Fauna of New Zealand
Ko te Aitanga Pepeke o Aotearoa

INVERTEBRATE SYSTEMATICS ADVISORY GROUP

Representatives of Landcare Research

Dr D.R. Penman
Landcare Research
Lincoln Agriculture & Science Centre
P.O. Box 69, Lincoln, New Zealand

Dr T.K. Crosby and Dr M.-C. Larivière
Landcare Research
Mount Albert Research Centre
Private Bag 92170, Auckland, New Zealand

Representative of Universities

Dr R.M. Emberson
Department of Entomology & Animal Ecology
P.O. Box 84, Lincoln University, New Zealand

Representative of Museums

Mr R.L. Palma
Natural Environment Department
Museum of New Zealand Te Papa Tongarewa
P.O. Box 467, Wellington, New Zealand

Representative of Overseas Institutions

Dr J.F. Lawrence
CSIRO Division of Entomology
G.P.O. Box 1700, Canberra City
A.C.T. 2601, Australia

SERIES EDITOR

‘FAUNA OF NEW ZEALAND’

Mr C.T. Duval (deceased 8 June 1998)
Landcare Research
Mount Albert Research Centre
Private Bag 92170, Auckland, New Zealand
Naturalised terrestrial Stylommatophora (Mollusca: Gastropoda)

Gary M. Barker

Landcare Research
Private Bag 3127, Hamilton, New Zealand

Lincoln, Canterbury, New Zealand 1999
Class Mollusca
Order Gastropoda

Naturalised terrestrial slugs and snails

Gastropods, or slugs and snails, are a very diverse group of molluscs. Most are marine, but many occur in freshwater and terrestrial habitats. Worldwide, terrestrial gastropods have been estimated to number about 35,000 species. New Zealand’s indigenous terrestrial gastropod fauna is among the richest in the world, with an estimated 1350 species. However, of the estimated global diversity of 71–92 families only 11 are represented in New Zealand’s indigenous fauna.

Through human activities, many species of terrestrial gastropod have been spread to and naturalised in areas outside their original range. Often these species have become pests in their new homes due to their damage to cultivated crops, their role in the transmission of parasitic diseases that affect humans and livestock, or their adverse effects on indigenous flora and fauna.

Our naturalised terrestrial gastropod fauna currently comprises 29 species, representing 15 families that were not part of the original New Zealand fauna. These species originate in Europe, North America, or the Pacific; some may have been introduced secondarily from populations first naturalised elsewhere. The species established in New Zealand are associated with man and his crops in their native range, with great propensity for passive dispersal, and have been widely distributed through human commerce. Several species established in New Zealand so early during the period of European settlement that zoologists of that time thought them to be members of the native mollusc fauna.

The general body plan in most terrestrial gastropods comprises the conical visceral mass coiled into a spiral within a single shell, and the head-foot which outwardly comprises a ventral muscular pad for locomotion and anteriorly a mouth and two pairs of tentacles. These (continued overleaf)
molluscs, commonly known as snails, are able to completely retract their head-foot into the shell for protection from desiccation and from predators. Features of the shell, and of the external morphology and internal anatomy of the head-foot, are important in the identification of snails. There are 15 species of snail in our naturalised fauna.

In the moist and humid conditions that prevail in many regions of the world, the ability to retract into a protective shell has been less important, and many groups of terrestrial gastropods have evolved forms with a reduced shell. In the initial stages of this evolution the shell is carried on the animal's back, but is no longer able to fully protect the entire animal. Animals at this stage of evolution, commonly known as semi-slugs, are represented in our naturalised fauna by a single species.

In the more advanced stages of this evolution the shell is reduced to a small plate or granules enclosed within the head-foot tissues, or lost completely. These animals, known as slugs, are simply snails with a reduced shell, and their identification is more dependent on the external morphology and internal anatomy of the head-foot. There are 14 species of slug in our naturalised fauna.

Contributor Gary Barker was born in Matamata, Waikato, but spent his youth on a farm surrounded by bush-clad hills in the Bay of Plenty. It was there that he developed an interest in wildlife, and invertebrates in particular. In 1972 Gary joined the Ministry of Agriculture at Ruakura Agricultural Research Centre. While working as a technician he obtained a New Zealand Certificate in Science at Waikato Polytechnic. Over a period of 24 years Gary published more than 100 papers on population and community ecology of invertebrates in agricultural systems. He has worked extensively with farmers and other researchers, in New Zealand and internationally, to develop sustainable pest management practices. In recognition of this contribution, in 1985 Gary was appointed as a senior research scientist with the Ministry of Agriculture. He also developed research interests and published in biogeography, systematics, and ecology of indigenous invertebrates, especially terrestrial molluscs. In 1996 he joined Landcare Research as a research scientist. His work is now centred on the systematics and community ecology of New Zealand indigenous invertebrates, and broader questions of biodiversity assessment.

I whānau mai te kaitihi nei, a Gary Barker, i Matamata, i roto o Waikato. Hei anō, i tana taitonga, noho ai ia ki tēnā pāmu e karapotia ana e te ngahere i te rohe o Te tētahi pāmu e karapotia ma e te ngahere i te rohe o Te Rōhu o Waikato. Heoi anō, i tana taiohinga, noho ai ia ki tēnā wāhi kōrero i tēnā rōnei, ki anō te rerekētanga i waenganui i tēnā, i tēnā momo ngata. O ngā ngātahi tātou katoa, kotahi anake e pēnei i Aotearoa, kotahi anake e tētahi pāmu e karapotia iwi i roto i ngā tau mano tini, kua iti ake ngā anga o ētahi. Ki te tinana o te huarahi e tētahi tētahi momo wae-uaua kua tīmata tā rātou takahi i tēnei huarahi, kua tēnei iwi, tēnei wāhanga, me āta titiro ki te hanga whakarōto o te ūpoko-waewae. Ko ngā mea kua roa tonu e takahi ana i te huarahi e tētahi wae-uaua kua tīmata tā rātou takahi i tēnei huarahi, kua tēnei iwi, tēnei wāhanga, me āta titiro ki te hanga whakarōto o te ūpoko-waewae. Ko ngā mea kua roa tonu e takahi ana i te huarahi e tētahi wae-uaua kua tīmata tā rātou takahi i tēnei huarahi, kua tēnei iwi, tēnei wāhanga, me āta titiro ki te hanga whakarōto o te ūpoko-waewae. Tēkau mā whā ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo wae-uaua. Ko ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo wae-uaua. Ko ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κara to roto iho i Aotearoa, 15 ngā momo pūtoko kua āhua tangata whenua tātou κατά την αναφορά μόνον τον άνθρωπο, η ικανότητα του άνθρωπου να αναπτύξει την αναφορά του ατόμου. Ο γάτας η γυναίκα, η μουσακάκια, η τέχνη, η τέχνη, είναι να αναπτύξει την αναφορά του ατόμου. Η γυναίκα, η μουσακάκια, η τέχνη, είναι να αναπτύξει την αναφορά του ατόμου. Η γυναίκα, η μουσακάκια, η τέχνη, είναι να αναπτύξει την αναφορά του ατόμου.
Moana a Tōr. Nō reira mai tana ngākau nui ki ngā mea oreore o te wao nui a Tāne, me tana aro nui anō ki ngā mea tūrā-kore. I te tau 1972 ka whai mahi a Gary i te Manatū Ahuwhenua, i te Pūtahi Rangahau Ahuwhenua o Ruakura. I a ta e mahi ana hei ringa hangarau, ka whakawhiwhia ia ki tana Tiwhikete o Aotearoa mō te Pātaiao, mai i te Kurutini o Waikato. I roto i te 24 tau, neke atu i te 100 ngā tuhinga kua whakaputaina e Gary e pā ana ki te maha me te āhua o te noho tahi a ngā hanga tūrā-kore i roto i ngā pānaha ahuwhenua. Kua kaha toto tana mahi tahi ki te hanga ahuwhenua me ētahi atu kairangahau, i tenei whenua me tāwahi anō hoki, kia takoto mai ai ētahi tikanga nanati i ngā kararehe takakino. Nā ēnei mahi āna, i te tau 1985 ka whiwhi a Gary i tētahi tūranga mō te kairangahau pūtuku matua i te Manatū Ahuwhenua.

Kua whāwhā atu anō hoki ia i ētahi atu momo mātāuranga, pēnei i te koiora-matawhenua, i ngā whakapapa me ngā pānaha whakarōpū i te ao o Tāne, me te āhua o te noho tahi a ngā hanga tūrā-kore o Aotearoa tūturu ki ō rātou ake taiao. I tenei kaupapa whakamutunga, ko ngā hanga-mohe noho ki uta ngā mea i ētahi tirotanga o ia. I tua atu i ngā mahi rangahau, kua whakaputa tuhinga ato ia e pā ana ki ēnei kaupapa. I ēnei rā, e ētahi whakapau kaha ana ia ki ngā whakapapa, ngā pānaha whakarōpū, me te āhua o te noho tahi a ngā hanga tūrā-kore tūturu o Aotearoa ki ō rātou taiao, tae atu ki te aromatawai i ngā huhua a Tāne.

He Kupu Āwhina — Glossary

aromatawai i ngā huhua a Tāne — biodiversity assessment (land-based)
hanga-mohe — soft-bodied > mollusc
koiora-matawhenua — biogeography
pāpokō — slug
pakoko — desiccated
papa hangariki — small plate
pītau — circinate frond of a fern > spiral
ringa hangarau — technician
 tikanga nanati i ngā kararehe takakino — pest management
weri — tentacle
wae-uaua — muscular foot, gastropod

Translation by H. Jacob
Huatau Consultants, Wellington
TRIBUTE

Cleveland Tymone DUVAL
8 November 1942 – 8 June 1998

New Zealand science lost a very experienced editor when Tymone Duval, after having been in remission for some months, died suddenly from acute lymphoblastic leukemia.

Tymone had been the series editor for the Fauna of New Zealand since its inception in 1982, and edited all 37 numbers published up until the time of his death. Even when on sick leave in 1998 he continued to bring this present work and other contributions closer to completion.

Tymone joined the Department of Scientific and Industrial Research (DSIR) as a science editor in 1973, with particular responsibility for the New Zealand Journal of Zoology. Previously he worked on insect control projects in Zambia (1965–68) and Botswana (1970–72), and was an editor for PANS (Pest Articles and News Summaries) (1969–70).
ABSTRACT

The naturalised terrestrial gastropod fauna of New Zealand is shown to comprise a total of 29 species representing 11 stylommatophoran families. Taxa previously recognised in New Zealand’s naturalised fauna and confirmed in this study are (with recommended common names): Agriolimacidae — *Deroceras laeve* (marsh slug), *D. panormitanum* (brown field slug), *D. reticulatum* (grey field slug); Ariolimacidae — *Arion hortensis* (Férussac’s orange soled slug), *A. intermedius* (glade slug); Cochlicopidae — *Cochlicopa lubrica* (slippery moss snail); Ferrucasia — *Cecilioides acicula* (blind pin snail); Helicidae — *Cantareus aspersus* (brown garden snail); Hygromiidae — *Candidula intersecta* (wrinkled snail); Limacidae — *Lehmannia nyctelia* (Bourguignat’s slug), *Limacus flavus* (yellow cellar slug), *Limax maximus* (tiger slug); Milacidae — *Milax gagates* (jet slug), *Tandonia budapestensis* (Budapest slug), *T. sowerbyi* (Sowerby’s slug); Papillidae — *Lauria cylindracea* (chrysalis snail); Testacellidae — *Testacella halionidea* (shelled slug); Valloniidae — *Vallonia excentrica* (eccentric grass snail); Vertigo — *Vertigo ovata* (grassland whorl snail); Zonitidae — *Oxychilus allarius* (garlic glass snail), *O. cellarius* (cellar glass snail), *O. draparnaudi* (Draparnaud’s glass snail), *Vitrea crystallina* (crystal snail).

Consistent with recent revisions, several generic-species epithet combinations are applied for the first time to the New Zealand naturalised fauna: these include *Cantareus aspersus* (formerly in genus *Helix*), *Limacus flavus* (formerly in *Limax* or *Lehmannia*), *Tandonia budapestensis* and *T. sowerbyi* (formerly *Milax*).

*Arion distinctus* (Ariolimacidae) (Mabille’s orange soled slug) is shown to have been long established and widespread in New Zealand, but previously not recognised as a component of *A. hortensis* s.l. *Zonitoides arboreus* (Zonitidae) (orchid snail) is formally recorded as a naturalised species, although its presence since the 1950s has been recognised in the popular press and unpublished plant protection records. *Helicodiscus singleyanus* (Helicodiscidae) (Singley’s subterranean discus snail) is recorded in the naturalised fauna for the first time with recognition of the presumably indigenous species *Hydrophrea academia* as a new junior synonym; this small, largely subterranean species has been known from widely scattered localities since 1970. *Lehmannia valentiana* (Limacidae) (Valencia slug) is recorded in New Zealand for the first time, although specimen material indicates it has been established at various localities in the North Island since the 1970s. *Prietoexella barbara* (Hygromiidae) (banded conical snail) is formally added to the naturalised fauna, although its establishment was recorded in 1983 but not published; this species is rapidly spreading through northernmost New Zealand. *Coneuplecta calculosa* (Euconulidae) (calculus cone snail) is the species most recently confirmed (1995) as a naturalisation, and is known at present from a single locality.

Family and generic diagnoses are presented; these were initially developed from the literature, but incorporate much new anatomical observation. All species are redescribed and illustrated on the basis of conchological and anatomical observations of New Zealand and extralimital material, with new or corrected anatomical data, and haploid chromosome numbers taken from the literature. The systematic status of each species is discussed, and information is presented on their distribution, history in New Zealand, and biology. A key to their identification is included. Methods for collection, preparation, and curation of these molluscs are briefly outlined. The systematic treatment of the taxa and the key are supported by a comprehensive description and discussion of the body plan and organ systems in Stylommatophora that are important in systematics and in taxon recognition. Most species are illustrated from life in a series of colour plates.

**CHECKLIST OF TAXA**

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Subg.</th>
<th>Species</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>AGRIOLIMACIDAE</strong></td>
<td>Prietocella</td>
<td>(Lessona &amp; Pollonera, 1882)</td>
<td>Laevorata</td>
<td>Brown field slug</td>
</tr>
<tr>
<td></td>
<td>Deroceras</td>
<td>(Rafinesque Schmaltz, 1820)</td>
<td>barbara</td>
<td>Banded conical snail</td>
</tr>
<tr>
<td></td>
<td>Deroceras</td>
<td>(Rafinesque Schmaltz, 1820)</td>
<td>laeve</td>
<td>Marsh slug</td>
</tr>
<tr>
<td></td>
<td>Deroceras</td>
<td>(Rafinesque Schmaltz, 1820)</td>
<td>panormitanum</td>
<td>Bourguignat's conical snail</td>
</tr>
<tr>
<td></td>
<td>Subg. Agriolimax</td>
<td>Murch, 1865</td>
<td>reticulatum</td>
<td>Grey field slug</td>
</tr>
<tr>
<td><strong>ARIONIDAE</strong></td>
<td>Limacus</td>
<td>Lehmann, 1864</td>
<td>flavus</td>
<td>Yellow cellar slug</td>
</tr>
<tr>
<td></td>
<td>Arion</td>
<td>d'Audebard de Férussac, 1819</td>
<td>distinctus</td>
<td>Mabille's orange soled slug</td>
</tr>
<tr>
<td></td>
<td>Limax</td>
<td>Linnaeus, 1758</td>
<td>maximus</td>
<td>Tiger slug</td>
</tr>
<tr>
<td><strong>MILACIDAE</strong></td>
<td>Milax</td>
<td>Gray, 1855</td>
<td>intermedius</td>
<td>Glade slug</td>
</tr>
<tr>
<td></td>
<td>Milax</td>
<td>Gray, 1840</td>
<td>cellarius</td>
<td>Cellar glass snail</td>
</tr>
<tr>
<td><strong>COCHLICOPIDAE</strong></td>
<td>Cochlicopa</td>
<td>d'Audebard de Férussac, 1821</td>
<td>gagates</td>
<td>Jet slug</td>
</tr>
<tr>
<td></td>
<td>Tandonia</td>
<td>Lessona &amp; Pollonera, 1882</td>
<td>lubrica</td>
<td>Slippery moss snail</td>
</tr>
<tr>
<td><strong>EUCONULIDAE</strong></td>
<td>Coneuplecta</td>
<td>Möllendorff, 1893</td>
<td>calculosa</td>
<td>Calculus cone snail</td>
</tr>
<tr>
<td><strong>FERUSSACIIDAE</strong></td>
<td>Cecilioides</td>
<td>d'Audebard de Férussac, 1814</td>
<td>cylindricalae</td>
<td>Chrysalls snail</td>
</tr>
<tr>
<td><strong>TESTACELLIDAE</strong></td>
<td>Testacella</td>
<td>Draparnaud, 1801</td>
<td>haliotidea</td>
<td>Shelled slug</td>
</tr>
<tr>
<td><strong>HELICIDAE</strong></td>
<td>Vallonia</td>
<td>Risso, 1826</td>
<td>aspersus</td>
<td>Brown garden snail</td>
</tr>
<tr>
<td></td>
<td>Cantareus</td>
<td>Risso, 1826</td>
<td>excentrica</td>
<td>Eccentric grass snail</td>
</tr>
<tr>
<td><strong>ZONITIDAE</strong></td>
<td>Oxychilus</td>
<td>Fitzinger, 1833</td>
<td>alleius</td>
<td>Garlic glass snail</td>
</tr>
<tr>
<td></td>
<td>Candidula</td>
<td>Kohlert, 1871</td>
<td>intersecta</td>
<td>Wrinkled snail</td>
</tr>
<tr>
<td><strong>HYDROMIIDAE</strong></td>
<td>Oxychilus</td>
<td>Fitzinger, 1833</td>
<td>interseam</td>
<td>Grassland whorl snail</td>
</tr>
<tr>
<td><strong>ZONITIDAE</strong></td>
<td>Candidula</td>
<td>Kohlert, 1871</td>
<td>intersecta</td>
<td>Wrinkled snail</td>
</tr>
</tbody>
</table>

-10-
**ACKNOWLEDGMENTS**

I am grateful to the many persons who over a period of 20 years have provided material for study. I thank Dr Frank M. Climo (formerly Museum of New Zealand, Wellington), Phil H. Colman (formerly Australian Museum, Sydney), Dr N.J. Evans and Dr Peter Mordan (Natural History Museum, London), Dave C.M. Munson and J. Ian Townsend (formerly Ministry of Agriculture and Fisheries, Plant Health and Diagnostic Station, Levin), Dr Simon Pollard (Canterbury Museum, Christchurch), and Anthony Harris (Otago Museum, Dunedin) for the opportunity to examine material in their care.

Dr Henrik W. Waldein (Natural History Museum, Göteborg), the late Dr Lothar Forcart (Naturalhistorisches Museum, Basel), Dr Jackie L. van Goethem (Koninglijk Belgisch Instituut voor Natuurwetenschappen, Brussels), Dr Dochita Lupu (Muséum d’Histoire Naturelle ‘Grigore Antipa’, Bucharest), Dr Robert A.D. Cameron (University of Birmingham, U.K.), Nora McMillan (Merseyside County Museum, Liverpool), Dr Alexandre V. Grossu (Bucharest) and Dr Andrzej Wiktor (Museum of Natural History, Wroclaw) checked my specific identifications, provided comparative specimen material, and/or offered comment on the New Zealand material.

Dr Jenny Dymock (Ministry of Agriculture and Forestry, Auckland) kindly provided unpublished biological information on *Zonitoides arboreus*, and Dr Robert E. Brockie (formerly Ecology Division, Department of Scientific & Industrial Research, Lower Hutt) provided unpublished data on the distribution of *Cantareus aspersus*.

I am indebted to my colleagues and others for untiring encouragement and for constructive comments on several drafts of this work, in particular Pauline C. Mayhall (Tauranga), Jim F. Goulstone (Auckland), Bruce F. Hazelwood (Auckland), Dr Richard C. Wilian (Museum of the Northern Territory, Darwin), and Bruce Marshall (Museum of New Zealand, Wellington).

Most of the exotic species established in New Zealand are of Northern Hemisphere origin, and are well known in many parts of the world. However, the extensive literature – including lengthy and often complex synonymies – is widely dispersed in both malacological and general zoological publications spanning nearly 250 years. Much of this literature was not readily available in New Zealand at the commencement of this project. I am indebted to Bruce Marshall (Museum of New Zealand, Wellington) and staff of the AgResearch library (Ruakura Agricultural Research Centre, Hamilton) for malacological literature. Dr Edmund Gittenberger (Rijksmuseum van Natuurlijke Historie, Leiden) and Dr Falco Giusti (Università Siena, Italy) assisted greatly by critically reviewing a draft of this work.

Production of the colour plates was funded by the New Zealand Lottery Board under Lotteries Research Grant no. 18186. I am indebted to Dr Gerhard Falkner (Worth-Horstkofen, Germany), Dr Heiko Bellmann (Jonsce, Germany), and Dr Vollrath Wiese (Cismar, Germany) for providing colour photographs.

**INTRODUCTION**

New Zealand has a large and phylogenetically diverse indigenous terrestrial mollusc fauna, most species of which are dependent on undisturbed forest or tussock grassland as habitat. In species number and sympatric diversity, the New Zealand indigenous terrestrial mollusc fauna is among the richest in the world per unit land area (Solem *et al.*, 1981; Solem 1984b, Emberton 1994a), with an estimated 1350 species. This indigenous terrestrial fauna contains one neritopsinan family (Hydrocenidae) and one caenogastropod family (Liareidae) but, as in most...
other regions of the world, is dominated by stylommatophoran Pulmonata.

The indigenous fauna is supplemented by a small and continually expanding naturalised fauna of Stylommatophora, which is the focus of this publication. These naturalised species are the slugs and snails familiar to the general public. There is little appreciation, however, of the number and phylogeographic diversity of species represented in the naturalised fauna, or of the extent to which they have pervaded the New Zealand landscape. They form an important element of the New Zealand biota, particularly in modified habitats.

The naturalised terrestrial mollusc fauna currently comprises 29 species, representing no less than 15 families of Stylommatophora. These species originate in Europe, North America, or the Pacific, although some may have been introduced secondarily from stock first naturalised elsewhere (Barker 1992). The species established in New Zealand are those which are synanthropes in their native range, with great propensity for passive dispersal, and which have been widely distributed through the activities of man.

**Methods and conventions**

A considerable part of this contribution is based on material gathered from the field throughout New Zealand. Many people contributed specimens, as acknowledged under Material Examined for each species. Specimen localities without a collector's name are those collected by the author. Detailed specimen collection records and distribution maps are presented for each species so as to be of value to later students of New Zealand's naturalised fauna.

For specimens collected in New Zealand, the two-letter codes at the beginning of each locality record or group of similar records alludes to the areas designated by Crosby et al. (1976, 1998), mapped on p. 248.

Unless otherwise indicated, material is deposited in the private collection of the author. Abbreviations for institutional repositories are as follows:

- **AMNZ** Auckland Museum, Auckland, N.Z.
- **AMSA** Australian Museum, Sydney, Australia
- **ANSP** Academy of Natural Sciences, Philadelphia, U.S.A.
- **BPBM** Bernice P. Bishop Museum, Honolulu, Hawaii
- **CMNZ** Canterbury Museum, Christchurch, N.Z.
- **MONZ** Museum of New Zealand, Wellington, N.Z.
- **NHMW** Naturhistorisches Museum, Vienna, Austria
- **OMNZ** Otago Museum, Dunedin, N.Z.

Initial specific determinations were made by reference to the literature. Identifications were confirmed by European and North American malacologists (see Acknowledgments) and, for many species, by examination of material from the species' native range collected by the author or gifted by colleagues. The family and generic diagnoses were initially developed from the literature, but incorporate much previously unpublished anatomical observation. The species descriptions and illustrations presented are based entirely on conchological and anatomical observations of the author, and for many species include new or corrected information.

Names of genera and species quoted in synonymy refer to world material, and include New Zealand synonyms (some new), as discussed in the text. These synonyms have been taken from the literature, without critical evaluation, unless otherwise noted.

The literature pertaining to most species is very extensive, but for the greater part is not readily available in New Zealand. It has not been possible owing to space limitations to provide a comprehensive list of references for each species, but a synopsis with key references is provided under Remarks. Furthermore, listings of junior synonyms for genera and species are supported by bibliographic references, to facilitate navigation through the often complex nomenclatural history of these taxa.

The category 'of authors' is included in these lists to indicate the generic placements (often) extensively used in the older literature, but which were subsequently shown to be inconsistent with generic limits as defined by type species. For example, *Helix* Linnaeus, 1778 was subsequently applied as the generic name for the majority of terrestrial snails, but following the designation by de Montfort (1810) of *Helix pomatia* Linnaeus, 1758 as type species, *Helix* was subsequently applied in a more restricted sense.

Public awareness of gastropods is facilitated by the use of common names. For each species recognised in the naturalised fauna, a common name is recommended. In general, if there was a name well established overseas (e.g., Godan 1983, Gittenberger et al. 1984) or in New Zealand (e.g., Ferro et al. 1977, Foord 1990) it was given priority. Where now common names were required, or where a choice was required between two or more common names in use, preference was given to names:

(i) based on a translation of the specific epithet,
(ii) descriptive of the animal or its habitat, and/or
(iii) informative about its origin or nomenclatural history.

Chromosome numbers were taken from the literature, namely Perrot (1938), Beeson (1960); Burch & Heard (1962), Laws (1965, 1966), Rainer (1967), Patterson (1968), Butot & Kiauta (1969), Kiauta & Butot (1969), Virmel et al. (1982), and Ramos & Aparicio (1985). The haploid numbers given in the family and generic diagnoses may be subject to change as further representatives of taxa...
Text-fig. 1 A phylogeny of the mollusc class Gastropoda, adopted from Ponder & Lindenberg (1996), showing distribution of terrestrial lineages (in bold) among the six main subclass taxa recognised (in capitals on right). Extant Cyclophoroidea are all terrestrial, while Neritopsina, Truncatellioidea, Littorinoidea, and Pulmonata are represented by families in marine, freshwater, and terrestrial environments. Stylommatophora represent that dominant terrestrial radiation within the Pulmonata, and worldwide are the dominant group of gastropods on land.

PHYLOGENY AND SYSTEMATICS

The Mollusca are in appearance, anatomy, ecology, and physiology a highly diverse group, for which the phylogenetic pathways and higher classification have been controversial since the very beginning of comparative investigation. Within the Mollusca, most systematic problems arise among the ecologically most disparate Gastropoda. Most gastropods are marine, but several lineages have colonised freshwater and/or terrestrial environments. Worldwide, terrestrial molluscs have been estimated to number about 35 000 extant species (Solem 1984b), and are represented in the gastropod clades Neritopsina, Caenogastropoda, and Heterobranchia (Text-fig. 1). In the heterobranch lineage, Pulmonata have radiated most extensively in terrestrial habitats, and in most regions of the world they dominate the faunas in species richness and [continued on p. 17]
Text-fig. 2 A phylogeny of the Stylommatophora inferred from the classification of Zilch (1958–60).

Text-fig. 3 A phylogeny of the Stylommatophora inferred from the classification of Solem (1978).
Text-fig. 4 A phylogeny of the Stylommatophora inferred from the classification and cladogram of Schileyko (1979).

Text-fig. 5 A phylogeny of the Stylommatophora inferred from the classification of Nordsieck (1986a).
Text-fig. 6. A phylogeny of the Stylommatophora inferred from the classification and cladogram of Tillier (1989).

Text-fig. 7. A possible phylogeny within Stylommatophora generated by maximum parsimony analysis of 57 morphological characters and conforming to a backbone tree suggested by RNA sequence data of Emberton et al. (1990) and Tillier et al. (1992, 1994). Heuristic search optimisation, with multi-state taxa interpreted as polymorphism. Tree length 1266, consistency index 0.58.
based on cladistic but largely phenetic analysis of new data. More recently, Tillier (1989) proposed a classification scheme developed by H.A. Pilsbry and H.B. Baker, based primarily on excretory, locomotor, and gross reproductive anatomy. Zilch and Solem used an intuitive evolutionary approach, presenting an hierarchically arrayed classification with no formal phylogeny. Schileyko's (1979) approach was similar to that of Zilch and Solem, yet his classification was profoundly different, being based primarily on shell and reproductive morphology. From a reinterpretation of the widely scattered literature on the morphology of the shell and various organ systems, and analysis of geographical distribution, Nordstedt (1985, 1986a) produced the first overtly cladistic stylommatophoran classification. More recently, Tillier (1989) proposed a classification based on cladistic but largely phenetic analysis of new data sets on the anatomy of the digestive, nervous, and excretory systems. Tillier's scheme has been rejected by Nordstedt (1992) and Emberton (in Emberton & Tillier 1995). The classification schemes for the Stylommatophora by Zilch (1959–60), Solem (1978), Schileyko (1979), Nordstedt (1986a), and Tillier (1989) are illustrated as cladograms in Text-fig. 2–6, with only those families mentioned in the systematic part of this paper identified as terminal taxa. These cladograms were constructed from the hierarchical classification presented by the respective authors. Phylogenetic analyses undertaken by the present author, using maximum parsimony of 37 anatomical characters and constrained to comply with backbones trees suggested by ribosomal RNA sequence data (Emberton et al. 1990, Tillier et al. 1992, 1994), suggest a quite different cladogram topology (Text-fig. 7) and raise serious doubts about the phylogenetic robustness of higher taxon categories in the previously published stylommatophoran taxonomies. The Orthurethra and Sigmurethra, as currently recognised, may not constitute natural phylogenetic groupings.

MORPHOLOGY AND DIAGNOSTIC FEATURES

In this section the morphology of the Stylommatophora is surveyed as a basis for highlighting trends in the evolution of these animals and introducing the characters that have been employed in systematics and taxonomy.

General body plan (Fig. 1–4)

In stylommatophoran land snails one can recognise the conical visceral mass (visceral hump), which is coiled into a spiral within the univalve shell, and the head-foot. The coiling of the visceral mass is generally dextral (clockwise spiral rotation from the embryonic shell down), but is sinistral (antihoroclockwise) in some species, or even individuals within a species. Any orientation stated or implied below refers to the condition in dextral animals. This coiling results in an asymmetrical body plan. The head-foot is concerned with sensory and locomotor activities, and is protruded from the protective shell during movement and feeding. Head-foot protrusion is mainly effected by hydraulic pressure, but its withdrawal is effected by contraction of muscles connecting the head-foot with the columella, of which the origin is the inner wall of the shell.

The pallial border or mantle collar forms the limit between the head-foot and the visceral mass, and is generally the only part not protected by the shell when the animal is retracted. The ventral surface of the foot is the pedal sole, which is used for crawling by means of ciliary or muscular waves. Locomotion is assisted by a carpet of mucus laid down on the substrate by the suprapedal gland, the opening of which is situated above the anterior extremity of the pedal sole. The part of the head-foot anterior to the pallial border is the cephalic region, or head, which bears the (usually) invaginable ocular peduncles and infer-
ior tentacles. Each ocular peduncle is equipped with an eye at its apex; eye usually pigmented black, but sometimes unpigmented in subterranean forms. The part of the foot posterior to the pallial border is the tail; its posterior extremity sometimes includes a caudal mucous gland.

Two principal cavities in the internal anatomy, the pulmonary cavity and the general body cavity, may be distinguished in land snails. The pulmonary cavity occurs above and behind the head, but within the shell. Its floor, the diaphragm, is formed by the dorsal surface of the head-foot, and its roof by the mantle skirt, a thin fold from the anterior face of the visceral mass. During ontogeny the pulmonary cavity forms by invagination at the border of the mantle edge, which secondarily fuses with the pallial cavity, which is homologous with the caenogastropod pallial cavity, to form the pneumostome or respiratory orifice (Regondaud 1964, Tillier 1984b).

The pneumostome opens on the right side of the pallial border, in the parieto-palatal angle of the shell aperture. The heart and kidney occupy the proximal part of the pulmonary cavity roof. This whole system of respiratory and excretory organs within the pulmonary cavity is frequently referred to as the pallial complex. For the land snail this cavity not only serves as the site for respiratory and excretory functions but also provides a space that can be occupied by the head-foot when the animal retreats to the protection of the shell.

The larger, general body cavity contains the digestive tract, central nervous system, arterial system, reproductive organs, and free muscle system. This cavity extends forwards into the cephalic region of the head-foot, but in snails does not extend into the tail. Only in the most evolved slugs is the visceral mass housed in a tail cavity (see below). In the snail, those organs that pass from the visceral mass into the head-foot are arranged and structured so as to maintain the pulmonary cavity as a retreat space.

**Shell (Fig. 5-9)**

The shell gives the mollusc partial or complete shelter for its body, and is composed of several layers: a thin outer organic layer or periostracum, consisting of tanned proteins, overlying much thicker layers of ostracum, which comprises crystalline calcium carbonate and proteinaceous conchiolin. The shell is formed by accretionary growth at the mantle edge. The mantle is a thin membrane which in the active animal extends minutely beyond the shell aperture, and at its edge adds a shell increment to the aperture margin so that each increment copies a configuration of the mantle edge at that time.

The shell tube coils in a logarithmic spiral, retaining isometric proportions between length, area, and volume parameters as it grows. The cross-sectional shape of the shell tube, and the rate at which the tube expands and descends, determine the overall shape of the shell. The inner wall that forms the axis of the shell coiling is referred to as the columella. The whole of ontogeny is conserved in the shell, as the larval shell, or protoconch, is retained as the apex to the post-embryonic shell, or teleoconch. Stylommatophoran snails have limited capacity to alter juvenile parts of their shell by internal resorption and deposition, and, with the exception of a few taxa in which the apical part of the shell may be lost through decollation, the exterior of the shell can not be modified.

The protoconch generally has a clearly defined termination, marking the growth change at the time of hatching from the egg. Usually the protoconch is small and completes a little over one 360-degree rotation or whorl. In some land snails, however, the protoconch may make three to four whorls, and this embryonic growth may account for over one-third of the total shell whorls in mature animals. The surface of both the protoconch and teleoconch is frequently sculptured, and evolutionary changes are often conserved as changes in sculpture running from the teleoconch back onto the protoconch. Many stylommatophorans exhibit indeterminate growth, whereby the shell continues to grow throughout the life of the animal. Others exhibit determinate growth, whereby increase in shell size is terminated about the time the animal reacquires adulthood. In these latter species onset of adulthood is frequently accompanied by changes in the allometric growth of the shell.

The colouring of the shell is produced by organic pigments acquired by the animal from its food. Most of the groups of pigment-producing cells are localised along the margin of the mantle, at the site of shell growth. The resulting colours are the outcome of the combination of four basic types of pigments: yellow carotenoids, black melanins, green porphyriins, and blue or red indigoids. The basic colour and pattern design are determined genetically, although many snails display much variation in colour due to environmental influences.

Because its appearance is characteristic for each species, the shell is very important in molluscan taxonomy, especially in species identification. Many species descriptions have been based solely on the shell. However, many unrelated taxa can through convergent evolution assume very similar shell morphologies. Furthermore, in some lineages there is little specific differentiation in shell characters. In these situations, knowledge of the anatomy of the animal is essential for identification and for resolving relationships.

Terminology for the various components of the shell is illustrated in Fig. 5-7. The shell must be observed in lateral, ventral, and dorsal orientation, and often at vary-
The size and general form of the shell are primary in snail identification. Among stylommatophoran snails the shell form varies from elongate to globular, and from depressed to discoidal. This general form can be described in an approximate way by the ratio of height to diameter. The shell may have many or few whorls, which may be rounded, angular, shouldered, or flattened. Generally the venter fills the shell cavity up to its top and the length of the visceral mass increases with the length of the shell (in whorls). The suture line where one whorl overlays and cement to the preceding one will be impressed to varying degrees, and may be channeled or crenulated.

The growth of the shell as a spiraling tube, with fusion of the inner walls where one spiral or whorl abuts the previous one, creates the axial columella. The columella may be solid, but more frequently comprises a hollow shaft, capped by the protoconch at the apex and open at the shell base. Shells with this hollow columella are generally referred to as perforated, with the hollow axis open to the shell base termed the umbilicus.

The opening of the shell tube is the aperture, and its free margin, minutely covered by the mantle collar in the active animal, is the peristome. The outline of the shell aperture may take many forms owing to the shape of the whorls and their interrelationships. The peristome may be thin and sharp throughout the life of the animal, but in some species with determinate growth the peristome may be variously thickened and/or turned back upon the animal reaching adulthood.

Development of various folds, calluses, tubercles, constriuctions, and plates that effectively narrow the shell aperture is a common phenomenon in Stylommatophora. Solem (1972b) referred to these aperture structures as 'barriers'. The general assumption has been that these barriers hinder possible predators from reaching the animal after it has retreated behind the barriers (Guilding 1829, Cooke 1895, Solem 1972b). Suvorov & Schileyko (1991) suggest that the presence of aperture barriers ensures that all soft parts withdraw along constant trajectories, reducing compression damage to organs. They also suggest that the lamellae developed on the columnella serve as blocks over which the pedal branches of the columnellar muscle are thrown, aiding lift of the shell apex during locomotion (see below for a description of the columnellar muscle system).

The number, position, shape, and size of these barriers (Fig. 8, 9) frequently have been used as diagnostic features for both genera and species, especially in families where the shell is rather uniform in appearance. Often these details provide the easiest and quickest means of identifying sympatric congeneric species that are similar in shell shape and size, although intraspecific variation should be recognised. The barriers that occur on the shell axial walls or columnella are referred to as columnellar lamellae, while those on the parietal wall are known as parietal lamellae. The folds on outer shell walls are referred to as palatal plicae. The palatal plicae result from folding of the secretory surface of the mantle during the life of the animal, but most frequently at the termination of post-embryonic development. In contrast, the columnellar lamellae appear even in embryogenesis and continue to lengthen as the shell grows. Frequently, as the barrier is formed at the shell aperture, that part formed earlier and now lying deep within the shell is resorbed.

On the basis of ontogeny, Schileyko (1979) regarded the presence of lamellae as a plesiomorphic character, while the plicae were considered to have evolved independently in several lineages. Nordsieck (1986a) emphasised, however, that irrespective of the ontogeny in extant taxa, the presence of lamellae and plicae must be evaluated as plesiomorphous, because they are found in taxa considered ancestral to the Stylommatophora.

Some species produce shells in which shape does not change with increasing size. However, most exhibit some degree of biphasic or triphasic allometry. The allometric variation often occurs as a slight change in direction of shell coiling at the onset of adulthood. In species with determinate growth, change in shell shape often occurs shortly before secretion of a definitive lip or reflection to the apertural peristome. Shells from adult animals are therefore most useful in identification.

Various sculptural features often occur on the surface of the protoconch and/or the teleoconch. These sculptures may be formed by the calcareous ostracum, overlain and elaborated by the periostracum, or formed solely by outgrowths of the periostracum. Often the sculpture is complex, and its true nature is revealed only at high magnification. The protoconch often becomes eroded during the post-embryonic life of the animal, as may some of the periostracal sculpture of the teleoconch.

**Shell loss (limacisation)** (Fig. 2, 4)
The term “slug” refers to a gastropod mollusc with the shell completely lost or so reduced as to be unable to contain the animal. The slug form has evolved many times in gastropods living in marine and terrestrial habitats (a process termed ‘limacisation’ by Solem 1974), and many taxa of widely divergent origins have, by parallel evolution, assumed a remarkable similarity. They have sacrificed the protection offered by possession of a shell for the mobility, faster body movement, and ability to occupy very small spaces gained by reducing or eliminating the shell. Slugs are simply snails with a reduced shell, and therefore not a
natural group of closely related animals.

In the course of limacisation among Stylommatophora, the number of whorls described by the visceral mass is reduced and its contents are incorporated into the head-foot (van Mol 1970, Solem 1974, Likharev & Wiktor 1979, Tillier 1984a). In semislugs, which represent the intermediate stage in the evolution towards the slug form, the shell is reduced to the extent that the animal can no longer withdraw its head-foot under the protective shell, and the organs associated with the distal part of the visceral mass are incorporated into the anterior head-foot. In these animals the stomach and associated digestive gland remain in the visceral hump, above the pallial border. In full slugs the visceral hump is still more reduced or absent, and the stomach is included in the pedal cavity of the head-foot. The pallial border or mantle collar extends over the surface of the reduced shell and may cover it totally, forming a dorsal mantle shield or 'clypeus'; the shell is absent in some full slugs. In the most limacised slugs, the shield itself can hardly be distinguished from the dorsal surface of the head-foot.

While on a global scale their species number is greatly exceeded by fully shelled taxa, slugs or semislugs are highly diverse, and in many regions make up a significant part of the stylommatophoran fauna. Among the New Zealand indigenous fauna the slug form is represented in the families Athoracophoridae, Rhytididae, and Charopidae. The naturalised Arionidae, Limacidae, Agriolimacidae, and Milacidae are readily distinguished from the native slugs by having no external shell and by carrying the ciliated sole above the foot margin. The naturalised Testacella Draparnaud, 1801 (Testacellidae) shows some similarities with the native rhytidid Schizoglossa Hedley, 1892 and the charopid Flammocoche Dell, 1952, but it is distinguished by having the shell at the extreme posterior of the body, the body scored by two branched longitudinal grooves, and the adult being considerably larger.

External pedal and cephalic features

The tegument or skin of the dorsal aspects of the head-foot is typically thick and of rugose, granular pattern. The skin is kept moist by mucus extruded onto the surface from secretory cells dispersed among the epithelial cells. The dorsal aspect of the tail in snails is generally without important features but species in some families (e.g., Lysinoe Adams & Adams, 1855 in Helminthoglyptidae, Oxychona Möhr, 1852 in Bulimulidae) possess distinct keels. Such keels are even more prominent in slugs of various families, including Milacidae, Limacidae, Agriolimacidae, Pseudocelidae, Trigonocholemyidae, and the arionid subfamily Ariopeltinae. A mucus pit, commonly but wrongly referred to as the caudal mucus gland, is a plesiomorphic character at the posterior extremity of the tail, sometimes with a projection above this juncture. The caudal mucus pit has been lost in many stylommatophoran lineages.

The ciliated ventral surface of the head-foot, the sole, functions as the locomotory pad. It is primitive in form, although commonly the outer edges are of different colour from the central zone. Locomotion in Stylommatophora is either by pedal cilia or by pedal muscular gliding. Ciliary movement is a smooth, uniform gliding with no differential movement of parts of the sole, propelled by cilia on the sole. This type of locomotion is generally confined among stylommatophorans to small species. Direct monotaxic pedal waves (Miller 1974) are the most common form of locomotion in stylommatophorans, and the only one found in the larger species. This locomotion involves rhythmic pedal waves, initiated at the posterior of the sole and moving to the anterior. In many species the pedal waves extend the full width of the pedal sole. In others the sole is tripartite, with two distinct furrows dividing it into three defined zones, and only the central zone is involved in the locomotory pedal waves. Both ciliary and pedal wave types of locomotory activity are present in lower gastropods (Miller 1974, and references therein). In active stylommatophoran snails the shell may be carried in an elevated position well above both tail and substrate, or an elevated position but supported by the body while resting on the tail, or may rest on the substrate and be dragged in a rhythmic hitching motion.

Two morphological conditions of the foot margin have been recognised in Stylommatophora. In some taxa a pair of grooves — the so-called parapodial grooves — occur along the side of the animal, just above the foot margin, so that the ciliated sole extends above the foot margin. This has been termed the holopod condition. In other taxa the holopod condition occurs, whereby the parapodial grooves may be fused into one and are sited at the margin of the foot; or the grooves may be entirely absent, such that the ciliated sole reaches to the lateral margin of the foot (but does not extend above).

Pilsbry (1896) divided the stylommatophoran order Sigmurethra (see below for definition of Sigmurethra and Orthurethra) into two suborders, Aulacopoda and Holopoda, on the basis of whether or not a pair of parapodial grooves occur along the side of the foot. However, Wächtler (1935) showed that the parapodial grooves are not absent from the Holopoda, but are merely indistinct. He showed that these grooves are similarly present but indistinct in various Orthurethra. Webb (1961a) independently repeated Wächtler’s discovery of the universality of parapodial grooves, and dismissed the recognition of
pore) into a ureter, which may be represented by an open
the excreta through a nephropore (nephridial or ureteric
system via a nephrostome (renopericardial pore) and expels
ory system of all Stylommatophora essentially consists of
became pallial rather than visceral in location. The excret-
paired ctenidia or gills in the pallial cavity. The pulmo-
Respiratory and excretory systems
Athoracophoridae.
A pallial kidney which receives wastes from the pericar-
and which retained only the left excretory organs that
Vetigastropoda, the excretory organs were paired and loc-
In the primitive gastropods, as exemplified by extant
veloped from the eye-bearing swellings or short pedun-
referred to as tentacles, implying homology with the ceph-
aulacopod foot and indeterminate growth result from paedomorphosis.
The cephalic region is simply an anterior elongation of
the head-foot that bears dorsally a pair of ocular pedun-
corresponding to distinctiveness of the grooves, on
the grounds of ecologically induced convergence. Webb
(1961a) thought the aulacopod condition better adapted to
burrowing in soil and the holoped condition, with less
pronounced grooves, more dry-adapted. Without reference
to Wächtler’s or Webb’s viewpoints, Solem (1978) main-
tained that the suborders “seemed coherent assem-
blages” and were thus retained in his sigmurethran clas-
dification. Drawing on the comparative morphology of the
parapodial grooves throughout the Stylommatophora,
Schileyko (1979) maintained that aulacopody arose repeatedly from the holoped condition.
In an analysis of pallial and foot character evolution in
Stylommatophora, Baker (1955) concluded that the an-
cestors of the Sigmurethra probably had, among other features, an aulacopod foot. Tillier (1989) noted the gen-
eral correlation between an aulacopod foot and a shell with
determinate growth. With the observation of aulacopody in
cabeyos and Hutchings of Orthurethra and holoped
Sigmurethra, Tillier surmised that both the aulacopod foot
and indeterminate growth result from paedomorphosis.
The cephalaic region is simply an anterior elongation of
the head-foot that bears dorsally a pair of ocular pedun-
cacies, anteriorly a pair of inferior tentacles or rhinophores,
and ventrally a mouth surrounded by oral labeis or lobes.
The ocular peduncles in Stylommatophora are frequently
referred to as tentacles, implying homology with the cepha-
lolic tentacles of lower gastropods. Such an homology has
not been demonstrated, and the ocular peduncles may have
developed from the eye-bearing swellings or short pedun-
cacies at the base of the cephalic tentacles seen in some
vegit gastropods and caenogastropods (Haszprunar 1985).
Interior tentacles are a synapomorphy of the exclusively
air-breathing pulmonates (Eupulmonata sensu Haszprunar
& Huber 1990). These structures have been secondarily
lost in some species of the families Urocoptidae, Verti-
ginidae, Pupillidae, and Succineidae, and in all species of
Athracophoridae.

Respiratory and excretory systems (Fig. 10–14)
In the primitive gastropods, as exemplified by extant
Vetigastropoda, the excretory organs were paired and located
in the visceral cavity, and respiration was effected by
paired ctenidia or gills in the pallial cavity. The pulmo-
nates evolved from gastropods that had lost the ctenidia
and which retained only the left excretory organs that
became pallial rather than visceral in location. The excret-
ory system of all Stylommatophora essentially consists of
a pallial kidney which receives wastes from the pericar-
dium via a nephrostome (renopericardial pore) and expels
the excreta through a nephropore (nephridial or ureteric
pore) into a ureter, which may be represented by an open
21
sening neither an orthureter on the nephridium nor a closed ureter, while Sigmurethra was defined as lacking an orthureter but possessing a ureter running along the anterior of the nephridium to the top of the pulmonary cavity and then, adjacent to the rectum, in the pneumostome. The ordinal category Heterurethra was created by Pilsbry for the Succineidae, the excretory system of which was said to differ from that of the Sigmurethra in that the nephridium extends transversely and the primary and secondary arms of the ureter are at right angles to each other. Baker (1955) applied the term Heterurethra to all stylommatophorans having a transverse nephridium but, as pointed out by Solem (1978) and Nordsieck (1985), this configuration is really a variant of the sigmurethran configuration.

The possession of an orthureter on the distal part of the nephridium is probably plesiomorphic in Stylommatophora because this configuration occurs in basal pulmonate groups (Delhaye & Bouillon 1972a, c, Nordsieck 1985, Tillier 1989). The differentiation of the orthureter in the excretory system among stylommatophorans has generally been recognised only in those taxa traditionally grouped as Orthurethra, namely Papilloidea, Chondrinoidea, and Partuloidea. Tillier (1989) has demonstrated, however, that a ureteric pouch-like differentiation is present in a number of non-orthurethran families. Despite the homology of these urethric pouch structures not being fully resolved by histological and functional studies, the ordinal status of Orthurethra is called into question. The validity of this ordinal category is further weakened by several orthurethrans possessing a retrograde closed ureter (Watson 1920, Solem 1964, Tillier 1989). Furthermore, many non-orthurethran taxa exhibit transitional states between the ureter morphology used originally to define the Sigmurethra and that of Sigmurethra (Nordsieck 1985, Tillier 1989).

Tillier (1989) proposed a new higher classification of non-orthurethrans within the Stylommatophora. Using the differentiation of kidney morphology, he recognised two phylogenetic lines within the Sigmurethra, one in which at first a dedifferentiation of the kidney took place which was followed by a partial closure of the ureter (Brachynephra sensu Tillier), and another in which at first a closure of the ureter took place, followed by a partial dedifferentiation of the kidney (Dolichonephra sensu Tillier). I concur with Nordsieck (1992) in considering Tillier’s hypothesis an overvaluation of the differentiation of the kidney. According to Schileyko (1979) sigmurethry is a feature in embryogenesis even in orthurethran forms without a ureter in the adult animal.

Among the marine pulmonates the kidney is differentiated into nephridial and ureteric parts and is without a ureter; this may be the plesiomorphic state in the Stylommatophora. The development of ureters in the terrestrial pulmonates may be correlated with resorption of ions and water. Reduction of the nephridial ureter among Stylommatophora results in an enlargement of the pulmonary cavity respiratory surface.

Reduction in shell size and incorporation of the visceral mass into the head-foot, associated with limacisation, necessarily involves alteration of the layout and size of the pulmonate organs just described for fully shelled stylommatophorans. Several patterns of pulmon organ modification are evident among lineages that evolved towards the slug form. Surface area for gaseous exchange is maintained by the venous vessels being highly developed in the vestigial pulmonary cavity or invading the mantle edge. Most semi-slugs and semi-slugs show extensive development of mantle lobes that partially or wholly cover the shell and extend forwards along the neck, providing increased surface area for gaseous exchange (Tillier 1983).

In the most highly evolved slugs a large part of the respiration takes place across the dermis (Duval 1982) and the mantle lobes may be secondarily reduced. Kidney size retention often involves its rotation and change in shape, including the development of lateral lobes. The presence of a closed sigmoid ureter has been considered a prerequisite for evolvement of the slug form (Solem 1974, Tillier 1989), but this paradigm is challenged by the absence of a substantive secondary ureter in testacellid slugs (De La Caze-Duthiers 1887, this study) and some atheraco-nychites (G.M. Baker, unpubl. data).

Digestive system (Fig. 15–20)

The digestive system comprises the buccal apparatus, oesophagus, stomach, into which open two lobes of the digestive gland, and intestine (Fig. 15, 16). The spheroidal buccal apparatus, located in the anterior head-foot, comprises a complex arrangement of muscles for protracting and retracting the radula and jaw (Fig. 17, 18). The jaw is located dorso-anteriorly in the buccal cavity, its base firmly anchored in the musculature of the buccal mass wall, and in stylommatophorans is used mainly to hold the food substrate, against which the radula can work.

Primitively the gastropods have two jaw plates, one on either side of the buccal cavity. In several gastropod lineages, including pulmonates, there has been a trend for these lateral plates to be complemented by a series of medially placed plates, which may fuse to produce a single medial plate. In Stylommatophora the lateral elements are absent and the component elements of the medial structure show varying degrees of fusion and variations in overall shape (Fig. 19). The jaw consisting of numerous separate plates united only by a common membrane is termed polyplacognathic. In the stegognathic condition the plates
Ontogenetic changes have long been recognised in life as the odontoblast cells mature or otherwise change. In the radular formation, the teeth develop further as new rows are added, and the radula becomes more complex. The radula is a characteristic feature of molluscs. When the animal is not feeding, the radula forms a tongue-like protrusion into the buccal cavity, covered by a radular membrane with few to many thousands of teeth in rows, and is posteriorly prolonged into the radular sac where teeth are formed by specialised cell clusters called odontoblasts. When the animal feeds, the radula is protruded from the mouth, and then withdrawn, to bring the food back into the buccal cavity and oesophagus (Runham 1975). Primarily this buccal system is designed for abrasion, cutting, and ingestion of vegetal matter.

Complex muscles control in and out movement of the radula, during which the radular membrane is rotated partly over the anterior tips of the underlying support of cartilage-like and muscle tissues, known as the odontophore. The rotation of the radular membrane over the anterior face elevates the cutting edge of the teeth above the membrane so that they can scrape, pierce, cut, or tear the object with which they come in contact. The teeth do, however, become gouged, chipped, or gradually ground down by ongoing abrasion. This wear problem is solved by having new rows of teeth formed at the posterior end of the radula throughout the life of the animal, while at the anterior end the radular membrane is resorbed and the worn teeth are shed to be swallowed and passed out in the faeces. The entire radular membrane with its rows of teeth grows forwards continuously.

The radula is a characteristic feature of molluscs. When the animal is not feeding, the radula forms a tongue-like protrusion into the buccal cavity, covered by a radular membrane with few to many thousands of teeth in rows, and is posteriorly prolonged into the radular sac where teeth are formed by specialised cell clusters called odontoblasts. When the animal feeds, the radula is protruded from the mouth, and then withdrawn, to bring the food back into the buccal cavity and oesophagus (Runham 1975). Primarily this buccal system is designed for abrasion, cutting, and ingestion of vegetal matter.

The pulmonate radula arises in the embryo as two separate areas comprising longitudinal rows of teeth. As the radula develops further tooth rows are added, and the two areas are united as a row of central teeth are added (Kerth 1979a). Thus the primary form of the stylophonophoran radula is a series of transverse rows, and the teeth at the same position on respective transverse rows are essentially mirror images as they are formed by the same odontoblast cells (Kerth & Hänsch 1977, Kerth 1979a, b, 1983a, b, MacKenstedt & Märkel 1987).

Ontogenetic changes in tooth form at a particular position on the radula may continue during post-embryonic life as the odontoblast cells mature or otherwise change. These ontogenetic changes have long been recognised in Stylommatophora (e.g., Sterki 1893b, Quick 1935) but their importance in reducing the reliability of radular differences as a taxonomic tool, or their value in resolving evolutionary trends, has to date received little attention.

Each radular tooth comprises a recurved cutting edge, usually with one or more pointed cusps, supported and affixed to the radular membrane by a basal plate (Fig. 20). The teeth are shaped such that in the elevated feeding mode, each is supported by the basal plate of the tooth immediately adjacent in the same row or in the next anterior transverse row (Solem 1972a, 1973, 1974). This inter-tooth support system reduces the risk of teeth being torn from the membrane when a hard substrate is contacted. The teeth do, however, become gouged, chipped, or gradually ground down by ongoing abrasion. This wear problem is solved by having new rows of teeth formed at the posterior end of the radula throughout the life of the animal, while at the anterior end the radular membrane is resorbed and the worn teeth are shed to be swallowed and passed out in the faeces. The entire radular membrane with its rows of teeth grows forwards continuously.

The form, size, and number of teeth in each transverse row are useful characters in stylommatophoran taxonomy, especially in species identification. Typically, in each transverse row it is possible to recognise a ‘central tooth’ (also referred to in the malacological literature as the median or rachidian tooth), a series of ‘lateral teeth’, and a series of ‘marginal teeth’. The central tooth is sited in the centre of the radular ribbon on the longitudinal axis, and is usually symmetrical in the shape of its basal plate and cuspid head. On either side, in the same transverse row, the central tooth is flanked by several to many lateral teeth, which may be symmetrical but more typically have the basal plate and cusps most strongly developed on that side of the tooth nearest the radular axis. These teeth in turn are flanked by a series of marginal teeth, which extend to the margins of the radular ribbon. The marginal teeth too may be symmetrical but more often are asymmetrical in shape. In many species the central tooth may be vestigial or even absent.

In taxonomic works the form of the teeth is usually given in the descriptive text, but the structure of the transverse row may be encapsulated in the simple formula:

$$N_m + N_l + C + N_p + N_m$$

where $N_m$ and $N_l$ are the number of marginal and lateral teeth on each half row respectively, and $C$ denotes the presence or absence of the central tooth. Thus the formula for a specimen with a central tooth, 6 lateral teeth on either side, and 20 marginal teeth on either side would be:

$$20 + 6 + C + 6 + 20$$

If a series of specimens are examined from a single species it is usual to find some variation in numbers of lateral and/
or marginal teeth. In the above example this may be expressed by

\[ 19-21 + 5-6 + C + 5-6 + 19-21 \]

indicating that in the material examined the number of lateral teeth varied from 5 to 6 and the marginal teeth from 19 to 21.

In some species there may be a zone of transition between the lateral and marginal fields in which teeth can not readily be classified as either lateral or marginal. This information can be captured in the formula, and in our example three transitional teeth may be identified by the expansion

\[ 16-18 + 3 + 5-6 + C + 5-6 + 3 + 16-18 \]

In many species the marginal and lateral teeth have assumed the same form. This can be identified in the radular formula as

\[ N_{l+} + C + N_{m+} \]

where \( N_{l+} \) is the number of teeth in the half row, with no distinction between marginal or lateral teeth.

Evolutionary change in the pattern of cusp and support structure is one of the prime ways in which stylommatophorans specialise to exploit different food resources. Consequently there is a large range in radular tooth form in Stylommatophora. Because of the apparent frequency of diet-related convergence in tooth form, the radula has generally been regarded as useful in systematics only at generic and species level (Solem 1978). Typically there is variation in tooth form and size along each transverse radular row. Furthermore, the transverse row is rarely straight (perpendicular to the longitudinal axis), more typically describing a V or some form of sweeping arc. These variations along the transverse row relate to the complex curvature of the functional face of the radula when the animal is feeding and the differential role in food gathering for teeth at different positions along the row. Evolutionary changes in the dentition generally occur first at the margins of the radula and progressively work their way towards the centre. Independently of such changes, the central tooth may be reduced.

The generalised stylommatophorans feed on decaying vegetation or fungal hyphae and have mostly tricuspid teeth. Typically their radula has 3000 to 4000 teeth. Many groups show specialisations for scraping phylloplane microbes from leaf surfaces and the cusps may become broad and spadelike. Several groups have developed radulae with numerous small multicuspid teeth, as many as 60 000, for raking and piercing algal and fungal cells. Others show a trend towards elongate lateral-marginal teeth on short basal plates, either as multicuspid sweeping structures, or tending to unicuspid, aculeate piercing structures. This elongation of the lateral-marginal teeth is often associated with an overall increase in tooth number to around 20 000.

Carnivory is generally associated with further development of the aculeate tooth form, so that in the most specialised carnivores all teeth on the radula are lance-shaped for catching and holding prey, and the number of teeth may be reduced to several hundred. Carnivory is usually accompanied by elongation and modified muscularisation of the buccal apparatus, primarily to allow ingestion of large live prey. In its fullest development the buccal apparatus of carnivores occupies a substantial part of the body cavity, and other organ systems are modified to accommodate this. The jaw is commonly reduced or lost in these carnivores, as it plays no role in prey capture.

The oesophagus opens dorsally from the anterior buccal mass and, in snails, runs backwards along the parietal side of the visceral cavity, and most generally expands into a gastric crop a short distance above the top of the pallial complex. Its internal ornamentation, if present, consists of longitudinal ridges. The oesophagus may be partly differentiated into an inflated oesophageal crop but, as pointed out by Tillier (1989), and contrary to the tenets of most treatises of zoology, many stylommatophoran species do not have an oesophageal crop. Two salivary glands are opposed to the oesophagus. Each comprises numerous acini the ducts of which converge into a main salivary duct, and this opens into the buccal cavity at the side of the oesophageal origin. The oesophagus and ducts of the salivary glands pass through the cerebral ring of the central nervous system. The gastric crop is prolonged by the caeca of the gastric pouch or stomach, which collectively extend apically from one-half to two whorls and occupying at least three-quarters of the cross-sectional area of those whorls. At its apex the stomach narrows and abruptly turns forward ventrally as the intestine, which runs along the columnellar side of the visceral mass, turns to the left under the anterior gastric crop or the posterior oesophagus, and turns upwards to cross over the aorta clockwise in dorsal view (periaortic bend), describing a posterior loop (prerectal bend) before turning forwards again. The rectum runs along the suture from the summit of the pallial complex to the roof of the pneumostome at the mantle collar. The anterior duct of the digestive gland opens into the concavity of the gastric pouch, between the openings of the stomach and proximal intestine; the posterior duct generally opens through the parietal wall of the stomach. When present, the ventral groove of the gastric crop leads to the opening of the anterior duct, from which one usually short typhlosole emerges into the proximal intestine. A second, longer typhlosole, issuing from the opening of the posterior duct, runs parallel to the first into the proximal intestine and reaches at most the beginning of the periaortic intestinal loop. The typhlosoles are prominent.
ciliated ridges that direct food particles and other gastric products into the proximal intestine. The large posterior lobe of the digestive gland occupies most of the space in the upper shell whorls. The anterior lobe, often reduced in size, lies adjacent to the stomach. Structural characteristics of digestive gland cells in Stylommatophora support the view that these cells are responsible for absorption and digestion of food material, as well as production and secretion of digestive enzymes (e.g., Dimitriadis & Houdret 1992).

The digestive tract of the Stylommatophora is rather simplified in comparison with many other gastropods. The oesophagus lacks glandular pouches, and the stomach lacks chitinised gizzard plates or a style sac. The simplification seen in Stylommatophora is correlated with a change from mechanical disintegration of the ingested food to a more chemical (enzymatic) process. In some Stylommatophora, notably the Succinidae and Athoracophoridae, a small caecum or diverticula sac occurs on the columnar side of the stomach near the opening of the anterior digestive gland lobe, and may represent a vestige of the coiled gastric caecum present in many lower gastropod groups. The long intestine is a feature of gastropod herbivores, while shortening of the intestine occurs in carnivorous species in various gastropod groups. Moreover, for stylommatophorans Tillier (1989) found intestinal length to be positively correlated with animal size. Formed faeces are of considerable importance for stylommatophorans because the anus is near the pneumostome, and firm faeces are less likely to foul this. Faeces formation in the distal intestine and rectum generally involves secretion of abundant mucus, squeezing of the mucus and rejected material to form firm bodies, and resorption of water.

The layout of the digestive tract in slugs is somewhat different to that observed in snails, owing to incorporation of the visceral mass into the foot. Tillier (1984a) has described the morphologies in the digestive tract in the course of allomotorisation. In most instances and at least in its early stages, allomotorisation involves dedifferentiation of the gastric pouch and development of a crop. At least in its early stages it also usually involves shortening of the intestine. In advanced slugs lengthening of the intestine may cause either secondary coiling or hypertorsion of the digestive tract, quite independent of the torsion and coiling seen in the ancestral snails, or development of intestinal caeca.

Reproductive system (Fig. 21–23)

Stylommatophora are hermaphrodites with a complex reproductive system. Their organs combine female structures associated with production of ova, receipt and storage of allosperm, and production of eggs containing fertilised ova, and male structures associated with production and delivery of autosperm. A generalised stylommatophoran reproductive system is illustrated in Fig. 21, and a generalised layout of the reproductive system in snails and slugs is illustrated in Fig. 22 and 23.

Increasingly, features of the reproductive system are being utilised in stylommatophoran taxonomy and for resolving phylogenetic relationships. However, extensive outgroup comparison is an essential prerequisite for recognising plesiomorphic conditions and their evolutionary changes in the Stylommatophora.

In the most primitive gastropods the sexes are separate (dioecious), and a single gonad lies near the apex of the visceral hump in the general body cavity. It communicates with the right kidney, the duct of which is therefore a renal-urinary duct and its aperture a urinogenital pore. At the most primitive level gametes are liberated into the pallial cavity and thence broadcast into the surrounding water, and fertilisation is external. There is therefore generally little or no elaboration of the genital duct or modification for copulation. In some Vetigastropoda, however, the distal portion of the right kidney duct is modified into a glandular region that produces a mucus layer in which eggs are deposited during spawning. The caenogastropods exhibit several developments on this primitive reproductive system.

While hermaphroditism has evolved in some marine caenogastropod families, most — including those families represented in terrestrial habitats — have remained dioecious. The (renogenital) duct from the gonad is separated from the functional kidney to open separately into the pallial cavity. Primitively, the male system comprises the gonoduct elaborated distally into an open ciliated and glandular groove in the pallial cavity, functioning as a prostatic gland, and a muscular phallus on the neck behind the cephalic tentacle. Sperm from the testis (autosperm), mixed with prostatic secretions, is conveyed to the phallus along an open ciliated groove, the sperm groove. In many caenogastropods the prostatic section of the male gonoduct is a closed tube, and the sperm groove has become internalised as a closed duct, the vas deferens. In the primitive caenogastropod female the gonoduct extends along the pallial cavity roof to the right mantle edge. Along its length it is modified into various glandular regions, more or less sequentially continuous, related to provision of nutrients (albumen gland) and protective coatings (capsule gland) in the egg capsules. While primitively this glandular pallial gonoduct is widely open to the pallial cavity, in many taxa the extent of opening has been reduced, with narrow orifices at both proximal and distal ends or, more commonly, just in the distal portion.
At the back of the pallial cavity a seminal receptacle occurs as a simple dilatation or a blind diverticulum for storage of allosperm received during copulation (Gust & Selmi 1985). An additional pouch, the bursa copulatrix or gametolytic gland, connected with the distal pallial gonoduct and opening to the pallial cavity, functions in digestion of spent or excess allosperm. The bursa copulatrix and seminal receptacle are connected by a groove, which Nordsieck (1985) termed the allo-spermiduct.

The gonad of Stylommatophora is formed by one or several clumps of acini which produce both oocytes and spermatozoa and is thus termed ovotestis (or hermaphroditic gland). It is typically embedded in the upper lobe of the digestive gland. From the ovotestis issues a single hermaphroditic duct which conveys both gamete types to the more distal parts of the reproductive system. The hermaphroditic duct is homologous with the gonoduct (reproductive duct) in lower gastropods that primitive conveyed gametes into the pallial cavity. In Stylommatophora the medial part of the hermaphroditic duct is generally dilated, and occasionally structurally elaborated, as a storage site for autosperm (seminal vesicle).

Those sections of the stylommatophoran reproductive system beyond the hermaphroditic duct that function in prostatic secretion, receipt, conduct, and storage of allosperm, and encapsulation of the fertilised ova were derived from — and are therefore homologous with — that section located in the pallial cavity of lower gastropods. Owing to modifications of the pallial cavity, the gonoduct shifted into the body cavity during pulmonate evolution. I shall refer to this section of the stylommatophoran reproductive tract as the pallial gonoduct to reflect this homology.

There has been considerable debate in the literature as to the origins of hermaphroditism and the plesiomorphic state of the pallial gonoducts in the Stylommatophora (e.g., Pelseneer 1896, Simroth 1910a, Hoffmann 1928, Duncan 1960, Nordsieck 1966, 1985, Solem 1972c, 1976, 1978, Visser 1977, 1981, Haszprunar 1985). Monauly of the pallial gonoduct is the plesiomorphic condition in the Stylommatophora (Nordsieck 1985), not diauly as Solem (1976, 1978) believed. Hermaphroditism is a basic feature of gastropods, which is merely suppressed in dioecious taxa. From the condition in the ancestral gastropod, the hermaphroditic pallial gonoduct in the stylommatophoran lineage apparently did not evolve from the female gonoduct or the male gonoduct alone, but arose from the combination of both gonoducts. This hypothesis is supported by the fact that the pallial gonoduct consists primarily of three channels: the outlet-channel for autosperm (termed autospermiduct), the inlet-channel for allosperm (allospermiduct), and the outlet-channel for eggs (oviducal gland).

In most species the pallial gonoducts assume the gross morphology of a saccular, secretory oviducal gland into which the autospermiduct opens and, with its associated prostatic follicles, is fused. This combined oviducal gland/autospermiduct is commonly referred to as a spermoviduct. The oviducal gland in Stylommatophora retains the function of secretion of mucopolysaccharides and calcareous crystals that form the egg-shell layers. In oviparous species the oviducal gland is commonly elongate and as such the autospermiduct and ribbon of prostatic follicles are similarly elongated. In some oviparous groups there has been some secondary shortening of the oviducal gland or, more frequently, of that section of the autospermiduct from which prostatic follicles issue. In ovoviviparous and viviparous species there is generally a short spermoviduct, with the prostatic follicles confined in reduced numbers at the proximal end. Several groups of stylommatophora exhibit a trend towards separation of the oviducal gland/autospermiduct combination from the autospermiduct, as closed tubes. Diauly of the stylommatophoran pallial gonoducts is therefore interpreted as a secondary phenomenon, and probably has occurred repeatedly.

The seminal receptacle, a diverticulum of the lower gastropod pallial gonoduct that served as a repository of allosperm, has become incorporated into the stylommatophoran reproductive system. Associated with the seminal receptacle is the accumulation pouch, which is the site of fertilisation of ova from the ovotestis. The combined seminal receptacle/accumulation pouch complex is termed the talon. The external form of the talon varies greatly between taxa, from a simple U-shaped bend in the terminal section of the hermaphroditic duct, through to a cluster of minute diverticular sacs, the stem of which arises from the junction of the hermaphroditic duct with the fertilisation chamber. It lies partially or deeply embedded in the columellar side of the albumen gland.

The plesiomorphic reproductive system of Stylommatophora is equipped with complex copulatory organs, with structures for producing and receiving spermatophores, and an auxiliary stimulatory organ. The free section of the autospermiduct distal to the prostatic follicles and oviducal gland, the vas deferens, is homologous with the structure for conveyance of autosperm evident in lower gastropods. The packaging of spermatozoa for insemination in the form of a spermatophore is of wide occurrence in the Gastropoda. Sperm transfer by spermatophores is neither an adaptation to terrestrial life (Nordsieck 1985) nor a trait developed independently in several stylommatophoran groups (Solem 1978), but a plesiomorphic trait in Stylommatophora inherited from their marine ancestors. In Stylommatophora the spermatophore is produced in the distal part of the vas deferens, which has a special structure.
and is termed epiphallus. In the plesiomorphic state the vas deferens does not insert terminally, and therefore the epiphallus has an appendage termed flagellum; this flagellum has a role in spermatophore formation. The shape of the epiphallus and its internal folds moulds the spermatophores into species-specific structures.

In many stylommatophoran groups there is an evident trend towards insemination without the need for spermatophores. In its early stages this trend manifests as simplified epiphallus structures, without a flagellum. Further epiphallus simplification results in spermatophores simplified in shape and ornamentation and with reduced thickness of the matrix that casheats the spermatophores. In many Stylommatophora a structure recognisable as an epiphallus is wanting and insemination is achieved by spermatophores suspended in a viscous fluid. In the plesiomorphic state of the stylommatophoran genitalia the epiphallus opens as a perforated papilla, termed verge, into the tubular phallus. As evidenced by the condition of the structure in Opisthobranchia and Pulmonata, including various Stylommatophora, a long verge papilla is plesiomorphic for the Stylommatophora. Only rarely in the Stylommatophora is the verge chitinised, and never does it function as a stylet as seen in some Basommatophora and Opisthobranchia. In many Stylommatophora the verge papilla is reduced in size or entirely absent; this is a secondary phenomenon.

The eversible and thus protrusible phallus in Stylommatophora, developed by invagination of the body wall at the base of the pedal phallic structure, is of widespread occurrence in the lower gastropods, including lower Heterobranchia. This invagination created a tubular structure bearing at its apex the formerly external pedal phallus, as an elongate papilla perforated by the vas deferens or sperm groove — the verge structure described above. This protrusible phallus, retractable primarily by a muscle attached to the diaphragm or columnella, is a synapomorphic character of higher heterobranch gastropods (clade Pentagangiata, sensu Haszprunar 1985) but may have developed independently several times with sinking of the pallial gonoduct into the haemocoel.

As exemplified by variations in contemporary archeopulmonate Ellobiidae (Morton 1955a, b, Berry et al. 1967), the phallic portion of the vas deferens in early Stylommatophora shifted from a course through the phallus wall to one in the haemocoel, but closely bound to the phallus by a muscular sheath. In contemporary Stylommatophora the vas deferens, or its epiphallus terminal section, has retained this association with the phallic sheath in some taxa while in others it has been lost and in yet others the sheath itself has been lost.

The phallus retractor muscle relaxes during mating to allow the phallus to evert. When copulation is completed, the muscle — which now lies inside the everted phallus — contracts. This invaginates the phallus as it is pulled back into the body.

Sinking of the pallial gonoduct into the haemocoel has been accompanied in Stylommatophora by a shift forwards of the female opening to unite with that of the male part as a common chamber, termed the atrium. The female component of the genitalia thus comprises a tubular extension of the pallial gonoduct. In Stylommatophora the bursa copulatrix has maintained both its association with the pallial cavity and its opening to the pallial gonoduct. Thus the primary form in Stylommatophora is a reservoir lying adjacent to the pericardium and bound by connective tissue and muscle to the diaphragm that constitutes the floor of the pulmonary cavity, and a distinct, usually rather long duct running to the cephalopodial part of the female reproductive tract. In many Stylommatophora the bursa copulatrix has developed an even more anterior entry to the reproductive tract, in some taxa communicating directly to the atrium or even with the phallus. A variant of this pattern is the opening of the bursa copulatrix to the proximal region of the female pallial gonoduct in some Achatinellidae.

Two basic types of bursa copulatrix are evident in Stylommatophora, those with a diverticulum on the duct, and those without such a diverticulum. The diverticulum on the bursa copulatrix is widespread in the Stylommatophora, and is apparently plesiomorphic. It is specifically constructed and positioned, relative to the bursa copulatrix duct opening, to function during mating as the site of spermatophore receipt from the copulatory partner. In many taxa the diverticulum is reduced or absent and the bursa copulatrix duct assumes the role of spermatophore receipt. The function of spermatophore receipt and the occurrence of allosperm in the reservoir part has led to the term bursa copulatrix being applied to this structure. However, a gametolytic rather than storage function has been demonstrated for this structure (Tompa 1984).

Furthermore, in many Stylommatophora spermatophores — or seminal mass, where spermatophores are not produced — are not received directly into the bursa copulatrix duct or its diverticulum, but are deposited in the oviduct. The seminal receptacle in the talon is the site for storage of allosperm, and it is only the excess allosperm that are retained or conveyed into the bursa copulatrix for lysis and resorption. Thus the term bursa copulatrix is not entirely appropriate, but is retained here for consistency with the modern literature. A trend evident in Stylommatophora, apparently related neither to site of entry to the reproductive tract nor to body cavity space alterations, is shortening of the bursa copulatrix duct and relaxation of the association of its reservoir with the pallial region.
The free oviduct is its narrower portion, between the distal end of the oviducal gland and the entrance of the bursa copulatrix duct. The vagina is that region of the oviduct between the base of the bursa copulatrix duct and that of the phallus.

Stimulatory organs can be found in the terminal genitalia of many Stylommatophora. There are different opinions concerning their evolution: some authors - Solem (1978) and Tompa (1984), for example - thought the stimulatory organs had evolved independently, while von Ihering (1892) and Schileyko (1979) considered all or only part of them to be homologous.

The stimulatory organ of the Orthurethra (sensu Pilsbry), developed as a phallic appendage, consists of a perforated papilla in a sheath, an adjoining gland, and a retractor muscle which is a branch of the phallic retractor. In many orthurethrans the bifid retractor is retained despite the stimulatory organ being somewhat reduced. In other orthurethran taxa the retractor to the stimulatory organ is retained but has become separated from the phallic retractor. A branch of the phallic retractor muscle inserting on the vestiges of the phallic stimulator, represented by a small lateral phallic caecum in Claussilidae, Zonitidae, Eucomulidae, and Perussaciidae, testifies to the former wide occurrence of a more fully developed stimulatory organ in the non-orthurethran Stylommatophora.

In at least one group of non-orthurethran Stylommatophora, the zonitoid Gastrodontinae, a stimulatory organ of very similar structure to that in Orthurethra, and supplied with a retractor muscle, is present as an appendage to the phallus. It contains, however, a well-developed calcareous dart. In Sagdidae too the stimulatory organ on the phallus is remarkably like that seen in Orthurethra, except for the absence of a retractor muscle and the presence of a vestigial dart. In several families of non-orthurethran Stylommatophora (e.g., Ariophantidae, Urocyclidae, Vitrimidae) this dart-bearing stimulatory organ has been retained, but displaced to the atrium or vagina, and the retractor muscle is still evident.

There is little doubt as to the homology of the unarmed stimulatory organ characteristic of the Orthurethra and the dart-equipped organs of these latter Stylommatophora. The difficulty lies in deciding which is the more plesiomorphic. The occurrence of a dart in the stimulatory organ across many superfamilies of non-orthurethran Stylommatophora (the occurrence in Orthurethra has yet to be confirmed - see Tompa 1984), including the vestigial dart of Sagdidae in a stimulatory organ built like the orthurethran stimulator, suggests that the dart-bearing structure is the primitive feature of Stylommatophora. This interpretation of plesiomorphy is further supported by the occurrence of auxiliary copulatory organs associated with the phallus in many other Heterobranchia, e.g., Cephalaspidea and other opistobranchs, Stiphonariidae, Amphibulidae, Aeucylidae, Onchidiidae, Vaginulidae, and Rathouisiidae. Nordseeck (1985, 1992) reached the same conclusion.

The reproductive system of Stylommatophora is systematic, with the common genital orifice opening on the right side. Syntremy permitted the change in position of the stimulatory organ from the male terminal genitalia to the female ones. Thus, among non-orthurethran Stylommatophora the stimulatory organ may be inserted on the phallus - the plesiomorphic position - or on the genital atrium and vagina. Further, loss of the stimulatory organ is widespread in the Stylommatophora. During evolutionary degeneration of the stimulatory organ, dart loss is a stage that precedes full organ loss; this pathway is evident, for example, in helicoid snails. In many taxa dart loss is accompanied by modifications of the previously dart-bearing papilla into a fleshy or hard-coated sarcobulum. Dart loss and stimulator loss are to be regarded as irreversible.

The plesiomorphic state within the Stylommatophora is for the genital opening to be located in the main body of the visceral stalk, near the pneumostome. In many lineages there has been a forward shift of the genital opening, into the cephalic region, and in many taxa the opening occurs immediately behind the right ocular peduncle.

External sperm exchange, by which allosperm is deposited on the mate's everted phallus without intromission, has evolved at least five times among stylommatophorans (Emberton 1994b). In the families Succineidae, Endodontidae, and Polygyridae both internal and external sperm exchange are known, while in Limacidae and Agriolimax exchange is exclusively external.

While the hermaphroditic reproductive systems of stylommatophorans typically possess both male and female genitalia (euphally), asexual individuals that lack the male copulatory organs are known from several families, including Vertiginidae, Valloniidae, Chondrinidae, and Agriolimaxidae. Asexual individuals can self-fertilize, or can outcross as female but not as male.

Tompa (1976, 1980) considered the provision of the embryo with calcium, by ionic mobilization of shell and/or digestive gland calcium stores and deposition as an egg shell by a specialized gonoduct epithelium, to be a synapomorphy of Stylommatophora. Other gastropods, especially in terrestrial habitats, are known to provide the embryo with calcium in the egg capsule, but the mechanisms for this differ from that in Stylommatophora (Tompa 1980). A hard, calcite egg shell thus can be taken as plesiomorphic in Stylommatophora, and the production of eggs with diminished calcium provision, and hence lacking a shell, as apomorphic. Some stylommatophorans
have adopted embryo brooding, whereby the eggs are deposited at an advanced stage of embryo development or retained in the oviduct until hatching (Tompa 1984).

Free muscle system (Fig. 22, 23)
The free retractor muscular system comprises branches of the columellar retractor, which is inserted on the inner shell surface along the columella — the only point at which the animal is attached to its shell. The primary form of the columellar muscle is a single stem with a broad fan attaching to the pedal musculature and organs in the body anterior. This condition is now rarely seen in the Stylommatophora. Instead there has been a general reduction in the bulk of the free muscle system, with branches to the various anterior organs and cephalic body walls becoming to various degrees separated from the columellar muscle stem. The buccal retractor inserts under the buccal mass, while the tentacular retractors divide distally into ocular and rhinophoral branches. In the primary state, the right ocular retractor passes over the base of the phallus to reach the ocular peduncle. The alternative course of the retractor, free of the terminal genitalia, has apparently arisen in many lineages independently. During limacisation the columellar stem to the pedal musculature is frequently lost, since there is no need for withdrawal of the anterior head-foot. In many slug taxa the buccal and tentacular retractors often lose their association with the columella (its region of origin) and instead arise from the body wall.

As indicated above, the phallus retractor muscle in most Stylommatophora arises from either the diaphragm or the columellar muscle stem. In some taxa the phallus retractor arises from the body wall outside the palatal region. In yet others the retractor is represented by rather weak muscle strands to the palatal gonoduct, or is entirely absent. The plesiomorphic state for attachment of the phallus retractor and the evolutionary changes within the Stylommatophora have not been resolved.

Nervous system (Fig. 24)
In the primitive gastropod the nerve centres are concentrated in the anterior head-foot, forming a loose ring around the oesophagus. There are three pairs of ganglia. The cerebral ganglia, linked by a cerebral commissure, are placed far forward dorsally over the buccal apparatus. Each cerebral ganglion sends ventrally two connectives, one each to the pleural and pedal ganglia located ventrally at the level of the anterior border of the foot. The left and right pleural ganglia are linked to the respective left and right pedal ganglia by a short connective. The pedal ganglia comprise long cords running the length of the foot and linked by many commissures. This arrangement, with the pleural ganglia sited closer to the pedal ganglia than to the cerebral ganglia, is termed hypoathroidy.

Paired visceral ganglia lie at the base of the visceral mass, linked to the pleural ganglia by connectives which traverse the neck and so are affected by torsion. In consequence the half-loop starting at the right pleural ganglion passes over the oesophagus to the visceral ganglion on the left, and the half-loop starting at the left pleural ganglion passes under the oesophagus to the visceral ganglion on the right, so giving the crossed condition of the visceral loop known as streptoneury. The dorsal pleural-visceral connective carries medially a ganglion (supravisceral) which innervates the left pallial gill (stenidia) and sensory organ (osphradium). The ventral connective carries a corresponding suboesophageal ganglion, innervating the same organs on the right.

The Stylommatophora are derived from gastropods in which the pedal ganglia had been concentrated and linked by a reduced number (two) of commissures, and the visceral loop had been shortened so that the pleural-visceral connectives were no longer crossed. This condition of the uncrossed visceral loop, referred to as euthyneury, had been accorded systematic significance in uniting opisthobranchs and pulmonates in the clade Euthyneura (Spengel 1881). However, the euthyneurous state of the visceral loop in pulmonates and opisthobranchs is now recognised as being due to convergence and derived independently in different lineages (Haszprunar 1985). Furthermore, vestiges of streptoneury are evident in several extant lower Pulmonata (e.g., Chilinidae, Ellobiidae) and Opisthobranchia (e.g., Diaphanidae, Philinidae). The opisthobranchs and pulmonates are, however, united by the autapomorphy of two additional ganglia - left and right parietal ganglia, derived from left and right pleural ganglia respectively - on the visceral loop. For this group Haszprunar (1985) proposed the taxon Pentaganglionata.

In Stylommatophora, with shortening of the connectives in the visceral loop, the oesophageal ganglia have been merged with the visceral ganglion, and the parietal ganglia frequently become appressed to or fused with the pleural or visceral ganglia. It seems reasonable that the length of the connectives in the visceral loop would be evolutionarily plastic (Tillier 1989); however, once two ganglia fuse in the course of evolution they are highly unlikely to separate again (but see Emberton 1991). The importance of visceral loop configuration for stylommatophoran systematics was initially investigated by Bargmann (1930), recommended by Bishop (1978), and extensively explored by Tillier (1989) and Emberton (1991). In the present work I have incorporated the configuration of the visceral loop into the taxon diagnoses.

The stylommatophoran central nervous system is sited at the posterior of the buccal mass. The oesophagus passes
below the cerebral commissure but above the visceral loop. For a visceral loop of a given length, the diameter of the perioesophageal ring is smaller when the cerebropleural connectives are shorter than the pleuropedal connectives, in contrast to when the pleural ganglia are closer to the pedal ganglia. Tillier (1989) reasoned that a short visceral loop is in general functionally impossible unless the pleural ganglia are close to the pedal ganglia, because it would strangle the osccophagus.

An extension of this argument would suggest that the hypothroid condition in Stylommatophora, where the pleuropedal connectives are shorter than the cerebropleural ones, is a secondary phenomenon affected by functionality of the digestive tract. However, the condition in many basal groups indicates that hypothroidy is plesiomorphic in Gastropoda (Haszprunar 1993). Furthermore, hypothroidy is retained or achieved in several heterobranchia, e.g., Aplysiomorpha, Ellobioidea, and Trimusculoidea (Haszprunar & Huber 1990), irrespective of the degree of shortening of the visceral loop. Moreover, many Caenogastropoda and other non-stylommatophorain Heterobranchia have achieved epipatry, whereby the pleuropedal connectives are longer than the cerebropleural ones, despite in many instances having a shortened visceral loop. On the basis of ontogeny, Haszprunar (1993) thought hypothroidy in heterobranchia to be derived secondarily from the epipatry condition.

Long cerebropleural connectives are correlated with a long supraoesophageal cerebral commissure, and this association is probably the plesiomorphic condition (Tillier 1989). A compact nerve ring with short cerebropleural connectives is a common feature in Stylommatophora, and the lengths of the right and left cerebropleural connectives are frequently subequal. In carnivorous taxa the retention or secondary derivation of a long anterior nerve ring, including a rather long visceral loop, can be explained easily by the functional necessity for extending around the voluminous buccal mass associated with carnivory.

The cerebral ganglia are also linked by a thin and easily overlooked sub-oesophageal cerebral commissure. The cerebrobuccal connectives pass from the lower surface of the cerebral ganglia to the buccal ganglia, which are pressed to the buccal mass on either side and below the origin of the osccophagus.

An essential autapomorphy of the pulmonates is the development of a neurosecretory procerebrum – an accessory lobe linked by two connectives to the metacerebral part of the cerebral ganglion – and a cerebral gland. Van Mol (1967, 1974) described morphoclines in the microscopic structure of the pulmonate cerebral ganglia, emphasizing greatest systematic significance in the degree to which the procerebrum is integrated with the metacerebrum (persistence of two procerebral commissures) and the position of the origin of the peritentacular nerve. As pointed out by Solem (1985) and Tillier (1989), the conclusions of van Mol cannot be accepted because observations in a single species cannot be generalized to family or even supra-family levels. Nonetheless, the Stylommatophora can be characterized by an enlarged procerebrum that is extensively fused with the cerebral ganglion.

The cerebral ganglia receive tactile and olfactory sensory input from tentacle on the head and from the lips around the mouth, and visual signals from the eyes; there is a single nerve to each ocular peduncle and to each inferior tentacle. The cerebral ganglia also innervate the buccal muscles. The pedal ganglia mediate locomotor movements of the foot. The pleural ganglia innervate the mantle edge, and the visceral ganglia the organs of the visceral mass.

**COLLECTING, PREPARATION, AND CURATION**

Empty shells are best stored dry in boxes (large specimens) or gelatin capsules (small specimens). Long-term storage in glass vials is often associated with deterioration of the shell. Field-collected live specimens are best killed by immersion for about 15 hours in de-aerated or narcotised water before preservation in 75% ethanol.

Snails may be extracted from the shell and stored in alcohol for subsequent anatomical examination. This extraction is most readily achieved, without destruction of the shell, if undertaken several hours after placement in the preservative but before the soft tissues have hardened substantially. For large animals preservation of the internal tissues is often improved by making an incision in the body wall to allow rapid penetration of the preservative. Mollusc shells deteriorate in formalin solutions, and formalin should be reserved for fixation and preservation of animal tissues to be used in histological investigations.

Specimens may be dissected under water or 75% ethanol, pinned to black wax in a shallow tray. Visibility of minute structures may be enhanced by addition to the dissection of small quantities of dye solution, such as methylene blue.

Jaws and radulae are extracted from the buccal mass by dissolution of the tissues in 10% sodium hydroxide solution and repeated washing in tap water. For light microscopy these structures can be mounted temporarily on glass slides in glycerol or permanently in Clearmount or DPX. For electron microscopy the jaws and radulae are best brought to 100% methanol and then air dried before being mounted on specimen stubs.
For many species, inspection of the protoconch and teleoconch sculpture at high magnification is required. For minute species this is best achieved by scanning electron microscopy. The specimens are first cleaned of most dirt and incrustations by soaking overnight in water, and then immersed for a few seconds in the water-filled tank of an ultrasonic cleaner. After air drying the specimens are mounted with the desired orientation on stubs.

**DESCRIPTIONS**

**Family AGRIOLIMACIDAE**

**Diagnosis.** Small to medium-sized aulacogonid slugs, herbivorous or facultatively carnivorous, with a rudimentary internal shell always present. Mantle a large, elongate-oval shield situated in anterior part of body, covering more than 0.3 of body. Posterior of body with a short keel. Pneumostome in right margin of mantle, usually in posterior part. Sole divided into 2 lateral zones with transverse grooves and a central zone with V-shaped grooves. Suprapedal gland embedded in foot tissues. Kidney broadly oval, often with a posterior lobe extending under rectum, partially enclosing heart at its anterior end. Secondary ureter separating from posterior end of kidney, terminating in urinary bladder. Buccal mass spheroidal. Jaw oxygastrenchic. Radula with marginal teeth dagger-like or sword-like. Intestine with a single forward-directed loop. Cephalic retractor muscles arising near body midline, a little posterior to pallial complex. Right ocular retractor muscle crossing the phallus or free of genitalia. Genital orifice immediately behind right ocular peduncle, or about 0.3 posterior between peduncle and pneumostome. Oviduct and atrium without accessory glands. Phallus sarcobelum (stimulator) and frequently with appendages. Genital orifice immediately behind right ocular peduncle. Rectal orifice immediately behind right ocular peduncle. Rectal caecum often present, short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact. Haploid chromosome number 30.

**Remarks.** The family Agriolimacidae has recently been reinstated (Wiktor & Likharev 1979, 1980, Likharev & Wiktor 1980) after having long been grouped with the Limacidae. This taxon comprises over 150 species, most confined naturally to the Holarctic region. Genera included are Deroceras Rafinesque Schmaltz, 1820, Krynichillus de Kaleniczenko, 1851, Lytopelte Boettger, 1886, Meso- limax Pollonera, 1888, Texolimax Simroth, 1899, Megalopelte Lindholm, 1914, and Furcopenis Castillejo & Wiktor, 1983.

**Genus Deroceras Rafinesque Schmaltz**

*Limax* of authors. (Not *Limax* of Limnaeus, 1758, type species *Limax maximus* Linnaeus, 1758, by original designation; Limacidae.)

*Limacella* of authors. (Not *Limacella* of Brand, 1815, type species *Limacella parma* Brand, 1815 = *Limax maximus* Linnaeus, 1758, designated by Turton (1831) — synonym of *Limax* Linnaeus, 1758; Limacidae. Not of de Blainville, 1817, type species *Limacella inexpectans* de Blainville, 1817 = *Limax carolinianus* Bosc, 1802, by monotypy — synonym of *Phthirius fasciatus* Schmaltz, 1820; Phthiriidae).

*Deroceras* Rafinesque Schmaltz, 1820; 10, type species *Limax gracilis* Rafinesque Schmaltz, 1820 = *Limax laevis* Müller, 1774, by original designation.

*Krynichillus* of authors. (Not *Krynichillus* of de Kaleniczenko, 1851, type species *Krynichillus melanocephalus* Kaleniczenko, 1851, by monotypy; Agriolimacidae.)


*Malaclimax* of authors. (Not *Malaclimax* of Malm, 1868, type species *Limax tenellus* Müller, 1774, according to Hesse (1926; Limacidae).


**Diagnosis.** Shell a broadly oval internal plate with concentric growth lines radiating from vestigial protoconch at posterior left margin. Keel on body very short. Pneumostome in posterior right margin of mantle. Mantle shield with concentric ridges, their nucleus to right of midline, over respiratory orifice. Kidney oval, with posterior lobe directed to right under rectum. Jaw oxygastrenchic, with a central protrusion. Right ocular retractor muscle passing to left of phallus and eviscerate. Phallus with an internal stimulator and frequently with appendages. Genital orifice immediately behind right ocular peduncle. Rectal caecum often present, short.

**Remarks.** Until very recently in European and some American literature the name *Agriliimactus* Mörch, 1865 was used for all representatives of this genus. I have followed Wiktor (1973) in giving priority to *Deroceras* Rafinesque Schmaltz, 1820.

*Deroceras* is represented by about 100 species in four subgenera, for which de Winter (1985) provides a summary of the diagnostic characters.

The genus is Holarctic in distribution, with greatest representation in Europe. Several species have been widely dispersed through human activities. Represented in New Zealand by three naturalised species.
Subgenus Deroceras Rafinesque Schmaltz

_Deroceras_ Rafinesque Schmaltz, 1820; 10, type species _Limon graciilis_ Rafinesque Schmaltz, 1820 = _Limon laevis_ Müller, 1774, by original designation.

_Maltno_ Gray, 1855: 178, type species _Limon bombicoides_ Morelet, 1845, by original designation.

_Hydrolimax_ Müller, 1868: 79, type species _Limon laevis_ Müller, 1774, according to Hesse (1926). (Not _Hydrolimax_ Heldemann, 1842, Vernon.)

_Eulimax_ of authors. (Not _Eulimax_ of Bower, 1881; _type species_ _Müller braondii_ van Mourens, 1880, by monotypy; _Lima-cidinae_.)

_Arctolimax_ Westerlund, 1894 (1892-94): 163, type species _Limon hyperboreus_ Westerlund, 1894 = _Limon laevis_ Müller, 1774, according to Pilsbry, 1948 (1939-48).

**Diagnosis.** Body narrow, with sides more or less parallel. Mantle large, almost 0.5 of body length. Skin soft, partly transparent, so shape of internal organs visible. Phallus with anterior part a stimulator in the shape of a hemispherical papilla or obtuse cone; posterior part with 1 or 2 appendices and with glandular papillae or flagella. Rectal caecum absent, or in the form of a small, shallow pocket.

**Remarks.** Slugs favouring high humidity, living near water in both open and forested habitats.

_Deroceras_ (Deroceras) _laeve_ (Müller)

_Figures 25, 28, 68, 109, 136, 165, 191, 219, C1, M32–34; Map 1_

_agrestis_ of authors (not of Linnaeus, 1758).

_laevis_ Müller, 1774: 1 (Limon).

_brandii_ Draparnaud, 1801: 104 (Limon).

_graciilis_ Rafinesque Schmaltz, 1820: 10 (Limon).

_undecula_ d'Orchigny, 1837 (1834-47): 222 (Limon).

_campestris_ Binney, 1843: 52 (Limon).

_porvidus_ Normand, 1852: 8 (Limon).

_semitectus_ Motch, 1857a: 281 (Limon).

_phallus_ Philipp, 1858: 22 (Limon).

_weinlandi_ Heynemann, 1862: 212 (Limon).

_gasties_ Gassies, 1867: 117 (Limon).

_araneus_ Tate, 1870: 134 (Krynickia).

_guatemalensis_ Crosse & Fischer, 1870: 297 (Limon).

_motagnensis_ Cockerell, 1914: 57 (as subsp. of _guatemalensis_ Crosse & Fischer) (Agriolimax).

_renschi_ Wagner, 1934: 89 (Agriolimax).


_2002_ Pilsbry, 1944: 16 (Deroceras).

_monocolophus_ Pilsbry, 1944: 16 (Deroceras).

_Slugs (Fig. 25) up to 25 mm in length, usually smaller, slim, posteriorly obtusely narrowing; keel short, ill defined. Mantle shield about 0.5 of body length. Body wall thin, transparent, usually chocolate brown, grey, or black, less frequently brownish cream, unicolorous in appearance but under magnification seen to be speckled or flecked. Border of pneumostome rather in conspicuous. Sole pale grey to brown, more transparent medially than laterally. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle._

_Shell (Fig. 28) thin, white, oblong-oval to avoid with right margin straight to convex, up to 3.1 x 2.1 mm. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, non-protruding, situated asymmetrically at left side. An organic sheet surrounding shell._

_Reproductive system. Fig. 68. Ovotestis compact, darkly pigmented. Hermaphroditic duct short, nearly straight, with talon at short albumen gland. Spermoviduct slightly twisted, voluminous; prostatic gland ribbon-like, attached along axis of female oviducal tract. Free oviduct sinuous. Vagina absent. Reservoir of bursa copulatrix oval to globular, on duct arising from junction of penis and free oviduct. Atrium tubular. Euphallic individuals with phallus sinuous, elongate, its proximal apical part with several small papillae (phallus glands); stimulator in distal phallus small, hemispherical or obliquely conical. Vas deferens thin, long, opening into phallus laterally about 0.3 from apex._

_Male copulatory organs often reduced, tending towards full aplasia. Phallus often shorter, persisting as a broadening or swelling on atrium into which a shortened vas deferens opens; further reduction may lead to its complete_
absence, the vas deferens becoming blind-ending, with no connection to atrium, or in the extreme with no free vas deferens. Female organs never reduced. Forms with reduced phallus somatically larger, with greater development of albumen gland and oviducal glands.

Phallus retractor muscle short, arising from diaphragm a little anterior to kidney, and inserted onto middle part of phallus.

Jaw (Fig. 109) of usual oxygnathous type, 1 mm in width.

Radular ribbon (Fig. M32-34) comprising about 80–110 rows of teeth, each varying in formula around 25+13+G+13+25. Central tooth with mesocone prominent, slender, flanked on either side by small, weak ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by a small endocone displaced towards mesocone tip and a small, pointed ectocone. Lateral teeth with mesocone progressively more slender, endocone becoming smaller and finally lost, and ectocone persisting until 11th to 15th tooth. Marginal teeth comprising only an elongate, slender mesocone, progressively smaller towards radular margin.

Digestive tract, Fig. 138. Buccal mass spheroidal. Oesophagus quickly expanding to large crop, which extends to about 0.6 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards a short distance to pass over anterior aorta, then producing a posterior loop nearly reaching body apex, before running forwards over stem of cephalic retractor to anus; rectum lacking a caecum. Palpal complex (Fig. 165) located in posterior part of mantle. Kidney rounded to oval, its longer axis transverse relative to body axis, partially enclosing heart at its anterior margin; a lobe arising from ventral medial part and extending to right below rectum. Secondary ureter arising from right posterior aspect of kidney, describing an arc to right anterior quarter of palpal complex, where it terminates in a barrel-shaped bladder. Heart with ventricle axis slightly right-inclined. Aortic stem long, extending below kidney lobe and rectum to outside right palpal margin before dividing into anterior and posterior branches. Lung with vascular network poorly developed.

Free muscle system, Fig. 191. Cephalic retractor arising on body midline a little posterior to palpal complex, passing forwards as a long common stem; buccal retractors dividing off well anterior from common stem, or occasionally from left tentacular branch.

Central nervous system (Fig. 219) with cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal than to cerebral ganglia. Visceral chain compact, with right pleural fused to right parietal ganglion; left parietal fused to visceral ganglion, which lies on median plane.

Type material. The whereabouts of the type material, from Frederiksdal, is unknown; it is presumed lost.

Distribution. D. laeve is a cosmopolitan terrestrial slug which has generally been assumed to be native to the Palearctic region. Chichester & Getz (1973) attribute the American distribution to natural spread in the Late Pleistocene or postglacial times. Van Regteren Altena (1966) and Barker & Pottinger (1983) considered the high mountains of Central America and the Andes of South America to be part of the natural range of D. laeve. This species has been introduced by man into most areas of the world.

Recommended common name. Marsh slug.


History in New Zealand. In an earlier revision of introduced slugs Barker (1979) treated records of D. laeve in New Zealand by Musson (1891), Suter (1913), Thomson (1922), Whitten (1955), and Coleman (1970) as misidentifications of D. panormitanum. The current rather restricted distribution of D. laeve suggests that this species has only recently established in New Zealand and supports my earlier referral of records to D. panormitanum. However, Quick (1960) examined material of D. laeve from New Zealand, suggesting its presence here in the late 1950s.

Biology. D. laeve is remarkable for its unusually diverse habitats, spanning an enormous geographical and ecological range. It is known from sea level to over 3500 m altitude, and from Arctic tundra to mesic and tropical for-
ests and croplands. It is hygrophilic and, while occurring in other habitats, is most abundant in wetlands at the edge of streams, rivers, and lakes and in wet grasslands and forests. It is even partially amphibious (Pearl 1901, Chichester & Getz 1968, Wichtor 1983a, Rollo & Shibata 1991). In wetlands subject to periodic flooding D. laeve thrives while other species such as D. reticulatum are drowned (Rollo & Shibata 1991).

Another feature of D. laeve is its ability to survive freezing temperatures, and it is active over the range 0–30°C. This probably explains why its global range extends further northwards and southwards than that of D. reticulatum. Carrick (1942) and Karlin & Naegele (1960) claimed that immersion kills Deroceras eggs, but Rollo & Shibata (1991) found that D. laeve eggs develop normally and hatch underwater (see also Kosiniak 1980 on D. sturanyi).

In New Zealand D. laeve is mostly restricted to the environs of nurseries, greenhouses, and gardens, but populations have been located in wet pastures and on stream banks in the Auckland and Waikato regions.

This species exhibits high plasticity in life history traits, with rapid growth and reproductive maturation within several months of hatching under favourable conditions, but with slow growth, delayed maturation, and extended lifespan under less favourable conditions. Mature slugs are thus always present to exploit unpredictable breeding opportunities in strongly seasonal, summer-dry climates, while in more equitable situations breeding can be maintained throughout the year (Rollo & Shibata 1991). Little information is available on the life cycle in New Zealand, but dissection of material from several continuously wet stream bank habitats suggests that breeding occurs throughout the year.

Mating in D. laeve occurs under cover, such as beneath timber and stones. This species apparently does not engage in the courtship trail-follwing and circling seen in D. reticulatum. The copulatory position is maintained for up to 1 hour (Gerhardt 1939, and this study). The translucent grey eggs, with sparse calcareous crystals embedded in the coating, vary from 1.8x1.45 mm to 2.0x1.3 mm, and are deposited as early as 3 days after mating, on or in soil, under logs, stones, and ground litter.

The male copulatory organs are frequently poorly developed (Baker 1930, Pilshury 1948 (1939–48), Quick 1960, Wichtor 1973, Els 1978, Barker & Pottinger 1983). In euphallic individuals the phalus is a long tubular structure with internal stimulator and apical glandular papillae. With progression towards aphallic the phalus may simply be shorter, or greatly reduced to a swelling on the atrium, and even completely absent, the blind end of the vas deferens having no connection with the atrium. In the extreme there is no free vas deferens. The female organs are never reduced. Forms with a reduced phalus are somatically larger, with the albumen gland and oviduct more strongly developed.

D. laeve has been reared in the laboratory unparentally for many generations (e.g., Maury & Reygrobellet 1963). This, coupled with marked deficiencies of heterozygotes in natural populations, led Foltz et al. (1982b) and McCracken & Selander (1980) to suggest the occurrence of self-fertilisation. Nicklas & Hoffmann (1981) demonstrated parthenogenesis and outcrossing as facultative reproductive modes for this species. The low heterozygosity of unparental laboratory and natural populations studied by Nicklas & Hoffmann (1981) has been attributed to automictic parthenogenesis by Hoffmann (1983). Further, the occurrence of populations of low genetic variability (as sampled by Foltz et al. 1982b, McCracken & Selander 1980), and others composed of single clones (Nicklas & Hoffmann 1981), led Hoffmann (1983) to suggest that there is geographic variation in the breeding system of the species, or that D. laeve consists of more than one cryptic species. Nicklas & Hoffmann (1981) were able to show that in their North American populations the variation in genital structure was affected by the temperature and photoperiod of the rearing environment.

Both euphallic and aphallic individuals are represented in New Zealand populations, with the latter strongly predominant.

D. laeve is omnivorous, with a proclivity for supplementing its diet of living plants and litter with faeces, carrion, and even living animals. It is opportunistically predaceous on slow-moving animals such as earthworms, aphids, mealybugs, and insects caught in spider webs (Karlin & Naegele 1960, Quick 1960, Fox & Landis 1973, Rollo in Rollo & Shibata 1991). It is highly aggressive towards other molluscs, and is cannibalistic (Karlin & Naegele 1960, Rollo & Wellington 1979). Reports on D. laeve as a pest of cultivated plants have been largely confined to floriculture (e.g., Alicata 1950).

Remarks. As a consequence of the great geographical range of this slug, numerous specific names have been erected. Little has changed since Baker (1930, pp. 41–42) remarked "... none of the describers or revisers of the names included in the foregoing synonymy [of D. laeve] has ever contributed satisfactory proof towards the separation of any of them from D. laeve of Europe"; or Meeuse & Hubert (1949, p. 25): "The relationship of the various forms which are usually included in D. laeve, but which have so far not been conclusively proved to belong to one and the same species, is far from clear." In Europe at least, until recently D. laeve has been confused with D.
Several variety names are to be found in the literature (e.g., Quicke 1960), relating to variations in body coloration.


**Deroceras (Deroceras) panormitanum**
(Lesson & Pollonera)

Figures 26, 29, 69, 110, 139, 166, 192a, b, 220a, b, 245, C2, M35–37; Plate 2.

agrestis of authors (not of Linnaeus, 1758).
laeve of authors (not of Muller, 1774).
queenslandicus Hedley, 1888: 150 (*Limax*).
pollonerae Sutroth, 1899a: 179 (*Agriolimax*).
carinaneae Pollonera, 1891: 3 (*Agriolimax*).
coconut Pollonera, 1896: 6 (*Agriolimax*).
agrestis var. nigra of authors (not of Morelet, 1845).
agrestis var. violacea of authors (not of Gassies, 1849).
coconut var. ilvatica Pollonera, 1905: 3 (*Agriolimax*).
dubius Hoffmann, 1941: 254 (*Agriolimax*).
meridionale Reygrobellet, 1963: 399 (*Deroceras*).

Slugs (Fig. 26) up to 30 mm in length, slim, posteriorly obliquely narrowing, with keel short and ill defined. Mantle shield about 0.4 of body length. Body wall thin and transparent, chocolate brown, grey, or black, unicoloured in appearance but under magnification seen to be speckled or flecked. Border of pneumostome pale. Sole pale grey.

Shell (Fig. 29) thin, white, oblong-oval to ovate but with right margin commonly concave, up to 4.6 x 2.8 mm in size. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, non-protruding, situated asymmetrically at left side or less frequently on midline. An organic sheet surrounds the shell.

Reproductive system, Fig. 69. Ovotestis rather large and darkly pigmented, partly exposed in viscera on the left, somewhat forward of hind body apex. Hermaphroditic duct short, nearly straight, with talon partially embedded in short albumen gland. Spermoviduct slightly twisted, voluminous. Prostatic gland ribbon-like, attached along axis of female oviducal tract. Free oviduct sinusous. Vagina absent. Bursa copulatrix reservoir oval, on a duct arising from junction of phallus and free ooviduct. Atrium tubular, short. Phallus large, distorting anterior body wall of mature animals, distinctly divided by a median narrowing into 2 parts: proximal part with a phallus gland of 4–6 slender, smooth or crenulate flagella located in a shallow recess between phallus lobe and digitiform phallus caecum; anterior part with a strong bulbous, glandular lateral outgrowth, narrowing to atrium, and internally with a conical sarcobelum. Vas deferens thin, opening into phallus at base of caecum adjacent to phallus gland flagella.

Phallus retractor muscle short, arising from diaphragm at anterior margin of kidney or a little forward, inserted on proximal part of phallus at base of caecum adjacent to entry of vas deferens.

Jaw (Fig. 110) of usual oxygyanous type, 1.3 mm wide.

Radular ribbon (Fig. M35–37) comprising about 90–110 rows of teeth, each varying in formula around 34–55+14–18+C+14–18+34–55. Central tooth with mesocone prominent, slender, flanked on either side by short, prominent ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by a small, weak endocone displaced towards mesocone tip and a prominent ectocone. Lateral teeth with mesocone progressively more slender, endocone becoming smaller and finally lost, and an ectocone often persisting in first few marginal teeth. Marginal teeth mostly comprising only an elongate, slender mesocone, progressively smaller towards radial margin.

Digestive tract, Fig. 139. Buccal mass spheroidal. Oesophagus quickly forming a large crop, which extends to about 0.6 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards a short distance to pass over anterior aorta, then producing a posterior loop nearly reaching hind apex of body, before running forwards over stem of cephalic retractor to anus. Rectum with a small caecum.

Pallial complex (Fig. 166) located in posterior part of mantle. Kidney rounded to oval, its longer axis transverse relative to body axis, almost entirely enclosing heart at its anterior margin; a lobe arising from ventral medial part and extending to the right below rectum. Secondary ureter arising from right posterior aspect of kidney, describing an arc to right anterior quarter of pallial complex, where it terminates in an oval bladder. Heart with ventricle axis slightly right-inclined. Aortic stem long, extending below kidney lobe and rectum to outside right pallial margin before dividing into anterior and posterior branches. Lung with vascular network poorly developed.
Free muscle system, Fig. 192a, b. Cephalic retractor arising on body midline a little posterior to pallial complex, passing forwards as a long common stem; buccal retractors anteriorly dividing off from left tentacular branch.

Central nervous system, Fig. 220a, b. Cerebral ganglia united by a commissure in length about equal to cerebral ganglion width. Cerebropleural connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact, with right pleural ganglion fused to right parietal; left parietal fused to visceral ganglion, which lies on median plane.

Type material. The whereabouts of the type material, from Palermo, Sicily, is not known.

Distribution. Originating in SW Europe, D. panormitianum has been spread to many parts of Europe, the Canaries Islands, southern Africa, North and South America, Australia, and New Zealand.

Recommended common name. Brown field slug.


History in New Zealand. *D. panormitanum* was first recognised in the New Zealand fauna by Barker (1979). It had long been established here (see also Barker 1992), but was apparently misidentified as *D. laeve* by Musson (1891), Longstaff (1912), Suter (1913), Thomson (1922), Whitten (1955), and Coleman (1970).

**Biology.** *D. panormitanum* is a slug of moist habitats, found in gardens, parks, and pastures, on arable land, stream banks, and roadsides, and in greatly disturbed areas of native forest.

Breeding apparently occurs throughout the year provided that moist conditions prevail. Mating has been described by Gerhardt (1939), Quick (1960), and Webb (1961b, 1965), and mating behaviour observed in New Zealand (Fig. 245) is in agreement with these accounts.

Courtship begins with a clockwise circling movement of two animals. As this circling continues, the sarcobela are protruded and the animals engage in biting each other's tail end. In some matings, intermittent slow circling occurs between periods of static tail-wagging and biting. After some 20–30 minutes the slugs come to rest alongside each other head-to-tail, with the body more or less curved, and the stimulators held rigidly turgid. In many instances, slugs at this stage of mating keep the head and tail uplifted and lunge laterally with the head to bite the other's flank and tail. The recipient of the bites often responds with violent side-to-side lashing of its tail, impacting against the anterior body of the aggressor. The strong arching and biting thrusts of the head result in the rigid stimulator-tip brushing swiftly along the flank of the other slug. As noted by Webb (1961b), in this movement the stimulator seems more frequently to contact the mate than the biting mouthparts. In the final phase of this precopulatory behaviour the stimulators become somewhat shortened. The slugs then reciprocally crawl forwards along the right side of the other until the atria but not the stimulators become contiguous. As soon as this body position is reached, the proximal lobe of the phallus is rapidly everted and entwined with the corresponding part from the other slug.

A period of 10–15 minutes of relative inactivity follows, broken by the sudden eversion and entwistment of the semen-bearing medial lobe of the phalluses. These medial lobes then begin to shrink, accompanied by rapid eversion of the phallus flagella, which when fully everted extend radially out like the fingers of a hand. The sex organs then soon become completely separated, and the phalluses continue to shrink and introvert. The animals separate, but complete introversion of the phallus structures to the precopulatory position, particularly that of the sarcobela, is not attained for some 30 minutes or more.

Webb (1961b, 1965) dissected animals shortly after mating and found that the semen received occupies the medial part of the phallus near the bursa copulatrix duct insertion. Semen was noted to have been almost entirely transferred into the bursa copulatrix system in an animal examined 8 minutes after copulation.

Gregg (1944) reported fertile eggs from unmated slugs of this species, and is supported by Quick (1960), who noted that individuals isolated from birth occasionally laid a few viable eggs.

The eggs vary from spherical, approx. 1.5 mm in diameter, to oval 1.75×1.4 mm, and are translucent grey with little or no calcareous crystal content.

As noted by Quick (1960), *D. panormitanum* is an active, rather fast-moving slug. It displays an irritable and pugnacious behavioural trend, frequently biting and tail lashing at its neighbours.

*D. panormitanum* feeds on a variety of living and decaying plant material and is often important as a pest in pastures, nurseries, greenhouses, gardens and commercial crops such as asparagus and lettuce. It has strong canibalistic tendencies, even when food is plentiful. Conspecifics weakened by molluscicide poisoning have been noted to be particularly favoured victims of such cannibalism.

**Remarks.** The taxonomic status of *D. panormitanum* has long been disputed. After critical examination of the original descriptions, type specimens, and fresh material from various European localities, Giusti (1973, 1976, 1986) has placed *D. pollonerae* (Simroth, 1889) and *D. caruaneae* (Pollonera, 1891) as junior synonyms. On the morphology of body, radula, and phallus complex these three nominal taxa cannot be clearly distinguished one from another. There has been much specific radiation of *Deroceras* in Europe, and Giusti (1986) has stressed that his proposed synonymy does not necessarily involve all populations.

Subgenus Agriolimax Mörch

Agriolimax Mörch, 1865: 378, type species Limax agrestis Linnaeus, 1758, designated by Malm (1868).

Chorolimax Westerlund, 1894 (1892–94): 163, type species Limax agrestis Linnaeus, 1758, by original designation.

Diagnosis. Body stout. Mantle 0.3 of body length in extended slugs, the posterior edge not attaining half of body length. Skin thick, not transparent. Phallus short, spheroidal or with a fissure in middle; proximal end with a gland in the form of a single or branched appendix, but other accessory structures absent; distal part with a conical sarcobulum, narrowed apically, less frequently flattened laterally. Rectal caecum usually several times longer than wide, exceptionally in the form of a shallow pocket.

Deroceras (Agriolimax) reticulatum (Müller)

Figures 27, 30, 70, 111, 140, 167, 193, 221, 246, C3, M38–40; Map 3

agrestis of authors (not of Linnaeus, 1758 as restricted by Luther, 1925).

laeve of authors (not of Müller, 1774).

reticulatum Müller, 1774: 10 (Limax).

canalicus d’Orbigny, 1839 (1836–42): 47 (Limax).

japonicus Gould, 1841: 3 (Limax).

niger Meeser, 1845: 24 (as var. of agrestis Linnaeus) (Limax).

violaceus Gassies, 1849: 64 (Limax).

minimus de Kaleniczenko, 1851: 224 (Krynickillus).

mortuus Hutton, 1879: 331 (Limax).

vitestis Nevill, 1880: 103 (Krynickillus).


pallidus of authors (not of von Schrank, 1848).

altenai Lupu, 1976: 10 (Deroceras).

Slugs (Fig. 27a–e) of extended length up to 50 mm, stout, posteriorly obliquely truncated, with a short, ill defined keel. Mantle shield about 0.3 of body length. Body wall thick, usually cream or pale brown, with blackish or brown spots distributed mainly in the skin grooves. Mantle similarly cream or pale brown, flecked or spotted black or brown. Pigmentation varying within populations from wholly dark to pale specimens. Border of pneumostome pale. Sole usually creamy, but brown in intensely coloured specimens. Mucus clear in undisturbed animals, but milky on irritation. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 30) thin, white, oblong-oval to oval but with right margin commonly convex, up to 5.5 x 3.8 mm in size. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, non-protruding, situated asymmetrically at left side. An organic sheet surrounds the shell.

Reproductive system, Fig. 70. Ovotestis elongate, lying anterior near apex of body cavity, partially exposed dorsally in viscera. Hermaphrodite duct short, with talon at its termination in lingiform albumen gland. Spermoviduct somewhat folded, broadest at proximal part; female part terminating in a straight or weakly contorted free oviduct; prostatic gland as a ribbon along entire glandular oviductal tract, giving rise to short vas deferens. Phallus rather large, with thick walls and a fissure in middle; phallus gland on proximal part a single, slightly flattened flagellum or consisting of several flagella branching from a very short stem; flagella always covered with nodulose glandular papillae. Vas deferens opening through phallus wall adjacent to body wall, a little below phallus gland. Bursa copulatrix reservoir oval to globular, opening into distal phallus via a short duct.

Phallus retractor muscle short, arising from diaphragm a little anterior of kidney, inserted onto medial region of phallus.

Jaw (Fig. 111) oxygnathous, 1.4 mm wide.

Radular ribbon (Fig. M38–40) with 80–125 transverse rows of teeth, each with the formula varying around 21–32+16–22+C+16–22+21–32, Central tooth with mesocone elongate, slender, flanked by shorter but prominent ectocones. Lateral teeth with mesocone more robust but equally long, a small endocone displaced towards tip of mesocone, and a small but prominently pointed ectocone, progressively more elongate and grading into sword-like marginal teeth. Marginal teeth progressively smaller towards radula margin, with endocone sometimes persisting in first few teeth, and ectocone frequently persisting as a minute cusp in teeth at radular margin.

Digestive tract, Fig. 140. Buccal mass spheroidal. Oesophagus quickly expanding to large crop, which extends about 0.6 length of body cavity. Stomach a simple tubule, with 2 ducts to the digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards a short distance to pass over anterior aorta, then producing a posterior loop extending below stomach to nearly reach the body apex, and finally running forwards over stem of cephalic retractor to anus. Rectal caecum well developed, several times longer than wide, lying dorsally over viscera.

Pallial complex (Fig. 167) located in posterior part of mantle. Kidney rounded to oval, its longer axis transverse relative to body axis, partially enclosing heart at its anterior margin; a lobe arising from ventral medial part and extending to the right below rectum. Secondary ureter arising from right posterior aspect of kidney, describing an arc to right anterior quarter of pallial complex, where it
terminates in a barrel-shaped bladder. Heart with ventricle axis slightly right-inclined. Aortic stem long, extending below kidney lobe and recurve to outside right pallial margin before dividing into anterior and posterior branches. Lung with vascular network poorly developed.

Free muscle system. Fig. 193a-c. Cephalic retractor arising on body midline a little posterior to pallial complex, commonly dividing from its root to form right ocular retractor and a common stem for left ocular and buccal retractors. Variants occur with stem united before branching anterior to right and left ocular retractors, and with buccal retractor arising near origin or at fork of ocular retractors.

Central nervous system. Fig. 221a, b. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to visceral ganglion, which lies to left of median plane.

Type material. Described from material from Frideriksdal, Norway. Holotype probably no longer exists. Topotypic specimens are described and illustrated by van Regteren Altena (1969).

Distribution. This European slug has been widely dispersed through the activities of man, and its natural range is not known. Occurring partly as a native and partly as a synanthrope, \textit{D. reticulatum} is the most common slug in the whole of northern and central Europe. It is less common in southern Europe, where it is replaced by other species (Wiktor 1983a). Introduced and established widely, including North and South America, South Africa, islands of the Atlantic and Indian oceans, Australia, and New Zealand.

Recommended common name. Grey field slug.

agrestis var. niger. Whitten (1957) recognised that his earlier (Whitten 1955) records of D. agrestis (as Agriolimax) in New Zealand were referable to D. reticulatum.

Limax molestus Hutton, 1879, described from New Zealand material, was previously referred to D. reticulatum, since Hutton's brief description is most consistent with Müller's species (Barker 1979); the holotype of L. molestus has not been examined. Hutton himself (1881, 1883) reduced L. molestus to synonymy with D. agrestis (= D. reticulatum (Müller, 1774)) (not of Linnaeus 1758), and this was followed by Suter (1913). By contrast, Grimpe & Hoffmann (1925) listed L. molestus as a synonym of D. laeve (Müller, 1774).

Quick (1960) examined material of this species from New Zealand.

**Biolo**. D. reticulatum shows wide ecological tolerance, but always living in open or poorly wooded habitats and never in closed forests. It occurs most frequently and abundantly in ruderal environments, refuse heaps, gardens and parks, ditches and roadsides, arable fields, and grazed pastures.

Because of its utility as a laboratory animal and its frequent pest status in cultivated crops there is an extensive literature on D. reticulatum. For an introduction to its biology and behavioural ecology in Europe and North America the reader is referred to Carrick (1938, 1942), Getz (1959), Arias & Crowell (1963), Newell (1966), Dmitrieva (1969), Hunter (1968, 1978), Runham & Lanyon (1968), Crawford-Sidebotham (1972), and South (1965, 1982, 1989a, b).

D. reticulatum is the most widely distributed and generally the most abundant slug in modified habitats in New Zealand, occurring throughout the North and South islands and on Stewart, Chatham, Auckland, and Campbell islands. In outdoor gardens and nurseries, arable crops, and pasture it is often of pest status. In recognition of this pest status in agriculture (Barker 1989), the population biology (Barker 1991a) and damage potential (Charlton 1978a, b, Ferguson & Barratt 1983, Barker 1990, 1991b, Barker et al. 1990, Barker & Addison 1992) of this species have been extensively studied in pasture situations. Information on its biology and the losses inflicted on other agricultural crops is incomplete, but is available for asparagus (Watson 1980, Watson & Townsend 1981) and no-tillage cereals (Barker et al. 1984, Hughes & Gaynor 1984). While its reproductive phenology can vary according to the microenvironmental conditions of a particular habitat, D. reticulatum is generally most reproducively active and in greatest abundance in autumn and, more especially, spring.
D. reticulatum is a heterozygous outcrossing species (Foltz et al. 1984). Its mating behaviour has been described by Simroth (1885), Gerhardt (1933, 1934, 1939), Karlin & Bacon (1960), Wiktor (1960), Webb (1961b, 1965), and others. Observations during the present study were consistent with these earlier descriptions. Mating (Fig. 246) is often initiated by directional following by one animal of the freshly laid mucus trail of another. If the pursued animal is receptive, copulation is preceded by a 'courtship dance' during which the animals encircle each other clockwise on an increasingly thick pad of mucus about 75 mm in diameter. This precopulatory behaviour occurs on both vertical and horizontal surfaces in sites above ground where eversion and play of the genitalia are not impeded. Each slug plays its sarcobela, extended by eversion of the distal phallic region, over the body of its partner as it circles. Gerhardt (1923, 1939) and Webb (1965) correctly stress the importance of the stimulator in courtship. As soon as the stimulators are brought into contact, each slug begins gnawing on the stimulator of the other. This seems to cause or aid reciprocal curvature of the foreparts so as to keep the stimulators in contact.

After about 30 minutes (but as much as 75 minutes) of circling and stimulator gnawing the animals align themselves so as to bring the reproductive openings into opposition. With the animals in rather loose enclaspment, the proximal phallic regions are rapidly and fully everted and then intertwined. The organs are violently rotated back and forth while intertwined and the sarcobela reach their greatest tumescence. Large quantities of clear, viscous seminal material borne on the exterior of the everted phalluses becomes smeared over the phallic structures as they intertwine, thus apparently effecting reciprocal insemination. During this phase of courtship, the phallus flagella are everted and become turgid rods radiated over the united phalluses. Webb (1965) suggested that these flagella function to entangle and anchor the semen so that it becomes engulfed as the phalluses are retracted. Seminal exchange in this species takes only about 30 seconds. Shortly after sperm transfer the slugs separate and crawl off.

As noted by Gerhardt (1939) and Webb (1961b), mature individuals often evince their sexuality by a prominence or dilation of the atrial pore, or by protrusion of the stimulator. Animals in this state are not infrequently observed, in the field and in laboratory cages, to approach conspecifics in an attempt to arouse a mating response.

The eggs, which measure about 3x2.5 mm, are translucent and weakly speckled with calcareous crystals which become absorbed during embryo development. At times, eggs are joined together by gelatinous strands, but generally they are deposited lacking this connection. Eggs are generally deposited on the soil surface, under plant litter or other cover.

Remarks. Many authors, especially in the 19th century, did not distinguish between D. reticulatum (Müller, 1774) and D. agrestis (Linnaeus, 1758), taking them for one species (Luther 1915). In Europe there are, in addition to D. reticulatum, several species closely related to and resembling D. reticulatum (e.g., D. turcicum (Simroth, 1894)) but distinguished by characters of the male genitalia.

Several variety names, founded on variations in body coloration, are to be found in the literature (e.g., Quick 1960).


### Family ARIONIDAE

#### Diagnosis.**

Herbivorous slugs or semi-slugs with a rudimentary shell. Body elongate; mantle small, not covering the entire back. Kidney arched, tending to surround pericardium. Cephalic retractors with a tendency towards division into several individual bands; right ocular retractor muscle either passing over male genitalia or free of genitalia to insert on ocular peduncle. Buccal mass spheroidal. Jaw odontognathic or oxygnathic. Radula with marginal teeth broad, on short basal plates. Intestine forming a single anteriorly directed loop. Genital orifice variously sited on foot, from immediately posterior to right ocular peduncle to visceral stalk below pneumostome. Epiphallus present. Phallus often reduced.

#### Remarks.**

The Arionidae as recognised here comprise six subfamilies: Ariolimacinae (Nearctic), Binneyinae (Nearctic), Anadeninae (Nearctic and Oriental), Oopeltinae (southern Africa), Ariopeltinae (southern Africa), and Arioninae (Palearctic). Only Arioninae occur in New Zealand, where they are represented by three naturalised species. Philomycidae (North America and Oriental) are here considered a distinct family, contrary to Tillier (1989), who reduced these slugs to subfamily status within the Arionidae.
Subfamily ARIONINAE

Diagnosis. Mantle small, round, covering about 0.3 of body, containing calcium granules which sometimes form a plate-like rudimentary shell. Pneumostome in anterior right margin of mantle. Back slightly rounded, sometimes with a vestigial keel. Body apex obtuse, with a pit-like caudal cavity just above foot edge. Anlapecoped, with well developed foot fringe. Sole undivided. Suprarectal gland embedded in foot tissues. Jaw odontognathic. Kidney arched, its extremities meeting so as to surround pericardium. Genital system with epiphallus well developed or wanting, and phallus greatly reduced or wanting. Free oviduct well developed, often with a ligula. Atrium of varying size and shape, often with lateral pockets. Spermatophores produced in outcrossing species. Genital retractor muscle divided into several small bands, one of them always fixed to bursa copulatrix duct, one to free oviduct, and one usually to atrium. Left and right tentacular retractors arising separately from pallial complex or body wall. Right ocular retractor not passing over male genitalia. Central nervous system with cerebropedal connectives equal in length and rather short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact. Haploid chromosomes number 25-29.

Remarks. Most Arioninae occur naturally in the western Palearctic between the Sahara and the Ural Mountains, but one endemic species is found in Siberia. In the western distribution centre they range north to 68 degrees in Scandinavia, and south to the Sahara, Bulgaria, and southern Ukraine, but are unknown from the Black Sea coast and the Caucasus.

The subfamily includes about 35 species. Because of a rather uniform external and internal body structure in Arioninae it is hard to delimit genera and subgenera. Nevertheless, three groups may be distinguished (Wiktor & Norris 1991), around the following genera. (i) Arion d'Audebard de Féru-sacc, 1819; (ii) Geomalacus d'Audebard de Féru-sacc, 1819; (iii) Letourneuxia Bourguignat, 1866 — slugs and snails.

Genus Arion d'Audebard de Féru-sacc

Limax of authors. (Not Limax of Linnaeus, 1758, type species Linax maximus Linnaeus, 1758, by original designation; Lininidae.)


Geomalacus of authors. (Not Geomalacus of Allman, 1843, type species Geomalacus maugeolus Allman, 1843, by monotypy — ICZN Opinion 335 (1955a: 48, 57); Arionidae.)

Letourneuxia d'Audebard de Féru-sacc, 1819: 10 (as section of Arion d'Audebard de Féru-sacc); type species Arion empricorum d'Audebard de Féru-sacc, 1819 = Limax ater Linnaeus, 1758, designated by Malm (1868).

Prolepis Maugeolus d'Audebard de Féru-sacc, 1819: 14 (as section of Arion d'Audebard de Féru-sacc); type species Limax ater Linnaeus, 1758, according to Hesse (1926).

Carnellia Mabile, 1868; 131, type species Arion tindus Morelet, 1845 = Limax ater Linnaeus, 1758, according to Hesse (1926).

Mabille, 1868; 14 (as a subgenus of Arion d'Audebard de Féru-sacc); type species Arion bourguignonii Mabile, 1868 = Arion circumscriptus Hesse, 1926, designated by Cockerell (1891c). (Not Carnellia of Johnstone, 1833; Not Carnellia of Swederus, 1839 (1812-45), in error for Carcinella Allman, 1843; Not Carcinella of Linnaeus, 1758, type species Limax ater Linnaeus, 1758, by original designation; Limacidae.)

Eugomalacus Mabile, 1870a: 121 (in part), type species not designated (several species referred to).


Microarion Hesse, 1926: 66, type species Arion intermedius Normand, 1852, by original designation.

Laevigati Mabile, 1870a: 123, for Geomalacus venus Mabile, 1860 and C. moitessierianus Mabile, 1867; no type selected but both included taxa are junior synonyms of Arion intermedius Normand, 1852.

Diagnosis. Shell internal, represented by separate calcareous granules. Mantle and back usually with lateral bands. Tail wide, obtuse; an indistinct keel present in some juveniles, but never in adults. Mantle shield without concentric ridges. Skin thick. Genital orifice immediately
below pneumostome. Cephalic retractors widely separate at origin from posterior margin of diaphragm. Genital retractor short, arising from diaphragm close to left cephalic retractor, inserted into free oviduct, bursa copulatrix duct, and phallus. Epiphallus strongly developed, rarely with a flagellum. Phallus vestigial, represented by an encompassing tissue ring around verge at entrance into atrium. Genitalia with or without a ligula. Epiphallus/phallus, free oviduct, and bursa copulatrix duct opening into atrium separately. Intestine with a single forward-directed loop, lacking a rectal caecum. Haploid chromosome number 25–29.

Remarks. Arion slugs are usually forest dwelling, omnivorous, and have a lifespan of about 1 year. The natural range of the genus is the same as that given for the subfamily. About 25 species are known.

The systematics and taxonomy of Arion is problematic owing to a general uniformity in external and internal body structure, and several of the long-established species are in fact a complex of sibling species. Various names have been applied to subgenera and sections of Arion, including taxa originally established at generic rank. As the validity and phylogenetic relationships of these infrageneric taxa are not known with any confidence, they are not applied here to New Zealand’s naturalised taxa. Taxa originally described at generic level, or subsequently elevated to that status, are here listed under the synonymy of Arion d’Audebard de Féreussac 1819, the earliest valid generic name for the slugs in question. Several additional names have been applied to sections of genus Arion. The reader is referred to Backeljau & de Bruyn (1990) for discussion of infrageneric taxonomy of Arion.

Arion distinctus Mabille

Figures 31, 71, 97, 112, 141, 168, 194, 222, C4, M1, M41–44; Map 4

subspecies of authors (not of Drupeau, 1805).

hormitis of authors (not of d’Audebard de Féreussac, 1821).
fasces of authors (not of Müller, 1774) var. fasciatus Magoni-Tandon, 1855: 2 (not of Nilsson, 1823) (Arion).
distinctus Mabille, 1868: 137 (Arion).
contraria Pollen, 1889: 634 (Arion).
oxerens Collinge, 1897a: 444 (Arion).

Small slug (Fig. 31), extended length of living specimens 25–40 mm. General colour variable, but typically yellowish-grey; on either side of body a longitudinal dark band; head and tentacles blue-black or grey; sole varying from pale yellow to bright orange; body mucus yellow-orange and sticky. Body wall groove into tubercles. Mantle not grooved into tubercles, but also showing a dark band on either side, this enclosing pneumostome on right side, often with a break or notch immediately dorsal to the orifice.

Shell granules (Fig. M1) discrete, variable in size, located under mantle.

Reproductive system, Fig. 71. Ovotestis grey, often with a reddish or violet tinge in fresh specimens, located in posterior part of body cavity, between lebes of digestive gland. Hermaphroditic duct long and coiled, dilated and folded medially, slender terminally and forming an indistinct talon partially embedded in elongate albumen gland. Spermatovoduct long. Free oviduct long and dimorphic; the slender proximal part always terminating in a firm, usually slightly dilated section, the distal part, capable of eversion during copulation, broadening towards atrium, but often lacking. Vas deferens moderately long. Epiphallus short, gradually widening towards vestigial phallus collar and verge at atrium; internal surface with rows of small polygonal papillae; verge a curved plate or low cone penetrated by epiphallial lumen in reaching atrium. Bursa copulatrix reservoir a large sac on a short, wide duct. Genital atrium divided into 2 parts: proximal part with outlets of free oviduct, bursa copulatrix duct, and epiphallus; distal part with genital pore opening to the exterior, a little anterior of pneumostome.

Genitalia provided with 2 retractor muscles, one on distal part of free oviduct and the other on bursa copulatrix duct, inserting on diaphragm beside one another or fused together, behind kidney.

Spermatophore (Fig. 97) markedly elongate and slender (5.0–7.5 mm long by 0.5–0.68 mm in diameter immediately behind collar); anterior end tapering to a straight or slightly curved, blunt nozzle; collar indistinct, partially encircling spermatophore shaft; an indistinct ridge, sometimes finely serrate, running longitudinally from collar to tapering, blunt, sometimes slightly curved or hooked posterior end.

Jaw (Fig. 112) about 1 mm wide, arcuate, composed of 8–12 fused ridged plates.

Radula (Fig. M41–44) with 100–120 transverse rows of teeth, each with the formula 28–35+C+28–35. Central tooth tricuspid, with a symmetrical basal plate; mesocone elongate, widest medially, terminally pointed; ectocones short and pointed to rounded. Transition from lateral to marginal teeth gradual. First lateral teeth robust, slightly larger than central tooth; external vertex prominent, on wide basal plate; mesocone robust, ovate and pointed; regressed endocone a slight swelling at about 0.4 of mesocone length; ectocone short, wide, and bluntly pointed.
Ectocones diminishing in size but increasingly elongate and pointed towards radular margin. Mesocone of outer lateral teeth markedly elongate and pointed. Teeth near margin of radula small, weakly cusped but multicuspid, with the short mesocone most prominent.

Digestive tract, Fig. 141. Buccal mass spheroidal. Oesophagus quickly enlarging to crop. Stomach large, with a prominent posterior gastric caecal sac lying on left, opposite origin of intestine, communicating with digestive gland via 2 openings. Intestine arising from right lateral part of stomach to coil 180 degrees around oesophagus before passing over anterior acetabulum; posterior loop not coiled around crop, extending to 0.7-0.8 of crop length before turning forwards to anus.

Pallial complex (Fig. 168) located more or less in middle of mantle. Heart occupying a central position, with ventricle axis left-inclined, relative to body axis, by about 45 degrees. Aortic stem moderately long, branching after crossing forward intestinal loop. Kidney horseshoe shaped, its extremities meeting above origin of aorta. Primary ureter very short. Secondary ureter long, separating from right anterior border to run to right posterior border of kidney before turning forwards and running to excretory orifice, immediately adjacent to anus. Urinary bladder absent, but ureter frequently saccular in distal part. Pulmonary vessel network anterior, extending a little posteriorly on either side of kidney.

Free muscle system, Fig. 194. Retractor muscles originating in posterior part of pallial complex; buccal retractor arising on body midline and dividing into two muscle bands well before passing through nerve ring; left and right tentacular retractors arising separately on left and right side respectively; right ocular retractor free of genitalia, inserting on ocular peduncle; genital retractor arising on left, between buccal and tentacular retractors.

Central nervous system, Fig. 222a, b. Cerebral ganglia united by a commissure about equal in length to cerebral ganglion width. Cerebropedal connectives short, their length less than cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal ganglion appressed to right pleural and visceral ganglia; left parietal fused to visceral ganglion, the latter sited to right of median plane.

Chromosome number unknown.

**Type material.** The type locality of *Arian distinctus* is Sèvres, near Paris. No original material survives (Davies 1979). A neotype (No. alcohol 9 120 in the Rijksmuseum van Natuurlijke Historie, Leiden), collected from Sèvres in 1983, was designated by de Winter (1984).

**Distribution.** Natural range in Europe not known, since *A. distinctus* has only recently been recognised as specifically distinct from *A. hortensis* (Davies 1977, 1979). This species is known to occur throughout much of Europe (British Isles, Netherlands, Germany, Belgium, Austria, Switzerland, France, Czechoslovakia, Sweden, Norway, Denmark) on the Azores, and in North America and New Zealand.

**Recommended common name.** Mabille's orange soled slug.


**History in New Zealand.** See under *A. hortensis*.

**Biology.** The biology of *A. distinctus* in New Zealand is poorly known, but observations suggest that reproductive behaviour and phenology are similar to what has been noted for this species in the British Isles by Davies (1977, 1979).

*A. distinctus* is a cross-fertilising species, and its mating behaviour is similar to that of *A. hortensis*. Copulation lasts no more than 30 minutes (cf. at least 80 minutes in *A. hortensis*); this shorter time is principally due to the more rapid transfer of spermatozoa. Individuals with differing forms of the free oviduct mate freely. The everted oviduct is a broad, rounded, tongue-like structure.

*A. distinctus* has a lifespan of about 12 months, and is reproductive throughout the period from late winter to early summer. It is more tolerant of extreme winter and summer conditions than *A. hortensis*, and therefore tends to be reproductive all year round in many localities.

Common in disturbed habitats, *A. distinctus* is easily found under stones, pieces of wood, and crowns of tussock-forming grasses. It is a pest in vegetables.

**Remarks.** Davies (1977, 1979) and others have shown that *A. distinctus* is part of a complex of three sibling species including *A. hortensis* d'Audebard de Férussac,
A.

Figures 32, 72, 98, 113, 142, 247, C5, Μ45-47; Map 5
Backeljau & de Bruyn (1990), and Vater (1991).

provided by Davies (1977, 1979), de Wilde (1983),

subfuscus

material of

Backeljau & van Beeck (1986), Dolan & Fleming (1988),

Backeljau (1985a), Backeljau & Marquet (1985),

Both forms of oviduct are apparent in the New Zealand

distinctus

May be tripartite, or bipartite with the eversible

plate or low cone penetrated by the epiphallus lumen; in


Backeljau (1985a), Backeljau & Marquet (1985),

Backeljau & Marquet (1985),


Both forms of oviduct are apparent in the New Zealand

material of A. distinctus.

Several variety names, founded on variations in body

coloration, are to be found in the literature (e.g., Hesse 1926, Quick 1949).

An introduction into the literature on A. distinctus is

provided by Davies (1977, 1979), de Wilde (1983),

Backeljau (1985a), Backeljau & Marquet (1985),

Buckeljau & van Beec (1986), Dolan & Fleming (1988),

Backeljau & de Bruyn (1990), and Vater (1991).

Arion hortensis d'Audebard de Férussac

Figures 32, 72, 98, 113, 142, 247, C5, M45-47; Map 5

fuscus (not of Müller, 1774).

fuscus (not of Müller, 1774) var. pyrenaeus Moquin-Tandon,

fuscus (not of Müller, 1774) var. oweni Davies, 1979. In an earlier

revision of New Zealand's naturalised slugs (Barker 1979) only A. hortensis s.s. of this complex was recognised as being present. A re-examination of the material studied by Barker (1979) and further collecting have revealed the presence in New Zealand of both A. hortensis s.s. and A. distinctus.

Since A. hortensis and A. distinctus show much variation in both general colour and banding pattern, their separation on the basis only of external appearance is always doubtful. For example, besides the typical blue-black A. hortensis with more dorsal mantle bands there are also paler forms with mantle bands situated more ventrally. On the other hand dark forms of A. distinctus exist with mantle bands enclosing a rather narrow, pale-coloured dorsal field. In a sample of a mixed population (sympatry occurs in New Zealand) it is possible to distinguish the species, since A. hortensis always appear darker, with more dorsally situated mantle bands, in comparison with the paler A. distinctus. The latter species always lacks any reddish or violet tinge in the head and ocular peduncles, often present in A. hortensis.

The only character by which A. distinctus and A. hortensis s.s. are reliably distinguished is the structure around the outlet of the epiphallus: in the former, verge a curved plate or low cone penetrated by the epiphallus lumen; in the latter, verge an oblong plate partially overhanging but not penetrated by the epiphallus lumen. The free oviduct in A. hortensis s.s. is always tripartite, while that of A. distinctus may be tripartite, or bipartite with the eversible part lacking (Davies 1977, Backeljau & de Bruyn, 1990). Both forms of oviduct are apparent in the New Zealand material of A. distinctus.

Several variety names, founded on variations in body coloration, are to be found in the literature (e.g., Hesse 1926, Quick 1949). An introduction into the literature on A. distinctus is provided by Davies (1977, 1979), de Wilde (1983), Backeljau (1985a), Backeljau & Marquet (1985), Buckeljau & van Beec (1986), Dolan & Fleming (1988), Backeljau & de Bruyn (1990), and Vater (1991).

1855: 14 (Arion).

1855: 14 (Arion).


delonatus Collinge, 1894: 66 (Arion).

? rubellus Sterki, 1911: 64 (Arion).

Small slug (Fig. 32), extended length of living specimens 25–50 mm. General colour variable, but in typical forms blue-black with a nearly black dorsum; on either side of body a longitudinal dark band; head, ocular peduncles, and inferior tentacles with a reddish or violet tinge; sole varying from pale yellow to bright orange; mucous yellow-orange and sticky. Bodywall grooved into tubercles. Mantle not grooved into tubercles, but also showing a dark band on either side, situated rather dorsally; right mantle band running over pneumostome, never showing a break or a notch.

Shell granules discrete, variable in size and distribution undermantle.

Reproductive system, Fig. 72. Ovotestis grey (often with a reddish or violet tinge in fresh specimens), located in posterior part of body cavity, between lobes of digestive gland. Hermaphroditic duct long and coiled, dilated and folded medially, slender terminally, forming an indistinct talon partially embedded in elongate albumen gland. Spermoviduct long. Free oviduct long, proximally slender, medially firm and slightly dilated, and with a long distal region, eversible as a slender process during copulation, broadening towards postum. Vas deferens short. Epiphallus of similar length to vas deferens, enlarging gradually in width towards vestigial phallus collar and verge at atrium, internally with rows of small polygonal papillae; verge an inconspicuous oblong plate, intimately associated with and partially overhanging epiphallus outlet. Bursa copulatrix reservoir a large, rounded sac on a short, wide duct. Genital atrium divided into 2 parts: proximal part with outlets of oviduct, bursa copulatrix duct, and epiphallus; distal part with genital pore opening to the exterior, a little anteriad of the pneumostome. Genitalia provided with 2 retractor muscles, one on distal part of firm portion of free oviduct, the other on duct of bursa copulatrix; retractors inserted on diaphragm beside one another or fused together, behind kidney.

Spermatophore (Fig. 98) short and relatively stout (4.5–5.2 mm long, 0.95–1.05 mm diameter immediately behind collar); anterior (apical) nozzle short, sharply pointed, and deflected up to 90 degrees from longitudinal axis; a distinct serrated ridge with about 25 tubercles per mm oriented towards apical end, rotating up to 90 degrees along shaft from collar to bluntly tapered and strongly hooked posterior end.

Jaw (Fig. 113) about 1 mm wide, arcuate, composed of
7–12 fused ridged plates.

Radula (Fig. M45–47) with 100–120 transverse rows of teeth, each with the formula 29–35+C+29–35. Central tooth tricuspid, with a wide symmetrical basal plate; mesocone slender and pointed; ectocone short and pointed to rounded. Transition from lateral to marginal teeth gradual. First lateral teeth robust, with only the external vertex prominent on a wide basal plate; mesocone long and robust, pointed; regressed endocone a slight indentation at about 0.5 of mesocone length; ectocone short, wide, and sharply pointed. Teeth near margin of radular ribbon small, weakly cusped but multicuspid, with the short mesocone most prominent.

Digestive tract, Fig. 142. Buccal mass spheroidal. Oesophagus quickly broadening to large crop. Stomach large, communicating with digestive gland via 2 openings; posterior gastric caecal sac prominent, lying on left opposite origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine.

Radula (Fig. M45–47) with 100–120 transverse rows of teeth, each with the formula 29–35+C+29–35. Central tooth tricuspid, with a wide symmetrical basal plate; mesocone slender and pointed; ectocone short and pointed to rounded. Transition from lateral to marginal teeth gradual. First lateral teeth robust, with only the external vertex prominent on a wide basal plate; mesocone long and robust, pointed; regressed endocone a slight indentation at about 0.5 of mesocone length; ectocone short, wide, and sharply pointed. Teeth near margin of radular ribbon small, weakly cusped but multicuspid, with the short mesocone most prominent.

Digestive tract, Fig. 142. Buccal mass spheroidal. Oesophagus quickly broadening to large crop. Stomach large, communicating with digestive gland via 2 openings; posterior gastric caecal sac prominent, lying on left opposite origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal origin of intestine.
ised fauna of New Zealand (e.g., Powell 1979). The absence of \textit{A. subfuscus} from the New Zealand fauna and the assignment of Hutton's \textit{A. incommodus} to the \textit{A. hortensis} complex was established by Barker (1979). The correct position of \textit{A. incommodus} within the \textit{A. hortensis} complex, however, remains problematic (see Remarks).

The presence of \textit{A. hortensis} s.l. was first recognised by Musson (1891), who had collected material from Auckland. Taylor (1902–07 (1902–21)) states that this record was in error, Musson's material being referable to \textit{A. intermedius} Norman, 1852. Musson's material, in AMSA, has been examined (Barker 1979) and found to be conspecific with \textit{A. hortensis}. Thomson (1922) gives Taranaki as a further locality for \textit{A. hortensis} and Quick (1952) lists Dunedin, but the source of this information was not given. From collections made in the 1950s, Whitten (1955) recorded \textit{A. hortensis} from the Thames district.

Quick (1960) mentions neither \textit{A. subfuscus} nor \textit{A. hortensis} as occurring in New Zealand but lists \textit{A. intermedius}, apparently modifying his earlier references to New Zealand (Quick 1949, 1952) to follow Taylor (1902–07 (1902–21)). Powell (1979) provided no new information on \textit{Ariam} in New Zealand, merely repeating the records given in Suter (1913).

Thus, for the century that followed Hutton's (1879) initial record, the malacological literature relating to \textit{A. hortensis} s.l. was confused as to nomenclature. Further, the scarcity of records indicated a very limited distribution.

Barker (1979) found \textit{A. hortensis} s.s. to be widespread and common in the North Island, but for the South Island had records only from Nelson and Dunedin, the latter based solely on the type locality for \textit{A. incommodus}. Following further extensive collecting, Barker (1982) concluded that \textit{A. hortensis} was found throughout the North and South islands, but less commonly in the southern South Island. Additional collecting over the past decade has confirmed that spatial pattern for \textit{A. hortensis} s.s. However, \textit{A. distinctus} is now recognised as being present at widely scattered localities in both North and South islands, often sympatrically with \textit{A. hortensis}.

It is thus probable that both \textit{A. hortensis} and \textit{A. distinctus} have long been resident and widespread in New Zealand.

**Biology.** \textit{A. hortensis} breeds by cross-fertilisation (Backeljau & de Bruyn 1990). Mating behaviour (Fig. 247) observed in New Zealand populations agrees closely with descriptions by Davies (1977, 1979) for this species in the British Isles. A sexually active slug may follow, and nibble, members of other \textit{Ariam} species or its conspecifics before finding a receptive partner. The mating pair encircle each other and settle before the genitalia are everted and joined. The everted oviduct is finger-like and mobile, and is withdrawn and everted several times and played over the partner's back during copulation. A period of 30–60 minutes elapses before spermatophores are exchanged. As the genitalia are retracted after mating, the received spermatophore becomes lodged in the atrium, with its collar region attached at the opening of the bursa copulatrix duct. Davies (1987) remarked that, during transfer, spermatophores are covered with a thick mucus.

These slugs are basically annual. Under New Zealand conditions breeding occurs 6–8 months after hatching, and sexual maturity generally is reached in autumn. Eggs measuring 2×2.5 mm and milky white from the calcite crystals suspended in their jelly capsule are produced in clutches of 10–50 throughout the period from autumn to late spring. Growth and breeding are generally arrested by dry summer conditions. In times of dry soil conditions, \textit{A. hortensis} activates under logs and stones in cells fashioned from body mucus and soil.

\textit{A. hortensis} is common in a wide range of disturbed habitats, including gardens, arable crops, roadsides, forest fringes, and grassy tracks in forest, but is less common in pastures. The slugs are easily found under stones, pieces of wood, and crowns of tussock-forming grasses. \textit{A. hortensis} feeds extensively on fungi and decaying leaf material, but in cultivated areas is frequently a pest in vegetables.

**Remarks.** Until recently a complex of three species has been confused under the name \textit{Ariam hortensis} (Davies 1977, 1979) (see above under \textit{A. distinctus}).

The correct assignment of \textit{A. incommodus} Hutton, 1879 remains uncertain. Barker (1979) tentatively listed it as a synonym of \textit{A. hortensis} s.s. A specimen in BMNH, which is probably Hutton's holotype, is in external appearance attributable to any one of the three species in the \textit{A. hortensis} complex, while the genitalia are similar to the condition in \textit{A. owenii} Davies, 1979. Topotypic material collected to date from Dunedin includes both \textit{A. distinctus} and \textit{A. hortensis} s.s.

De Winter (1986) comments on the possibility of \textit{Ariam anthracius} Bourguignat, 1866 being a valid species.

Various variety names, based on variations of body coloration and markings, are to be found in the literature (e.g., Taylor 1902–07 (1902–21), Hesse 1926, Quick 1949, 1960).

**Arion intermedius** Normand

Figures 33, 73, 99, 114, 143, 169, 195, 223, C6, C7, M2, M48–50; Map 6

flavus Müller, 1774: 10 (not of Linnaeus, 1758) (Limax).
fuscus of authors (not of Müller, 1774).
hortensis of authors (not of Andréard de Pérousse, 1819).
fuscatus Moleret, 1845: 32 (not of d'Andréard de Pérousse, 1819) (Arion).
intermedius Normand, 1852: 7 (Arion).
bourguignoni Mabille, 1867: 58 (Geomalacus).
? poladithamus Mabille, 1867: 60 (Geomalacus).
? monsterialus Mabille, 1867: 61 (Geomalacus).
hiaulae Drueet, 1867: 59 (Geomalacus).
mabillii Baudon, 1868: 142 (Geomalacus).
pacalicanus of authors (not of Mabille, 1868).
vendeanus Letonneux, 1869: 51 (Geomalacus).
verrucosus Breuvière, 1881: 310 (Arion).
mobiliarius Baudon, 1884: 260 (not of Bourguignani, 1866)
(1863–70) (Arion).
mimix Sinroth, 1885: 227 (Arion).
intermedius var. apenninal Pollonera, 1889: figs 11, 12 (Arion).
mollaria Pollonera, 1889: 639 (Arion).
vejrovskyl Balcer & Kostál, 1893: 1 (Arion).
bouchi Sinroth, 1894: 295 (Arion).
obsoluctus Reischütz, 1973: 229 (Arion (Microarion)).

Small slug (Fig. 33) 10–25 mm in extended length when mature. General coloration variably greyish- or greenish-yellow or yellowish-white, with head and tentacles often darker; usually on either side of body a longitudinal dark band; sole yellowish-grey; mucus yellow. Body wall grooved into tubercles which, when raised in the contracted live animal, have a serrated ridge. Mantle not grooved into tubercles but also usually showing a dark band on either side; bands often united along posterior mantle margin to form a lyre-like pattern.

Shell granules (Fig. M2) minute, sometimes aggregated into an irregular mass, located under mantle.

Reproductive system, Fig. 73. Ovotestis deeply pigmented, lying between lobes of digestive gland, partly exposed dorsally. Hermaphroditic duct long, weakly contorted and dilated in medial section, narrowing towards its termination with an indistinct talon partially embedded in linguiform albumen gland. Spermoviduct moderately short but voluminous. Free oviduct and vagina very short and stout, lacking internal ligula-like structures. Vas deferens slender, about 1.5x length of combined free oviduct and vagina, thin-walled with some folds on inner surface. Epiphallus rapidly broadening towards atrium, terminating in a pronounced vestigial phallus collar; inner surface with rows of small polygonal papillae; verge a vestigial, papillate fold, forming a raised rim about the epiphallus entrance into atrium. Bursa copulatrix reservoir large and spherical; duct very short, stout, its distal part with a ring-shaped thickening from which, on side facing epiphallus, a tongue-like structure protrudes slightly into genital atrium. Atrium elongate, with bursa copulatrix duct, epiphallus, and vagina opening close together in proximal part; walls glandular. Genital orifice immediately below pneumostome.

Genital retractor system comprising many small muscles. A large muscle arising from body wall near left margin of diaphragm, distally divided to send one branch to vestigial phallus on distal part of epiphallus and adjacent vagina and another to spermathecal duct. A slender accessory retractor arising from body wall near anterior margin of pallial complex and ending in wall of vestigial phallus, facing vagina. Another slender muscle arising in body wall near genital orifice and ending where phallus collar attaches to proximal atrium.

Spermatophore (Fig. 99) 3–3.8 mm in length; anterior nozzle about 0.6 mm in length, conical, with sharply pointed apex; body elongate, widest medially, often with an ill-defined serrate longitudinal crest, particularly at anterior end.

Jaw (Fig. 114) about 1 mm wide, composed of 7–15 fused plates.

Radula (Fig. M48–50) with 95–120 transverse rows of teeth, each with the formula 28–35+C+28–35. Central tooth tricuspid, with a wide symmetrical basal plate; mesocone long, slender and pointed; ectocones short (about half length of mesocone) and pointed. First lateral teeth robust, with only external vertex prominent on wide basal plate; mesocone long and robust; endocone retracted, a slight indentation at about 0.6 of mesocone length; ectocone short but wide and sharp. Basal plate gradually reducing in height, and mesocones and ectocones in size, with more lateral placement of teeth on radial ribon, with a gradual transition from lateral to marginal teeth. Teeth near extreme lateral margins distinguished by their marked reduction in size, short, bluntly pointed mesocone, and endocone broken into several small points.

Digestive tract, Fig. 143. Buccal mass spheroidal. Oesophagus quickly enlarging to crop. Stomach large, communicating with digestive gland via 2 openings; posterior gastric caecal sac absent or small. Intestine issuing from right side of stomach and coiling 180 degrees around oesophageal crop before passing over anterior aorta; posterior loop not coiled around crop, extending nearly to level of stomach, before running forwards to anus.

Pallial complex (Fig. 169) located in middle of mantle, with heart occupying a central position; ventricle axis left-inclined by 45 degrees relative to body axis. Aortic stem short, branching as it crosses forward intestinal loop. Kidney horseshoe-shaped, its extremities meeting above
origin of aorta. Primary ureter very short. Secondary ureter long, separating from right anterior border of kidney to run to right posterior border before turning forwards and running to excretory orifice immediately adjacent to anus. Urinary bladder absent, but ureter frequently secular in distal part. Pulmonary vascular network not well developed. Largely confined to area anterior to kidney.

Free muscle system, Fig. 195. Buccal retractor arising a posterior margin of diaphragm, on or slightly to left of body midline. Left and right tentacular retractors arising separately at left and right posterior margins of pallial complex; right tentacular retractor arising a little forward of origin of left retractor; right ocular retractor not crossing over genitalia, inserting on cuticular peduncle.

Central nervous system, Fig. 223. Cerebral ganglia united by a commissure about equal in length to cerebral ganglion width. Cerebropedal connectives short, their length less than cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal ganglion pressed to right pleural and visceral ganglia; left parietal fused to visceral ganglion, the latter sited to right of median plane.

Haploid chromosome number 28.

Type material. The type locality is "environs de Valenciennes", France. The whereabouts of the type material is unknown, and it is presumed lost.

Distribution. *A. intermedius* is naturally distributed throughout central and western Europe, and has been introduced passively into South Africa, North America, Australia, and New Zealand.

Recommended common names. Glade slug.


History in New Zealand. Taylor (1902–07 (1902–21)) refers the Auckland record of A. hortensis by Musson (1891) to this species, as he does for Hutton’s (1879) A. incommodus from Dunedin. Musson’s material belongs to A. hortensis s.s., while Hutton’s A. incommodus belongs to the A. hortensis complex. Taylor (1902–07 (1902–21)) also gives Manapouri (SL) and Paradise (OL) as localities for A. intermedius, following reports by W.D. Roebuck in 1905 of this species in gardens.

Longstaff (1912) wrote of Mrs Longstaff finding specimens of A. intermedius on Rangitoto Island and at Matahiwi near Masterton in 1910. These records suggest that A. intermedius was well established and of widespread occurrence in New Zealand by the early 20th century. Longstaff’s two records were repeated in the literature, as A. minimus, by Suter (1913), Thomson (1922), Whitten (1955), Coleman (1970), and Powell (1979). Only Whitten (1955) added new information, with confirmation of A. intermedius on Rangitoto.

Barker (1979, 1982) confirmed the widespread occurrence of A. intermedius in New Zealand, including offshore islands.

Biology. A. intermedius apparently has a predominantly uniparental, probably autogamic, breeding system (see Remarks). It is most abundant in relatively undisturbed areas, and as such is a characteristic element in the faunas of woodland and ecotonal habitats. In New Zealand it can be locally abundant in pastures, but is most frequently encountered in hedgerows, scrubland, plantation forests, and native forest areas. Slugs of this species are encountered often in forest and scrub areas disturbed by man’s activities such as mining and logging, and from these areas frequently penetrates several kilometres into dense, relatively undisturbed native forest and subalpine scrubland.

The reproductive and population biology of A. inter-
**Family COCHLICOPIDAE**

**Diagnosis.** Herbivorous snails. Shell elongate, under 10 mm in height, imperforate, glossy, subtranslucent, capable of housing retracted animal; aperture ovate, longer than wide, sometimes armed with barriers; lip not expanded, but thickened within; columella slightly sinuate to truncate at base. Sole holopod, undivided or indistinctly tripartite. Foot without a caudal mucous pit. Suprapedal gland embedded in foot tissues. Buccal mass spherical, jaw autotactic, radula with marginal teeth short, broad, multi-cuspid. Intestine with a single loop directed forwards. Kidney very long, divided internally into 2 distinct regions, the anterior region functioning as a primary ureter; some taxa with a closed secondary ureter extending to top of pulmonary cavity. Columellar muscle dividing a short distance from its origin into left and right cephalic retractors; buccal retractor associated with left branch. Right ocular retractor bundles; buccal retractor associated with right branch. Right ocular retractor crossing phallus. Phallus retractor arising from diverticulum. Epiphallus well developed. Phallus with or without an appendix, sometimes armed internally with spines. Central nervous system with long cerebropedal connectives, the right one slightly shorter than the left. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral ganglion chain moderately concentrated.

Haploid chromosome number 26.

**Remarks.** The Cochlicopidae comprise the four genera Cochlicopa d'Audebard de Férussac, 1821, Azecca Fleming, 1828, Hypophila Bourguignat, 1858, and Cryptazaecia de Rolin & Bérlion, 1877.

**Genus Cochlicopa d'Audebard de Férussac**

*Helix* of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

*Turbo* of authors. (Not *Turbo* of Linnaeus, 1758, type species *Turbo perhasto* Linnaeus, 1758, designated by de Montfort (1810); Turbinidae.)

*Bulimus* of authors. (Not *Bulimus* of Gmelin, 1798, type species *Bulimus castratum* Gmelin, 1798, designated by Gray (1847) - synonym of *Megalobulimus* Müller, 1774; Acavidae.)

*Oleacina* of authors. (Not *Oleacina* of Roding, 1798, type species *Oleacina voluta* Roding, 1798 = *Bulla voluta* Gmelin, 1791, by monotypy; Oleachiidae.)

*Achatina* of authors. (Not *Achatina* of de Meester de Lamarck, 1799, type species *Achatina fulica* Linnaeus, 1758, by monotypy; Achatinidae.)

*Colonna* of authors. (Not *Colonna* of Perry, 1811, type species *Buccinum colonna* Müller, 1774, by monotypy; Achatinidae.)

*Glandina* of authors. (Not *Glandina* of Schunacker, 1718, type species *Glandina olivacea* Schunacker, 1718 = *Oleacina voluta* Gmelin, 1791, by monotypy; synonym of *Oleacina* Roding, 1798; Oleachiidae.)

*Cochlicopa* d'Audebard de Férussac, 1821: 84 (as sub-genus of *Helix* Müller, 1774), type species *Helix lubrica* Müller, 1774, designated by Gittenberger (1983).

*Ferussacia* of authors. (Not *Ferussacia* of Risso, 1826, type species *Ferussacia granulata* Risso, 1826, according to Pilsbry (1908 (1908-10); Ferussaciidae.)

*Achatinella* of authors. (Not *Achatinella* of Swainson, 1828, type species *Monodonta semingula* de Monet de Lamarck, 1821 = *Turbo apesfulva* Döderlein, 1788, designated by Pilsbry & Cooke (1912 13); Achatinellidae.)

*Cionella* Jeffreys, 1830: 347, type species *Helix iburica* Müller, 1774, designated by Kobelt (1880 (1876-81)).

Zoe Lesbian, 1831: 82, type species *Helix iburica* Müller, 1774, by monotypy.

*Sieväder* Rühinger, 1833: 105 (in part), type species not designated. For *Buccinum acicula* Müller, 1774, in *Ferussacia* Müller, 1774, in Cochlicopidae.

*Folliculus* de Charpentier, 1837: 14, type species *Helix iburica* Müller, 1774, by monotypy.

*Hydatas* Parreys, 1849: 98, type species *Helix iburica* Müller, 1774, by monotypy.

*Opesia* of authors. (Not *Opesia* of Albers, 1850, type species *Stenogyra gravidil* Müller, 1822 = *Bullina pumilis* Pfeiffer, 1840, designated by von Martens (1866); Subulinidae.)

**Diagnosis.** Shell less than 8 mm in height; aperture lacking barriers, but thickened within by a callous rim continuous to upper insertion. Prostatic gland large, extensively fused to female pallial gonoduct to form a spermo-oviduct. Bursa copulatrix duct rather long, with a short diverticulum. Epiphallus well developed. Phallus with appendix well developed, lumen lacking spines.

**Remarks.** *Cochlicopa* d'Audebard de Férussac, 1821 and *Cionella* Jeffreys, 1830 are strict synonyms in having the same type species, *Helix iburica* Müller, 1774. Most European malacologists at present accept *Cochlicopa* as the valid name, as was done also until relatively recently by American workers, including Pilsbry (1908 (1908-10) in his earlier revision of the genus. Pilsbry later (1948 (1939-48)) decided that *Cionella* was the correct name, being influenced by Kennard's (1942) claim that d'Audebard de Férussac's *Cochlicopa* was an invalid name. Watson (1943) has shown, however, that Kennard's interpretation of the rules of nomenclature was erroneous in this instance. The same conclusion was reached by
Cochlicopa lubrica (Müller)

Figures 34, 74, 115, 144, 170, 196, 224, C8, M3, M4, M51–53, M113; Map 7

lubrica Müller, 1774: 104 (Helix).
muscorum Pennant, 1777: 131 (not of Linnaeus, 1758) (Turbo).
glubra da Costa, 1778: 87 (Turbo).
sublubrica Gmelin, 1791: 3652 (not of Linnaeus, 1758) (Helix).

Shell (Fig. 34, M3, M4) elongate oval, to 7.8 mm high by 2.5 mm wide; spire gradually widening from an obtuse apex, of 5.5–6 moderately convex whorls, thin, smooth, yellowish conomous, subtransparent and very glossy, imperforate, protoconch of approximately 1.5 whorls, smooth; aperture subvertical, ovate, without barriers, the outer lip evenly arched, bordered with yellow or red outside, in mature snails having a narrow, smooth, and continuous callous rib within; columella somewhat straightened, calloused, often very indistinctly notched or sinuous at its junction with basal lip; parietal callus thin, transparent.

Animal with sides of foot, mantle collar, and sole pale to dark grey; mantle collar speckled white, with flake-shaped glands. Foot rather short in active animal; sole indistinctly tripartite.

Reproductive system, Fig. 74. Ovotestis comprising 4 lobes, each made up of numerous acini, embedded in upper lobes of digestive gland. Hermaphroditic duct moderately long, distended and convoluted in its middle section, terminating in carrefour region with a small, bulbous talon partially embedded in albumen gland. Female pallial gonoduct sacculate, in its middle section differentiated by a zone of morphologically distinct glandular cells. Free ovotestis rather short, stout. Vagina long, Busc cepalatrict duct rather stout at its origin on oviduct, but for the greater part rather slender, ending in a saccular reservoir, and giving off a short diverticulum at about same level as origin of vas deferens. Prosthetic gland rather long, fused to female pallial gonoduct section to form sperm-oviduct; follicles most strongly developed in proximal part of these.
but weak or absent in middle section, adjacent to specialised middle section of female tract. Vas deferens slender, accompanying free oviduct and then folding back around right ocular retractor to run to epiphallus, into which it abruptly expands. Epiphallus generally arched, opening into phallus with a small vaginal papilla immediately distal of phallic retractor muscle insertion. Phallus rather slender, internally with fleshy stimulatory pads in proximal section, bearing apically an appendix with a bulbous base giving rise to a glandular sac on a slender duct. Atrium short, somewhat indistinct.

Spermatophore unknown.

Phallus retractor muscle arising from anterior part of diaphragm, to insert on distal epiphallus without branching.

Jaw (Fig. 115) aulacognathic, 0.5 mm wide, composed of about 20 narrow plates denticulating the lower border.

Radular ribbon (Fig. M51-53) with about 80 transverse rows of teeth, each with the formula 12-15+7-9+C+7-9+12-15. Central tooth narrow, incuspid, with prominent mesosecone and poorly developed but distinct ectocones, on an elongate basal plate. Lateral teeth somewhat larger than central tooth, bicusp, with large mesosecone and well-developed ectoceme, on a rectangular basal plate. Marginal teeth multispid, with mesosecone first rounded then becoming serrate, and ectocone also becoming progressively more serrate towards margin of ribbon.

Digestive tract, Fig. 144. Buccal mass spheroidal. Oesophageus long, terminating in gastric pouch without a crop. Gastric pouch cylindrical, extending about half a whorl to end in a sacculate stomach which is not externally differentiated. Intestine producing a short, anteriorly directed loop to abut the kidney, then describing a posteriorly directed loop before again turning forwards and running to anus in mantle collar.

Pallial complex, Fig. 170. Pulmonary cavity in active animal extending for about 1 whorl. Kidney proper short, barely exceeding length of pericardium, extended to about 0.8 of pulmonary cavity length by a slender ureteric pouch. Retrograde closed ureter absent, but a ciliated groove extending for a short distance from excretory orifice towards top of pulmonary cavity. Pulmonary vein with no large branches.

Free muscle system, Fig. 196. Columellar muscle dividing below origin into left and right bundles. Left bundle giving rise first to buccal retractor, then dividing into ocular and inferior tentacular retractors. Right columellar branch giving rise near its base to a broad tail fan, divided more anteriorly into ocular and inferior tentacular retractors. Inferior retractor on both sides sending out a branch which ramifies to anterior cephalic body wall.

Central nervous system, Fig. 224. Cerebral commissure length about equal to cerebral ganglion width. Cerebro-pedal connectives subequal in length, the right one about equal to cerebral ganglion width. Pleural ganglia slightly closer to cerebral ganglia than to pedal ganglia. Parietal ganglia closer to visceral ganglia than to pleural ganglia; right parietal ganglion fused with visceral ganglia, which lies to right of median plane.

Haploid chromosome number 26.

Type material. Müller (1774) did not give a type locality with his species description. His material is assumed to have come from Frederiksdal near Copenhagen, Denmark. The whereabouts of this material is unknown; it is probably lost.

Distribution. Holarctic and circumpolar in natural range. Widespread in Eurasia, from Iceland, northern Europe, and Siberia south to northwestern Africa and east to Japan; in North America from north of the Arctic Circle in Alaska, south to Alabama in the east and at high elevations to Mexico. Introduced into St Helena, South Africa, Venezuela, Australia, and New Zealand.

Recommended common name. Slippery moss snail.


**Biology.** In its native range *C. lubrica* is known from a wide variety of habitats, including grassland, arable land, woods, and gardens. Krull & Mapes (1952), who studied
C. lubrica on farmland in New York State, U.S.A., found the snails to be most abundant in wet places under bushes or shrubs, occurring in considerable abundance in grassy pasture and other dry habitats. In New Zealand this species is most prevalent in moist, shaded areas in gardens. It is often abundant in patches of remnant, modified forest, especially those in urban areas and on limestone rock outcrops. It is unknown from closed, relatively undisturbed native forest. During periods of dry weather the snails aestivate with the shell aperture sealed to the substrate by a thin, colourless epiphragm. During dry weather the animals may burrow into the soil.

Little is known of the biology of C. lubrica in New Zealand. As noted in the Northern Hemisphere (e.g., Mapes & Krull 1952, Quick 1954, Baker 1969), eggs and juveniles can be found at most times of the year but with a trend for greater abundance in winter and summer. No information is available on the abundance of individuals in New Zealand habitats, but estimates for grassland in Europe and North America range up to 577 snails per m² (Mapes & Krull 1952, Boyd 1960, Baker 1969). In a Polish Alnus forest Umiński & Focht (1979) recorded populations up to 60 snails per m². Their sampling indicated that C. lubrica took 21–24 months to reach maturity and that the adult snails lived in excess of one year. These observations concur with those of Krull & Mapes (1952) for populations in New York farmland.

Both in New Zealand and in their native range these snails are often found congregated in large numbers on rocks, stone walls, and concrete paths. The suggestion by Pilsbry (1948 (1939–48)) that these aggregations are associated with breeding has not been confirmed. C. lubrica is a species of deterministic shell growth: snails held in the laboratory commenced oviposition within 5 days of thickening of the peristome. The eggs are spherical to oval, with a greater diameter of 1.1–1.5 mm, and comprise a flexible shell (Fig. M113) of calcareous granules embedded in a gelatinous matrix. The eggs are deposited singly, and are frequently covered with strands of faecal material and plant litter. While rather variable in size, the male genitalia of all New Zealand C. lubrica dissected (n = 18) were always well developed. Outeiro et al. (1990) record but do not discuss the occurrence of aphalic specimens in their Spanish collections.


Mapes & Krull (1952) noted that C. lubrica fed upon both green and dead plant material under laboratory conditions, but found no evidence of green plants being consumed under natural conditions. In the present study, snails collected from coastal forest at Opoutere had tissues from both live and dead leaves in their intestinal tracts.

Remarks. An introduction into the very extensive literature on C. lubrica is provided by Germain (1930), Pilsbry (1948 (1939–48)), Likharev & Rammel'meier (1952), Quick (1954), Bequaert & Miller (1973), Backhuys (1975), Schileyko (1984), Grossu (1987), Outeiro et al. (1990), and Starobogatov (1996).

Family EUCONULIDAE

Diagnosis. Herbivorous aulacopod snails, ovoviviparous or oviparous. Shell minute to small, with 5th whorl diameter less than 10 mm, capable of fully housing the retracted animal, or reduced and not able to accommodate the animal. Shell lappets often developed on mantle collar. Foot with a well developed suprapedal groove and foot fringe. Sole tripartite. Caudal mucous pit often overhung by a caudal horn. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw oxygnathic. Marginal teeth elongate, multicuspoid or bicuspid but lacking endocones, on slender basal plates. Intestine with a single forward-directed loop. Kidney with a closed sigmoid ureter, opening at pneumostome. Right ocular retractor passing over phallus. Phallus retracting arising from diaphragm, inserted on epiphallus or phallus. Genital cricite located immediately behind right ocular peduncle or a little posterior. Sometimes with a diverticular sac on the talon. Male and female pallial gonoducts fused to spermoviduct. Free oviduct often glandular. Bursa copulatrix weakly developed, opening to phallus, atrium, or vagina, or absent. Epiphallus often with a short flagellum. Phallus variably developed, often with a sheath; appendix often present. Central nervous system with short cerebropedal connectives, the left one often shorter than the right. Right pleural ganglion near right cerebral ganglion. Visceral ganglion chain moderately concentrated.

Haploid chromosome number: 28.


The Euconulidae, comprising about 20 genera, are represented in most regions of the world, with maximum diversity in the central and west Pacific. The limits of many genera are uncertain, as the anatomy of many species has not been examined. The family is represented in New Zealand by a single naturalised species.
Genus Coneuplecta Möllendorff

Helix of authors. (Not Helix of Linnaeus, 1758, type species Helix pomatia Linnaeus, 1758, designated by de Montford (1810); Eulidae.)

Zonites of authors. (Not Zonites de Montfort, 1810, type species Helix algera Linnaeus, 1758, by original designation; Zonitidae.)

Nanina of authors. (Not Nanina of Gray, 1843, type species Helix virina Linnaeus, 1758, designated by Gray (1847); synonym of Nanina Sowerby, 1842, in Ariophanidae.)

Nanina of authors. (Not Nanina of Sowerby, 1842, in error for Nanina Gray, 1843; Ariophanidae.)

Hyatula of authors. (Not Hyatula of Albers, 1850, type species Helix callavia Müller, 1774, designated by von Meijenfeldt (1866) — synonym of Oxychilus Hitzinger, 1833, in Zonitidae.)

Staita of authors. (Not Staita of Adams, 1865, type species Helix taphina Benson, 1848, designated by Adams (1865); Ariophanidae.)

Trochonanina of authors. (Not Trochonanina of Mousson, 1869, type species Helix morganica Pfeiffer, 1855, designated by Nevill, 1878; Atractidae. Not of Gürter, 1884, type species Nanina schmelziana Mousson, 1865, by original designation — synonym of Inveolate Gude, 1913, in Microcystidae.)

Coneuplecta von Möllendorff, 1893: 64, type species Helix scalarina Pfeiffer, 1851, by original designation.


Parasitala Thiele, 1929-31: 398, type species Parasitala avantiensis Thiele, 1931, by original designation.

Sitalina Thiele, 1929-31: 635, type species Sitalina circumcincta Reinhardt, 1883, by monotypy.

Turrisitala Iredale, 1933: 55, type species Turrisitala normalis Iredale, 1933, by original designation.

Oviparous species. Shell small, moderately conical, angulate, narrowly perforate, corneous to greenish-brown or reddish-brown, finely striated or costulate; aperture without armature; peristome thin, not continuous. Shell lobes absent. Radula with a 5-cuspid central tooth, and with no more than 2 lateral teeth which are almost as elongate as marginals and have more than one ectocone. Genital orifice immediately posterior to right opercular peduncle. Divergent sac on talon. Free ovicrypt with a glandular zone. Bursa copulatrix present. Phallus without an appendix. Phallic retractor inserted on epiphallus. Cerebropedal connectives short, the left one shorter than the right. Pleural ganglia closer to cerebral ganglia than to pedal ganglia. Right parietal ganglia fused with visceral ganglion, which is on right of median plane.

Chromosome number not known.

Remarks. Snails of Asia, Indonesia, Philippines, New Guinea, northern Australia, and numerous islands in the Pacific. In the absence of a revision of the Indo-Pacific Euconulidae I have essentially followed the taxonomy established by Baker (1941), who regarded Durgellina Thiele, 1928, Conibycus Thiele, 1928, Parasitala Thiele, 1931, and Sitalina Thiele, 1931 as junior synonyms of Coneuplecta von Möllendorff, 1893 and yet applied Durgaelliina and Sitalina at subgeneric rank without providing subgeneric diagnoses. Coneuplecta calculosa (Gould, 1852) was assigned to the subgenus Durgellina as it is conspecific with the type species D. virina Thiele, 1928. Other authors, such as Zilch (1959-60), treat Durgellina, Conibycus, Parasitala, and Sitalina as genera distinct from Coneuplecta. The status of Turrisitala Iredale, 1933, tentatively placed in synonymy with Coneuplecta by Baker (1941), has not been resolved (Smith 1992).

The anatomy of most Coneuplecta species is not known.

Coneuplecta calculosa (Gould)

Figures 35, 75, 116, 143, 171, 197, 225, M5-8, M9-12, M54, M55, M114, M115; Map 8

calculosa Gould, 1852: 48 (Helix).

microconus of authors (not of Mousson, 1865).

pinnocki Iredale, 1876: 100 (Helix).

virina Thiele, 1928: 136 (Durgellina).

Shell (Fig. 35) conoid-turbinate, convex basally, up to 5.5 mm high by 5 mm in diameter, narrowly perforate, distinctly angulate when young, becoming almost evenly rounded at 5 whorls, but always with a low peripheral thread, when mature with 5-6 rapidly increasing whorls, very thin, corneous to very pallid, horn-coloured at apex, dullish, with satin-like finish above but more glossy below. Protoconch (Fig. M5-8) of 1.5-2 whorls, with closely spaced, rounded growth-threads, beaded by subequally spaced, spiral, impressed lines. Teleoconch (Fig. M9-12) with growth threads and more widely spaced spiral striae separating broader wrinkles; growth threads obsolescent shortly below periphery; sutures deep. Umbilicus superficial, its width 0.06 of shell diameter. Aperture broad, evenly rounded; peristome thin; columella sharply and broadly reflected above, closing more than half the perforation.

Animal very pale, with brown coloration of viscera visible through foot tissues and shell. Tail elongate, extending well beyond shell in active animal; a poorly developed horn over caudal mucus pit. Sole tripartite. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right opercular peduncle.
Reproductive system, Fig. 75. Ovotestis consisting of 2 clusters each of 4 or 5 claviform lobes, embedded on dorsocolumellar side of digestive gland. Hermaphrodite duct rather short, for the greater part dilated but narrowing to its entry in talon, bearing a diverticulum. Spermoviduct short; prostatic gland with follicles confined to distal part. Free oviduct moderately long, with a glandular zone in medial part. Bursa copulatrix reservoir an oval sac on a short, stout duct; fine muscle threads arising from spermoviduct inserted on apex of reservoir. Hermaphrodite duct rather short, for the greater part dilated but narrowing to its entry in talon, bearing a diverticulum. Spermoviduct short; prostatic gland with follicles confined to distal part. Free oviduct moderately long, with a glandular zone in medial part. Bursa copulatrix reservoir an oval sac on a short, stout duct; fine muscle threads arising from spermoviduct inserted on apex of reservoir. Vagina short. Vas deferens long. Epiphallus short, its entry to phallus apparently without a papilla. Phallus elongate, with proximal 0.75 thick-walled, closely packed internally with papillae; distal 0.25 thin-walled, its internal lining smooth or weakly ridged. Sheath heavy and muscular, surrounding greater part of proximal phallus, with bands to epiphallus and onto phallus retractor. Atrium short.

Phallus retractor arising from diaphragm, investing base of epiphallus. Vagina receiving a branch from right lateral retractor.

Jaw (Fig. 116) broadly crescentic, 0.45 mm wide, with a weak medial projection.

Radula (Fig. M54, 55) of about 135-155 V-shaped rows of teeth, each with the formula 130–135+1+C+1+130–135. Central tooth very elongate, with 5 cusps constituting the elongate mesocone, shorter but prominent ectocones, and very small secondary ectocones. Lateral teeth elongate, with prominent endocone, mesocone and ectocone, and with 2 small secondary ectocones. Marginal teeth multicuspid, with prominent mesocone and ectocone and several smaller secondary ectocones. All teeth on elongate basal plates.

Digestive tract, Fig. 145. Buccal mass spheroidal. Oesophagus long, without a crop. Gastric crop cylindrical. Stomach a simple curvature bearing ducts to digestive gland, not differentiated externally from gastric crop. Intestine short.

Pallial complex, Fig. 171. Pulmonary cavity 2.5× as long as it is wide, extending over about 0.7 whorls. Venation apparently absent apart from pulmonary vein. Kidney triangular, occupying about 0.25 of length of pulmonary cavity. Ureter sigmoid, running along anterior face of kidney to top of pulmonary cavity, then recurving to run adjacent to rectum, close to pneumostome.

Free muscle system, Fig. 197. Columellar muscle giving off buccal retractor muscle almost immediately and right and left tentacular retractors very shortly afterwards. Tentacle retractors arising dorsally from lateral retractors, each dividing anteriorly to insert on ocellar peduncle and interior tentacle; right ocular retractor crossing over phallus.

Central nervous system, Fig. 225. Cerebral ganglia united by a very short commissure. Cerbropleural connectives short, the left one shorter than the right. Pleural ganglia nearer to cerebral ganglia than to pedal ganglia. Left parietal ganglia adjacent to left pleural ganglion. Right parietal ganglion fused with visceral ganglion, which is on right of median plane.

Type material. Described from Tahiti, Society Islands. Syntypes USNM 5465 (but see Baker 1941 for discussion on their status).

Distribution. Widely distributed on islands of the Pacific.

Recommended common name. Calculus cone snail.


History in New Zealand. This is the first record of C. calculosa established in New Zealand, confirmed by collection of live material from the field.

Biology. C. calculosa is widely distributed in the Pacific, at altitudes from sea level to nearly 700 m, suggesting that it has a requirement for subtropical to tropical climatic conditions. It has evidently been carried from island to island by human agency (Baker 1941, Solem 1959). The Pacific collection records quoted by Baker (1941) suggest that it is arboreal. The species of Java are known to be arboreal on low vegetation (van Benthem Jutting 1950). In contrast, Smith (1992) states that it occurs in litter of closed forest in coastal Northern Territory, Australia. The New Zealand material was gathered from the soil surface under broadleaf forest litter. Only two live animals were found amongst several hundred shells collected, possibly indicating that those on the forest floor had fallen from vegetation above. Searches of vegetation to 2 m height did not, however, yield any specimens.

Oviparous. The eggs are spherical, about 0.85 mm in diameter, with a white shell (Fig. M114, 115) composed of calcite crystals.
Family FERUSSACIIDAE

**Diagnosis.** Herbivorous aulacopod snails, oviparous or ovoviviparous. Shell small, oblong or lanceolate, smooth and glossy, unicortous, with apex blunt, aperture pyriform, and columella often bearing a prominent spiral fold and parietal wall a medial lamella, capable of housing retracted animal. Eyes unpigmented in Cecilioides. Foot with a well developed suprapedal groove and foot fringe. Suprapedal gland embedded in foot tissues. Caudal muscle pit present in some species. Buccal mass spheroidal or weakly oval. Jaw aulacognathic. Radula with marginal teeth short, on broad basal plates. Intestine with a single loop directed forwards. Kidney short, transversely extended to hindgut, which it may follow some distance forwards; ureter closed, retrograde, extending to anterior margin of pulmonary cavity, opening via separate ducts to rectum and to exterior near pneumostome. Anal gland present in pallial cavity above pneumostome. Buccal retractor arising from left branch of colomellar muscle. Right ocular peduncle retractor passing forwards over phallus. Genital orifice a short distance posterior to right ocular peduncle. Male and female pallial gonoducts, below cærorefour, separate or fused. Phallus retractor arising from diaphragm or on right branch of colomellar muscle, inserted on apex of epiphallus and, in some genera, on phallic appendix. Bursa copulatrix duct rarely long, often dilated at entry to oviduct, where a pilaster may occur. Epiphallus compact, bulbous, applied intimately to proximal phallus, with a low vergic papilla, this often somewhat vestigial. Phallus with dilated proximal section occupied by pilasters and often a sacroblem-like papilla, and bearing a variously developed lateral appendix; distal section tubular and somewhat slender. Central nervous system with cerebropedal connectives in length equal to or less than cerebral ganglion width; left and right connectives of similar length. Pleural ganglia closer to pedal ganglia than to cerebral ganglion. Visceral chain moderately compact; right parietal ganglion fused with visceral ganglion.

Haploid chromosome number 30.

**Remarks.** Most systematists of the Stylommatophora have recognised the ferussacids at the family level, with close affinities to the Achatinidae and Subulinidae. Pilsbry (1946 (1939-48)) regarded these snails as a subfamily of the Subulinidae.

The Ferussacidae comprise 12 genera, mainly Eurasian. Their systematics has not been fully resolved, as the majority of species have not been studied anatomically. In contrast to Watson (1928) and Giusti (1973, 1976), I take the bulbous structure at the proximal end of the male genitalia in Ferussacidae to be the epiphallus rather than part of the phallus.

Genus Cecilioides d’Audebard de Férussac

**Buccinum** of authors. (Not Buccinum of Linnaeus, 1758, type species Buccinum undatum Linnaeus, 1758, designated by de Monfort (1810); Buccinidae.)

**Helix** of authors. (Not Helix of Linnaeus, 1758, type species Helix pomatia Linnaeus, 1758, designated by de Monfort (1810); Helicidae.)

**Bulimus** of authors. (Not Bulimus of Scopoli, 1766-88, type species Bulimus hebraeus Müller, 1758, designated by Gray (1847) - synonym of Megalobulimus Müller, 1878; Achatinidae.)

**Achatina** of authors. (Not Achatina of de Monet de Lamare, 1799, type species Achatina limosa Linnaeus, 1758, by monotypy: Achatinidae.)

**Polyphemus** of authors. (Not Polyphemus of de Monfort, 1810, type species Polyphemus vulgatus Röding, 1798, by monotypy - synonym of Ovotoma Röding, 1798; Ovotomidae.)

**Columba** of authors. (Not Columba of Perry, 1811, type species Bucinum columna Müller, 1774, by monotypy: Achatinidae.)

*Ferussacia* of authors. (Not Ferussacia of Linnaeus, 1758, type species Ferussacia promicacea Riso, 1826, according to Zilch (1959); Ferussacidae.)

*Achatinella* of authors. (Not Achatinella of Swainson, 1828, type species Achatinella seminigra de Monet de Lamare, 1822 = Turbo operculata Döderlein, 1788, designated by Pilsbry & Cook (1912-14); Achatinellidae.)

*Acicula* of authors. (Not Acicula of Hartmann, 1821, type species Acicula miliaris Müller, 1774, designated by Gittenberger (1983); Aciculidae.)

*Oleacina* of authors. (Not Oleacina of de Lamarck, 1799, by monotypy - ICZN Opinion 335 (1955a: 48).)

**Cecilioides** of D’Audebard de Férussac, 1814: 48, type species Bulimus acicula Bruguières, 1789 = Bucinum acicula Müller, 1774, by monotypy - ICZN Opinion 335 (1955a: 48).

**Cochlicopa** of authors. (Not Cochlicopa of d’Audebard de Férussac, 1821, type species Helix laboriosa Müller, 1774, designated by Gittenberger (1983); Coellicopidae.)

**Acicula Risso, 1826: 81, type species Acicula eversea Riso, 1826 = Bucinum acicula Müller, 1774, by monotypy. (Not Acicula of Hartmann, 1821, type species Bulimus culmen De Panzanand, 1801 ICZN Opinion 344, 1955c: 312; Aciculidae.)

**Ferussacia** of authors. (Not Ferussacia of Risso, 1826, type species Ferussacia promicacea Riso, 1826, according to Zilch (1959); Ferussacidae.)

**Achatinella** of authors. (Not Achatinella of Swainson, 1828, type species Achatinella seminigra de Monet de Lamare, 1822 = Turbo operculata Döderlein, 1788, designated by Pilsbry & Cook (1912-14); Achatinellidae.)

**Acicula** of authors. (Not Acicula of Jeffreys, 1830, type species Helix laboriosa Müller, 1774, designated by Koebele (1880); Aciculidae.)

**Styloides** of authors. (Not Styloides of Hartmann, 1821, type species Buccinum acicula Müller, 1774, designated by Pilsbry (1946 (1939-48)).

**Boulevard** of authors. (Not Boulevard of Shuttleworth, 1854, type species Bulimus teretens de Monet de Lamare, 1801, according to Zilch (1959); Subulinidae.)

**Cecilioides** of authors. (Not Cecilioides of de Lamarck, 1799, type species Cecilioides acicula Müller, 1774, by monotypy: Achatinidae.)

**Macropria** of authors. (Not Macropria of Swainson, 1840: 171, type species Helix exsima Gmelin, 1789 = Cecilioides acicula (Müller, 1774), designated by Pilsbry (1931).)

**Cecilioides** of authors. (Not Cecilioides of de Lamarck, 1799, type species Cecilioides acicula (author not given) = Buccinum acicula Müller, 1774, by monotypy: Achatinidae.)

**Macrotricca** of authors. (Not Macrotricca of de Lamarck, 1799, type species Macrotricca eburnea Müllar, 1774, designated by Pilsbry (1931).)

**Cecilioides** of authors. (Not Cecilioides of de Lamarck, 1799, type species Cecilioides acicula (author not given) = Buccinum acicula Müller, 1774, by monotypy: Achatinidae.)

**Macrotricca** of authors. (Not Macrotricca of de Lamarck, 1799, type species Macrotricca eburnea Müllar, 1774, designated by Pilsbry (1931).)

**Cecilioides** of authors. (Not Cecilioides of de Lamarck, 1799, type species Cecilioides acicula (author not given) = Buccinum acicula Müller, 1774, by monotypy: Achatinidae.)

**Macrotricca** of authors. (Not Macrotricca of de Lamarck, 1799, type species Macrotricca eburnea Müllar, 1774, designated by Pilsbry (1931).)
Glandina of authors. (Not Glandina of Schumacher, 1817, type species Glandina ovataeae Schumacher, 1817 = Oletina ovataeae Cunia, 1791, by monotypy – synonym of Oletina Röding, 1798; Oletinidae.)

Acicula Westerlund, 1886 (1886: 87): 175 (as section of subgenus Caecilianella Bourguignat of genus Cecilioides Jeffrey). Type species Buccinum acicula Müller, 1774, according to Pilsbry (1909 (1908–10)).

Diagnosis. Ovoviviparous species. Shell very narrowly lanceolate, imperforate, transparent (weathering to opaque white); aperture pyriform, its height usually less than half that of shell, its outer lip arching forward in middle, with columella concave and more or less distinctly truncate at base. Animal white or unpigmented, the eyes unpigmented. Sole undivided. Caudal mucus pit absent. Hermaphrodite with extensive proximal pilasters; lateral appendix, when present, poorly developed. Phallus retracting from dia-phragm, inserted apically on epiphallus.

Remarks. Cecilioides species are calcicolous, burrowing snails found deep in the soil or hidden under leaf litter. They occur naturally in western and southern Europe, southern Asia, and the tropics.

Several sections or subgenera of Cecilioides have been distinguished on the basis of shell characters (Pilsbry 1909–10 (1908–10), Thiele 1929–31, Zilch 1959–60).

Subgenus Cecilioides

Diagnosis. Shell with spire slender, columella distinctly truncate at base; columellar and parietal walls of aperture without a conspicuous callosity, but a low parietal nodule sometimes developed.

Cecilioides (Cecilioides) acicula (Müller)

Figures 36, 76, 117, 146, 172, 198, 226, C9, M13, M14, M56, M57; Map 9

acicula Müller, 1774: 159 (Buccinum).

octana Gmelin, 1791: 36 (in part) (Helix).

? ribesii Jacob, 1798: 639 (Buccinum).

terrestre Montagu, 1803: 248 (Buccinum).

eburnea Risso, 1826: 81 (new name for acicula Müller, 1774) (Acicula).

aciculoides de Cristoför & Jan, 1832: 2 (Columna).

miliaris de Cristoför & Jan, 1832: 2 (Columna).

pulchra Scacchi, 1836: 16 (Achatina).

punctata Compagno, 1837: 92 (Achatina) (nude name).

alba Brown, 1837: 49: 22 (Achatina) (nude name).

glandulifera Pfeiffer, 1850: 80 (Achatina).

spinifera Benson, 1856: 343 (Achatina).

? vera Benson, 1856: 343 (Achatina).

anglica Bourguignat, 1856: 384 (Caecilianella).

resille Bourguignat, 1856: 385 (Caecilianella).

aglae Bourguignat, 1857: 15 (Caecilianella).

hydrola Bleiz, 1859: 296 (Acicula).

corpora Bourguignat, 1860: 158 (Caecilianella).

ricetanus Benoit, 1862: 245 (Achatina).

stephaniæa Benoit, 1862: 246 (Achatina).

gemmellariana Benoit, 1862: 248 (Achatina).

unifasciata Bourguignat, 1864: 55 (Caecilianella).

buresi Bourguignat, 1866: 1803–70: 184 (Ferussacia).

laetae Moitessier, 1867: 371 (Caecilianella).

anversitatis Dohni, 1869: 10 (Caecilianella).

manniana Bourguignat, 1870: 54 (Caecilianella).

mermines Bourguignat, 1870: 54 (Caecilianella).

ribertiana Benoit, 1875: 136 (Achatina) (nude name); Benoit, 1882: 89 (Caecilianella).

cuheristosa Servais, 1880: 121 (Caecilianella).

riberti Servais, 1880: 131 (Caecilianella).

cristallina Benoit, 1882: 120 (Caecilianella).

latae Poideau, 1886: 46 (Acicula).

gaturi Westerlund, 1892 (1892: 94): 195 (Clonella (Caecilianella)).

melanesis Westerlund, 1892 (1892: 94): 196 (Clonella (Caecilianella)).

peltopera Westerlund, 1892 (1892: 94): 196 (Clonella (Caecilianella)).

uniova de Gregorio, 1896: 206 (Caecilianella).

praelata Westerlund, 1898: 196 (Caecilianella (Acicula)).

reacta von Rosen, 1903: 181 (Caecilianella).

amarelle Schnebb, 1906: 184 (as a var. of octana Gmelin (Stenogyra)).

Shell (Fig. 36) very narrowly lanceolate with regularly tapered spire, 4.5 mm high by 1.2 mm in diameter, with 5 or 6 scarcely convex whorls, polished and smooth except for very weak spiral striae, thin, transparent, tinged yellow or golden brown in live specimens owing to colour of underlying digestive gland, imperforate; protoconch (Fig. M13, M14) blunt, rounded, smooth or with faint growth lines; aperture pyriform, 0.3 of shell height, narrowed and acutely truncate, rounded at base, with outer lip thin and flexuous, and parietal wall not calloused; columella slightly calloused, with a columellar fold in juveniles, and abruptly truncate at its union with basal margin of aperture lip in adults.

Animal white, with eyes unpigmented. Active animal with head and tail much elongated, the latter often fitted off substrate but not reaching behind shell.

Reproductive system, Fig. 76. Ovotestis occupying uppermost whorls of viscera, consisting of a single large,
ungimented acinus. Hermaphroditic duct proximally straight and slender, but distally much dilated and convoluted, at entry to telench slender and bent back upon itself in a U-shape. Albumen gland large, linguiform. Male and female pallial gonoducts fused into spermoviduct condition; walls of female part dilated but not apparently folded; male part a narrow internal groove passing along entire ventral side, into which open follicles of prostatic gland. Free oviduct short, Bursa copulatrix a small oval sac on a short, slender duct. Vagina rather long. Vas deferens very slender, inserted apically on male genitalia, adjacent to retractor muscle attachment. Male genitalia an oval, bulbous structure on a slender stem to atrium; proximal third of bulb, delimited by a slight constriction, representing vestigial epiphallus, internally with much folded walls; entry into phallus with a small verge papilla. Proximal region of phallus occupied for the most part by several large pilasters; distally human free immediately before narrowing to extend to short, slender atrium.

Spermatophore unknown, probably not produced.

Phallic retractor arising as a slender branch of right division of columnar retractor system.

Jaw (Fig. 117) 0.3 mm wide, crossed by 26–28 folds which denticulate the edges.

Radular ribbon (Fig. M56, 57) with about 80 transverse rows of teeth, each with the formula 10 + 5 + C + 5 + 10. Central tooth small and narrow, with a short mesocone flanked by minute ectocones. Lateral teeth larger, tricuspid, on quadrangular basal plates. Marginal teeth rather broad, bearing 6 or 7 minute cusps.

Digestive tract, Fig. 146. Buccal mass spheroidal to weakly oval. Oesophagus slender and long, extending to gastric pouch without formation of an oesophageal crop. Gastric pouch capacious, extending 0.7 of a whorl, constricted before giving rise to stomach. Intestine issuing from upper reaches of stomach to extend directly forwards before describing a posteriorly directed loop of about half a whorl, then running forwards to anus. Anal gland associated with anus in pulmonary cavity system.

Pallial complex, Fig. 172. Pulmonary cavity extending around cuticle body whorl in adult, shorter in juveniles. Kidney short, barely exceeding length of pericardium, but prolonged transversely across top of pulmonary cavity to about hindgut. Ureter closed, extending across anterior margin of kidney and then along hindgut to mantle collar, there opening via minute ducts to rectum and to body exterior below pneumostome. Vascular network of pulmonary cavity roof and main pulmonary vein weakly developed.

Free muscle system, Fig. 198. Columnar muscle with a short common stem, dividing into left and right branches. Left branch giving rise to buccal retractor and, further forward, to tentacle retractor and anterior pedal retractor. Right branch quickly giving off a broad but rather short tail fan; main stem dividing further forward into tentacular retractors and anterior pedal retractor; right branch to ocular peduncle passing over phallus.

Central nervous system, Fig. 226. Cerebral commissure shorter than cerebral ganglion width, rather slender. Left and right cerebropedal connectives equal, their length about equal to width of cerebral ganglion. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Left parietal ganglion separated from both left pleural ganglion and visceral ganglia by short connectives, but closer to visceral ganglion. Right parietal ganglion separated from right pleural ganglion by a short connective but fused to visceral ganglion, the latter lying to right of median plane.

Haploid chromosome number unknown.

**Type material.** Müller's material was collected from Thuringia - Thangelstedt near Weimar, Germany. The whereabouts of this material is unknown, and it is presumed lost.

**Distribution.** The natural range of *C. acicula* is believed to be central and western Europe, the Mediterranean, Arabia, North Africa, and Central Asia. Introduced to Northern Europe, the U.S.A., Bermuda, Barbados, Hawaii, the Azores, the Canary Islands, South Africa, Australia, and New Zealand.

**Recommended common name.** Blind pin snail.

**Material examined.** New Zealand. AK. Epsom, La Roche (MONZ M84650); Tamaki, 1 Nov 1993, B.F. Hazelwood. BP. Tauranga, 1984, B. McFadgen (MONZ M86174).


**History in New Zealand.** First reported from New Zealand by Suter (1913). Further material was collected from the Epsom, Mt Eden, and Mt Albert areas in Auckland City in the 1950s (Whitten, 1955). An established population was discovered near Tauranga in 1984 during archaeological excavations and the species is known from Nelson (D. Roscoe, pers. comm.), indicating that it may be more widespread than is suggested by the material in malacological collections.

**Biology.** Largely subterranean in habit, and in Europe most frequently encountered in rather dry pastures and other grassy areas, gardens, and caves. Also well known from graves in Europe, where the snails can be found in numbers associated with bones (see Pilshy 1909–10
Definitive information on the food of *C. acicula* is lacking, but these snails are believed to feed on vegetable matter such as fungi and possibly fine roots.

Wächtler (1929a, b) describes various aspects of the biology of *C. acicula*, which is oviparous. Eggs 0.75 mm in diameter, with a calcareous shell, are laid singly in the soil.


Family HELICIDAE

Diagnosis. Herbivorous snails with shell capable of housing animal. Sole undivided. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw odontognathic, with degree of plate fusion variable. Radula with marginal teeth broad, on short basal plates. Intestine with a single forward-directed loop. Kidney with a retrograde closed duct usually terminating between lung top and pneumostome, or at pneumostome. Cephalic retractors strongly developed, arising as a single stem from columella, with right ocular retractor passing forwards between phallus and vagina. Phallus retractor arising from floor of body cavity. Genital orifice immediately behind right ocular peduncle, or a short distance posteriorly. Accessory organs of genitalia comprising a single stylophore and 2 tubular, often branched, mucus glands opening into vagina. Bursa copulatrix reservoir adjoining pericardium, with a diverticulum variously developed, sometimes reduced or absent, never bound to spermoviduct by a muscular or connective membrane. Central nervous system with cerebropedal connectives in length less than twice cerebral ganglion width, the left connective generally longer than the right one.

Haploid chromosome number 22–30.

Remarks. The Helicidae are European and circum-Mediterranean. Nordsieck (1987) recognised them as comprising two groups, the Ariantinae and Helicinae. In Schileyko's (1991) system the genus *Euparypha* Hartmann, 1843 is separated out from the latter group to form the monogeneric subfamily Euparyphinae.

The escargots or edible snails of Europe belong to this family, and members of several genera have been widely introduced, often becoming pests in their new range.

Subfamily HELICINAE

Diagnosis. Shell moderate-sized to large, commonly turbinate or globose, more rarely flattened; aperture lacking parietal barriers, but prominences or plates often present on basal and palatal margins; columellar margin sometimes with a callus. Genitalia with mucus glands variously ramified, with a minimum of 2 branches. Bursa copulatrix duct with diverticulum variously developed, sometimes reduced or absent, never bound to spermoviduct by a vascular membrane. Central nervous system with cerebropedal connectives in length less than twice cerebral ganglion width, the left connective generally longer than the right one.

Haploid chromosome number 22–30.

Remarks. The subfamily comprises about 26 genera, one of which is represented in New Zealand by a single naturalised species.

Genus Cantareus Risso

*Helix* of authors. (*Not* *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

*Serpula* of authors. (*Not* *Serpula* of Linnaeus, 1758, type species *Serpula vermicularis* Linnaeus, 1767, designated by Hartman (1959); Annelida.)

*Cornu* von Born, 1778: 371, type species *Helix aspersa* Müller, 1774, by monotypy (introduced for a taxonomical specimen).

*Cochlea* of authors. (*Not* *Cochlea* of da Costa, 1778, type species *Helix pomatia* Linnaeus, 1758, designated by Winckworth (1926); Helicidae.)

*Crypomphalus* de Charpentier, 1837: 5, type species *Helix aspersa* Müller, 1774, designated by Moquin-Tandon (1855).
Costanæa of authors. (Not Costanæa of Held, 1838 (1837-38), Zer iaspersa, lucana, laticeca, pomata, etc., synonym of Helix Linnaeus, 1758; Helicidae.)
Tapada Gray, 1840: 127, type species Helix aperta von Born, 1778, by monotypy.
Colinæa of authors. (Not Colinæa of Scudder, 1882: 56, type species Helix pomatia Linnaeus, 1758, according to Pilsbry (1939 (1939 48)) synonym of Helix Linnaeus, 1758; Helicidae.)
Megastoma of authors. (Not Megastoma of Scudder, 1882, type species Helix pomatia Linnaeus, 1758, according to Pilsbry (1939 (1939 48)) synonym of Helix Linnaeus, 1758; Helicidae.)
Eschelida of Maria di Monterosato, 1894: 168, type species Helix mazzullii de Cristofori & Jan, 1832, by monotypy.

**Diagnosis.** Shell moderate-sized, globose, imperforate, with peristome either simple or expanded; protoconch smooth. Jaw with strong ribs demarcating both margins. Kidney triangular, rather longer than the pericardium on its left side, occupying 0.25-0.5 of lung length. Secondary urter close to pneumostome. Genital orifice a short distance posterior to right ocular peduncle. Bursa copulatrix reservoir a spheroidal to oval sac, bound to bursa seminalis. Keratoconch (Fig. M15) of 1.5 whorls large, containing a single dart with 4 blades and a fluted base. Phallus subdivided to proximal and distal portions by robust annular pad; proximal phallus with papilla and a pseudopapilla; distal phallus with small pleats and crest-like structure at entry to atrium. Phallus nerve from right cerebral ganglion.

**Cantareus aspersus** (Müller)

Figures 37, 77, 100, 118, 173, 199, 227, 248, C10, C11, M15, M58-60, M116; Map 10
aspera Müller, 1774: 59 (Helix).
hoverensis Pennant, 1777: 136 (not of Müller, 1774) (Helix).
calcaris da Costa, 1778: 72 (Cochlea).
capreus van Burt, 1778: 371 (Cornu).
lessuris da Ranzouwsky, 1879: 274 (not of Müller, 1774) (Helix).
grevia Gmelin, 1791: 3649 (in part) (not of Linnaeus, 1758) (Helix).
variegata Gmelin, 1791: 3650 (Helix).
cornuscapina Gmelin, 1791: 3745 (Serpula).
feroxensis Costa, 1839: 19 (Helix).
senconda Costa, 1839: 19 (Helix).
corn survey Moquin-Tandon, 1859: 175 (as subsp. of aspersa Müller) (not conceived Draparnaud, 1801) (Helix).
senosea Lowe, 1861: 111 (Helix).
solitariana Paulucci, 1879: 119 (as subsp. of aspersa Müller) (Helix).
adjacent to origin of very long, slender flagellum. Epiphalus sinuous, cylindrical, forming a broad arch or sharply folded into a U-shape, entering phallus with a small, spheroidal, finely nodulated papilla. Phallic rather short, proximal part bulbous, housing a solid pseudopapilla arising from walls, separated from distal part by a prominent annular pad; distal phallic bearing weak longitudinal folds or crests that fuse to a plastron-shaped plate on distal vaginal wall. Antron very short.

Spermatophore (Fig. 100) with anterior section about 32 mm long and 1 mm wide, comprising 5 longitudinal ridges that spiral gradually throughout its length; ridges smooth. Mid-section or body spindle-shaped, about 13 mm long and about 3 mm in maximum diameter; 4 longitudinal ridges from anterior part extending over entire length of mid-section, then crest irregularly serrate. Tail a whip-like filament, 80 mm in length, for the greater part U-shaped in cross-section and lacking ornamentation.

Phallic retractor arising from diaphragm, inserted on epiphalus a little proximal to its insertion on phallus. Jaw (Fig. 118) about 3.7 mm wide, broadly crescentic, with anterior cutting margin strongly concave, scored with a variable number of prominent vertical ribs or folds strongly denticulating the upper and lower margins, and with distinct transverse striation.

Radula (Fig. M58-60) with about 125 transverse rows of teeth, each varying around the formula 23+20+Cr+20+23. Central tooth tricuspid, on a quadrate basal plate, with a broadly elongate mesocone and short but distinctly pointed ectocones. Lateral teeth tricuspid or bicuspid, on a quadrate basal plate, with mesocone broader and shorter than on central tooth; endocone generally absent, and ectocone small but distinct; 20th tooth transitional, with mesocone bifurcated and ectocone more prominent. Marginal teeth on small, broadly rectangular basal plates, of 3 or 4 cusps owing to division of mesocone and ectocone, teeth on outermost parts of radial ribbon often represented by basal plates lacking cusps.

Digestive tract, Fig. 147. Buccal mass spheroidal. Oesophagus slender and short, abruptly giving rise to a dilated crop. Stomach separated from crop by a constriction, short but dilated, occupying about 0.5 of penultimate whorl. Intestine extending in a short anteriorly directed loop to abut kidney, then producing a short posteriorly directed loop before running forwards to anus in mantle collar.

Pallial complex, Fig. 147. Pulmonary cavity short, in active animal about 2x longer than wide, extending to about 0.5 of body whorl; venation of roof strongly developed. Kidney triangular, extending to about 0.3 of pulmonary cavity length, with pericardium extending along the greater part of its left wall. Ureter sigmoid, closed to pneumostome, rather broad in its primary arm along anterior of kidney but rather slender in its secondary part along rectum.

Free muscle system, Fig. 199. Columellar muscle extending forwards as a broad tail fan, attaching to pedal and lateral body walls, and near its origin giving rise to paired tentacular retractors, each of which divides anteriorly into branches to ocular peduncle, inferior tentacle, and cephalic body wall. Right ocular retractor passing across phallic. Buccal retractor originating from columellar stem adjacent to and immediately in front of tentacular muscles, extending anteriorly as a broad ribbon, then bifurcating before its attachment to posterior and lateral aspects of buccal mass.

Central nervous system, Fig. 227. Cerebral commissure moderately short. Left cerebropedal connective slightly longer than the right, in length about 1.5x width of cerebral ganglion. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Right parietal ganglion fused to visceral ganglion and closely appressed to left pleural ganglion. Left parietal ganglion apparently partially fused to visceral ganglion and closely appressed to left pleural ganglion. Visceral ganglion to left of median plane.

Haploid chromosome number 27.

Type material. Described from material collected in Italy. The whereabouts of this material is unknown, and it is presumed lost.

Distribution. Native in Western Europe to the borders of the Mediterranean Sea and Black Sea. Introduced to parts of Europe and North Africa as far back as the eighth century B.C. with the Phoenician, Greek, and then Roman settlements and trading posts established around the Mediterranean. Subsequently introduced into further European countries, southern Russia, Israel, the Azores, Madeira, St Helena, the Canary Islands, Canada, the U.S.A., Mexico, Bermuda, Haiti, Guatemala, Dominican Republic, French Guiana, Ecuador, Peru, Chile, Argentina, Brazil, West Africa, Zimbabwe, South Africa, Réunion, Tristan d’Acunha, Ascension, Mauritius, the Mascarene Islands, Taiwan, New Zealand, the Loyalty Islands, Pitcairn, Easter Island, Australia, and New Zealand. Introductions were often unintentional with garden plants and freight, but not infrequently deliberate as a food snail.

Recommended common name. Brown garden snail.


**History in New Zealand.** *C. arboresus* is popularly believed to have been first introduced into New Zealand by the French in the 1860s. The earliest record in New Zealand's malacological literature appears to be that of Hutton (1883), who lists Auckland, Nelson, and Greymouth as localities. However, the species was well established by that time, particularly at the seaport towns (Musson 1891, Suter 1891). Further, the snails are known to have been abundant in some districts as early as the 1860s (Thomson 1891). Damage in gardens and crops was reported in 1890s (e.g., Brown 1897).

The pattern of greater abundance of *H. aspersa* in the North Island than in the South Island was evident by the early twentieth century (Thomson 1922).
inbreeding manifests first in fecundity and fertility, then in founder stock, or in severely depleted natural populations, 

C. aspersus is highly prized by Europeans as an edible snail. It continues to be collected in vast numbers in the Mediterranean area for human consumption, but, as wild stocks are declining, there is increasing emphasis on farming (heliciculture). Currently the centre of commercial production is France, but significant quantities are produced in other Mediterranean countries such as Italy, Spain, and Greece. C. aspersus is also farmed for both local consumption and export in other parts of the world, including New Zealand. Heliciculture methods vary from simple outdoor pens to a largely automated indoor battery pen system. Information on commercial culture of C. aspersus can be found in Avagnina (1983), Chevallier (1983, 1985), Daguzan (1983, 1989), Frömming (1982, 1989), Runham (1989), de Grisse (1991), and Associazione Nazionale Elicicoltori (1986-90).

A consequence of this interest in heliciculture, and the importance of the species as a pest in several crops, is that there is considerable information available on the biology of C. aspersus.

As to food plants, C. aspersus is selective, but feeding does occur on a large variety of living and dead plant tissues. A fundamental prerequisite of intensive heliciculture is the availability of suitable feedstock. It has been demonstrated that snails will grow at an acceptable rate on dry feed diets with high ash and relatively low protein content, provided they have access to water (Daguzan 1981). Studies on the performance of H. aspera fed on commercially available animal feedstuffs demonstrated their preference for diets based on vegetable rather than animal protein (Stephanou 1986a, Jess & Marks 1989).

The selection of raw materials, particularly the cereal component, is also known to be an important factor in the palatability of snail diets (Brittan 1984). C. aspersus consumes significant quantities of soil as part of its normal diet. In heliciculture, the provision of a soil substrate has demonstrated significant beneficial effects on snail growth rates (Gomot et al. 1986, 1989a, Jess & Marks 1989, Albuquerque de Matos 1990).

C. aspersus, like other helicids, is an obligate outcrossing species (Frömming 1954, Albuquerque de Matos 1989). Highly sensitive to degeneracy effects of inbreeding, as may occur when farms are established from limited founder stock, or in severely depleted natural populations, inbreeding manifests first in fecundity and fertility, then in size and survivorship, till finally, within three or four generations of sib matings, the lines become wholly infertile (Albuquerque de Matos & Serra 1984, 1988, Albuquerque de Matos 1989). Each mature snail will mate several times in a single season, with an interval between matings of as little as 3 days (Basinger 1931). Observations on courtship behaviour in C. aspersus have been published by Herzberg & Herzberg (1962), Giusti & Lepri (1980), and in detail by Chung (1987) and Adamo & Chase (1988). In the course of the present study, courtship behaviour was observed in snails brought to the laboratory during the spring and summer months.

Three phases of courtship (Fig. 248) have been described by Chung (1987) and Adamo & Chase (1988). An introductory phase consists of labial-head contact behaviour. Each snail probes the head and labial region of the other with its mouth and labial palps. With the head raised off the substrate and the tentacles fully extended, the snails move their jaw and radula actively, intermittently biting or nuzzling each other. The genital pore shows some swelling, or the terminal genitalia may be partially everted. The second phase comprises labial probing of the genital region and dart shooting behaviour. Labial probing occurs when a snail presses its mouth and labial palps on the genital pore, or on the skin next to the genital pore of the partner. This behaviour can occur with or without genital eversion in either snail, although full genital eversion usually begins at this time. When the behaviour occurs simultaneously and reciprocally in both snails, the everted genitalia will be appressed and apposed. A snail usually assumes a characteristic body posture and behaviour, whereby the sole is contracted and reduced in size but the anterior head-foot becomes swollen and distended, with ocular pedicules shortened but not invaginated. The snail pushes its swollen and very turgid everted genitalia against its partner. Dart shooting occurs when a snail rapidly everts the dart sac from the vaginal region of the already everted terminal genitalia. The dart, which is attached by its base to the base of the dart sac, is rapidly pushed out so as to (usually) pierce the flesh of the partner. The dart carries approximately 2 mg of white mucus secreted by the glands associated with the stylophore (Chung 1986a). The dart sac is then withdrawn. The dart is never propelled through the air, but is torn from the dart sac on becoming lodged in the partner's tissues. Occasionally the dart either does not hit the partner or does not lodge in the flesh, and is then withdrawn partially or entirely back into the dart sac. The erotic impulse includes full phallic eversion simultaneously with, or shortly after, shooting the dart.

Contrary to assertions by Chung (1986b), snails engaging in courtship behaviour for the first time usually possess a dart (Giusti & Lepri 1980). Snails that have gone
through dart shooting within the previous 5–7 days (in an earlier courtship), and have not yet regrown a fully formed dart, eliminate this behaviour from their courtship.

Once dart shooting behaviour has occurred, the dart is not used again. Dissections by Chung (1987) showed that darts which fail to lodge in the partner's tissues are discarded into the producer's bursa copulatrix diverticulum shortly before reception of a spermatophore from the partner during copulation. A new dart starts to grow within 5 hours of expulsion of a dart, and is fully grown within 5–8 days (Giusti & Lepri 1980, Tompa 1982, Chung 1987).

The third courtship phase consists of repeated phallus eversion and attempted copulation. Snails enter into this phase of mating only after dart shooting behaviour, and do not depend on receipt of a dart from the partner. In the normal development of this phase the snail, while oriented with its everted atrium pressed against the body of the partner, exhibits a momentary tensing of the body wall of the anterior headfoot. This is followed immediately by increased turgor of the everted atrium and then by phallus eversion. The everted phallus invaginates immediately if the snail does not achieve successful intromission. If intromission fails, the snail usually pauses before attempting copulation again. Normally the everted atria of the two snails are apposed when phallus eversion occurs. However, a snail can also evert its phallus when the everted atrium is pressed against any other part of its partner, indicating that tactile stimulation of the genitalia is necessary for triggering of the penial eversion behaviour.

Courting animals can make as many as 50 intromission attempts, or as few as one, before achieving copulation. Copulation does not occur unless intromission is simultaneous. In successful intromission the everted phallus is allowed to penetrate the vagina of the partner and to lodge in the vaginal canal. The snail, attaining intromission takes on the mating posture, in which the head is lifted off the substratum, the tentacles are shortened and held vertically, and the snail remains immobilised until it deposits its spermatophore into the partner's bursa copulatrix diverticulum. Adamo & Chase (1988) observed that usually only the second or third simultaneous intromission leads to successful spermatophore transfer. Transfer of the spermatophore to the partner is not strictly simultaneous for both snails. Once a snail has transferred its spermatophore it comes out of the mating posture, retracts its phallus, and waits for its partner to finish.

Digestion of the received spermatophore occurs in the bursa copulatrix diverticulum (Giusti & Lepri 1980, Adamo & Chase 1988).

Giusti & Lepri (1980), Chung (1987), and Adamo & Chase (1988) observed that the duration of courtship in *C. aspersus* varies considerably. The time from start of courtship to dart shooting averages about 35 minutes, while dart shooting to copulation takes another 15–45 or, rarely, as much as 240 minutes. Copulation was observed to last from 4 to 12 hours. Spermatophore transfer takes an hour or more towards the end of intromission.

Herzberg & Herzberg (1962), Cowie (1980), Giusti & Lepri (1980), Chung (1987), and Pos (1994a, b) have noted precocious mating in young *C. aspersus* lacking a deflected lip on the shell. These snails produce fertile eggs. For a South Auckland population, Pos (1994a) noted that over 30% of snails mated and 23% laid eggs before cessation of shell growth.

The function of the dart and of dart-shooting behaviour in the courtship and reproductive physiology of *C. aspersus* and other land snails has long been debated. Nonetheless, the function remains unclear (see Tompa 1984, Chung 1986a, 1987, and Adamo & Chase 1988 for the most recent discussions).

While courtship behaviour varies little, the reproductive output of *C. aspersus* varies greatly between individuals and populations. Studies of natural populations (Millar 1978), experiments in the laboratory (Herzberg 1965, Dan & Bailey, 1982) and experience in heliciculture (Lucas 1984, Daguzan 1985, 1989, Marciano 1986, Stephanou 1986a, Elmslie 1989) show that crowding effects at high population densities result in reduced growth rate, increased mortality, and reduced and more variable adult snail weight, all of which contribute to reduced fecundity. Albuquerque de Matos (1989, 1990) found high heritability values for adult size, but diet has an overriding effect on snail growth rates and size at maturity. The season of the year in which snails are reproductive in the wild varies between populations and even among individuals within a population; this variation is largely governed by environmental conditions, but there is apparently a genetic component (Albuquerque de Matos 1989, 1990, Elmslie 1989). It has been well established (Bailey 1981, Enée et al. 1982, Le Guhennec & Daguzan 1983, Laurent et al. 1984, Gomit & Gomit 1985, Aupinel & Daguzan 1989, Gomit et al. 1989b, Lazaridou-Dimitriadou & Bailey 1991) that long days stimulate whereas short days inhibit growth rates and egg laying. While the first oviposition of the season is indifferent to photoperiod, long days are needed in order to induce more egg-layings (Enée et al. 1982).

A period of hibernation (or artificially imposed quiescence) has been shown to increase the reproductive activity and fecundity of *C. aspersus* (Bonney-Claudet & Denny 1984). Hibernation in *C. aspersus* is controlled primarily by photoperiod, although temperature may determine its duration (Bailey 1981, 1983, Aupinel 1987); this hibernation condition is more correctly termed...
diapause. Reproduction becomes non-seasonal within several generations when the snails are maintained under optimum conditions (Albuquerque de Matos 1990); three or four generations can be produced each year.

Like most Mediterranean snails, C. aspersus can survive in a dormant aestivatory state for many months during dry weather. Under New Zealand conditions the majority of mature snails begin mating in spring (October/November) and oviposition continues throughout the late spring, summer and autumn provided that activity is not arrested by aestivation during dry weather (Pos 1990, 1994a, b, G.M. Barker, unpubl. data). Millar (1978) found that C. aspersus populations increased following seeding of lupin (Lupinus arboreus) into Manawatu coastal dunes. Under these conditions of actively expanding populations, snails reached maturity in about 12 months. High snail numbers were maintained for as little as 3 years, however, as lupin growth and survival was adversely affected. In declining populations, Millar found that the snails required 2–3 years to reach maturity.

Egg laying commences 3–6 days after first fertilisation, but can occur within hours of subsequent matings. Under unfavourable conditions, egg laying in fertilised snails may be delayed by a period of aestivation (Basinger 1931). C. aspersus deposit their eggs into pockets in moist soil. These pockets are usually excavated by the snails themselves through movement of the head and anterior foot, though occasionally natural cavities will be used (Basinger 1931, Herzberg & Herzberg 1962, Pos 1990). Not all nest excavations that are initiated will be successfully filled with eggs; many are apparently abandoned before one is finally considered suitable. After oviposition the nests are covered with soil and are abandoned. The number of eggs in each clutch varies from 10 to 176 (e.g., Basinger 1931, Ingram 1947, Herzberg & Herzberg 1962, Daguzan 1989, Pos 1990, 1994a, b) and deposition of a single clutch may take as long as 36 hours (Pos 1990).

Under optimum conditions in indoor farms, individual snails can produce 2500 eggs in a year (Runham 1989).

The eggs are spherical to oval, varying in greater diameter from 3 to 4.9 mm. The egg shell (Fig. M116) is partly calcified, with discrete crystals of calcium carbonate dispersed in the inner of two flexible jelly matrix layers. During embryogenesis the egg embryo dissolves and absorbs calcium from the egg shell (Tompa 1984). Guéméné & Daguzan (1983) observed that eggs produced by different snails varied from translucent to opaque, according to the quantity of calcium carbonate crystals in the egg shell. They were able to demonstrate that embryo development and hatching success were higher in those with high calcium provisions. Reproductive snails have a high calcium requirement (Tompa 1984), and egg production by snails exposed to calcium-poor soil was approximately doubled when CaCO$_3$ was supplied (Crowell 1973).

The incubation period of the eggs has been shown by Guéméné & Daguzan (1983) to vary according to the relative humidity of the incubation environment. In one experiment at 20°C, for example, they recorded that the incubation period increased from 13.8±1.9 days to 40.0±9.9 days as the relative humidity declined from 100% to 70%. Survivorship of the eggs similarly declined with decreasing humidity, from 91.5% to 14%. The young hatching snails remain in the nest for 1–16 days (Basinger 1931, Ingram 1947, Herzberg & Herzberg 1962). During this time, egg cannibalism can occur (Elmslie 1988).

Field populations of C. aspersus tend towards an annual breeding cycle. In laboratory culture, the animals tend not to exhibit any seasonality of breeding.

C. aspersus is gregarious, and very high numbers of snails can occur in favourable habitats such as garden shrubbery, coastal dunes and cliffs, and scrub on limestone outcrops. The gregarious behaviour is particularly apparent over the winter months, when the diapausing snails aggregate in protected sites. During this diapause hibernation the shell aperture is sealed with an epiphragm or several epiphragms. In the Manawatu dunes Millar (1978) observed hibernation to begin in May and to reach a peak in July. The snails became active again in mid August. According to Taylor (1906–14 (1902–21)) the juvenile snails are less sensitive to the cold and thus less inclined to diapause. There are few reported estimates of population size, but from an average of 40 snails per lupin plant Brockie (1957) estimated 20,000 snails per hectare in the Paekakariki dunes north of Wellington.

The species has a very well developed homing instinct. Snails return regularly to the same retreat each morning after their nightly forays.

The pest status of C. aspersus in New Zealand is discussed by Cederman (1951).

**Remarks.** Cantareus Risso, 1826 (type species Helix aperta Born, 1778) has long been recognised as a genus distinct from Helix Linnaeus, 1758 (type species Helix pomatia Linnaeus, 1758). Giusti et al. (1995) have demonstrated that Helix aspera Müller, 1774 has strong systematic affinities with Cantareus aperta, and accordingly transferred this species to the genus Cantareus. Unlike members of Helix, species of Cantareus possess a solid pseudopapilla arising from the wall of the proximal phallos and a crestlike structure in the distal phallos that extends to and fuses with a pilaster-shaped pleat in the vagina.

Cantareus takes precedence over two supraspecific taxa.
founded on *Helix aspersa* Müller, 1774. *Cryptomphalus* Charpentier, 1837 is junior by date of description with respect to *Cantareus*, and *Cornu* Born, 1778 is unavailable because it was deliberately introduced for a teratological (scalariform) specimen, and as such is excluded in terms of Art. 1 (b) (2) of the International Code of Zoological Nomenclature (1985).

Numerous varieties of *C. aspersus*, founded on shell variation, are recorded in the literature. Shell polymorphism in size, shape, markings, and colour has been extensively studied, with recognition of several endemic forms in North Africa (Taylor 1906–14 (1902–21), Chevallier 1977). Recent work on the genetic variability of allozymic characters (Crook 1981, Bleakney et al. 1989, Madee 1989, 1991) and life-history traits (Madec & Daguza 1993) has suggested that the more distinct morphs, *C. aspersus aspersus* and *C. aspersus maximus* Taylor, can be recognised as subspecies. Guiller et al. (1994) found that the morphological heterogenic Moroccan populations could not, however, be distinguished by allozymic variation, thus again calling into question the subgeneric status of *C. aspersus maximus*. They raise the possibility that *C. aspersus maximus* is a ‘man-made’ morph, associated with early selective breeding in cultivation, rather than a natural morphotype.

Material from New Zealand (Auckland, Hokitika) was included in the allozyme study of Bleakney et al. (1989).

One of the principal helicid snails used for human consumption in Europe, especially the Mediterranean region, *C. aspersus* has been cultivated since at least the time of the Romans.


### Family HELICODISCIDAE

**Diagnosis.** Herbivorous snails. Shell under 5 mm in diameter, strongly depressed, with few whorls that do not increase rapidly in size, always capable of fully housing the retracted animal; sculpture of spiral periostracal ridges or fringes, reduced in some taxa; aperture frequently with barriers or nodules, sometimes deflected and/or thickened when adult. Foot with a well developed pedalial groove, sole uniform, with no waves of progression. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw polyplacognathic. Radula with marginal teeth broad, on short basal plates, sometimes lacking cusps on outermost teeth. Intestine with a single loop directed forwards. Kidney often with a small rectal lobe reaching to and often partially overlying the rectum, and with a closed retrograde urer opening next to rectum at posterior of pulmonary cavity. Cephalic retractors arising almost at same level as separate branches from columellar stem. Right ocular retractor crossing phallos. Phallos retractor arising from diaphragm. Genital orifice immediately posterior to right ocular peduncle. Prostatic gland and oviduct fused to form a spermoviduct. Telen very elongated, without a distinctly expanded head. Phallos with or without a verge and pilasters, with or without a lateral caecum. Epiphallus frequently with a separate retractor muscle.

Central nervous system and chromosome number unknown.

**Remarks.** The helicodiscid snails have been widely recognised as having close affinities to the arionacean endodontoids. Their family status has long been disputed, however, reflecting the unstable systematics of the endodontoids. The subfamily unit Helicodiscinae, in the Endodontidae, was credited to Pilsbry in a paper by Baker (1927). It was defined on the basis of kidney form, with *Helicodiscus* Morse, 1864, *Chanomphalus* Streb & Pfeffer, 1880, and *Radiodiscus* Pilsbry & Ferriss, 1906 included. Thiele (1929–31) and Pilsbry (1948 (1939–48)) excluded *Radiodiscus* and defined the subfamily on the basis of the ovotestis, shell coiling, and radula. Solem (1957) included *Polygyriscus* Pilsbry, 1948 in the Helicodiscinae, while later (Solem 1975) *Chanomphalus* and *Radiodiscus* were assigned charopid affinities.

The helicodiscid snails have subsequently been variously accorded subfamily rank in the Endodontidae, Charopidae, Punctidae, and Discidae, or recognised as a separate family, Helicodiscidae. The latter is accepted here. The above family diagnosis is largely taken from Solem (1975, 1984a), who considered the Helicodiscidae to contain only three genera: *Helicodiscus* Morse, 1864 and *Polygyriscus* Pilsbry, 1948 from North America, and
Stenoplyés Fulton, 1914 from Indonesia, the Philippines, New Guinea, the Solomon Islands, and Australia.

Genus Helicodiscus Morse

Helix of authors. (Not Helix of Limnaeus, 1758, type species Helix pomata. Limnaeus, 1758, designated by de Mornfort (1810); Helicidae.)
Zonites of authors. (Not Zonites of de Mornfort, 1810, type species Helix aspera. Limnaeus, 1758, by original designation; Zonitidae.)
Hyalina of authors. (Not Hyalina of Albers, 1850, type species Helix cellaris. Müller, 1774, designated by von Martens (1809) — synonym of Ozychilus (Hützinger, 1833; Zonitidae.)
Helicodiscus Morse, 1864. 25, type species Helix limata. Say, 1817 (not of Olivi, 1792) = Helicodiscus parvulitus. (Say, 1822), by monotypy.
Phrixognathus of authors. (Not Phrixognathus of Fulton, 1883, type species Helix fajna. Hutton, 1886 = Phrixognathus celta. Hutton, 1883), designated by Pilsbry (1892–93 (1890–95); Pinmitidae).


Diagnosis. Ovoviviparous species. Shell aperture without a reflected lip but usually with pairs of tubercles deposited at intervals on parietal and/or palatal walls. Animal generally unpigmented except for orange coloration on mantle collar in some species. Ocular peduncles rather stout, without swollen apices, and without pigmented eyes (animal blind). Ovotestis very long, unbranched, subcylindrical, occupying about 1 whorl in upper digestive gland. Phallicus with a small vergic papilla but lacking pilasters. Radula with 3 or 4 tricuspid lateral teeth in each half row.

Remarks. Helicodiscus is known from Jamaica, Cuba, northern Mexico, and the eastern and northwestern U.S.A., regarded by most authors as the extant range of the genus. The occurrence of Helicodiscus in Europe and the Madeiran Archipelago has generally been attributed to stocks of H. singleyanus (Pilsbry, 1890) introduced from North America. Most such occurrences have been noted in habitats associated with the activities of men, such as greenhouses and gardens. However, the probability of European Helicodiscus being a natural occurrence has been raised by other collections of H. singleyanus having been made in areas remote from human disturbance (e.g., Chatfield 1977, Schlickum 1979) and the discovery of a Helicodiscus species endemic to the Tuscan Archipelago (Gìsti 1976). The occurrence of H. singleyanus as an apparent subfossil in European Pleistocene strata (e.g., Ložek 1964) needs to be verified by dating of the shell material, because the species is frequently recovered as a contaminant of soil from archaeological excavations (Chatfield 1977; and see Remarks under H. singleyanus).

Three subgenera have been recognised (Pilsbry 1948 (1939–48)); Helicodiscus s. str., Helvetodiscus Baker, 1929 and Pseudiscus Morrison, 1942. These subgenera are based entirely on shell characters and have not been critically examined from the perspective of anatomy, which for many Helicodiscus is unknown.

Subgenus Helvetodiscus Baker

Helvetodiscus Baker, 1929: 86, type species Helicodiscus (Helvetodiscus) singleyanus inermis Baker, 1929, by original designation.


Diagnosis. Shell entirely smooth or with microscopic spiral threads; aperture lacking internal teeth in adults.

Remarks. Bequaert & Miller (1973) regard Helvetodiscus as sufficiently distinct from Helicodiscus to be accorded generic rank, but give no details to support their assertion.

Helicodiscus (Helvetodiscus) singleyanus (Pilsbry)

Figures 38, 78, 119, 148, 174, 200, M16, M61–63; Map 11

sci[400]nilla Lowe, 1852: 115 (Helix).
singleyanus Pilsbry, 1889: 197 (Zonites) [nude name]. Pilsbry, 1890–91 (1890–95); 84 (Zonites).
inermis Baker, 1929: 86 (as subsp. of singleyanus Pilsbry) (Helicodiscus).
laeviuscula Sterki, 1892: 53 (Hyalina).
texana Sterki, 1892: 54 (Hyalina) [nude name].
intermedius Morrison, 1942: 378 (Helicodiscus (Helvetodiscus)).
academia Climo, 1970: 211 (Laoma (Phrixognathus)). New synonymy.

Shell (Fig. 38) strongly depressed, to about 2.4 mm in diameter by 0.9 mm high, of 4–4.5 tightly coiled, rounded whorls with deep sutures, thin, translucent white to pale straw, somewhat glossy with weak growth lines. Protoconch (Fig. M16) of 1.5 whorls, generally smooth but occasionally with fine microscopic spiral threads. Umbilicus widely open, 0.28–0.33 of shell diameter. Aperture lunate, with no teeth at any stage of growth. Peristome simple.
Animal unpigmented, translucent white. In active animal tail short, not extending behind shell, which tends to be dragged. Genital orifice immediately posterior to right ocular peduncle.

Reproductive system, Fig. 78. Ovotestis undivided, elongate, subcylindrical, embedded in digestive gland. Hermaphroditic duct not convoluted, slender at extremities, medially distended. Talon markedly elongate, slender, weakly expanded at apex, exposed on ventral surface of large, linguiform albumen gland. Pallial gonads fused to form spermoviduct; prostatic gland a ribbon along entire, rather sacculate glandular oviduct. Free oviduct stout. Bursa copulatrix reservoir small, elongate, on a long, slender duct. Vagina short. Vas deferens slender throughout. Epiphallus elongate, convoluted in proximal part, somewhat dilated medially. Phallus short, slightly dilated proximally at entry of epiphallus as a rounded, vorticose papilla; pilasters lacking, but internal wall somewhat glandular, thrown into weak longitudinal folds. Atrium distinct but short and slender.

Spermatophores unknown.

Phallus retractor originating from diaphragm, attaching at juncture of epiphallus and phallus. Epiphallus also provided with a retractor muscle, from the right tentacular retractor, inserted on epiphallus proximal apex.

Jaw (Fig. 119) a broad arch, about 0.4 mm wide, composed of 15 fused, approximately oval plates.

Radular ribbon (Fig. M61–63) with about 85 transverse rows of teeth, varying little about the formula 4+4+C+4+4. Central tooth narrower and often slightly shorter than 1st lateral tooth, tricuspid, the cusps rather small, with mesocone longer than the flanking ectocones; basal plate narrowly rectangular. Lateral teeth tricuspid, with elongate mesocone and short endocone and ectocone, on broad, quadrate basal plates. Marginal teeth serrate, with progressively shorter mesocone and progressively more divided endocone and ectocone; basal plate broad, short.

Digestive tract, Fig. 148. Bucal mass spheroidal. Oesophagus long, terminating in a gastric pouch without apparent crop formation. Gastric pouch subcylindrical, extending about 0.3 of whorl to end in sacculate stomach, which is not externally differentiated. Intestine producing a long, anteriorly directed loop to abut the visceral-pallial wall, then reflected to a short, posteriorly directed loop before running forwards to anus in mantle collar.

Pallial complex, Fig. 174. Pulmonary cavity long, about 2.5x length of kidney. Principal pulmonary vein without evident tributaries. Kidney extending anteriorly to about twice length of pericardium, laterally with a small lobe abutting or partially overlying rectum. Primary ureter large, dilated, looped between limbs of kidney. Secondary ureter running adjacent to rectum, closed to about opposite middle of kidney and then continued by an open groove to near pneumostome.

Free muscle system, Fig. 200. Columellar muscle slender, on reaching base of haemocoele widening considerably to give off at almost the same level right and left tentacular retractors, large but very short buccal retractor, and small tail retractor with radiating fibres. Ocular branch of right peduncle retractor passing over phallus.

Central nervous system not examined.

Haploid chromosome number not known.

Type material. From New Braunfels, Comal County, Texas (ANSP 160068).

Distribution. H. singleyanus is endemic to North America, occurring naturally from New Jersey south to Florida, and west to Arizona. It has been introduced to California, and apparently also to Europe and New Zealand, where it now occurs.

Recommended common name. Singley's subterranean discus snail.


History in New Zealand. H. singleyanus was first recorded by Climo (1970, 1974) from subterranean water sources at Christchurch and Nelson in the South Island (see Remarks). It has since been found at a number of localities in the North Island. It is highly probable that H. singleyanus has been long established in New Zealand, and is now widely distributed.

Biology. H. singleyanus apparently lives a predominantly subterranean existence in soil, and hence material collected alive is rare in collections. The most common source of material is flood drift. The animal is colourless and blind,
and is known to be ooviviparous (Pilsbry 1948 (1939–48)).

Remarks. Helix scintilla Lowe, 1852 has priority over
Zonites singleyanus Pilsbry, 1890. It is in accordance with
ICZN Article 23b to render scintilla obsolete in favour of
the well established name singleyanus (Pilsbry), but a case
to ICZN for this action has not been made.

When Laoma (Phrixognathus) academia was described
from New Zealand (Climo 1970) the type specimen was
assumed to be an original component of a Quaternary
deposit, 400–500 years old, found beneath about 2 m of
Waimakariri River alluvium. In 1974 further specimens
were collected in water pumped from wells and bores near
Nelson, also in the South Island (Climo 1974). The site of
the original specimen and the habitat of the subsequent
Nelson material seemed to suggest a snail of phreatic
(aquatic, subterranean) existence, and led Climo (1974)
to introduce the name Hydrophrea. In that paper shells,
terminal genitalia, the foot, buccal mass, and radular teeth
were illustrated. The shells (Climo 1974, fig. 5A–F) are
typically those of subadult Helicodiscus singleyanus
(Pilsbry 1948 (1939–48), fig. 346).

Anatomical features of the single dissected specimen
(radula – fig. 5; reproductive terminalia – fig. 5G) illustrated
by Climo (1974) also point to Hydrophrea academia
being a synonym of H. singleyanus. The number of teeth
were four fewer in a half radular row in the New Zealand
specimen than in H.B. Baker’s dissection of New Jersey
(U.S.A.) material. Climo’s illustration does not show as
635, fig. 345), but the salient features are the same in both.
The male terminal genitalia of Climo’s New Zealand
specimen match Baker’s description for H. singleyanus
(Pilsbry 1948 (1939–48), p. 637). While helicodiscid
snails typically have a long bursa copulatrix duct (Pilsbry
1948, Solen 1975, 1984a), such a structure was described
as absent in H. academia (Climo 1974). This may have
been an error in observation (F.M. Climo, pers. comm.).
The unpigmented body and eyes further point to H.
academia being conspecific with H. singleyanus (Pilsbry

Subsequently further specimens of this helicodiscid
have been collected from a number of localities in the
North Island, including a series of live animals from
Tauranga and Hamilton. The anatomy and radula of these
specimens are consistent in character with both Hydro-
phrea academia (except for the presence of a long bursa
copulatrix duct) and North American H. singleyanus.
There is a remote possibility, however, that Helicodiscus
is an indigenous element of the New Zealand fauna.

H. singleyanus has a burrowing habit, and in friable
soils and gravels could easily get into groundwater sys-
tems, hence the retrieval of Climo’s specimens from wells
and bores.

Bequaert & Miller (1973) note that among North Amer-
ican material the subspecies H. singleyanus inermis Baker
cannot consistently be distinguished, even by geography,
from typical H. singleyanus. Pilsbry (1948 (1939–48))
earlier admitted that these two forms are “so similar that
their separation is most difficult.” Hübricht (1975) has
maintained that singleyanus and inermis are specifically
distinct, with the shell smaller and having shallower
sutures in H. inermis, and suggested that the difference
in shell sculpture by which these two forms were originally
differentiated is a poor character. Waldén (1983) has also
maintained that singleyanus and inermis are distinct
species, but gives no supporting information. Until the
intragenic phylogeny of Helicodiscus has been resolved
from anatomical characters, inermis is best regarded as
conspecific with singleyanus.

An introduction into the literature on H. singleyanus
is provided by Pilsbry (1948 (1939–48)), Klener (1956),
Bequaert & Miller (1973), Riedel & Wiktor (1974),
Chatfield (1977), Flasar (1977), Schlickum (1979), and
Altoraga (1989b).

Family HYGROMIIDAE

Diagnosis. Herbivorous snails. Shell small to moderate in
size, capable of fully housing the animal; aperture with lip
frequently present, situated at some distance from aperture
margin. Animal with sole holopedal, undivided. Suprapedal
gland embedded in foot tissues. Buccal mass spheroidal.
Jaw odontognathic, with ribs varied in development.
Radula with marginal teeth broad, on short basal plates.
Intestine with a single loop directed forwards. Kidney
with a closed retrograde meter, opening between top of
lung and pneumostome, or at pneumostome; some taxa
with a long ureteric diverticulum extending along rectum
below uroter opening. Cephalic retractors arising as a
common stem on columella; right ocular retractor some-
times passing between phallus and vagina, sometimes free
from genitalia. Phallus retractor arising from diaphragm.
Genital orifice located immediately behind right ocular
peduncle, or somewhat more posterior. Genitalia prim-
arily with stylophores (when present, and not extremely
regressed or modified) forming a dart-sac complex con-
sisting of 1 or 2 double units with a common base and
distinct distal sacs lying side by side in the same plane.
Darts (when present) short to long, straight or slightly
curved. Digitiform mucus gland tufts variable in number,
inserted on proximal vagina, more-or-less close to where
dart sacs open into vagina. Reservoir of bursa copulatrix

-71-
adhering to spermoviduct, not connected with wall of pulmonary cavity, its duct of medium length to short and lacking a diverticulum. Male genital ducts with a spermatozoon-producing epiphallus, with flagellum. Phallus generally with a vergic papilla. Central nervous system with cerebropedal connectives in length less than twice cerebral ganglion width; left connective often longer than the right one. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 21–27.

Remarks. The Hygromiidae are a group of helicoids of western Palaearctic distribution, recently separated from the Helicidae as a distinct family. Several Hygromiidae have been widely distributed through the activities of man. Two genera — Candidula Kobelt, 1871 and Prietocella Schileyko & Menkhorst, 1997 — are each represented in the New Zealand naturalised fauna by a single species.

The scope and subfamilial systematics of the Hygromiidae continues to change as new data on anatomy and hence phylogenetic relationships are made available. Suprageneric names and diagnoses are consequently not attempted here. In his classification of the hygromiids, Nordsieck (1993) places Candidula Kobelt, 1871 in the Hygromiinae Helicella-Candidula Group (= Helicellini von Ihering, 1909) (with genera Xerotricha di Maria Monterosato, 1892 and Helicella d’Audebard de Férussac, 1821), and Cochlicella d’Audebard de Férussac, 1821 in the Monachaec Cochlicelina Schileyko, 1972 (with the genus Montilearia Mousson, 1872). Schileyko & Menkhorst (1997) maintain that a close phylogenetic relationship exists between Montilearia and Cochlicella, which they formalised by creating the family Cochlicelidae. These authors also erected the genus Prietocella Schileyko & Menkhorst, 1997 for Helix barbara Linnaeus, 1758, which had long been included in the genus Cochlicella.

The systematic status of the cochlicellid snails has long been controversial, and for the present I have retained their placement in the Hygromiidae. The genus Prietocella is, however, accepted as several reproductive characters of the sole species, P. barbara (Linnaeus, 1758), distinguish this taxon from Cochlicella and Montilearia. In particular, Prietocella lacks the calcareous envelope around the phal- lus papilla that occurs in Cochlicella.


Genus Candidula Kobelt

Helix of authors. (Not Helix of Linnæus, 1758, type species Helix pomatia Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Helicella of authors. (Not Helicella of d’Audebard de Férussac, 1821, type species Helix ericetorum Müller, 1774 = Helicella taiga (Linnaeus, 1758), designated by Herrmannsen (1847) [ICZN Opinion 431,1958: 350]; Hygromiidae.)

Jacosta of authors. (Not Jacosta of Gray, 1821, type species Helix (Jacosta) utica Draparnaud, 1801 = Helix explanata Muller, 1774, by monotypy — synonym of Leucochiona Beck, 1837; Hygromiidae.)

Zenobia of authors. (Not Zonobia of Gray, 1821, type species Helix (Zenobia) binaperta Gray, 1821 = Helix cuthartiana Müller, 1774, by monotypy — synonym of Zenobiella Gada & Woodward, 1921; Hygromiidae. Not of von Okan, 1815–16; Lepidoptera.)

Theba of authors. (Not Theba of Risso, 1826, type species Helix pisana Müller, 1774, designated by Gray (1847); Helicidae.)

Helicopsis of authors. (Not Helicopsis of Fitzinger, 1833, type species Helix striata Müller, 1774, by monotypy, Hygromiidae.)

Sthelina of authors. (Not Sthelina of Fabre, 1808; Lepidoptera.)

Xerophila of authors. (Not Xerophila of Held, 1838 (1837–38), type species Helix pisana Müller, 1774 = Theba pisana (Müller, 1774), designated by Herrmannsen (1847); Helicidae.)

Heliomane of authors. (Not Heliomane of Browne, 1840 (1837– 49); listed in synonymy of Cernuella Schiller, 1838, Hygromiidae, by Zilch (1959–60), type designation not traced. Not of Newman, 1840; Cuckooera.)

Candidula Kobelt, 1871: 22, type species Gischnus (Helix) candidula Studer, 1820 = Helix unifasciata Poiret, 1801, by monotypy.

Sthelina of authors. (Not Sthelina of Clessin, 1876 (1876– 77), type species Gischnus (Helix) candidula Studer, 1820 = Helix unifasciata Poiret, 1801, source of designation not traced — synonym of Heliomane Fitzinger, 1833; Hygromiidae.)

Xeroteca di Maria di Monterosato, 1892: 22, for H. eucaperia, hertepisii, gigasii, undulatasa, type apparently not subsequently designated.

Xeroteca of authors. (Not Xeroteca of di Maria di Monterosato, 1892, type species Helix retulatena Pfieffer, 1850, designated by Kobelt (1892); Hygromiidae.)

Diagnosis. Shell globose to moderately depressed, umbilicate, pale-coloured, often with dark spiral bands; sculpture weak, radial. Genital orifice sited behind right ocular peduncle, at about 0.3 of distance posterior to pneumostome. Female genitalia with 2 stylophores on one side of vagina, one of them large and externally evident, the other vestigial and invisible. Proximal phallus a simple
tube penetrated by shaft of vergic papilla, the latter not joined to distal phallus wall by frenula. Right ocular retractor not crossing between phallus and vagina.

Haploid chromosome number 26 or 27.

Remarks. Chiefly western European in distribution.

*Candidula intersecta* (Poiret)

Figures 39, 79, 101, 120, 149, 175, 201, 228, C12, M17, M64, M65; Map 12

Bivalve of authors (not of Linnaeus, 1758).

*? fasciolata* Poiret, 1801: 79 (*Helix*).

*intersecta* Poiret, 1801: 81 (*Helix*).

*spirata* Drupaulard, 1801: 91 (in part) (not of Miller, 1774) (*Helix*).

*polychilis* Bourguignat, 1866 (1863-70): 180 (*Helix*).

*herbarum* Servais, 1880: 92 (*Helix*).

*pallidula* Mabille, 1881: 123 (*Helix*).

*deferiana* Bourguignat, in Locard, 1882: 107, 322 (*Helix*).

*subintersecta* Bourguignat, in Locard, 1882: 113 (*Helix*).

*polyconum* Bourguignat, in Locard, 1882: 338 (*Helix*).

*scabiosula* Locard, 1889: 87 (*Helix*).

*expedenta* Locard, 1899: 113 (*Helix*).

*intermedia* Locard, 1899: 113 (*Helix*).

Shell (Fig. 39) small, subglobose, up to 8 mm high by 13 mm in diameter; perforate, of 5-6.5 slightly convex whorls with shallow sutures, slightly angulated at the periphery, opaque, coloured buff to pale brown with dark brown to black irregular blotches; sculpture of coarse radial wrinkles and ribs. Umbilicus moderately wide, 0.14-0.17 of shell width. Protoconch (Fig. M17) of 1.25 whorls, narrowing but for weak growth lines. Aperture ovate-lunate. Lower lip reflected, with an internal white rib set back from edge.

Animal grey, paling towards tail and foot margin, speckled white in head region; foot fringe below pedal groove strongly speckled grey; sole densely speckled grey towards lateral margins; mantle collar with grey margin. Active animal with tall not extending behind shell. Locomotion by muscular pedal waves generated from posterior of sole.

Reproductive system, Fig. 79. Ovotestis embedded in posterior lobe of digestive gland. Hermaphrodite duct long, contorted and distended for much of its length, ending at base of albumen gland with a small diverticulate tuba. Albumen gland large, lingiform. Spermoviduct moderately long; female tract sacculate, folded; male part with prostatic folicules distributed as a broad ribbon along entire length. Free oviduct very short, stout. Bursa copulatrix reservoir a large oval sac on a moderately long duct which generally broadens towards its origin in oviduct. Vagina large, bearing proximally paired mucus glands above a well developed, bulbous stylophore which opens towards atrium with a single protruding dart; dart about 2 mm long, straight or slightly curved, rounded in cross-section, narrowing from base embedded in stylophore wall to a fine point; mucus glands with 3 or 4 tubular, sometimes branched, finger-like processes arising from a very short, sacculate stem; internal wall of vagina opposite stylophore carrying a longitudinally folded stimulatory shield, with vestiges of a second, unarmed stylophore sac. Vesic retractor long, slender, terminating in epiphallus lateral to its short apical flagellum. Epiphallus about 3x as long as phal- lus; cylindrical. Phallus sacculate, broader than epiphallus, covered with a thin muscular sheath which extends over vagina and stylophore; a large, elongate, conical epiphallus papilla occupying most of the internal space; lumen wide with minute papillae, spinose in proximal part. Atrium very short.

Spermatophore (Fig. 101) about 9 mm long, slender, narrowing to bluntly pointed extremities, bearing a longitudinally spiralled ridge which is ornamented with double row of spines in its middle section.

Phallus retractor arising from diaphragm about midway along pulmonary cavity; inserted on epiphallus at about 0.65 from its proximal end.

Jaw (Fig. 120) 0.8 mm wide, weakly ribbed, with anterior margin strongly concave, the lateral extremities broadly rounded and projecting anteriorly.

Radular ribbon (Fig. M64, 65) with 95-102 transverse rows of teeth, each row varying about the formula 14+9+C+9+14. Central tooth tricuspid, on a quadrate basal plate, with a prominent, rather broad mesocone and small, pointed exocone. Lateral teeth bicuspid, on quadrate basal plates, with a large mesocone and a short but prominent exocone. Marginal teeth on reduced but broad basal plates, with mesocone and ectocone retained, tending to become serrate towards radial margin.

Digestive tract, Fig. 149. Buccal mass spheroidal. Oesophagus short. Crop occupying about 1.2 whorls, divided by a median constriction into a cylindrical oesophageal part and a more sacculate gastric part. Stomach sacculate, not externally differentiated from gastric crop. Intestine producing a short anteriorly directed loop to abut the kidney, then reflected to a short posteriorly directed loop, before running forwards to anus in mantle collar.

Pallial complex, Fig. 175. Pulmonary cavity about 3x longer than wide. Kidney triangular, extending from posterior of pulmonary cavity to about 0.3 of its length. Ureter sigmoid, its primary arm along anterior of kidney closed, opening at posterior of pulmonary cavity into a
ureteric gutter which extends adjacent to rectum to the mantle collar. Pericardium applied to left side of kidney. Pulmonary vein well developed, but vascularisation of mantle rather weak.

Free muscle system, Fig. 201. Left tentacular and buccal retractors arising from a short common stem with origin on columnella. Buccal retractor a broad sheet anteriorly, not bifurcating before its insertion on buccal mass. Right tentacular retractor a separate branch from its origin, not passing over phallus to its insertion in ocular peduncle and inferior tentacle.

Central nervous system, Fig. 228. Cerebral commissure short, less than half cerebral ganglion width. Left cerebral-pedal connective slightly longer than the right, its length about twice width of cerebral ganglion. Pleural ganglion closer to pedal ganglion than to cerebral ganglion, closely appressed to parietal ganglia. Visceral ganglion fused to left parietal ganglion and closely appressed to right parietal ganglion, lying to left of median plane.

Haploid chromosome number 26.

Type material. Described in a paper on species in the environs of Paris, without a precise type locality. The whereabouts of the type material is unknown; presumably it is lost.

Distribution. The native range is Western Europe, from the British Isles, western and northern France, Belgium, and The Netherlands, to scattered localities in Portugal, Germany, Denmark, and southern Sweden. Introduced into Australia and New Zealand.

Recommended common name. Wrinkled snail.


History in New Zealand. The first record of C. intersecta in New Zealand is that of Sturt (1891) for a colony at Nelson. Suter (1913) lists Paakakariki and Nelson as localities. Moore (1952) added Waitakura (Thames coast), and Whitten (1955, 1957) added several southern North Island localities. Powell (1979) indicated that C. intersecta was "now widespread in both North and South Islands but less common in the north."

According to Taylor (1921, 1902–21), F.W. Watton recorded Helicella itala (Linnaeus, 1758) from Wellington in 1892, said to have been imported five or six years earlier with English grass seed. H. itala had established in York Peninsula, South Australia at about the same time, apparently also via importation of grass seed (Taylor 1921, 1902–21). Taylor commented that the Wellington shells closely resembled those established in South Australia, which in turn he likened to a further European species, H.
obvia (Menke, 1828). As neither H. itala nor H. obvia is known from the Wellington region or anywhere else in New Zealand, it would seem that Taylor misidentified the material collected by Waton. C. interseca is common in the Wellington area, and I refer Taylor's records to this species. Quick (1952) perpetuated the Wellington records of H. itala without examining any material from New Zealand.

Biology. C. interseca is regarded as an "open country" species in Europe (e.g., charfield 1975, Kerney & Cameron 1979, Reuse & Evans 1994). In New Zealand it is found in open, dry habitats such as coastal dunes, exposed limestone outcrops, open scrub, and pasture. It ranges from sea level to over 800 m in altitude. During dry weather the snails bury themselves.

Remarks. In Europe, C. interseca may be readily confused conchologically with several other Candidula species, especially C. helicenaria (servain, 1880), C. gigaxa (Pieffer, 1848) and C. unifasciata (Pieffer, 1801), and with unrelated hygromiid species such as Trachoides geyeri (Soes, 1926).

Germain (1930), Backhuys (1975), and Gittenberger (1993b) provide an introduction into the European literature on C. interseca.

Genus Prietocella Schileyko & Monkhorst

Helix of authors. (Not Helix of Linnaeus, 1758, type species Helix pomatia Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Bulimus of authors. (Not Bulimus of seeppii, 1786 (1786-88), type species Bulimus hamsterpesius Linnaeus, 1758, designated by Gray (1847) - synonym of Megaloohalimia Miller, 1878; Aercidae.)

Helicella of authors. (Not Helicella of d'Audebard de Férussac, 1821, type species Helix ericetorum Müller, 1774 = Helicella ulla (Linnaeus, 1758), designated by Herrmannsen (1847) - ICZN Opinion 431 (1956: 350); Hygromiidae.)

Cochlicella of authors. (Not Cochlicella of d'Audebard de Férussac, 1821, type species Helix conoidea Draparnaud, 1801, designated by Gray (1847) - ICZN Opinion 325 (1955: 48, 56; Hygromiidae.)

Xeropila of authors. (Not Xeropila of Held, 1838 (1837-38), type species Helix pisana Müller, 1774 = Theba pisana (Müller, 1774), designated by Herrmannsen (1847) - synonym of Theba Risso, 1826; Helicidae.)

Xerocassia of authors. (Not Xerocassia of Maria di Montresor, 1892, type species Helix cretica Müller, 1841, designated by Kobelt (1892) - synonym of Xerocassia di Maria di Montresor, 1892; Hygromiidae.)

Prietocella Schileyko & Monkhorst, 1997: 54, type species Helix barbara Linnaeus, 1758, by original designation and monotypy.

Diagnosis. Shell small, more or less turritform or conical, higher than wide, narrowly umbilicate, varying from opaque white with brown bands or flecks to largely concave with opaque white streaks; aperture small, the lip thin and simple, reflected at columellar margin. Genital orifice immediately posterior to right ocular peduncle. Stylophore bearing apical mucus glands, opening into atrium. Bursa copulatrix duct unbranched. Epiphasium with a small flagellum.

Haploid chromosome number 23.

Remarks. Prietocella comprises three European species, one of which has been established in New Zealand.

Prietocella barbara (Linnaeus)

Figures 40, 80, 102, 121, 150, 176, 202, 229, C13, M18, M66-68, M117, M118, Map 13

barbara Linnaeus, 1758: 733 (in part) (Helix).

acens of authors (not of Müller, 1774).

ventricosa Draparnaud, 1801: 68 (not of Bruguière, 1791 (1789-1816); Bradybaenidae) (Bulimus).

ventricosa d'Audebard de Férussac, 1821: 56 (new name for Helix ventricosa Draparnaud, 1801) (Helix (Cochlicella)).

bulimoides Moqun-Tandon, 1855: 277 (Helix (Cochlicella)).

Shell (Fig. 40) high conic, up to 12 mm high by 5 mm in diameter, of 6-7.5 thin whorls, perforate with umbilicus minute, pale brown, generally profusely streaked and flecked with opaque buff, but this pattern often lacking, especially on body whorl; body whorl often with a brown band; surface slightly glossy; growth lines rather distinct, especially immediately below suture. Protoconch (Fig. 80) of 1 whorl, its surface irregularly pitted and with microscopic striae. Aperture rounded-oval, the lip thin. Columella erect, reflected.

Animal densely speckled grey-brown dorsally, sparsely speckled grey at sides of foot; sole off-white or pale grey; mantle collar speckled grey towards anterior margin. Genital orifice a little posteriad of right peduncle.

Reproductive system, Fig. 80. Ovotestis embedded in posterior lobe of digestive gland, comprising 3 progressively larger clusters of acini along first part of hemiprod-duct. Hemiprod-duct only briefly slender, for the greater part dissected and highly convoluted, but straightening to end in talon at base of large albumen gland. Spermoviduct of moderate length; female part much folded, male part a broad ribbon of prostatic follicles extending full length of duct. Free oviduct short, broad-
enlarge towards duct of bursa copulatrix. Bursa copulatrix duct long, broad and thick-walled for 0.2 of its length from origin in ovicavit, remainder thin-walled with saccular terminal and subterminal distensions. Vagina short, stout. Vas deferens long, slender, inserted in epiphallus at base of short flagellum. Epiphallus long, cylindrical, somewhat contorted proximally, internally with longitudinal folds; entry into phallus with a long verigae papilla capped by a nodulose pad. Phallus short, bulbous, occupied for the most part by verigae papilla; internal lining smooth. Atrium short, carrying opposite phalii a succulate stylephore upon which issue 4–6 slender, tubular mucous glands.

Spermatophore (Fig. 102) 1.75 mm long, slender, slightly spirally twisted, tapered to a point at both ends, ornamented with 2 serrate ridges.

Phallus retractor arising from diaphragm, inserted on epiphallus a little proximal of junction with phallus. Jaw (Fig. 121) about 0.8 mm wide, with anterior margin strongly concave, irregularly ribbed.

Radular ribbon (Fig. M66–68) with 93–100 transverse rows of teeth, each row varying about the formula 8+10+ C+10+8. Central tooth tricuspid, on a quadrated basal plate, with a prominent, rather broad mesocone and small, weakly pointed ectocones. Lateral tooth bicuspid, on quadrated basal plates, with a large mesocone and short but prominent ectocone. Marginal teeth on reduced but broad basal plates, with mesocone and ectocone retained, tending to become serrate towards radular margin.

Digestive tract, Fig. 150. Buccal mass spherical. Oesophagus short, expanding abruptly into a long, cylindrical crop which grades imperceptibly into stomach. Intestine long, from stomach forming an anteriorly directed loop abutting kidney, then turning back in a posteriorly directed loop before making a complete whorl anteriorly to reach anus in mantle collar.

Central nervous system, Fig. 229. Cerebral commissure length about half cerebral ganglion width. Left cerebral-pedal connective slightly longer than the right, its length about 1.5× cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia, the left closely appressed to left parietal ganglion, the right apparently fused to right parietal ganglion. Visceral gangliion fused to left parietal ganglion and closely appressed to right parietal ganglion, lying to right of median plane.

Haploid chromosome number 23.

Type material. No type locality was given by Linnaeus (1758). The whereabouts of the type material is unknown; presumably it is lost.


Recommended common name. Banded conical snail.


History in New Zealand. P. barbara was first discovered in New Zealand on farmland at Tapora, south-west of Wellsford, in May 1983. Surveys by staff of the Ministry of Agriculture and Fisheries revealed it to be well established at that time in the Tapora area, with population densities as high as 600 per m² in lucerne fields (R. Kleinpaste, pers. comm.). This is the first formal record of the species in New Zealand. The species is now widely distributed in Northland and north Auckland.

Biology. The habitat of P. barbara in its native range is, according to Kerney & Cameron (1979, p. 184), "dry exposed sites near the sea, especially dunes, occasionally inland in S. France." The habitat in New Zealand agrees closely, the species becoming increasingly more widespread and abundant on coastal dunes and in summer-dry pastures in Northland.
**P. barbara** is frequently present in large numbers, as indicated above. More recent surveys (1992–95) by this author indicate that abundance varies markedly between sites, even where the snail has been established for more than 5 years. In the Te Hana and Hakarim areas, for example, populations in pasture vary from 2 per m² to in excess of 1000 per m². The snails feed on both living and decaying plant material. There have been no reports of damage to lucerne or pasture.

These snails are very tolerant of dry conditions, though in extremes they seal the aperture of the shell with an aeries of epiphragms to prevent moisture loss. The first-formed, outer epiphragm frequently incorporates, or has adhering to it, small fragments of plant litter.

Eggs (Fig. M117, 118) are 1.0 x 1.2 mm, with a flexible shell comprising numerous calcite crystals embedded in a jelly layer.

Remarks. Germain (1930), Giusti (1970, 1976), and Forcalt (1976) provide an introduction into the European literature on **P. barbara**.

**Family LIMACIDAE**

**Diagnosis.** Large unihaploids, primarily herbivorous, with a rudimentary, internalised shell. Body elongate, tapering posteriorly; keel varying in length, sometimes reaching posterior margin of mantle shield. Mantle less than half of body length, situated in anterior part of body. Pneumostome usually in posterior right margin of mantle, exceptionally in anterior right margin. Sole divided into 3 longitudinal zones, with transverse grooves. Suprapedal gland embedded in foot tissues. Kidney approximately oval, without any lobe, partially enclosing heart on right side; secondary retractor separated from kidney, terminating in urinary bladder. Cephalic retractors arising near body midline, a little posterior to pallial complex. Buccal mass spheroidal. Jaw oxygnathic. Radula with marginal teeth dagger-like or sword-like. Intestine with 2 anteriorly directed loops. Right ocular retractor crossing phallic free of genitalia. Genital orifice immediately below right ocular peduncle, or posteral from peduncle about 0.5 of distance to pneumostome. Male and female pallial gonaducts united as spermoviduct. Oviduct and atrium without accessory glands. Epiphallus absent; spermatophores not produced. Phallicus with stipulated folds. Central nervous system with cerebropedal connections equal in length and rather short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 24–31.

**Remarks.** This taxon has recently been raised to family rank, distinguishing it from the agriolimacid slugs (Likharev & Wiktor 1980, Wiktor & Likharev 1979, 1980). Limacid slugs occur naturally in North Africa, Europe, the Caucasus, Central Asia, and Asia Minor. Included genera are **Limax** Linnaeus, 1758, **Lehmannia** Heynemann, 1862, **Malacolimax** Malm, 1868, **Limax** Lehmann, 1864, **Eulimax** Boettger, 1881, **Gastromelicata** Boettger, 1883, **Bielzia** Clessin, 1887, **Metalimax** Simroth, 1896, **Turcomelica** Simroth, 1901, **Caspira** Hesse, 1926, and **Lehmannia** Likharev & Wiktor, 1980. Several species of **Limax** and **Lehmannia**, and the sole species of **Limacus**, have been widely distributed through the activities of man.

**Genus Lehmannia Heynemann**

*Lehmannia* Heynemann, 1862: 211, type species *Limax marginatus* Muller, 1774, by original designation.

**Agriolimax** of authors. (Not *Agriolimax* of March, 1865, type species *Limax agrestis* Linnaeus, 1758, designated by Malm (1868): Agriolimacidae.)

**Malacolimax** of authors. (Not *Malacolimax* of Malm, 1868, type species *Limax tenellus* Muller, 1774, according to Hesse (1926): Limaxidae.)

**Eulimax** of authors. (Not *Eulimax* of Moquin-Tandon, 1855, type species *Limax maximus* Linnaeus, 1758, designated by Plisby (1922) - synonym of *Limax Linnaeus*, 1758: Limaxidae.)

**Simrothia** Clessin, 1884 (1884–85): 62, listed in synonymy by Wiktor (1923), type designation not traced.

**Ambigolimax** Pollonera, 1887: 1, type species *Limax valentianus* d'Assebrood de l'Étangue, 1823, by monotypy.

**Mesolimax** of authors. (Not *Mesolimax* of Pollonera, 1888, type species *Mesolimax brauni* Pollonera, 1888, by monotypy, Agriolimacidae.)

**Metalimax** Pollonera, 1891: 4, type species *Limax magneticus* Lessona & Pollonera, 1882, designated by Hesse (1926).

**Diagnosis.** Shell internal, an asymmetrical, broadly oval plate with concentric growth lines radiating from vestigial protoconch at left posterior margin. Keel of posterior body short and ill defined. Pneumostome in right posterior part of mantle. Mantle shield with concentric ridges, their nucleus lying in mid-dorsal line. Jaw oxygnathic, with a medial projection. Right ocular retractor crossing over phallicus. Phallicus short, cylindrical to club-shaped, often with a whip-like apical caecum, always with a well-developed retractor. Bursa copulatrix duct connected to distal phallicus. Prostatic gland fused to oviduct for its entire length. Vas deferens well developed, Vagina absent. Rectal caecum always present, extending to posterior of body cavity. Genital orifice immediately behind and below right ocular peduncle.

Haploid chromosome number 24.
**Remarks.** European and North African slugs, mostly of forested mountain areas. The genus contains 16 nominal species. Represented in New Zealand by two naturalised species.

**Lehmannia nyctelia** (Bourguignat)

Figures 41, 45, 81, 122, 151, 177, 203, 230, C14, C15, M69-72; Map 14

Marginata of authors (not of Müller, 1774).

Arborus of authors (not of Boucard-Chantecour, 1837).

Nyctelia Bourguignat, 1851: 305 (Limax).

Legrandi Tate, 1881: 16 (Limax).

Bourget Bahor, 1898: 41 (Mesolimax).

Kervillei Germain, 1917: 154 (Agriolimax (Malacolimax)).

Extended animal (Fig. 41a–c) 40–60 mm long, with an ill-defined keel at hind end. Mantle about 0.35 of body length. Body pale greyish yellow to greyish chocolate brown. Mantle with lateral bands and diffuse central band of dark brown or black; border around pneumostome pale. Back with a pale medially zone, sides with 1 or 2 pairs of more or less visible bands of brown or black, these sometimes broken up into spots or entirely lacking. Sole uniformly creamy-grey. Mucus clear. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 45) white and iridescent, oblong-oval, up to 7x4.8 mm, varying in degree of calcification and thus irregular in thickness and outline. Dorsal surface convex, with distinct growth lines. Ventral surface concave. Visceral protoconch near posterior margin, usually not protruding, situated centrally or asymmetrically at left. Organic sheet surrounding the shell, usually extending well beyond calcified part.

Reproductive system (Fig. 81). Ovary small, deeply pigmented, exposed dorsally between lobes of digestive gland near posterior of body cavity. Hermaphroditic duct initially straight, then convoluted and swollen, with pale tan near large, oval albumen gland. Spermoviduct folded, dominated by female tract proximally. Free oviduct of moderate length, often slender. Vagina absent. Vas deferens short, running directly from origin in prostatic gland to phallus apex, adjacent to insertion of phallus retractor. Phallus cylindrical, often somewhat folded, inflated at proximal apex, internally with 2 prominent folds. Bursa copulatrix reservoir large, oval, on a short duct opening to phallus near atrium.

Phallus retractor short, arising from diaphragm at left lateral margin of kidney.

Jaw (Fig. 122) 1.8–2.0 mm wide, with a medial projection and transversely scored with fine striae.

Radula (Fig. M69–72) with about 106 transverse rows of teeth, each with a formula varying around 43+30+C+30+43. Central tooth tricuspid, with mesocone prominent, flanked on either side by small ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by small well-defined endocone and ectocone. Mesocone progressively more slender and elongate on lateral teeth, without accessory cusps, and then on marginal teeth shorter and serrate-edged.

Digestive tract. Fig. 151. Buccal mass spheroidal. Oesophagus expanding to large crop, extending to 0.6–0.7 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach to run forwards and over anterior aortic branch, then producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor, then forming a further short, posteriorly directed loop and running forwards to anus; rectal caecum arising from last intestinal loop, running along right side to posterior of body cavity.

Pallial complex (Fig. 177) located in posterior of mantle. Kidney bean-shaped, with long axis oblique to body axis, partially enclosing heart on its left anterior side. Secondary ureter separating from kidney at left posterior and describing an arc to right anterior part of pallial complex, where it inflates to form a urinary bladder. Heart ventricle producing a long aortic stem directed posteriorly and to the right. Lung heavily vascularised.

Free muscle system, Fig. 203. Cephalic retractor attached on dorsal body wall a little posterior to pallial complex, and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising as a branch from stem or from left tentacle retractor; second anterior loop of intestine passing over cephalic retractor muscle stem near its origin.

Central nervous system, Fig. 230. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia, closely appressed to parietal ganglia. Visceral chain compact, but pleural, parietal, and visceral ganglia distinct; visceral ganglia to right of median plane.

Chromosome number unknown.

**Type material.** Bourguignat's original material was collected from Algiers; its whereabouts are unknown, and it is presumed lost.

**Distribution.** *L. nyctelia* occurs in natural environments in the Balkans and in the mountains of eastern and central Europe, indicating that it is probably native there (Wiktor...
On the basis of ecological requirements, the presence of *L. nyctelia* in North Africa has been attributed to introduction through the activities of man. According to Grossu & Lupu (1965) the species was originally distributed over a large area including the Mediterranean region, while its present distribution is relict. As a synanthrope it has been introduced into Europe, North America, South Africa, Great Britain, Egypt, Australia, and New Zealand.

**Recommended common name.** Bourguignat’s slug.


**History in New Zealand.** *L. nyctelia* was first reported in New Zealand by Barker (1979) on the basis of material collected at Hamilton and Mapua during 1977. Because of the apparent restricted distribution, Barker (1979, 1992) suggested that *L. nyctelia* had established in New Zealand relatively recently, probably during the latter part of the 1970s in association with imported plant material. This concept is supported by the current situation, with (i) an apparently very restricted distribution, largely confined to urban areas, and (ii) populations at establishment sites still in a phase of rapid increase and local dispersal.

However, the species may have established considerably earlier. *L. marginata* Müller, 1774 (as *Limax arborum* Bouchard-Chantereaux, 1837) was recorded from New Zealand and Australia by Taylor (1902–07 (1902–21)) on the basis of specimens collected in 1905 by W.D. Reebuck and associates. These records were repeated in subsequent literature without critical review (e.g., Quick 1949, 1960, Cotton 1954, Burch 1960), although Quick (1960) did examine specimens from Australia. Van Regteren Altena (1966), Wiktor (1967, 1983a, b) and Grossu & Lupu (1965) suggested that the species was originally distributed over a large area including the Mediterranean region, while its present distribution is relict. As a synanthrope it has been introduced into Europe, North America, South Africa, Great Britain, Egypt, Australia, and New Zealand. It is also possible that a population of *L. marginata* had established in Wellington around the turn of the century but subsequently perished. The situation is further complicated by the fact that many records of *L. marginata* or *L. arborum* have proved to be referable to *L. valentina* d’Audebard de Férussac, 1823 (Waldén 1961), a species also now established in New Zealand.

I confirm my earlier proposal (Barker 1979) that *L. marginata* be withdrawn from the New Zealand list of naturalised molluscs until such time as its presence is confirmed by collection and accurate identification of fresh material.

**Biology.** The natural habitat of *L. nyctelia* in Europe is mountainous deciduous forests and subalpine herbfields, where it feeds mainly on lichens upon rocks and trees (Wiktor 1983a). In New Zealand this species is at present known only from within nurseries and domestic gardens, or areas immediately surrounding them. It is found under rocks, logs, pots, and planter trays and around the roots of plants, and can occur in high numbers, inflicting significant damage on some cultivated plants.

Mating and egg laying have not been observed in New Zealand, though translucent yellow eggs have been found in spring, measuring 2.1x1.5 mm to 2.3x1.6 mm.

**Remarks.** Dissections are required to separate *L. nyctelia* from *L. valentina*.

An introduction to the literature on *L. nyctelia* is provided by Quick (1960), Grossu & Lupu (1965), van Regteren Altena (1966), Wiktor (1967, 1973, 1983a, b), Giusti (1976), and Jakharov & Wiktor (1980).

**Lehmannia valentina** (d’Audebard de Férussac)

Figures 42, 46, 82, 123, 152, 178, 204, 231, C16, M75–76; Map 15

marginatus of authors (not of Müller, 1774).

valentiana d’Audebard de Férussac, 1823 in d’Audebard de Férussac & Deshayes, 1820–51: 96 (*Limax*).

arborum of authors (not of Bouchard-Chantereaux, 1837).

pointiert Mobilile, 1885: 52 (*Limax*).

ganica Grossu, 1970: 109 (*Lehmannia*).

Animal (Fig. 42a–c) 60–75 mm when extended, with an ill-defined keel at hind end. Mantle about 0.25 mm width. Body pale greyish yellow, brown, or red-brown. Mantle with a median band and 2 conspicuous lateral bands; lateral and anterior margin spotted or mottled; border around pneumostome pale. Back usually with a pale medial zone flanked by a band on either side, and below these variously spotted or with diffuse lower bands. Bands on mantle and
body often broken into spots, or entirely lacking, or occasionally entire body with a motiled reticulated pattern. Bands, spots, and motting brown. Sole uniformly creamy grey. Mucus clear. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 46) white and iridescent, oblong-oval, up to 7.5x5 mm, varying in degree of calcification and thus thickness. Dorsal surface convex, with distinct growth lines. Ventral surface concave. Visceral protococonch near posterior margin, usually non-procering, situated centrally or asymmetrical on left. An organic sheet surrounding the shell, usually extending a short distance beyond calcified part.

Reproductive system, Fig. 82. Ovotestis large, superficially pigmented, exposed dorsally between lobes of digestive gland adjacent to stomach. Hermaphroditic duct initially straight, then convoluted and swollen, with pale talon near large, ovate albumen gland. Spermatocyst folded proximally. Free oviduct short, stout. Vagina absent. Bursa copulatrix reservoir on a moderately long duct to base of phallus. Vas deferens short, running directly from origin in prostatic gland to phallus apex. Phallus with a short cylindrical section arising from atrium, then bifid apically with one limb — the phallus apex proper — penetrated by vas deferens, the other a short cylindrical appendix; internally phallus with 2 prominent folds arising from base of appendix and extending, one further than the other, into distal section.

Phallus retractor short, arising from diaphragm at left lateral margin of kidney and inserted in middle part of phallus below bifurcation.

Jaw (Fig. 123) about 2.3 mm wide, transversely scored with fine striae and bearing a prominent medial projection.

Radula (Fig. M73-76) with 100-160 transverse rows of teeth, each with a formula varying around 45+15+C+15+45. Central tooth tricuspid, with mesocone prominent, slender, flanked on either side by small ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by small but well defined endocone and ectocone. Mesocone of lateral teeth progressively more slender and elongate, without accessory cusps in mature animals. Teeth progressively shorter towards radular margin; mesocone at first with a small accessory mesocone, then serrate-edged.

Digestive tract, Fig. 152. Buccal mass spheroidal. Oesophagus expanding to large crop, extending to 0.6-0.7 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach to run forwards and over anterior aortic branch, then producing a posterior loop overlying crop, again running forwards to pass over stem of cephalic retractor, then forming a further short, posteriorly directed loop, and finally running forwards to anus; rectal caecum arising from last intestinal loop to run along right side to posterior of body cavity.

Pallial complex (Fig. 178) located in posterior of mantle. Kidney bean-shaped, with long axis oblique to body axis, partially enclosing heart on its right anterior side. Secondary ureter separating from kidney at left posterior and describing an arc to right anterior part of pallial complex, where it inflates to form urinary bladder. Heart ventricle producing a long aortic stem directed posteriorly and to the right. Lung heavily vascularised.

Free muscle system, Fig. 204. Cephalic retractor arising as a bifid stem on dorsal body wall a little posterior to pallial complex, and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising as a branch from stem or from left tentacle retractor; second anterior loop of intestine passing over cephalic retractor muscle stem near its origin.

Central nervous system, Fig. 231. Cerebral ganglia united by a very short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact, but pleural, paired, and visceral ganglia distinct; visceral ganglion to right of median plane.

Chromosome number unknown.

Type material. The type material, from Valencia, Spain, no longer exists.

Distribution. Native to the Mediterranean area, especially the Iberian Peninsula, and Atlantic islands. Carried by man to many parts of the world, including Europe, the Azores, the U.S.A., Colombia, Chile, Peru, Juan Fernandez, Easter Island, South Africa, Australia, and New Zealand.

Recommended common name. Valencia slug.


History in New Zealand. This is the first record of L. valentiana in New Zealand, with specimens first collected in Auckland and the northern Waikato during 1979. It is present confined to a small number of localities in the
North Island, principally in association with greenhouse plants such as orchids. This is highly suggestive of recent introduction and establishment in New Zealand.

**Biology.** *L. valentiana* is strictly terrestrial and not arboreal, unlike several other *Lehmannia* species. From the material examined it is apparent that this species, living outdoors, reaches maturity during the New Zealand summer, with eggs present from late summer to early spring. Mature slugs and eggs were evident throughout the year in material from greenhouses. Mating was not witnessed during this study.

Webb (1961b, pp. 44, 46) describes mating in this species (as *L. marginata*) as follows. "Courtship commences when one slug begins to follow at the tail of the other. After a short chase the pursued slug turns back and contacts the right side of the pursuer slug. The slugs continue to entwine their foreparts so that their heads and necks are thus borne upwards above the rest of their bodies. Soon the entwining foreparts bring the atrial pores into contact and coitus ensues as the penises are very rapidly entwined together as they erect. ... At first the contiguous atrial pores appear much dilated, then swollen. Next a diskoid body with a screw-shaped keel appears. This is the penis which continues to erect while it entwines with the erecting penis of the other slug. As initially erected, the organs appear more elongate than later. The period of engagement of the sex-organs is so very transient, a matter of seconds."

Webb found that the phallic flagellum is everted along with the phallus during mating, and suggested that it may aid in the retention of semen during phallus retraction.

The translucent yellow eggs, 2.0–2.2x1.8 mm in size, were found in soil and under planter trays in clutches of 10–60 during spring in an Auckland greenhouse.

*L. valentiana* can be a pest in gardens and greenhouses (e.g., Frömming 1954, Waldén 1961), but there have been no reports of plant damage in New Zealand to date.

**Remarks.** *L. valentiana* is polymorphic in body coloration and banding (e.g., Waldén 1961).

Owing to general similarities in body form and great variation in body pigmentation, dissection is needed to separate this species from *L. nyctelia*, which also occurs in New Zealand (see above). Also, because of close similarity in external appearance and somewhat similar phallus morphology, *L. valentiana* has often been confused with *L. marginata* (Muller, 1774).


---

**Genus Limacus Lehmann**


_Simrothia Chessen, 1884 (1884–85): 62, type species *Limacin breckworthianus* Lehmann, 1864 = *Limax flavus* Limacus, 1758, according to Wiktor (1983a)._

**Diagnosis.** Phallus cylindrical, shorter than half of body length, with no internal folds starting from proximal phallic apex. Bursa copulatrix duct short, opening to oviduct. Vagina very short. Prostatic gland fused with oviduct in all but its very anterior part. Vas deferens almost half length of phallus. Phallic retractor well developed, inserted at phallic apex, intestine with last loop very short, and with rectal caecum extending towards posterior of body cavity.

Haploid chromosome number 31.

**Remarks.** The number of species representing the genus *Limacus* is in dispute (Likharev & Wiktor 1980, Wiktor & Norris 1982, Wiktor 1983a, Evans 1978b, 1986, Forcart 1986, Wiktor 1994). A species of very similar external morphology, *Limax maculatus* Kaleniczenko, 1851, is known in Europe (Black Sea, Crimea, Caucasus, Turkey, probably Romania, Bulgaria). This species is also known by some of its junior synonyms (*L. grossus* L. 1970 – Romania, Crimea; and *L. pseudoflavus* Evans, 1978 – British Isles). *L. flavus* has been introduced into various parts of the world, and has long been represented in New Zealand.

---

**Limacus flavus** (Linnaeus)

Figures 43, 47, 83, 124, 153, 179, 205, 249, 317, 318, M77–79; Map 17

*Flavus Linnaeus, 1758: 652 (Limax).\*\*\

_variegatus* Draparnaud, 1801: 103 (in part) (Limax).

_angularius* Bond, 1815: 115 (Limacella).

_virens* d'Audebard de Férussac, 1819: 10 (Limax).

_megalodones* Quey & Gaimard, 1824: 428 (Limax).


_umbrosus* Philippi, 1844: 102 (Linax).

_canarinis* d'Orbigny, 1839 (1836–42): 47 (Linax).

_olivaceus* Godd, 1852: 4 (Linax).

_ehrenbergi* Bourguignat, 1853: 3 (Linax).

_deshayesi* Bourguignat, 1863 (1863–70): 179 (Linax).

_enulatus* Bourguignat, 1864: 35 (Linax).

_breckworthianus* Lehmann, 1864: 145 (Linax).

_bicolor* Selenka, 1865: 105 (Linax).

_breccivorus* Mahille, 1888: 145 (Linax).
Animal (Fig. 43a—c) up to 120 mm in body length. Mantle about 0.3 of body length. Dorsum rounded, with keel at hind end very short. Dorsum and mantle with an irregular network of dark grey-olive to greyish-green spots on paler whitish-yellow or orange-olive background; on sides dark pigment does not reach edge of foot. Sole pale yellow. Mucus yellow. Loculation of muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right opercular peduncle.

Shell (Fig. 47) thin, shiny white, oblong-oval, up to 13×8.8 mm. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Ventral surface concave. Vestigial protoconch near posterior margin, not prominent, situated asymmetrical at left side. Organic sheet surrounding the shell, usually extending a short distance beyond calcified part; partially decalcified shells not uncommon.

Reproductive system, Fig. 83. Ovotestis rounded, completely embedded in lobes of digestive gland. Hermaphroditic duct short, mostly convoluted, ending in rounded talon partially embedded in lingiform albumen gland. Female part of spermoviduct posteriorly tubular, broadening anteriorly. Free oviduct moderately long, slender. Bursa copulatrix reservoir small, on a short duct. Vagina very short. Prostatic gland very long and slender, not fused to oviduct at its very anterior end. Vas deferens short, opening just below phallus appendix, adjacent to which, at the distal phallus, are followed by only 3 short but large folds of lobulate or crenulate margin. Atrium very short.

Phallus retractor short, arising from left margin of diaphragm below kidney in posterior of pallial complex.

Jaw (Fig. 124) 2.5 mm wide, marked transversely with fine striae which reticulate with finer striae following jaw contour.

Radula (Fig. M77—79) with 130—170 transverse rows of teeth, each varying around the formula 50—65+C+50—65. Ectocones and endocones of all teeth very poorly developed or absent. Central tooth on a broad basal plate; mesocone prominent, elongate. Transition from lateral to marginal teeth marked by basal plate becoming progressively smaller, and mesocone becoming progressively elongate and aculeate. Twenteth to 23rd tooth in each row most elongate, largest, then teeth becoming progressively smaller towards margin.

Digestive tract, Fig. 153. Buccal mass spheroidal. Oesophagus expanding to large crop, extending to about 0.7 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to about half length of crop, passing over anterior aorta branch, and producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor to form a further short posteriorly directed loop and running forwards to anus. Rectal caecum long, arising from last intestinal loop and extending along right side to reach posterior of body cavity.

Pallial complex (Fig. 179) located in posterior part of mantle. Kidney bean-shaped, its longest axis oblique to body axis, partially enclosing heart on its left side. Secondary ureter separating from left posterior part of kidney and describing an arc to right anterior part of pallial complex, where it inflates to form a urinary bladder. Heart in left anterior quarter of pallial complex, with ventricle directed posteriorly and to the right; aortic stem short. Lung heavily vascularised.

Free muscle system, Fig. 205. Cephalic retractor arising on dorsal body wall a little posterior to pallial complex and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising from left tentacular retractor branch near its origin from stem.

Central nervous system with cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closely joined to pedal ganglia than to cerebral ganglia. Visceral chain compact but with pleural, parietal, and visceral ganglia distinct; visceral ganglion to right of median plane.

Haploid chromosome number 31.

**Type material.** Described from Europe without precise type locality, but presumably from Sweden or England. The type material no longer exists.

**Distribution.** Because of the confusion of *Limacina flavus* with members of the genus *Limax* and its strong synonyms, the original distribution is not known. Britz & al. (1959) considered *L. flavus* to be of Mediterranean origin. It occurs widely in western Europe, and has been introduced to many parts of the world, including Japan, China, St. Helena, Madagascar, Canada, the U.S.A., South Africa, Australia, Rarotonga, Vanuatu, and New Zealand.

**Recommended common name.** Yellow cellar slug.

L. flavus was first recorded in New Zealand from Dunedin by Hutton (1879). A few years later Hutton (1883) added Greytown as a locality. These records were quoted by Musson (1891), Suter (1891), and others without additional information. Taylor (1902-07(1902-21)) listed as localities Dunedin and Greytown, after Hutton, plus Hokitika on the basis of specimens collected in 1905 by W.D. Roebuck. Suter (1913) considered the species both common and injurious to vegetables, but gave no further locality information. Thomson (1922) also regarded L. flavus as common, but gave only Dunedin, Greytown, and Taranaki as localities. These records were repeated in subsequent literature without additional information (e.g., Whitten 1955, Powell 1979). While recognising the wide distribution of L. flavus in New Zealand, Barker (1979, 1982) noted that the extent of its dispersal was not fully documented.

**Biology.** L. flavus is a nocturnal, rather secretive animal. Despite its large size and being widespread in moist urban habitats, it is infrequently seen. It is not considered an abundant species, and is poorly represented in New Zealand malacological collections.

In New Zealand L. flavus has been observed only in habitats closely associated with human dwellings, namely gardens, crevices of walls or wood stacks, on damp carpets and other floor coverings, and in cellars and outhouses. These are essentially the types of habitat most often occupied in Western Europe, although the species also occurs in woodland there (Quick 1960, Evans 1978b, 1986, Cook & Radford 1988). Kerney (1966) regarded L. flavus as a synanthropic species.

L. flavus feeds on decaying vegetable matter, fungi, and lichens (Taylor 1902-07, 1902-21; Frömming 1954, Cook & Radford 1988). It is an occasional pest in dwellings and commercial premises, making night forays to feed on moist, decaying carpet and associated microflora. Like L. maximus, this species exhibits marked homing behaviour, and several individuals tend to aggregate together at a single home site (Taylor 1902-07, 1902-21; Cook 1981, Chelazzi et al. 1988).

Individuals live for several years, and in Ireland Cook & Radford (1988) found them to be reproductive in their first autumn. Juveniles are most frequently encountered in New Zealand during winter to spring, reflecting the summer to early winter timing of egg laying. The eggs are commonly 6x4 mm but may be as large as 11 mm, translucent pale amber, and laid in chains of 20 or more. They hatch at 1-2 months at ambient temperatures, but are sensitive to low temperature (e.g., 5°C) (Cook & Radford 1988). The hatchlings are pale greenish yellow with characteristic blue ocular peduncles; the spotted pattern of the dorsal skin and mantle appears later in development.

L. flavus is capable of self-fertilisation (Evans 1983), but the frequency of this mode of reproduction, relative to mating and cross-fertilisation, is not known. In the present study mature slugs were observed to engage in trail following, without any apparent 'courtship' behaviour before mating (Fig. 254). The copulating slugs rapidly everted and spirally intertwined their phallic structures. Spermatodesae enclosed in a mucous mass were exchanged, and were transferred to the bursa copulatrix on withdrawal of the genitalia at the completion of copulation, which lasted less than 2 minutes. Further details on mating in this species are given by Gerhardt (1933).


L. flavus tends to be polymorphic in body colouration, and numerous variety names are to be found in the literature (e.g., Taylor 1902-07, 1902-21; Hesse 1926, Quick 1960).

Genus Limax Linnaeus

Limax Linnaeus, 1758: 652, type species Limax maximus Linnaeus, 1758, designated by d'Audebard de Férussac (1819).

Krynickillus of authors. (Not Krynickillus of de Kaleniczenko, 1851, type species Krynickillus melanochephalus Kaleniczenko, 1851, by monotypy; Agriolimacidae.)

Parmacella of authors. (Not Parmacella of de Cuvier, 1804, type species Parmacella olivieri de Cuvier, 1804, by monotypy; Parmacellidae.)

Limacella Brard, 1815: 107, type species Limacella parma Brard, 1815 = Limax maximus Linnaeus, 1758, designated by Turon (1831). (Not of de Blainville, 1817, type species Limacella lacrescens de Blainville, 1817 = Limax carvalloanus Bose, 1802, by monotypy - synonym of Philomythus Rofinaque Schwitz, 1820: Philomychidae.)

Eulimax Moquin-Tandon, 1855: 22, type species Limax maximus Linnaeus, 1758, designated by Phibs (1922).

Diagnosis. Shell an asymmetrical, broadly oval internal plate with concentric growth lines radiating from vestigial protoconch at left posterior margin. Keel on body well developed but often very short. Pneumostome in right posterior part of mantle. Mantle shield with concentric ridges, their nucleus in mid-dorsal line. Jaw oxygnathic, with a median projection. Right ocular retractor passing forwards over phallus. Vagina absent; bursa copulatrix duct arising from distal phallus. Phallus long, with internal system of folds. Genital orifice immediately behind and below right ocular peduncle.

Remarks. About 90 species of Limax are recognised in 8 subgenera. Most are broadly Mediterranean, occurring from North Africa to eastern Europe and Asia Minor.

Subgenus Limax

Limax Linnaeus, 1758: 652, type species Limax maximus Linnaeus, 1758, by original designation.

Heynemannia Malm, 1868: 54, type species Heynemannia cellarius Malm, 1868.

Gastroa Pini, 1876: 83, type species Gastroa maximus Pini, 1876, designated by Wiktor (1983a).


Opilimax Pini, 1876: 92, type species Opilimax punctulatus Sundell, 1876, designated by Wiktor (1983a).

Stabilea Pini, 1876: 97, type species Stabilea parva Bourgignat, 1862, designated by Wiktor (1983a).


Diagnosis. Phallus long, cylindrical, with a retractor muscle. Bursa copulatrix reservoir small, on a short duct to distal phallus. Prostatic gland not fused with oviduct anteriorly. Vas deferens always well developed. Rectal caecum absent.

Haploid chromosome number 31.

Remarks. Subgenus Limax contains about 20 species, mostly native to the Mediterranean and Asia Minor. Represented in New Zealand by a single naturalised species.

Limax (Limax) maximus Linnaeus

Figures 44, 48, 84, 125, 154, 180, 206, 232, 250. C19, M80–82; Map 16

maximus Linnaeus, 1758: 652 (Limax).

collarius Dezallier d'Argenville, 1757: 28 (Limax).
cinereoniger Meller, 1774: 5 (in part) (Limax).
parsa Brard, 1815: 110 (Limacella).

antiquorum d'Audebard de Férussac, 1819: 68 (in part) (not Limax antiquorum d'Audebard de Férussac, 1819 = Limax cinereoniger Wolf, 1803) (Limax).

maculatus Nunailey, 1837: 46 (Limax).
sylvaticus Morselt, 1845: 53 (Limax).
vaigasi Moquin-Tandon, 1855: 28 (new name for Limax cinereus var. f. Meller, 1774, but as subsp.) (Limax).

mamelianus Bourgignat, 1869: 4 (Krynickillus),

bocagei da Silva e Castro: 1873: 245 (Limax).

Slugs (Fig. 44a–f) up to 200 mm long, with specimens 100 mm long usually mature. Mantle about 0.3 of body length. Hind body distinctly keeled. Body yellowish white or grey; back usually with 6, 4, or 2 dark bands, these frequently interrupted to form a more or less spotted pattern; mantle irregularly spotted or marbled with dark pigment. Sole uniformly pale. Mucus clear. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 48) thin, shiny white, oblong-oval, up to 14 x 6.7 mm. Dorsal surface weakly convex, with distinct growth lines. Ventricle surface concave. Protoconch vestigial, anteriorly. Vas deferens always well developed. Rectal caecum absent.

Reproductive system, Fig. 84. Ovotestis elongate, reaching apex of body cavity or almost so, embedded in digestive gland. Hermaphroditic duct long, at first straight and slender, then wider and convoluted before narrowing to tube, which is deeply embedded in albumen gland. Female part of spermoviduct folded and voluminous. Free oviduct long and mostly slender, but dilated at entry into atrium. Bursa copulatrix reservoir small, oval, on a short duct opening to base of phallus, very close to atrium. Vagina absent. Prostatic gland fused to female oviduct.
proximally, free anteriorly. Vas deferens thin, opening at apex of phallic adjacent to insertion of retractor muscle. Phallus cylindrical, its length half or more that of body, strongly convoluted, internally with a cord expanded proximally into a cord. Comb short.

Phallus retractor short, arising from left margin of phallic in posterior part of pallial complex.

Jaw (Fig. 125) 3.5 mm wide, with a prominent median projection and transversely scored with fine striae.

Radular ribbon (Fig. 120-82) comprising about 150 rows of teeth, each near the formula 20+40+C+50+20. Central tooth tricuspid, with a prominent mesocone flanked on either side by small, weak ectocones. First lateral tooth usually tricuspid, with prominent mesocone flanked by small median and ectocone. Lateral teeth with mesocone progressively more slender and elongate towards outer lateral field of radula; endocone generally absent in 2nd or 3rd lateral tooth; endocone persisting to perhaps the 20th tooth. Marginal teeth markedly smaller than lateral teeth, with mesocone outer edge somewhat serrated.

Digestive tract, Fig. 154. Buccal mass spheroidal. Oesophagus quickly expanding to large crop, extending to about 0.6 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta, then producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor, and finally producing a long, posteriorly directed loop along right side of body cavity before running to anus.

Pallial complex (Fig. 180) located in posterior part of mantle. Kidney bean-shaped, its longest axis somewhat obliquely positioned relative to body axis, partially enclosing heart on its left side. Secondary retractor separating from left posterior part of kidney and describing an arc to right anterior quarter of pallial complex, where it inflates to form an elongate, tubular urinary bladder. Heart in left anterior quarter of pallial complex, with ventricle directed posteriorly and to the right; aortic stem short. Lung with a small, weak ectocone. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta and enter hepatic glands. Oesophagus quickly expanding to large crop. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta, then producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor, and finally producing a long, posteriorly directed loop along right side of body cavity before running to anus.

Pallial complex (Fig. 180) located in posterior part of mantle. Kidney bean-shaped, its longest axis somewhat obliquely positioned relative to body axis, partially enclosing heart on its left side. Secondary retractor separating from left posterior part of kidney and describing an arc to right anterior quarter of pallial complex, where it inflates to form an elongate, tubular urinary bladder. Heart in left anterior quarter of pallial complex, with ventricle directed posteriorly and to the right; aortic stem short. Lung with a well developed vascular network.

Free muscle system, Fig. 206. Cephalic retractor attached on dorsal body wall a little posterior to pallial complex and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising as a branch from stem, or from left tentacle retractor, second anterior loop of intestine passing over cephalic retractor stem near its origin.

Central nervous system, Fig. 232. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia markedly closer to pedal ganglia than to cerebral ganglia. Visceral chain compact but with pleural, parietal, and visceral ganglia distinct; visceral ganglion to right of median plane.

Type material. Described by Linnaeus without precise type locality, but presumably from Sweden, as the *Fusana Suecica* is cited. The whereabouts of the type material is unknown; it is probably lost.

Distribution. Native to southern and western Europe and probably North Africa. Its original distribution is difficult to establish, since it has spread as a synanthrope to many areas, including Scandinavia, Russia, the Ukraine, and the Caucasus. It has also frequently been mistaken for *L. cinereoniger* Wolf, 1803 and other species in southern Europe (Wiktor 1983a). In addition to New Zealand, *L. maximus* has been introduced into Northern Europe, Canada, the U.S.A., Hawaii, Mexico, South America, and Australia.

Recommended common name. Tiger slug.

refuse, and will make nightly forays to the compost bin. Perhaps because of its liking for soft-bodied carrion, and its at times aggressive behaviour toward other slugs (Rollo & Wellington 1977, 1979), this species is often erroneously regarded as a predator.

The life cycle of *L. maximus* in New Zealand, described by Barker & McGhie (1984), closely follows that reported for the British Isles (Quick 1960) and North America (Sokolove & McCrone 1978). Growth occurs throughout the year, and, given that individuals live for 3 or 4 years, there is always a wide range of body size in any given population. Mating occurs from February to May and is followed shortly by egg-laying. Greatest numbers of juvenile slugs occur from May to September. The maximum size attainable in New Zealand appears to be 95 mm resting (150 mm extended), whereas gains are made in body weight but not in length. In dissected animals the genitalia become discernible in slugs over 40 mm in length, though there is little relationship between sexual maturity and body size.

Mating (Fig. 250) occurs at night. Preliminary courtship behaviour was observed to consist of circular crawling motions, with repeated body contact. After a period the slugs intertwine their bodies and become suspended by a stout mucus thread from an overhanging surface. While suspended with intertwined bodies for 10–20 minutes, the pair evert their terminal genitalia and interwine their voluminous phallices. Copious mucus production accompanies rotating motions of the phallices, during which seminal material is apparently exchanged. Slow withdrawal of the genitalia occurs as the slugs re-ascend the mucus thread. The reader is referred to Adams (1898), Kew (1901), Gerhardt (1933, 1934), and van Regteren Altena (1960) for further information on the mating behaviour of this species.

The eggs, varying greatly in size about a mean of 5.0x5.5 mm, are soft, translucent, and amber-coloured. They are laid in clusters of 20–100, and hatch in about 1 month in the field (approx. 14 days at 18–20°C: Prior 1983). The hatchlings are pale, translucent grey with a faint band visible on the mid dorsum and vinous ocular peduncles and inferior tentacles. Within 3 weeks the other body bands have appeared and begin breaking up, and the mantle becomes increasingly spotted or mottled.

**Remarks.** *L. maximus* is polymorphic in body coloration. Numerous variety names are to be found in the literature (e.g., Taylor 1902-07(1902-21), Hesse 1926, Quick 1960).

Entry into the extensive literature on *L. maximus* is provided by Germain (1930), Pilsbry (1948(1939-48)), Likharev & Rammel'meier (1952), Quick (1960), Bequaert & Miller (1973), Wiktor (1973, 1983a, 1989), Backhuys (1975), and Likharev & Wiktor (1980).
Family MILACIDAE

Diagnosis. Herbivorous slugs up to 130 mm long, with internalised rudimentary shell. Body elongate, tapering posteriorly, with a keel usually along back from posterior edge of mantle to end of body. Mantle anterior, covering less than 0.3 of body, with horse-shoe-shaped groove opening posteriorly; pneumostome in posterior right margin. Sole divided into 3 longitudinal zones, with chevron-shaped wrinkles on its surface. Supragastric gland free in body cavity. Kidney elongate oval, aligned with body axis, partially enclosing heart on the right, with a large posterior lobe extending over rectum; secondary ureter separated from kidney, terminating without a bladder. Cephalic retractor arising from posterior edge of pallial complex. Right ocular retractor not passing over phallus. Buccal retractor arising from posterior edge of pallial complex. Visceral chain compact.

Remarks. The priority of Aspidoporus limax (Draparnaud) as the type species of Milacidae has been established by Wiktor (1981). The genus comprises two genera (Milax Gray, 1855 and Tandonia Lessona & Pollonera, 1882), with about 50 species naturally distributed about the Mediterranean, the coasts of the Black Sea, and adjacent regions of southern and western Europe, Asia Minor, and northern Africa (Wiktor 1981, 1983a)

The Milacidae are represented in New Zealand only by naturalised species.

Genus Milax Gray

Limax of authors. (Not Limax of Linnaeus, 1758, type species Limax maximus Linnaeus, 1758, by original designation; Linnaeidae.)

Aspidoporus of authors. (Not Aspidoporus of Fitzinger, 1833, type species Aspidoporus limax Fitzinger, 1833, by monotypy — synonym of Tandonia Lessona & Pollonera, 1882; Milacidae.)


Amalia Moquin-Tandon, 1855: 19 (as a section of Limax Linnaeus, 1758), type species Limax gagates Draparnaud, 1801, designated by Wiktor (1981).

Lallemandia Mabille, 1868: 143, type species Limax polyphyclus Bourgignat, 1859 = Limax gagates Draparnaud, 1801, by monotypy.

Palizzolia Bourguignat, 1877: 15, type species Palizzolia monrosi Bourguignat, 1877, by monotypy.

Sansenna Bourguignat, 1881: 11, type species Sansenna furcula Dujon, 1870, by monotypy.

Pyralinea Lessona & Pollonera, 1882: 57, type species Pyralinea gagates Draparnaud, 1801, by original designation.

Remarks. The priority of Milax Gray, 1855 over Amalia Moquin-Tandon, 1855 was established by Mörch (1865). The genus has been divided according to various systems (Simroth 1910a, Hesse 1926, Wagner 1930a, b), but Wiktor (1981) has shown that these are ill founded. Twelve Milax species are known, with a natural distribution from the Canary Islands through the Mediterranean and Black Sea regions to Transcaucasia. Several species have been distributed widely by man, and one has established in New Zealand.

Milax gagates (Draparnaud)

Figures 49, 52, 53, 103, 126, 155, 181, 207, 233, 251, C20, C21, M38–86; Map 18

gagates Draparnaud, 1801: 100 (Milax).
marginita of authors (not Amalia marginita Draparnaud, 1805 = Limax rusticus Müller, 1843).
maurus Quoy & Gaimard, 1824: 427 (Limax).
ascensionis Quoy & Gaimard, 1832: 145 (Limax).
carenata d'Oroigvy, 1839 (1836–42): 47 (Limax).
cartina d'Orihargy, 1842 (1836–42): 3 fig. 4–8 (not of Risso, 1826) (Limax).
fulginosus Gould, 1852: 5 (Limax).
antiperdianus Gray, 1855: 177 (Milax).

-87-
plumpia Moquin-Tandon, 1855: 19 (as var. of gagates Drapa-
naud) (Limax (Amalia)).
polypterus Bourguignat, 1859: 144 (new name for Limax
carenatus d'Orbigny) (Limax).
pectinatus Selenaia, 1865: 103 (Limax).
averans Mabille, 1868: 144 (Milax).
kwstomi Cooper, 1872: 147 (Limax (Amalia)).
emarginatus Hutton, 1879: 331 (Milax).
insularis Tate, 1881: 16 (Milax).
rigriculus Tate, 1881: 17 (Milax).
guaidini Mabille, 1883: 51 (Milax).
veremini Mabille, 1883: 51 (Milax).
raymondiana Sharroth, 1888: 69 (as var. of gagates Drapa-
naud) (Amalia).
rawa Williams, 1888: 89 (Amalia).
pallida Cockenell, 1891a: 340 (as var. of antipodarum Gray)
(Amalia).
perry Collinge, 1895a: 7 (Amalia).
haberi Collinge, 1897b: 294 (Amalia).
santosi Torres Minguez, 1928: 117 (Amalia).

Crawling slugs (Fig. 49) up to 50 mm long. Mantle about
0.25 of body length. Body dark grey or blackish, rarely
brown or orange-brown, paler towards foot margin, never
spotted or banded: keel of similar coloration to body or
darker. Sole uniformly pale grey, or with darker grey or
blackish lateral zones and paler medial zone. Mucus clear.

Shell (Fig. 52) oval, white and shining, up to 5.5x2.8
mm. Dorsal surface concave, highest at posterior. Ventral
surface flat. Vestigial protoconch located centrally or
slightly to left in posterior part. Growth lines distinct.
Irregular shells occur frequently owing to decalcification.

Reproductive system, Fig. 85. Ovotestis rather small, the
surface concave; left parietal ganglion appre-
ssured; cerebral ganglia. Visceral chain very compact, with all
ganglia closer to pedal ganglia than to
united by a short but distinct commissure. Cerebral ganglia
part of kidney and describing a short arc to its orifice at
right mediolateral margin of pallial complex. Heart par-
tially enclosed by kidney from right, its ven-tricle directed
posteriorly and slightly to the left; aortic stem long, ex-
tending behind pallial complex before branching. Lung
with a well developed vascular network.

Free muscle system, Fig. 207. Cephalic retractor arising
from a single root at posterior end of pallial area but
dividing immediately into 2 branches, the tentacular and
cerebral retractor, which themselves divide anteriorly into
left and right branches. Right tentacular retractor not crossing
phallus to insert on ocular peduncle.

Central nervous system, Fig. 233. Cerebral ganglia
united by a short but distinct commissure. Cerebrosedal
connectives short, their length less than width of cerebral
pigment. Pleural ganglia closer to pedal ganglia than to
cerebral ganglia. Visceral chain very compact, with all
ganglia closely appressed; left pedal ganglion appa-
rently fused with visceral ganglion, which lies to left of
median plane.

Haploid chromosome number 33 or 34.
Type material. The whereabouts of Draparnaud's types is unknown; they are presumed lost. The type locality is France, presumably near Montpellier.

Distribution. *M. gagates* is often associated with modified habitats. It is native probably only to the Canary Islands and the coastal zone and islands of the western Mediterranean. It occurs in south-western Europe, and is certainly introduced to Germany, Finland, Japan, North and South America, Bermuda, Australia, New Zealand, and numerous islands of the Atlantic (e.g., St. Helena) and Pacific (e.g., Juan Fernandez).

Recommended common name. Jet slug.


History in New Zealand. *M. gagates* has been known from New Zealand since material was collected in the Bay of Islands in 1840 as a result of the United States Exploring Expedition in the South Pacific. This material was described under the name *Limax fuliginosus* Gould, 1852. On the basis of further New Zealand material, this species was subsequently described as new taxa, *Milax antipodarum* Gray, 1855 and *Milax emarginata* Hutton, 1879. The name *Milax gagates* was first applied to this species in New Zealand by Musson (1891).

Biology. *M. gagates* is widely distributed in the North and South islands, and occurs on the Chatham Islands. It is found in gardens and nurseries, field crops, pastures, and less commonly in greenhouses. It is often subterranean in habit, and has been associated with potato tuber and carrot root damage in both gardens and commercial plantings.

Mating (Fig. 251) has been observed on several occasions between animals held in captivity. In the initial stages, which generally occurred late in the evening, the slugs often circled clockwise, but movement was slow. Protrusion of the stimulator followed, and in some matings this was seen to be played briefly over the body of the partner. The pairing slugs assumed a near motionless state, with bodies closely appressed and curved. The stimulators became concealed by the close proximity of the slugs, and it appeared that each animal inserted the stimulator into the atrium of its partner. The termination of precopulatory courtship behaviour and the onset of copulation proper were difficult to distinguish as there was little external evidence of genital eversion and penetration.

The animals remained in a presumed copulatory state for 8–15 hours, during which there was little movement and little or nothing of their genitalia visible. As the animals separated, there was again little notable evidence of genital eversion, except that part of the received spermatophore was often seen protruding from the still partially dilated atrium. Full uptake of the spermatophore was achieved rapidly by movement in the atrium. Dissection of animals within 5 minutes of copulation revealed a spermatophore lodged in the bursa copulatrix of each slug.

These observations are generally consistent with those by Taylor (1902–07(1902–21)), Gerhardt (1936), and Wiktor (1987a, b), except that the reported period in copulation varies greatly. The prolonged copulatory period in this and other milacid species has generally been assumed necessary to effect spermatophore production and transfer. The presence of several spermatophores in the bursa copulatrix (Bett 1960) suggests that these slugs mate repeatedly during their breeding season. Karlin & Bacon (1960) reported *M. gagates* isolated from birth to be capable of self fertilisation and production of viable eggs.

Adults are most apparent in Waikato pastures in spring.
and autumn, when mating pairs are occasionally discovered under shelter. Eggs and juveniles are most prevalent in late spring to summer and again in early winter, as are spent adults, which die on the soil surface several weeks after reproductive activity. This pattern of activity suggests a 6-month life cycle, similar to the breeding cycles of the related species *M. nigricans* (Philippi, 1836) under laboratory conditions (Quattrini 1970, Forcardi & Quattrini 1972).

The transparent eggs are relatively small at 2.0x1.5 mm to 2.8x1.8 mm. In clutches of 12–20, the eggs are usually deposited in chambers 30–50 mm deep, formed by the slugs borrowing into the soil. On occasion the eggs are deposited under cover on the soil surface.

**Remarks.** As discussed by Wiktor (1987b), several species— including *M. nigricans* (Philippi, 1836), *M. gasulli* Altena, 1974, and *M. ater* Collinge, 1895—closely resemble *M. gagates*. Examination of the papillation of the atrial stimulator and spination of the spermatophore is required for their separation. The validity of many identifications of *M. gagates* in earlier works consequently requires confirmation.

*Limax fuliginosus* Gould, 1852, *Milax antipodaranum* Gray, 1855 (= *M. antipoda* Pfeiffer of some authors), *M. emarginata* Hutton, 1879, and *Amalia antipodaranum* var. *pallida* Cockerell, 1891 were all erected for specimens collected in New Zealand and thought to be native to this country. They are here placed in synonymy with *M. gagates*, as been done previously (e.g., Suter 1913, Barker 1979).

I have examined, without dissection, the holotype of Cockerell’s (1891a) var. *pallida* (in BMNH) and found it to be an immature *M. gagates*. Type material of *Limax fuliginosus* is apparently lost (Dr C. Kessler, MCZH, pers. comm.), but Gould’s (1852) description and figure fall within the range of variation of *M. gagates*. Type material corresponding to the species of Gray (1855) and Hutton (1879) could not be located.

Quick (1960) recognised a number of varieties in *M. gagates*, but several of these are now regarded as belonging to *M. nigricans*.


**Genus Tandonia Lessona & Pollonera**

*Limax* of authors. (Not *Limax* of Linnaeus, 1758, type species *Limax maximus* Linnaeus, 1758, by original designation; *Limacidae*.)

*Amalia* of authors. (Not *Amalia* of Moquin-Tandon, 1855, type species *Limax gagates* Draparnaud, 1801, designated by Wolter (1981) — synonym of *Milax Gray, 1855; Milacidae*.)

*Milax* of authors. (Not *Milax* of Gray, 1855, type species *Limax gagates* Draparnaud, 1801, designated by Hesse (1920); *Milacidae*.)

*Tandonia* Lessona & Pollonera, 1882: 54, type species *Limax marginatus* Draparnaud, 1805 = *Limax maximus* Müller, 1843 (not *Limax marginatus* Müller, 1774; *Limacidae*), designated by Hesse (1920).

*Subamalia* Pollonera, 1887a: 5, type species *Amalia rohdei* Sinar, 1885, designated by Hesse (1920).

*Macronyx* Wagner, 1930a: 46 (as a subgenus of *Milax* Gray), type species *Milax publanensis* Wagner, 1930, by original designation and monotypy.

*Promax* Wagner, 1930a: 59 (as a section of *Milax* Gray), type species *Amalia baldensis* Simroth, 1910, designated by Wiktor (1981).

**Diagnosis.** Shell internal, a broadly oval arched plate with concentric lines of growth radiating from vestigial protoconch situated posteriad. Body keel variously arched. Jaw oxygnathic, with a median projection. Genital accessory glands 2 or more in number, opening laterally to vagina below insertion of spermathecal duct. Atrium small, without a stimulator inside.

Haploid chromosome number 33 or 34.

**Remarks.** About 36 species of *Tandonia* are known, most from the Balkan Peninsula. Several have been widely dispersed through the activities of man. The genus is represented in New Zealand by two naturalised species.

**Tandonia budapestensis** (Hazay)

Figures 50, 53, 86, 104, 127, 156, 182, 208, 234, 252, C22, M87–90; Map 19

*gagates* Menegazzi, 1855: 64 (not of Draparnaud, 1801) (*Limax*).

*gracilis* Leydig, 1876: 276 (not of Rafinesque Schmaltz, 1829) (*Limax*).

*budapestensis* Hazay, 1881: 37 (*Amalia*).

*villiniensis* von Kimakowicz, 1884: 103 (*Amalia*).

*vulnicausa* Growa & Lupu, 1961: 135 (as a subspecies of *gracilis* Leydig) (*Milax*).

Slender, crawling slugs (Fig. 50) up to 70 mm long. Mantle about 0.25 of body length. Keel weakly arched. Body blackish to dark brown in appearance owing to dense, dark speckling on a dull cream or orange background, never
flanked by strong ectocones. Lateral teeth tricuspid, with a strong mesocone; endocone progressively reducing in size but persisting in early marginal teeth. Marginal teeth mostly unicuspid, elongate and slender, spirally twisted amongst lobes of digestive gland. Hemaphroditic duct long, proximally slender and straight, distally distended and convoluted, producing a small saccular talon at entry to modest albumen gland. Spermoviduct folded and voluminous, with a well developed prostatic gland running throughout its length. Free oviduct short, slender. Bursa copulatrix reservoir oval, sometimes clearly narrowed at apex, on a stout duct. Vagina very short. Vas deferens very slender, long, terminating asymmetrically in apex of epiphallus. Epiphallus cylindrical or claviform, broad at proximal end, constricted on entry to phallus. Phallus irregular in shape but somewhat rounded, approximately as long as epiphallus, internally with a small conical papilla at entry of epiphallus. Atrium short, tubular, with internal surface minutely papillate but lacking a stimulator. Accessory glands 2 in number, closely adhering to vagina and connected to it by several thin tubules. Spermatophore (Fig. 104) slender, about 16 mm long, its exterior surface covered with short, branched processes. Phallus retractor well developed, arising from diaphragm at left posterior of pallial complex, inserted on epiphallus or at junction of epiphallus and phallus. Jaw (Fig. 127) about 1.5 mm wide, with a rounded anteromedial projection.

Radular ribbon (Fig. M87–90) comprising about 90–110 rows of teeth, each with a formula varying around 40+74C+74+40. Central tooth slightly smaller than lateral teeth on either side, tricuspid, with a strong mesocone flanked by strong ectocones. Lateral teeth tricuspid, with a strong mesocone; endocone progressively reducing in size so as to be absent in early marginal teeth; ectocone similarly reducing in size but persisting in early marginal teeth. Marginal teeth mostly unicuspid, elongate and slender, reducing in size towards radular margin.

Digestive tract, Fig. 156. Buccal mass spheroidal. Oesophagus quickly giving rise to a large crop extending to about 0.65 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta, then producing a posterior loop which extends well beyond stomach, and finally running forwards to anus.

Pallial complex (Fig. 182) located under posterior part of mantle. Kidney oval, its longest axis approximately parallel to body axis, and with a large posterior lobe extending to the right under rectum and ureter. Secondary ureter separating from right posterior part of kidney and running directly to orifice at right mediolateral margin of pallial complex. Heart partially enclosed by kidney from right, its ventricle directed posteriorly and slightly to the left; aortic stem long, extending behind pallial complex before branching. Lung with a moderately developed vascular network.

Free muscle system, Fig. 208. Cephalic retractors arising from a single root at posterior end of pallial area, but soon dividing into 2 branches, the tentacular and buccal retractors, which themselves divide anteriorly into left and right branches. Right ocular retractor not passing over phallus to insert on ocular peduncle.

Central nervous system, Fig. 234. Cerebral ganglia united by a very short and indistinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal and pleural ganglia closely appressed; left parietal and pleural ganglia fused; visceral ganglion to right of median plane.

Haploid chromosome number 33.

Type material. Leydig’s type material was collected from the environs of Tubingen, Germany.

Distribution. The original range of *T. budapestensis* has not been ascertained. It probably occurred in the southern Alps and the northern Balkans of Europe, and spread as a synanthrope (Wiktor 1987b). It is now known from Austria, Italy, Germany, Switzerland, Hungary, Romania and — clearly as an introduction — from Turkey, Bulgaria, Yugoslavia, Czechoslovakia, Poland, Belgium, Netherlands, Great Britain, and New Zealand.

Recommended common name. Budapest slug.

Killarney, Kerry, 24 Aug 1990, under stones in garden.
Bucharest, Oct 1964, D. Lapu, in park. Scotland. Audincourt,
Dumfries & Galloway, 12 Sep 1990, in garden.

History in New Zealand. First recorded in New Zealand by Barker (1979), at a time when it was apparently restricted to the northern North Island (Northland, Auckland, Waikato).

Biology. T. budapestensis occurs in New Zealand in gardens, nurseries, greenhouses, and less commonly in pastures. It is known in Europe as a pest of root crops such as potatoes, and instances of this type of damage have been recorded in New Zealand.

Mating behaviour (Fig. 257) has not been observed in New Zealand. Pairs in copulation have been collected in spring, and frequently had spermatophores in the bursa copulatrix. In Britain mating of T. budapestensis occurs from November to January (Quick 1960), while in Czechoslovakia mating has been observed from April to September (Hudec 1963). According to Quick (1960), courtship and copulation is prolonged, usually beginning at night and extending to the afternoon of the following day, or even longer. During copulation the atra, phalluses, and accessory glands are everted.

The yellow, leathery eggs, 3.0x2.25 mm, are laid in clutches of 8-15 in the soil. Juvenile slugs have been collected during spring and summer.


Tandonia sowerbyi (d'Audebard de Férussac)


marginatus of authors (not of Müller, 1774; not of Draparnaud, 1805).
carinatus Risso, 1826: 56 (Limax).
argillaceus Gassies, 1856: 232 (Limax).
etruscus Ivel, 1868: 69 (Limax).
barrabes Mabile, 1865: 60 (Milax).
julio Paulucci, 1879: 22 (as var. of Limax marginatus Draparnaud; not of Müller, 1774) (Amalia).
marginalis Paulucci, 1879: 23 (as var. of Limax marginatus Draparnaud; not of Müller, 1774) (Amalia).
kessel Boettger, 1882: 96 (Amalia).
kobelti Hesse, 1882: 93 (Amalia).
tyrensis Lessona & Pollonera, 1882: 56 (Amalia).
benoiti Hesse, 1882: 105 (as var. of Limax gagates Draparnaud) (Amalia).
nuevoda Collinge, 1895b: 336 (not of Koch & Heynemann, 1874) (Amalia).
torrez Collinge, 1895b: 336 (not of Koch & Heynemann, 1874) (Amalia).

Crawling slugs (Fig. 51) up to 70 mm long. Mantle about 0.25 of body length. Keel very strongly arched. Coloration rather variable, with body and mantle usually brownish yellow in appearance owing to diffuse blackish pigment forming irregular reticulation, never spotted or banded; keel yellow or orange, without dark speckling; pneumostome with a pale border. Sole creamy, with orange along margins. Mucus very thick, viscous, transparent orange or yellow.

Shell (Fig. 54) evocally oval, white, up to 5.6x3.2 mm. Dorsal surface concave, highest at posterior. Ventral surface flat or convex. Vestigial protoconch located centrally in posterior part. Growth lines distinct.

Reproductive system Fig. 87. Ovotestis large, consisting of numerous follicles forming an elongate cluster, spirally twisted amongst lobes of digestive gland. Hermaphrodite duct long, proximally slender and straight, distally distended and convoluted, producing a small saccular talon at entry to modest albumen gland. Spermovivuct folded and voluminous, with well developed prostatic gland running throughout its length. Free oviduct moderately long, slender. Bursa copulatrix reservoir elongate with a narrow apical prolongation, on a short, slender duct. Vagina very short. Vas deferens very slender, long, terminating asymmetrically, almost laterally, in apex of epiphallus. Epiphallus elongate conical, but terminating from a small apical knob at proximal end, its insertion on phallus marked by a sharp constriction. Phallus irregular cylindrical, approximately 0.3–0.5 of length of epiphallus, internally with a small, conical papilla at entry of epiphallus. Atrium short, bulbous, internally with fine folds and plate-like thickening, but lacking a stimulator. Accessory glands comprising numerous finger-like tubules and ducts surrounding vagina at entry to atrium.

Spermatophore (Fig. 105) elongate, at first very slender and surrounded by fan-like membranous processes in 4 rows before broadening to a smooth medial section, then covered with small branched processes before narrowing slightly to rounded tip.

Principal phallus retractor well developed but rather
short, arising from diaphragm at left posterior of pallial complex near origin of cephalic retractors, inserted on epiphallus. A pair of short supplementary muscles arising from body wall and inserted at distal end of epiphallus.

Jaw (Fig. 128) about 1.5 mm wide, with a rounded anterior mediolateral projection.

Radular ribbon (Fig. M91–94) comprising about 110–120 rows of teeth, each with a formula varying around 35+12+C+12+35. Central tooth slightly smaller than lateral teeth on either side, tricuspid, with a strong mesocone flanked by strong ectocones. Lateral teeth tricuspid, with a strong mesocone, endocone progressively reducing in size so as to be absent in early marginal teeth; ectocone similarly reducing in size but persisting in early marginal teeth. Marginal teeth mostly unicuspids, elongate, reducing in size towards radular margin.

Digestive tract, Fig. 157. Buccal mass spheroidal. Oesophagus quickly giving rise to a large crop extending about 0.7x length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, rotating 270 degrees around crop to run forwards over anterior aorta, then producing a posterior loop which extends well beyond stomach, and finally running forwards to anus making a further rotation of 360 degrees.

Pallial complex (Fig. 183) occupying posterior part of mantle. Kidney oval, its longest axis approximately parallel to body axis, with a large posterior lobe extending to right under rectum and ureter. Secondary ureter separating from right posterior part of kidney and running directly to its orifice at right mediolateral margin of pallial complex. Heart partially enclosed by kidney from right, its ventricle directed posteriorly and slightly to the left; aortic stem long, extending behind pallial complex before branching. Lung with a moderately developed vascular network.

Free muscle system, Fig. 209. Cephalic retractors arising from a single root at posterior end of pallial area, but immediately dividing into 2 branches, the tentacular and buccal retractors, which themselves divide into left and right branches. Right ocular retractor not crossing over phallus to insert on ocular peduncle.

Central nervous system (Fig. 233) with cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain very compact; left parietal ganglion fused with visceral ganglion, which is slightly to the left of median plane.

Haploid chromosome number 34.

Type material. The types, collected from the vicinity of London, England, are presumed lost (ICZN Opinion 336, 1955b: 107).

Distribution. The original range has been difficult to establish because T. sowerbyi tends to be highly synanthropic. It now occurs in coastal Mediterranean and southwest European areas, and has been introduced into South America and New Zealand.

Recommended common name. Sowerby’s slug.


History in New Zealand. Quick (1960) suggested that T. sowerbyi may occur in New Zealand. This was confirmed by Barker (1979), who found it to be widely distributed in both North and South islands.

Biology. In Europe T. sowerbyi occurs mainly in open habitats such as grasslands, arable fields, and gardens, sheltering under stones and pieces of wood. In New Zealand it has been collected principally from pasture. It burrows actively in soil and, on the basis of European experience, has the potential to inflict considerable damage on root crops such as potatoes and carrots.

Little is known of the life cycle of T. sowerbyi. In Europe mating occurs in autumn (Quick 1960, Wiktor 1987b). According to Quick (1960), after a courtship involving trail following and circling the pair copulate and remain united for 12–18 hours. Taylor (1962–67(1962–21)) noted the occurrence of more than one spermatophore in the bursa copulatrix, indicating that multiple matings sometimes occur. The pliable eggs, 4x3.5 mm to 5x4 mm and translucent pale amber, are laid in the soil in clusters of about 12. Hatchlings are 8 mm long, with a conspicuous dark median streak, which may be retained into adulthood.
Remarks. *T. sowerbyi* is easily distinguished from other *Tandonia* species by the characteristics of the bursa copulatrix, phallus, and epiphallus. In the literature it may have been confused with *T. rustica* (Millet, 1843).

Quick (1960) recognised several varieties of *T. sowerbyi* based on variation in body coloration.

An introduction into the literature on *T. sowerbyi* is provided by Germain (1930), Quick (1960), Giusti (1976), Wiktor (1983a, 1987b), and Martin & Augulo (1986).


**Subfamily LAURINAE**

Diagnosis. Epiphallus lacking a flagellum. Phallus frequently with an apical caecum.

**Genus Lauria Gray**

*Helix* of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

*Turbo* of authors. (Not *Turbo* of Linnaeus, 1758, type species *Turbo nucuminus* Linnaeus, 1758, designated by de Montfort (1810); Turbinidae.)

*Rutinus* of authors. (Not *Rutinus* of Scopoli, 1786–88, type species *Rutinus metcalfii* Linnaeus, 1758, designated by Gray (1847) — synonym of *Megalobulimus* Miller, 1787; Acaulidae)


*Clausilia* of authors. (Not *Clausilia* of Draparnaud, 1802, type species *Turbo bijon* Montagu, 1803 = *Turbo bulimatus* Ström, 1766, designated by Turton (1834) [ICZN Opinion 119, 1921: 23; Opinion 335, 1955a: 56]; Clausiliidae.)

*Odoestoma* of authors. (Not *Odoestoma* of Fleming, 1813, type species *Turbo plautus* Montagu, 1803, designated by Gray (1847); Pyramidulidae.)

*Cochlodonta* d’Audebard de Férussac, 1821; 63 (as a subgenus of *Helix* Linnaeus, 1758, type species *Pupa ambilicata* Draparnaud, 1801 = *Turbo cylindracea* Costa, 1778, designated by Pilsbry (1922–26).)

*Pupilla* of authors. (Not *Pupilla* of Férussac, 1828 (1827–28), type species *Pupa margarita* Draparnaud, 1801 = *Turbo margarita* Linnaeus, 1758, by monotypy [ICZN Opinion 335, 1955a: 49, 58]; Pupillidae.)

*Cochlidium* Lowe, 1831; 62 (as a subgenus of *Helix* Linnaeus), type species *Helix (Cochlidium) anconostoma* Lowe, 1831 = *Turbo cylindracea* Costa, 1778, designated by Pilsbry (1922–26) (coordination of *Cochlodonta* d’Audebard de Férussac, 1821).

*Lauria* Gray, 1840; 193 (as a subgenus of *Pupa* Draparnaud), type species *Pupa ambilicata* Draparnaud, 1801 = *Turbo cylindracea* Costa, 1778, designated by Hermanssen (1847) [ICZN Opinion 335, 1955a: 49, 57].

**Family PUPILLIDAE**

Diagnosis. Herbivorous holopod snails, oviparous or ovoviviparous. Shell small, cylinidracea to conical, frequently with apertural teeth; capable of fully housing the animal. Sole uniform, without a caudal mucus gland. Suprapedal gland embedded in foot tissues. Buccal mass spherical. Jaw autophragnistic. Radula with marginal teeth bearing numerous cusps, on broad, short basal plates. Intestine with a single loop directed forwards. Kidney very long, divided internally into 2 distinct regions, the anterior region functioning as a primary ureter, but without a secondary ureter. Cerebro-pleural connectives subequal in length and relatively long. Pleural ganglia closer to cerebral ganglia than to pedal ganglia. Visceral ganglion chain moderately concentrated.

Chromosomal number unknown.

Remarks. The phylogeny of pupilloid snails has not been fully resolved, and the limits of the family Pupillidae have often been disputed. The family name is used here in its restricted sense for Pupillinae + Laurinae + Argininae.
Fr. E. Swainson, 1840: 334 (as subgenus of Clasusia Draparnaud). Type species Pupa umbilicata Draparnaud, 1801 = Turbo cylindracea da Costa, 1778, designated by Hermanssen (1847).

Sowerbottae of authors. (Not Sowerbottae of Morsen, 1843.
Listed in synonymy of Abidu Tutar, 1834. Chondrinidae, by Zilch (1959–60), type designation not traced.)

Costa, 1778) dominates the entire genus by its comparably very large natural distribution, which largely coincides with that of the genus.

Costa, 1778) dominates the entire genus by its comparably very large natural distribution, which largely coincides with that of the genus.

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22, M95, M96; Map 21

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22, M95, M96; Map 21

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22, M95, M96; Map 21

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22, M95, M96; Map 21

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22, M95, M96; Map 21

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22, M95, M96; Map 21

Almost all taxa placed in Lauria s. s. have similar shells. Given this, and the fact that the anatomy for most is unknown, the systematic relationships and species limits of nominal Lauria remain uncertain.
Animal steely blue to grey dorsally, shading to pale grey at sides and on sole. Tail rather short, not extending behind shell in active animal. Locomotion by muscular pedal waves generated from posterior of sole.

Reproductive system, Fig. 88. Ovotestis comprising a series of single acini opening to proximal hermaphroditic duct, embedded in digestive gland. Hermaphroditic duct rather long, markedly distended and convoluted in middle section, terminating in a multilobate, diverticular tainon embedded in alburnum gland. Spermicduct and oviduct fused to form spermoviduct; female part proximally slender but for the most part sacculate, in gravid animals greatly distended by embryos; prostatic gland short, fused with proximal female oviduct. Free oviduct and vagina short, stout. Bursa copulatrix reservoir small, bulbous, on a long, slender duct. Vas deferens long and very slender, at its distal end expanding abruptly into an epiphallus which lacks a flagellum. Phallus rather short, thick-walled, bearing apically an elongate caecum armed internally with spinate papillae, and laterally carrying an appendix with a bulbous base giving rise to a glandular sac on a slender duct; entry of epiphallus direct, not through a papilla. Atrium short but distinct.

Spermatophores unknown.

Phallic retractor arising from diaphragm, bifurcating to insert laterally on phallus and on bulbous base of phallic appendix.

Jaw (Fig. 129) about 0.2 mm wide, crescent-shaped, with numerous fused plates.

Radular ribbon (Fig. M95, M96) with about 110 transverse rows of teeth, each of formula 10+2+4+7+C+7+2+10. Central tooth well developed, tricuspid, with a large mesocone and short ectocones on a quadrate basal plate. Lateral teeth bicuspid, with a large mesocone and a smaller but prominent ectocone, on quadrate basal plate. Teeth transitional between lateral and marginal characterised by bifurcation of ectocone and shortening of basal plate. Marginal teeth with a shortened mesocone and a serrate ectocone (cusps lacking on extreme marginals), on a broad but short basal plate.

Digestive tract, Fig. 158. Buccal mass spheroidal. Oesophagus long, terminating in gastric pouch without any apparent crop formation. Gastric pouch cylindrical, extending about 0.6 of a whorl to end in a sacculate stomach which is not externally differentiated. Intestine producing short, anteriorly and posteriorly directed loops before running as a long rectum to anus in mantle collar.

Pallial complex, Fig. 184. Pulmonary cavity long, extending about 2.25 whorls. Kidney proper short, barely exceeding length of pericardium, extended to about 0.85 of pulmonary cavity length by a slender ureteric pouch. Retrograde ureter absent, but a ciliated groove extending for a short distance from excretory orifice towards top of pulmonary cavity. Pulmonary cavity poorly vascularised.

Free muscle system, Fig. 210. Columnar muscle dividing shortly after its origin into 2 primary branches; left branch to left ocular and inferior tentacles, giving rise to buccal retractors in its middle section; right branch dividing into a well developed, extensively radiating tail fan, and tentacle retractors. Retractor branch to right ocular peduncle passing over phallus.

Central nervous system, Fig. 236. Cerebral commissure length about equal to cerebral ganglion width. Cerbro-pedal connectives subequal in length, the right one about 1.5x as long as width of cerebral ganglion. Pleural ganglia markedly closer to cerebral ganglia than to pedal ganglia. Parietal ganglia closer to visceral ganglion than to pleural ganglia; right parietal apparently fused with visceral ganglion, which lies to right of median plane.

Type material. The type locality is England. The whereabouts of the type material is unknown.

Distribution. Widely distributed in western Europe and the eastern Atlantic islands, eastwards to the Caucasus and Asia Minor. Introduced into St Helena, Reunion, the U.S.A., Canada, Jamaica, South Africa, and New Zealand.

Recommended common name. Chrysallis snail.


History in New Zealand. This species was first collected in New Zealand by Whitten (1955, 1957) but wrongly assigned to Pupilla muscorum (Linnæus, 1758) (Willan 1977). Whitten’s (1955) material was collected from Mt Pleasant, Thames in 1944 and Western Springs, Auckland in 1955. Whitten (1957) noted this species from Parnell, Auckland in 1956. Further specimens from Thames were misidentified as P. muscorum by Powell (1979). Willan (1977) and Barker (1982) confirmed the establishment of L. cylindracea at several localities in Auckland City.

During the present study L. cylindracea has been recorded from numerous localities in the northern North Island and from the Nelson region of the South Island.

Biology. The habitat of L. cylindracea is varied, but commonly it is found in rocky or stony sites, on walls, in crevices of tree stumps, under bark of fallen trees, and in coastal grassland. In Britain Lauria is common in woodland, rocky open areas, and grassland (e.g., Cameron & Redfern 1972, Chatsfield 1975, Rouse & Evans 1994). L. cylindracea has not been found in areas of native forest in New Zealand.

Ovoviviparous. Gravid animals have been collected in New Zealand from late spring to autumn.

Remarks. The shell form of the species established in New Zealand is clearly that which would be assigned to L. cylindracea in Europe, but the anatomy of the dissected series (from Auckland and Hamilton) differs in detail from that described for L. cylindracea by Steenberg (1925): (a) the acini of the ovotestis are not clustered into several lobes, but arise singly along the proximal hermaphroditic duct; (b) the hermaphroditic duct does not terminate in a small bulbous talon, but at the base of a large, sacculate and multilobate receptacle; (c) the bursa copulatrix reservoir does not lie against the prostatic gland follicles but more distally, against the sacculate part of the oviduct, indicative of a shorter bursa copulatrix duct; (d) rather than being shorter, the phallic caecum extends the length of the epiphallus; and (e) rather than about 4x, the total length of the phallic appendix exceeds that of the epiphallus by about 2x. The relative portions of the epiphallus, phallic caecum, and phallic appendix are similar in the material described and illustrated by Steenberg (1925) and Schileyko (1975, 1984). However, Schileyko’s material differed from Steenberg’s and the present New Zealand material in that the phallic branch of the phallic retractor muscle was inserted on the distal epiphallus near the base of the phallic caecum, rather than laterally on the proximal phallus, and the bursa copulatrix duct arose very close to the atrium, resulting in a very short vagina or none, rather than more proximally with a distinct vagina.

This varied combination of character states suggests the possibility of a sibling species complex within what at present is known as L. cylindracea. Any analysis of this complex would necessarily include the other common European species L. sempronii (de Charpentier, 1837), the typical form of which is indistinguishable from L. cylindracea from non-calcareous soils or dry habitats (Manganelli et al. 1990).

Entry into the literature on L. cylindracea is provided by Pilsbury (1922–26), Germain (1930), Likharev & Rammel’ meier (1952), Giusti (1973), Backhuys (1975), Schileyko (1975, 1984), and Manganelli et al. (1990).

Family TESTACEILLIDAE

Diagnosis. Carnivorous slugs. Shell small, auriform, situated at posterior end of body, covering the pallial organs but not capable of housing retracted animal. Dorsum with a pair of branched lateral grooves arising from prepalial groove and running forwards. Ocular peduncles not bulbous at apex. Caudal mucus pit absent. Sole uniform. Suprapedal gland lying free in body cavity. Jaw absent. Buccal bulb much enlarged, containing radula with V-shaped rows of barbed aculeate teeth, protrusible for impalement and capture of earthworms and other prey, and with strong posterior and (usually) lateral retractor muscles. Intestine reduced in length, describing a broad, anteriorly directed loop before running to anus at mantle collar. Kidney with a short secondary ureter. Genital orifice near base of right ocular peduncle. Genitalia without accessory glands, but phallus with a small diverticulum and an apical flagellum. Right ocular retractor passing forwards over phallus. Cerebral commissure very short; cerebropleural and cerebropedal commissures moderately long.

Haploid chromosome number 32.

Remarks. The family is represented by a single genus native to the western Palaearctic region.

Genus Testacella Draparnaud

Helix of authors. (Not Helix of Linnæus, 1758, type species Helix pomatia Linnæus, 1758, designated by de Montfort (1810); Helicidae.)

Testacella Draparnaud, 1801: 116, type species Testacella haliotidea Draparnaud, 1801, by monotypy. (Not Testacella of de Monet de Lamarck, 1801 (nude name) [ICZN Opinion 335, 1955a: 58, 59].)

Daudebordia of authors. (Not Daudebordia of Hartmann, 1821, type species Helix rufa Draparnaud, 1805, by monotypy: Daudebordiidae.)
Diagnosis. Characters as for family.

**Testacella haliotidea** Draparnaud

Figures 56, 57, 89, 159, 185, 211, 237, C25, M97-99; Map 22

*haliotidea* Draparnaud, 1801: 116 (Testacella).
*munguca* de Roëzy, 1805: 13 (Testacella).
*gulbae* van Osten, 1816 (1815-16): 95 (Testacella).
*seauvage-ceanileanae* of authors (not of d'Audebard de Fersasse, 1819).
*noves-ceanileanae* of authors (not Pfeiffer, 1862).
*calathus* Fauton, 1892: 42 (Testacella).
*bacchinomensis* Pollonera, 1888: 4 (Testacella).
*dubia* Pollonera, 1888: 4 (Testacella).
*anamala* Torres Minques, 1924: 113 (Testacella).

Extended animal (Fig. 56) 80-120 mm long, with small external shell carried over pallial organs at posterior apex of body. Two very distinct grooves, about 2 mm apart at their origin, arising from anterior edge of mantle and describing a lateral arc over back, one on either side, before converging near body anterior. Body usually dull greyish brown to yellow, with pale yellow-white foot fringe and sole. Mucus clear.

Shell (Fig. 57) to 7x5 mm, convexly auriform, subtriangular, with brown periostracum often abraded. Dorsal surface with distinct growth lines. Ventral surface with a crescentic muscle scar. Protoconch vestigial but none-theless distinct on right aspect of shell posterior apex. Columella expanded to a rounded callosity posteriorly, and usually slightly truncate anteriorly.

Reproductive system, Fig. 89. Ovotestis pale, at apex of visceral mass between lobes of digestive gland. Hermaphroditic duct long, slender, much folded, with a bulbous tation at its termination in large albumen gland. Spermoviscer duct much folded. Free oviduct very short, stout. Busa copulatrix reservoir oval to spherical, on a short, rather stout duct. Vagina of moderate length, narrowing towards atrium. Vas deferens long and slender, inserted without a papilla at apex of phallus, adjacent to flagellum. Phallus (and its flagellum) slender and tubular, with a small mediolateral caecum, and internally with numerous conical papillae.

Spermatophore unknown, probably not produced.

Phallus retractor long, slender, arising from dorsal body wall at third end of body cavity and inserted at apex of phallus.

Radular ribbon (Fig. M97-99) of about 50 V-shaped rows of teeth, 18 teeth on either side of midline. Central tooth usually absent, occasionally vestigial. Teeth barbed acutely, each with a vestigial mesocone midway between base and apex, gradually increasing in size up to the penultimate one; marginal (18th) tooth shorter.

Digestive tract, Fig. 159. Buccal mass large, cylindrical. Oesophagus short. Crop thick-walled, cylindrical, merging with thick-walled stomach at level of posterior limit of buccal mass, conspicuously connected with dorsal and lateral body wall by a number of thin muscle strands. Intestine arising from left lateral aspect of stomach, forming a broad anteriorly directed loop before running to anus at right posterior of body.

Pallial complex (Fig. 185) at posterior of body, overlain by shell and mantle. Kidney rectangular, lying below and largely in front of pulmonary chamber, opening into a very short ureteric tube. Pulmonary chamber a thin-walled air sac. Heart in pericardium on right side of kidney, with ventricle in front of auricles; aortic stem extending forwards beyond pallial complex before branching. Osphradium in floor of pulmonary chamber, comprising a ridge of cells innervated from visceral ganglion.

Free muscle system, Fig. 211. Ocular retractors arising asymetrically from lateral body wall a little anterior of pallial complex; right retractor arising from pedal musculature and passing between phallus and vagina. Buccal retractor arising from left posterior body wall, inserted laterally on left side of buccal mass as numerous muscle bundles.

Central nervous system, Fig. 237a, b. Cerebral ganglia appressed, united by a very short and indistinct commissure. Right cerebropedal connectives slightly longer than those on the left, their length about equal to width of cerebral ganglion. Pleural ganglia close to pedal ganglia, to which they are linked by short connectives. Visceral chain compact; pleural ganglia closely appressed to pleural ganglia; visceral ganglion to left of median plane, closely appressed to left pleural ganglion and linked to right pleural ganglion by a very short connective.

Haploid chromosome number 32.

**Type material.** Represented by two syntype specimens in NHMW (Acq. No. 1820. xxvi. 151). The type locality is assumed to be Montpellier, France.

**Distribution.** Naturally distributed in the Western Palaearctic region from the Atlantic isles to the Balkans, and from the North African coast to southern Scotland. Introduced into Canada, the U.S.A., Cuba, Australia, and New Zealand.

Recommended common name. Shelled slug.

**Material examined.** New Zealand. AK. Auckland, shells only, T.F. Cheeseman (CMNZ M252, lectotype, and CMNZ...

History in New Zealand. Testacellid slugs were first recorded for New Zealand as Daudebardia novoseelandica (not of Pfeiffer) by Hutton (1881), and later described as a new species, Testacella vagans, by Hutton (1882a). Musson (1891), Suter (1891), and Hedley (1892) correctly pointed out that Hutton's slug was a naturalised species, possibly T. maugeri d'Audebard de Férussac. Subsequently T. maugeri appeared regularly in Estings of molluscs introduced into New Zealand. Recorded localities were Ashburton and Nelson (South Island), Waikato and Auckland (North Island).

Although the type specimen of Hutton's slug had not been traced and hence could not be examined, 1 earlier (Barker 1979) listed T. vagans in the synonymy of T. haliotidea, primarily based on the basis of radial form. Shell material collected in Mt Eden, Auckland and deposited in MONZ by R.K. Dell during the 1950s was referred to T. maugeri by Whitten (1955), but appears to be of T. haliotidea (Barker 1979). However, Hutton's type material was discovered in CMNZ during the present study. The form of the lectotype and (2) syntype shells of T. vagans indicates that this taxon is conspecific with T. maugeri. It remains uncertain as to whether both T. maugeri and T. haliotidea have established in the Auckland area, where no testacellid slugs have been seen for at least 35 years.

During 1978 and subsequently, testacellid slugs have been collected on a number of occasions from localities in the Poverty Bay and Hawkes Bay regions of the North Island. Dissections of preserved animals (Barker 1979 and this study) have shown these to be T. haliotidea.

Biology. Testacella is largely systema in Britain (Kerney 1966), and primarily subterranean in gardens and other cultivated soils. During the day the slugs remain underground, emerging at night to prey upon earthworms, slugs, snails, and other soil animals such as centipedes on the soil surface. Feeding behaviour and the function of the buccal mass in Testacella has been described by de Lacaze-Duthiers (1887), Webb (1893), Taylor (1902-07 (1902-21)), Barnes (1950), Barnes & Stokes (1951), and Crumpton (1975). During dry or particularly cold weather T. haliotidea retreats into the soil to depths often greater than 1 metre. Under these conditions the slugs may go into a form of aestivation in earthen cells lined with viscid mucus.

Because of their subterranean habit, testacellid slugs are rarely observed, and hence little is known of their biologies. According to Taylor (1902-07 (1902-21)) and Barnes & Stokes (1951) the slugs are most active in spring and autumn, when mating occurs either in the soil or under cover on the soil surface. Copulation lasts for 4 or 5 hours. Chemin (1939a, b) reported self-fertilisation in T. haliotidea isolated young. Eggs are ellipsoidal, 7x4 mm, with a calcareous shell which changes from white to yellow, and are deposited in clusters deep in the soil. Gassies (1849) reported that eggs took 10–22 days to hatch, while Barnes & Stokes (1951) recorded development times of 144–201 days. According to Taylor (1902-07 (1902-21)), Testacella takes about 18 months to reach sexual maturity, and may live for 5 or 6 years.

Remarks. Many old records of T. haliotidea can be referred to T. squamulatum Sewesby, 1821, as the latter was considered by many authors to be only a variety of T. haliotidea, and was not distinguished in the literature.

Several variety names of T. haliotidea appear in the literature, based on variation in shell characters and body coloration (e.g., Quick 1960).

Entry into the European literature pertaining to T. haliotidea are provided by Germain (1930), Quick (1960), Diaz et al. (1986), and Martin & Rallo (1986).

**Family VALLONIIDAE**

**Diagnosis.** Herbivorous holopod snails, oviparous or ovoviviparous. Shell cylindriform, low-conical, or turbinate, less than 5 mm in height, umbilicate, sometimes with periostracal ribs or processes, frequently with aperture barriers, capable of fully housing the retracted animal. Animal lacking inferior tentacles in some taxa. Sole uniform, without a caudal muscul pit. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal, jaw macrogomatic. Radula with marginal teeth multisulcated on broad, short basal plates. Intestine with a single loop directed forwards. Kidney very elongate, divided internally into 2 distinct regions, the anterior region functioning as a primary retractor; secondary retractor absent except in Acathina, which has a short, closed retrograde duct. Columellar muscle branching at or a short distance from origin into left and right cephalic retractor bundles; buccal retractor associated with left branch, tail fan associated with right branch. Right ocular retractor crossing phallus. Genital orifice near right ocular peduncle, or sited on visceral stem near pneumostome. Spermovicul duct formed; prostatic gland short, confined to proximal pallial groove in ovoviviparous forms, longer in oviparous forms. Bursa copulatrix...
duct of moderate length or rather short, in some taxa with a diverticulum. Aphally common: male genitalia (when present) with an epiphallus and phallus equipped with a well-developed appendix and gland; phallus frequently with an apical caecum. Phallus retractor muscle arising from diaphragm, bifurcating to insert on phallus and its appendix. Cerebropedal connectives frequently subequal in length but never long. Right pleural ganglion closer to right cerebral than to right pedal ganglion. Visceral ganglion chain moderately concentrated, on right of medium plane.

Haploid chromosome number 28.

**Remarks.** The limits of the Valloniidae and their affinities to other orthurethran families have not been fully resolved. Zilch (1959-60) and Tillier (1989) divide the nominal family into several subfamily taxa: Valloninae, Acunthiuninae, Strobilopsinae, and Speleodiscinae. The Valloniidae in this sense are closest to the Achatinellidae, Pupillidae, and Pyramidulidae in Tillier's (1989) classification. Pilsbry (1948(1939-48)) and Giusti & Manganelli (1986) question the validity of the current subfamily divisions of the Valloniidae. I have therefore used Valloniinae in the broad sense of Zilch and Tillier, without recognition of subfamily units. In this sense the family is represented by 15 extant genera.

The Valloniidae are widely distributed in temperate and tropical regions, and are represented in New Zealand by a single naturalised species.

**Genus Vallonia Risso**

*Helix* of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); *Helicidae*.)

*Zarana* Leach, 1819: 108, type species *Helix paludella* Müller, 1774 (≡ *V. paludella* (Müller, 1774) + *V. costata* (Müller, 1774), by original designation.


*Amplexis* Brown, 1837: figs 76 & 77, type species *Amplexis paludosa* da Costa = *V. paludella* (Müller, 1774), designated by Pilsbry (1927-35); amended to *Amplexis* by Brown (1844 (1837-49)). (Not *Amplexis* of Sowerby, 1814; Cnidaria.)

*Chilostoma* of authors. (Not *Chilostoma* of Fitzinger, 1833, type species *Chilostoma zonata* Studer, 1820 = *Helicigona fontana* Studer, 1820, designated by Gray (1847); *Helicidae*.)

*Corneola* Beck, 1837 (1837-38): 23 (as subgenus of *Helix* Linnaeus, 1758), type species *Helix paludella* Müller, 1774, designated by Herrmannsen (1847) - synonym of *Chilostoma* Fitzinger, 1833; *Helicidae*.)

*Lucina* Gray, 1840: 142, type species *Helix paludella* Müller, 1774, designated by Moquin-Tandon (1855).


**Diagnosis.** Shell depressed, helicoid, broadly umbilicate; peristome continuous or nearly so, thickened and reflected, in some species with periostal ribs; aperture always lacking teeth. Animal with inferior tentacles. Oviparous. Bursa copulatrix duct short, lacking a diverticulum. Genital orifice well posterior of right ocular peduncle, at base of visceral stalk. Central nervous system with left pleural and parietal ganglia closely appressed; right parietal ganglion fused with visceral ganglion.

Haploid chromosome number 28.

**Remarks.** Gerber (1996) recognised 40 species and subspecies in *Vallonia*. The genus has a wide distribution in Europe, North Africa, Atlantic islands, North America, North and Central Asia, and Japan. Several species have been dispersed by human commerce.

**Vallonia excentrica Sterki**

Figures 58, 90, 130, 160, 186, 212, 238, 253, C26, M23, M100, M101, M119, M120; Map 23

*pulchella* of authors (not of Müller, 1774).

*pulchella* da Costa: 1778: 59 (*Helix*), *excentrica* Sterki, 1893a: 249 (*Vallonia*), *excentricoides* Weirs, 1894: 151 (as var. of *pulchella* Müller) (in error for *excentrica* Sterki) (*Vallonia*).

Shell (Fig. 58) to 1.2 mm high by 2.3 mm in diameter, with 3–3.5 rapidly increasing rounded whorls, the last quarter-whorl expanding noticeably, whitish or straw coloured, somewhat translucent. Protoconch (Fig. M23) with slight roughness and lined by numerous thin spiral grooves. Teleoconch furnished with growth lines, as well as rare, weak traces of irregularly disposed and branched periostal striae. Umbilicus open, elliptical, about 0.25 of shell diameter. Aperture circular, rather obliqueEventide and inclined. Peristome not continuous, abruptly thickened to form a white lip but weakly reflected.

Animal translucent white. Tail in active animal very short. Sole undivided, narrow, with margin weakly crenulate: progression by advancing muscular waves. Genital orifice at base of visceral stalk.

Reproductive system, Fig. 90. Ovotestis embedded in digestive gland, composed of 3 clusters of 3–5 acini. Her-
ma-phrodite duct slender and straight proximally, much swollen and contorted in middle part, before again becoming slender to run to an elongate talon with bulbous head. Female pallial gonaduct sacculate, especially immediately below that part fused with prostatic gland. Free oviduct rather short. Bursa copulatrix reservoir oval, on a rather short duct. Vagina moderately long. Prostatic gland with elongate follicles, confined to proximal pallial gonaduct, where it fuses with female tract to form a spermoviduct. Vas deferens long and slender. Epiphallus arched, dilated at entry to phallus, where it houses a short conical papilla. Phallus comprising a rather sacculate proximal part and short tubular distal part, the lumen of both lined with low folds, an appendix arising from proximal phallus, with a bulbous base, housing a fleshy, elongate papilla, giving rise to a glandular sac on a slender stem. Atrium short, indistinct. Male terminal genitilia often absent.

Spermatophores unknown.

Phallus retractor arising from anterior part of diaphragm, bifurcating to attach to medial part of epiphallus and basal part of phallus appendix.

Jaw (Fig. 130) arcuate, 0.23–0.25 mm wide, sculptured with 18–26 low folds which denticulate the margin, often with a slight median projection.

Radular ribbon (Fig. M100, 101) with 70–77 transverse rows of teeth, each varying around the formula 10–12+3–4+3–4+10–12. Central tooth narrower than adjacent laterals, tricuspid, with mesocone not half as long as rectangular basal plate. Lateral teeth bicuspid with basal plates squarish; mesocone large, in length equal to or exceeding basal plate height; ectocone small. Marginal teeth multicuspid, on broad but short basal plates.

Digestive tract, Fig. 160. Buccal mass spheroidal. Oesophagus long, slender, terminating in a gastric pouch without crop formation. Gastric pouch inflated, cylindrical, extending about 0.3 of a whorl to merge with sacculate stomach, which is not externally differentiated. Intestine producing long anteriorly and posteriorly directed loops, then running to anus at mantle collar.

Pallial complex, Fig. 186. Pulmonary cavity rather short, extending about 0.6 of a whorl. Kidney short, barely exceeding length of pericardium, extended to about 0.9 of pulmonary cavity length by a conical ureteric pocket. Retrograde urerter absent, but a ciliated groove extending for a short distance from anterior excretory pore towards top of pulmonary cavity. A spongy tissue mass overlying rectum immediately before anus.

Free muscle system, Fig. 212. Columellar muscle dividing at origin into a left cephalic bundle and a right, short but broad tail fun. Cephalic bundle dividing into left and right branches, which run to ocular peduncles, inferior tentacles, and anterior body wall. Buccal retractor arising from left branch of cephalic retractor. Right ocular retractor passing between male and female branches of terminal genitilia.

Central nervous system, Fig. 238. Cerebral commissure rather short, its length less than cerebral ganglion width. Length of cerebro-pedal connectives exceeding width of cerebral ganglia; left connective slightly longer than the right. Right pleural ganglion closer to cerebral ganglion than to right pedal ganglion; left pleural ganglion sited midway between left cerebral ganglion and pedal ganglion. Left parietal ganglion separated from both left pleural ganglion and visceral ganglion by short connectives, but closer to the former. Right parietal ganglion separated from right pleural by a short connective, but fused to visceral ganglion, which lies to right of median plane.

Chromosome numbers unknown.


Distribution. Apparently native to the Mediterranean, western Europe, Atlantic islands, and North America. Introduced to St Helena, South Africa, Australia, and New Zealand.

Recommended common name. Eccentric grass snail.


-101-


History in New Zealand. Crosse (1893) recorded V. pulchella (Müller, 1774) from New Zealand, without collection data. In the same year Suter (1893b) listed V. pulchella as having been found in Albert Park, Auckland by Cheeseman. This record apparently formed the basis of Suter's (1913) listing of V. excentrica from Auckland. In addition to listing Taranaki as a new locality for V. excentrica, Thomson (1922) referred to records of V. pulchella from Auckland by Musson (1891), who however does not list any New Zealand localities for V. pulchella. It would seem that Crosse (1893) was in error in thinking that Musson had recorded Vallonia from New Zealand, and that this error was subsequently repeated by Thomson (1922). Unless shown otherwise by material in the collections of Musson, the first authentic record of Vallonia in New Zealand (specifically, V. excentrica) is that of Suter (1893b).

Whitten (1955) lists Leigh, Auckland, Taranaki, and Nelson (incl. Tahunanui) as localities for V. excentrica. Whitten (1957) added Papakura and Taipa Beach as localities. This pattern of widespread distribution in the North Island and restriction to the Nelson region in the South Island is confirmed by Barker (1982 and this study).

Whitten (1957) recorded V. costata (Müller) from Devonport. I have not been able to confirm the presence of this species in New Zealand.

Biology. Vallonia excentrica is a xerophile, common in grasslands (e.g., Boycott 1934, Kerney 1966, Cameron & Redfern 1972, Rouse & Evans 1994). Kerney & Cameron (1979) give its habitat as "open, usually dry calcareous places: short-turfed grassland, screes, sand-dunes; not normally in woods or marshes." This applies equally to New Zealand, except that the species occurs in pastures over a wide range of soil acidity (pH 4.5–7) and thus is not restricted to calcareous sites. V. excentrica has become a conspicuous element of the pasture fauna on many northern New Zealand soils. Barker (1985) provided information on its biology in two Waikato pastures, which suggested that dispersion and abundance are governed by microclimatic factors such as drainage.

V. excentrica displays deterministic growth. Barker (1985) found that under favourable conditions the snails grow steadily until maturity when peristome thickening occurs in shells of 2.2–3 mm diameter. In the laboratory, snails took an average of 48 days at 25°C to attain maturity. Snails commenced oviposition within 7 days of peristome thickening, producing an egg every 1–3 days (mean 0.86 eggs per day) when first reproductive. After several months both oviposition rate and egg viability declined, when the spent snails died. Analysis of population census counts taken from Waikato pastures, where abundance as high as 1500 per m² was recorded, indicated that two generations occur each year, with recruitment in spring to early summer and in late summer to autumn.

Watson (1920) found English examples of V. excentrica and V. pulchella to be aphallitic. In contrast, among 45 specimens of V. costata examined by Watson, 3 were euphallic and 42 were aphallitic. Giusti & Manganelli (1986) maintain that constant aphallia is a character of the pulchella group, in which they include V. excentrica. Both euphallic and aphallitic individuals are represented in New Zealand populations of V. excentrica; this apparently is the first report of euphalia in V. excentrica. In a sample from Waikato pastures dissected by Barker (1985), 29 were
found to be aphallic and 7 euphallic. Dissection of a larger sample assembled from other New Zealand localities during the present study indicated a similar incidence of dimorphism (n = 45: 37 aphallic, 8 euphallic), although several sites yielded exclusively aphallic specimens.

Copulation (Fig. 253) in euphallic *V. excentrica* was observed by Barker (1985). The mode of reproduction in aphallic individuals is not known. Boycott (1917) suggested cross-fertilisation by vaginal copulation between aphallic forms of *Acanthinula* Beck, 1847 and *Spermatokea* Westerlund, 1902. Watson (1934) noted that structural differences in genitalia suggest that the euphallic forms reproduce by cross-fertilisation and aphallic forms by self-fertilisation. In discussing male copulatory organ deficiency in *Stylommatophora*, Riedel (1953) suggested alternative reproductive modes: (1) vaginal coupling between aphallic forms; (2) copulation between a euphallic individual, functioning as a male, and an aphallic individual, functioning as a female; or (3) aphallic forms reproducing without copulation, by parthenogenesis or self-fertilisation. Whitney (1938) has documented self-fertilisation and production of fertile progeny in *V. pulchella* isolated from birth.

Eggs of *V. excentrica* are deposited singly on the soil surface, usually amongst plant litter. They vary from spherical, 0.65 mm in diameter, to slightly flattened spheroids 0.7x0.65x0.58 mm. As in all *Vallonia* species (see Tompa 1976), a brittle shell (Fig. M119, 120) of calcite crystals imparts a pure white appearance to the eggs. From laboratory studies Barker (1985) estimated that approximately 148 degree-days above a threshold of 10°C is required for complete embryo development and egg hatch. Barker (1985) recorded high mortality of *V. excentrica* in Waikato pasture during the egg stage, especially during autumn. Whitney (1938), working with *V. pulchella*, found the eggs to be very sensitive to desiccation.

Remarks. The specific distinction between *Vallonia pulchella* Müller, 1774 and *V. excentrica* Sterki, 1893 has been the subject of debate for many years. Some authors (e.g., Wagner 1935, Hubendick 1950, 1952, 1953, Jacobson 1950, Varga 1972, Giusti 1976) consider *excentrica* to be merely an ecological variant of *pulchella*. Other authors (e.g., Küpper 1951, Mandahl-Barth 1951, Sparks 1953, Hubricht 1969) have presented evidence in favour of *excentrica* being recognised as a distinct species. This latter view has been accepted by most authors over the past few decades. Giusti & Manganeli (1986) argue that the present *Vallonia* taxonomy, founded on weak conchological peculiarities, is rather subjective. They hold that the high frequency of aphallic ("constant aphally", in their wording) in the *pulchella* group suggests an aggregation of genetically distinct entities whose affinities are not distinguishable on a morphological basis.

In the most recent revision of the genus, Gerber (1996) treated *V. excentrica* as a species distinct from *V. pulchella*. I have used *excentrica* for the populations naturalised in New Zealand, in the hope that the status of this entity may be resolved at some later date, perhaps by molecular techniques. Because many early authors did not distinguish between these entities, earlier references to *V. pulchella* may in fact refer to *V. excentrica*.

Entry into the literature on *V. excentrica* is provided by Pilsbry (1948 (1939-48)), Hubendick (1950, 1953), Sparks (1953), Bequaert & Miller (1973), Backhuys (1975), Grossu (1987), and Gerber (1996).

Family VERTIGINIDAE

Diagnosis. Herbivorous holopod snails. Shell dextral or sinistral, under 5 mm in height, ovate, ovate-cylindrical, cylindrical, or exceptionally cylindrical-conical or spindleshaped, capable of housing retracted animal; aperture simple or armed with barriers formed at sexual maturation. Animal often lacking inferior tentacles. Sole undivided; progression by pedal waves initiated from posterior. Caudal macus pit lacking. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw autalognathic. Radula with marginal teeth multicuspid, on broad but short basal plates. Intestine with a single loop directed forwards. Kidney very long, divided internally into 2 distinct regions, the anteriormost functioning as a primary ureter; secondary ureter lacking. Colbular muscle dividing at or a short distance from origin into left and right cephalic retractor bundles; buccal retractor associated with left branch, tail fan with right branch. Right ocular retractor crossing phallus. Phallus retractor arising from diaphragm, unidivided or bifurcate. Genital orifice a short distance behind ocular peduncle. Bursa copulatrix reservoir on a long duct. Epiphallus simple, without a flagellum, or absent. Phallus with or without appendages; aphallic evident in some species. Central nervous system with moderately long cerebropedal connectives. Pleural ganglia closer to cerebral ganglia than to pedal ganglia. Visceral ganglion chain moderately concentrated.

Chromosome number unknown.

As pointed out by Pokryszko (1990a), the systematic position of the majority of taxa classified with the Vertiginidae is obscure, as members of only 9 of the 16 genera have been studied anatomically. Pokryszko proposed restriction of the Vertiginidae to the genera Vertigo Müller, 1774, Truncateella Lowe, 1852, and Columella Westerlund, 1878, with provision for inclusion of other genera should anatomical investigation show that they too are characterised by the simple structure of the copulatory organs. In the present work Zilch's (1959–60) definition of Vertiginidae is used, with the simple male genitalia taken as a diagnostic character at the subfamily level.

Fusion of the right parietal ganglion with the cerebro-pedal connective noted by Tillet (1989) in the central nervous system of Bothriopupa breviconus Pilsbry, 1917 (Truncateellinae) and Sterkia cyriest (Drouet, 1859) (Nesopupininae) are not apparent in Vertigo. In the Vertigo species considered here and V. moulinstana (Dupuy, 1849) examined by Sneath (1925), the nervous system is characterised by the five ganglia of the visceral chain being distinct and the left cerebro-pedal connective being longer than the right. These differences have been incorporated into the diagnoses presented here, but further anatomical study of Vertiginidae is warranted.

Subfamily VERTIGININAE

Diagnosis. Oviparous snails. Shell dextral or sinistral, less than 3 mm high; aperture armed with 1–11 barriers, exceptionally simple, its margin in adults thickened. Animal lacking inferior tentacles. Prostatic gland small, comprising one to several processes, fused to female pallial gonoduct to form a short spermoviduct. Epiphallus present. Phallus retractor undivided, inserted on apex of epiphallus. Male terminal genitalia without accessory organs. Central nervous system with right cerebro-pedal connective slightly shorter than the left, and ganglia of visceral chain not fused.

Remarks. Represented by a single genus, Vertigo Müller, 1774, with about 100 species widely distributed in the Holarctic region.

Genus Vertigo Müller

Vertigo Müller, 1774: 124, type species Vertigo pastila Müller, 1774, by monotypy [ICZN Opinion 335, 1955: 50, 59].

Pupa of authors. (Not Pupa of Röding, 1798, type Pupa grisebia Röding, 1798 = Voluta solidula Linnaeus, 1758, designated by Suter (1913) - synonym of Solidula Linnaeus, 1758; Acteonidae. Not Pupa of de Manet de Lamarck, 1801, type species Turbo ovata Linnaeus, 1758, by monotypy - synonym of Carion Röding, 1798; Cernuicidae. Not Pupa of Draparnaud, 1801, type species Pupa secula Draparnaud, 1801, by monotypy - synonym of Abula Turton, 1831; Caenidae.)

Zoones of author. (Not Zoones of de Montfort, 1810, type species Helis algera Linnaeus, 1758, by original designation; Zoontid).

Isthmia Gray, 1821: 239 (as a subgenus of Helis Linnaeus), type species Helis Isthmia) cylindrica Gray, 1821 = Vertigo pygmeus (Draparnaud, 1801), by original designation.

Alacea Jeffreys, 1830: 357, type species Alacea palustria Leach, in Turton, 1831 = Vertigo antivertigo (Draparnaud, 1801), selected by Gray (1847).

Staurodon Lowe, 1855: 214 (as a subgenus of Pupa), type Pupa pygmea Draparnaud, 1801, by original designation. (Not Staurodon of Lowe, 1852, type species Pupa saxicola Lowe, 1852, designated by Pilsbry (1918–20); Vertigidae.)


Haplopupa Pilsbry, 1898: 119 (as a section of Vertigo Müller), type species Vertigo dalliana Steer, 1890, by monotypy.

Diagnosis. As for the subfamily (see above).

Remarks. Zilch (1959–60) recognised five subgenera of Vertigo, characterised by the apertural barriers and general shape of the shell: Alloptyx Pilsbry, 1953; Angustula Sterki, 1888; Vertilla Moquin-Tandon, 1855; Vertilloidea Pilsbry, 1919; and Vertigo s.s. As proposed by earlier authors (e.g., Kennard & Woodward 1926), Zilch reduced many early subdivisions of the genus to synonymy with Vertigo s. str. This approach was followed by Schileyko (1984), except that he recognised Isthmia Gray, 1821 as being subgenerically distinct from Vertigo s.s. Following Taylor (1960), Bequaert & Miller (1973) reduced Angustula to a junior synonym of Vertigo s.s. In a detailed study of the Vertigo of Poland, Pokryszko (1990a) could find no anatomical characters supporting recognition of Vertilla as a separate subgenus. This finding lends weight to the suspicion that current subgeneric division in Vertigo is a matter of taxonomic convenience, with no phylogenetic basis. The sole species established in New Zealand, V. ovata (Suy, 1822), has shell characters consistent with the current definition of Vertigo s.s., and subgeneric divisions of Vertigo are not recognised here.

Vertigo is represented in North America by about 60 species, in Eurasia by about 30 species, and in Africa by 3–5 species.
Vertigo ovata (Say)

Figures 59, 91, 131, 132, 161, 187, 239, 254, C27, M24, M25; Map 24

pugmata of authors (not of Draparnaud, 1801).

ovata Say, 1822: 375 (Pupa).

antiquorum Cockerell, 1891b: 18 (as form of ovata Say) (Pupa).
diabolu Pilshy, 1919 (1918–20): 88 (as subsp. of ovata Say) (Vertigo).

mariipusa Pilshy, 1919 (1918–20): 88 (as subsp. of ovata Say) (Vertigo).

hibbardi Baker, 1938: 126 (Vertigo).

Shell (Fig. 59) dextral, ovate, from very short and broad to strongly elongate, perforate, up to 1.8–2.7 mm high by 1.2–1.7 mm in diameter, of 4.5–5.5 rounded whorls with deep sutures, glossy to almost matt yellowish brown to chestnut, with sculpture of fine growth lines. Protoconch (Fig. M24) of approximately 1.2 whorls, smooth in appearance but with fine, irregular reticulate sculpture under high magnification. Aperture (Fig. M25) nearly semicircular, in adults with margin continuous, white and slightly thickened, reflected in all but upper palatal section, internally with 4–6 white barriers; outer margin usually bent inwards slightly and bearing an auricle. Palatal wall with a prominent medial barrier. Columella with a prominent perpendicular fold or knob, base often with a small, knob-like barrier set somewhat deeper than other barriers. Palatal wall with 2 high medial lamellae extending about 0.2 of a whorl in depth; upper palatal wall often with a vestigial barrier. Upper body wall with external palatal crest a little behind aperture margin. Umbilicus open and deep but extremely narrow, rarely closed.

Animal with sides of foot, mantle collar, and sole pale grey and head, tentacles, and dorsal part of foot steel blue-grey. Tail moderately long, extending to level of shell apex in active animal.

Reproductive system, Fig. 91. Ovotestis grey, comprising 2 lobes each of 4–6 pear-shaped acini embedded in digestive gland. Hermaphroditic duct relatively short, proximally slender and not convoluted, medially distended and mildly contorted, then abruptly narrowing to form a U-shaped talon on ventral surface of the large, linguiform albumen gland. Female pallial gonoduct sacculated, thick-walled. Free oviduct long, narrowing to insertion of bursa copulatrix duct. Bursa copulatrix sac-like, elongate, appressed against lateral aspect of proximal spermoviduct, on a slender, long duct. Vagina very short, stout. Prostatic gland comprising 2–4 elongate acini, often partially fused, opening over a very short length of male pallial gonoduct. Prostatic gland fused with female tract to form a short spermoviduct. Free vas deferens slender, inserted in proximal apex of epiphallus adjacent to insertion of phallic retractor muscle. Epiphallus slender, widest proximally and narrowing gradually to insertion into phallus. Phallus elongate, about 2x length and width of epiphallus, distinctly dilated at entry of epiphallus, internally with a small conical vergic papilla and few longitudinal folds. Atrium short.

Spermatophores unknown, apparently not produced.

Phallus retractor arising from diaphragm, running to insertion on epiphallus as a single muscle strand.

Jaw (Fig. 131) 0.12 mm wide, strongly arched, comprising 13 or 14 fused plates, each finely strate.

Radula (Fig. 132) with about 86 transverse rows of teeth, each varying in formula around 20 or 21 + C + 20 or 21. Central tooth well developed, tricuspid, with a large mesocone flanked on either side by a minute accessory cusp and a large ectocone, on a large rectangular basal plate. First lateral teeth similar to the central, but mesocone shortened to same length as ectocone and endocone. Laterals grading into marginals by gradual reduction in length of primary cusps, division of minute accessory cusps, and shortening of basal plate. Teeth on extreme margin of nodular ribbon serrate.

Digestive tract, Fig. 161. Buccal mass spherical. Oesophagus long, slender, not differentiated into a crop. Gastric pouch cylindrical, extending about 0.5 of a whorl to merge with stomach, which is not externally differentiated. Intestine producing one forward loop and one posteriorly directed loop before running as rectum to anus in mantle collar.

Pallial complex, Fig. 187. Pulmonary cavity extending about 0.8 of body whorl, lacking all vascularisation but the primary vein. Kidney short, about as long as pericardium, sacculated, extending to about 0.8 of pulmonary cavity length by an elongate ureteric pouch, with excretory orifice laterally near anterior extremity. Closed retrograde ureter lacking, but a very short gutter directed towards lung top.

Free muscle system, Fig. 213. Columellar muscle dividing at origin into left and right branches. Left branch giving rise to stout buccal retractor before anteriorly dividing into ocular peduncle retractors and labial retractors. Right branch giving rise to tentacular and labial retractors before ramifying into a broad tail fan; branch to ocular peduncle crossing over phallus.

Central nervous system, Fig. 239. Cerebral commissure length about equal to cerebral ganglion width. Cerebral pedal connectives slightly longer than cerebral ganglion width, the right connective slightly shorter than the left. Pleural ganglia markedly closer to cerebral ganglia than to pedal ganglia. Parietal ganglia sited medially between pleural and visceral ganglia. Visceral ganglion slightly to
right of median plane, owing primarily to shortness of right cerebropleural connective.

Haploid chromosome numbers unknown.

Type material. Philadelphia, Pennsylvania was selected as type locality by Pilsbry (1918–20).

Distribution. V. ovata is widely distributed in its native North America, from Alaska and northern Canada southwards over most of the U.S.A. to Florida, the Gulf of Mexico, the Mexican border, and California. The only known naturalised occurrence outside of North America is New Zealand.

Recommended common name. Grassland whorl snail.


History in New Zealand. Barker (1982) stated that in the early 1980s V. ovata was unknown outside the Auckland region, basing this on records of Vertigo pygmaea (Draparnaud, 1801) from Auckland by Willan (1977) (see Remarks for identity of New Zealand V. pygmaea). However, Vertigo was first recorded in New Zealand by Whitten (1955) for a single shell collected from McGregor’s Bay, Whangarei in 1955. In addition, Mannering (1971) had reported on material from the Port Waikato area, Gardner (1977) from McGregor’s Bay (Whangarei Heads), Punguru (Hokianga Harbour), Waikaretu, and Te Aku, and Furey (1982) recorded Vertigo during an archaeological study at Whangapoua State Forest, Coromandel. Material examined in the course of the present study confirmed V. ovata to be widely distributed in the North Island, and to have been present outside the Auckland area before 1982.

Biology. Little information is available on the biology of Vertigo in New Zealand. All known populations are from pasture, grassy areas adjacent to forest, or grassy ledges on partially deforested limestone outcrops. V. ovata is widely distributed and known from a variety of habitats in North America, including woodland and grassland. According to Franzen & Leonard (1947), in Kansas V. ovata lives only in moist environs afforded by shaded slopes near streams and shores of ponds. Similarly, Requaert & Miller (1973) indicated that V. ovata in the acid southwest U.S.A. often lives in muddy litter and on damp logs or semiaquatic plants, close to the edge of ponds and shallow creeks. The available data on European Vertigo (e.g., Shileyko 1984, Walden 1969, 1971, 1986, Zeissler 1960, Pokryszko 1990a) suggests that the most widely distributed species exhibit regional preferences in habitat, particularly at the limits of their range.

Aspects of the reproductive biology of Vertigo have been described by Watson (1923), Steenberg (1925), and Pokryszko (1987, 1990a, b). Both self-fertilisation and outcrossing, the latter involving either euphallic or ephallic/aphallic partners, have been reported for Vertigo. Observations on five New Zealand V. ovata have, to date, been confined to collections made in January 1993 from grassland near Whatawhata. Five individuals from this population have been dissected and were found to be sexually mature, with fully formed male genitalia. Mating (Fig. 254) was observed twice between snails from this population; on both occasions copulation involved reciprocal insemination via everted phallic structures. Further study is needed to determine if this population — and indeed V. ovata — is dominated or constituted solely by euphallic individuals.

Mating was apparently initiated by one snail following and eating the mucus trail of another. The trail-layer was approached and palpated with the ocular peduncles, and its shell was mounted. In the two matings observed, several attempts at shell mounting were required for the snail initiating courtship to establish a firm hold and proper orientation. This phase took some 35–45 minutes, during which the individual receiving the attention showed no apparent interest, continuing to move about and feed. Eversion of the phallus and its tactile play over the head region, accompanied by secretion of a viscous mucus, initiated a response in the mounted individual, with cessation of movement and eversion of its phallus. Reciprocal intromission quickly ensued. Copulation lasted for 7–11 minutes, after which the phalluses were quickly retracted, the upper snail dismounted the lower individual, and both snails moved off to resume feeding as retraction of the phallus was completed.

Eggs of V. ovata have not been observed in the field in New Zealand. In the laboratory eggs were deposited singly on moist filter paper and among grass leaf litter. These
eggs were slightly oval, with a greater diameter between 0.5 and 0.55 mm, translucent, and gelatinous, and had no trace of calcium carbonate crystals.

**Remarks.** This small vertiginid, noted in the Northland and Auckland regions in the 1950s to 1970s, was referred to *V. pygmaea* (Draparnaud, 1801) (Whitten 1955, Manning 1971, Willan 1977, Gardner 1977). As noted by Barker (1982), comparisons with shell lots of *V. pygmaea* from Europe and *V. ovata* from North America—not of the type series—by Dr F.M. Climo (formerly MONZ) suggested that the New Zealand shells belong to the latter. Since 1982 further populations of *Vertigo* have been discovered in northern New Zealand. All New Zealand populations are characterised as follows: (1) A protoconch of rather flat apex and rapidly expanding whorls. (2) Moderately convex teleoconch whors without spiral striate sculpture. (3) Aperture with 4–6 barriers, always with only one (medial) parietal lamella, one columnellar lamella, and superior and inferior palatal plicae; when present, basal fold more subcolumnar than palatal. (4) Palatal plicae on an internal ridge associated with a more-or-less prominent crest on shell exterior. (5) Aperture margin slightly thickened, and reflected in columnellar and inital regions. (6) Peristome continuous. (7) Outer margin of aperture with an auricle, but inward bend weakly developed. On these shell characters the New Zealand stock is intermediate between the *V. ovata* group *sensu* Pilsbry (1948 (1939–48)) and *V. pygmaea* in the sense of Pilsbry (1948 (1939–48)) and Pokryszko (1990a).

The aperture in juvenile New Zealand shells is square in outline, cf. circular in *V. pygmaea*. The anatomy of the reproductive system in the New Zealand material departs from *V. pygmaea* and other European Vertigo (see Steenberg 1925, Schileyko 1984, Pokryszko 1990a) in the following combination of character states: very elongate phallus, very short epiphallus, and distal insertion of bursa copulatrix duct. To my knowledge no North America *Vertigo* has been studied anatomically, including the North American forms of *V. pygmaea*, so that no definitive conclusion on affinities of the New Zealand stock can be drawn. Assignment of the New Zealand populations to *V. ovata* is tentatively retained, pending anatomical investigation of North American taxa.

The bipartite structure of the phallus referred to by Pokryszko (1990a, b) is here interpreted as comprising a proximal epiphallus and a distal phallus, with only the latter everted during copulation. This is consistent with Steenberg (1925) and Schileyko (1984).

An introduction into the literature on *V. ovata* is provided by Pilsbry (1922–26, 1948 (1939–48)), Fransen & Leonard (1947), and Begnaert & Miller (1973).

---

**Family ZONITIDAE**

**Diagnosis.** Herbivorous or carnivorous aulacopod snails able to withdraw completely into the shell. Shell generally thin, glossy and translucent, globulose to strongly depressed or discoidal, ambiculate or imperforate. Posterior cardinal pit not overhung by a horn-like prominence. Mantle without prominent lobes reflected over shell. Sole divided into longitudinal zones, or undivided. Sepal pedal gland embedded in foot tissues. Buccal mass spherical (herbivores) to elongate (carnivores). Jaw oxygnathous, with a median anterior projection. Radula with aculate marginal teeth. Intestine with a single loop directed forwards, kidney triangular, less than twice length of pericardium. Ureter sigmoid, closed to pneumostome. Central nervous system with cerebro pedal connectives equal in length, or left connective the longer, 1.2–3x cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact. Haploid chromosome number 20–31.

**Remarks.** In the Zonitidae I recognise two subfamilies, Gastrodentineae and Zoniteae.

---

**Subfamily ZONITINAE**

**Diagnosis.** Shell minute to moderately large. Genital orifice located at some distance posterior to right ocular peduncle. Genitalia without a dart sac or epiphalic papilla. Bursa copulatrix duct without a diverticulum. Pleural ganglia close to pedal ganglia, on short but distinct pleural/ pedal connectives. Visceral chain compact, often with some ganglia fused. Haploid chromosome number 24–31.

---

**Genus Oxychilus Fitzinger**

*Helix* of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

*Zonites* of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix emarginata* Linnaeus, 1758, by original designation; Zonitidae.)

*Oxychilus* Fitzinger, 1833: 100, type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847) [ICZN Opinion 431, 1956: 350].

*Vitrea* of authors. (Not *Vitrea* of Fitzinger, 1833, type species *Glisculus (Helix) diaephyra* Studer, 1820, by monotypy [ICZN Opinion 335, 1955a: 50, 59]; Zonitidae.)

*Vortex* of authors. (Not *Vortex* of Beck, 1837 (1837–38), issued in synonymy of *Helicodonta* d’Audebard de Férussac, 1819, Helicidae, by Zich (1959–60), type designation not traced.)
**Polina Held,** 1838 (1837–38); 916, type species **Helix cellaria** Müller, 1774, designated by Hermannsen (1847).

**Hyalinia de Charpentier,** 1837: 13 (as subgenus of **Helix** Linnaeus), type species **Helix helix** Draparnaud, 1801, designated by Bourgainchaud (1889). (Not **Hyalinia** of Sowerby, 1820, listed in synonymy of **Vitrina** Draparnaud, 1801, Verrillidae, by Zilch (1959–80), designation not maed. Not **Hyalinia** of Schumacher, 1817, type species **Hyalinia pellucidula** Schumacher, 1817, by designation not maed. Not **Hyalinia** of Albers, 1857: 91 (as group of **Charopidae.**)

**Heliocella Gray,** 1847: 173, type species **Heliocella Müller,** 1774, by original designation. (Not **Helicella** d'Audebard de Férussac, 1821, type species **Helicella ericetorum** Müller, 1774 = **Helicella itala** (Linnaeus, 1758), designated by Hermannsen (1847) [ICZN Opinion 431, 1956: 359]; **Hylomastacidae.**)

**Amphidoxa** of authors. (Not **Amphidoxa** of Albers, 1850, type species **Helix maromella** Pflüger, 1845, designated by Pilshry (1893–95 (1890–95)); **Endodontidae.**)

**Vitrina** Albers, 1850: 66 (as group in **Helix** Linnaeus), type species **Helix cellaria** Müller, 1774, designated by von Martens (1860).

**Lucilla** Lovera, 1855: 177, type species **Helix cellaria** Müller, 1774, by original designation.  
**Aplostoma** Maquin-Tardon, 1855: 72 (as section of **Zonites** de Montfort), type species **Helix cellaria** Müller, 1774, designated by Lindboim (1927).

**Euhyalina** Albers, 1857: 91 (as group of **Hyalinia** de Charpentier, 1837), type species **Helix cellaria** Müller, 1774, by original designation.

**Zonites** of authors. (Not **Zonites** de Léman, 1862, type species **Helix natica** Müller, 1774, designated by Lindboim (1927).

**Flammulina** of authors. (Not **Flammulina** of von Martens, 1873, type species **Vitrina zebra** Lo Guillot, 1842, according to Pilshry (1893–95 (1890–95)); **Charopidae.**)

**Germotia** of authors. (Not **Germotia** of Hutton, 1853a, type species **Germotia pantherina** Hutton, 1852a, by monotypy; **Charopidae.**)

**Calymna** of authors. (Not **Calymna** of Hutton, 1884, type species **Amphidoxa cornula** Hutton, 1882, by monotypy – synonym of **Flammulina** von Martens, 1873, **Charopidae.**)

**Euhyalina** Taylor, 1907 (1906–14 (1902–21)); 18 (as subgenus of **Hyalinia** de Charpentier), cranided name (or **Euhyalina** Albers, 1857.

**Diagnosis.** Essentially vegetarian species, but with a tendency to predaceous feeding on snails and slugs. Shell small to medium-sized (diameter to 30 mm), thin, strongly depressed, with spire only slightly raised, umbilicate, with 4–7 rounded, gradually to rapidly expanding whors; aperture rounded to elliptical; lip thin, with no internal callus or barriers. Animal with glandular phalcycles and pits in right anterior skin. Foot long and narrow, with distinct pedal grooves and posterior caudal mucus pit; sole tripartite, in progression showing distinct waves over central area. Buccal mass tending to elongate. Jaw arched, smooth, with a central projection. Radula with marginal teeth elongate, aculeate. Intestine with a simple loop directed forwards. Kidney triangular, not much longer than pericardium. Ureter sigmoid, its secondary part closed to pneumostome. Genital orifice approximately midway between pneumostome and right ocular peduncle. Genitalia characterised by a proximal vaginal gland, an epiphallic tube sometimes with a small flagellum, entering phallus apically or subapically, and a muscular sheath about distal part of phallus, the latter typically enclosing terminal part of vas deferens. Bursa copulatrix duct simple, never long. Right ocular retractor passing between phallus and vagina.

**Haploid chromosome number** 24–30.

**Remarks.** The genus **Oxychilus,** represented by in excess of 300 species, occurs throughout Europe. The uniformity in shell form is remarkable, and reliable identifications are dependent on study of anatomy.  
On the basis of characters of the shell, radula, and genitalia, Forcatt (1957) and Riedel (1980) recognised respectively 8 and 22 subgenera of **Oxychilus.** Of relevance to the species established in New Zealand, both of them classified **O. draparnaudi** (Beck, 1837) in subgenus **Oxychilus** s.s., along with the type species **O. cellarius** (Müller, 1774), while **O. alliarius** (Müller, 1822) was classified in subgenus **Ortizius** Forcatt, 1957, typified by **O. helvetica** (Blum, 1881). In support of earlier observations (Manganello & Giusti 1985, Altonaga 1986, Manganello et al. 1991), de Brito (1992) has shown **Ortizius** to be a junior synonym of **Oxychilus** s.s.

The four **Oxychilus** species represented in Britain have been widely distributed through the trading activities of man. Three of these have established in New Zealand. The keys developed by Lloyd (1970b, c) for separation of the British **Oxychilus,** based on glandular features of the anterior body wall, can – in conjunction with shell characters – be usefully employed for identification of New Zealand material when live specimens are available but anatomical dissections are not practicable.

**Subgenus Oxychilus** Fitzinger

**Oxychilus** Fitzinger, 1833: 166, type species **Helix cellaria** Müller, 1774, designated by Hermannsen (1847).

**Mediterranea Clausin,** 1880a: 257 (as group of **Hyalinia** de Charpentier, group **Vitrina** Fitzinger), type species **Helix hydatina** Rossaínssler, 1838, by original designation.

**Hydatina Westerlund,** 1886 (1886–87): 29, 37 (as section of **Hyalinia** Charpentier, group **Vitrina** Fitzinger), type species **Helix hydatina** Rossaínssler, 1838, by monotypy. (Not **Hydatina** of Ehrenberger, 1828; **Rostheria.**)

**Hydatina de Maria di Monterosato,** 1892: 7 (as group of

Hyalina Wagner, 1907: 128, as amended name for Hyalina Westerlund, 1886.

Diaphanella Hesse, 1916: 124, new name for Hyalina Westerlund, 1886. (Not Diaphanella of Clossin, 1880, type species Glaischerius (Helix) diaphana Stoder, 1820, by original designation – synonym of Vinzenz Fitzinger, 1833; Zonitidae. Not Diaphanella of Thiele, 1912, type species Bulls fragilis Velain – synonym of Notodiaphana Thiele, 1917; Gastropoda, Diaphanidae.)


Retinella sensu Lindholm, 1927: 325, type species Helix fuscosa Rossmaessler, 1838, by original designation. (Not Retinella of Fischer in Shuttleworth, 1877, type species Helix alliariae Gnadin, 1791, designated by Kohelt (1880 (1876–81)); Zonitidae.)

Lindholmella Boettger, 1930: 580, type species Helix fuscosa Rossmaessler, 1838, by original designation; new name for Retinella sensu Lindholm, 1927.

Oxychilus Forcart, 1957: 123 (as subgenus of Oxychilus), type species Hyalina (Polita) helvetica Blum, 1881, by original designation.

Diagnosis. Central tooth tricuspid, narrow and generally shorter than adjacent lateral teeth. Vaginal gland enclosing basal part of spermathecal duct. Epiphallus opening subterminally into phallus.

Oxychilus (Oxychilus) alliarius (Miller)

Figures 60, 63, 92, 106, 133, 162, 188, 214, 240, 241, 240, 28, M26, M102, M103, M121, M122; Map 25

nitus of authors (not of Miller, 1774).

nition of authors (not of Gmelin, 1791).

alliarius Miller, 1822: 379 (Helix).

foetida Brown, 1827: figs 48, 52 (Helix).

remota Benson, 1851: 263 (Helix).

steenstrupii Mörch, 1857b: 75 (Helicella).

jansensis McLaughlan, 1854: 40 (Oxychilus).

Shell (Fig. 60) up to 3.5 mm high by 7 mm in diameter, strongly depressed, convex above, flattened below, of 4–4.5 rather rapidly expanding whorls, with suture moderately distinct. Coloration translucent pale yellowish brown to brown above, paler around umbilicus below, glossy, with weak, rather regular striations. Protoconch (Fig. M26) smooth. Umbilicus about 0.17 of shell diameter. Aperture slightly elliptical. Columella not reflected. Peristome thin.

Animal (Fig. 63) slate blue-black dorsally paling to grey at sides of foot; mantle collar grey; sole uniformly grey. Tail short, extending only a little beyond shell during locomotion. Locomotion by muscular pedal waves generated from posterior of sole. Mucus colourless. Phylacities well developed, densely clustered in body wall immediately anterior to mantle collar. Glandulae crypts in anterior body wall few and inconspicuous, confined to right side.

Reproductive system, Fig. 92. Ovotestis whitish, composed of a few clusters of acini scattered amongst lobes of digestive gland. Hermaphroditic duct long, slender, not convoluted, medially distended, ending in a talon partially embedded in basal portion of large, liguiform albumen gland. Spermoviduct multilobate, slender proximally but rather voluminous distally, narrowing abruptly to free oviduct. Vagina stout. Vaginal gland enclosing basal part of bursa copulatrix duct and vagina, extending almost to genital atrium. Bursa copulatrix reservoir elongate oval to globulous, on a slender duct that broadens towards its insertion on oviduct. Vas deferens slender, arising at distal end of spermoviduct prostatic portion, united with epiphallus amongst muscle fibres of phallus sheath. Epiphallus slender, inserted subterminally in phallus. Phallus elongate, cylindrical, with a poorly defined medial constriction below which it is enclosed by a thin muscular sheath, extending above insertion of epiphallus as a flagellum about 0.25 of length of phallus, internally the flagellum and region around epiphallus entry with slender pleats, and the distal phallus with papillate longitudinal folds. Atrium short.

Spermatophore (Fig. 106) a slender rod about 2.5 mm long, variably curved but always narrowed and pointed at ends, lacking elaborate external sculpture but with fine longitudinal striations.

Phallus retractor arising from diaphragm, inserted at apex of phallus flagellum.

Taw (Fig. 133) about 0.5 mm wide, with a prominent medial projection.

Radular ribbon (Fig. M102, 103) with about 35 transverse rows of rather large teeth, each with a formula varying around 9–12+2+2+4+2+1–12. Central tooth similar in size to first lateral tooth, tricuspid, with mesocone slender but prominent and ectocone rather weak. First 2 lateral teeth with mesocone and ectocone prominent, and ectocone weak; 3rd tooth transitional, with mesocone and endocone but lacking ectocone. Marginal teeth aculeate, unicusp, decreasing in size rapidly towards radular margin.

Digestive tract, Fig. 162. Buccal mass longer than broad. Oesophagus abruptly widening into a bulbus crop.
then briefly narrowing before producing a voluminous gastric pouch that extends approximately half a whorl. Ducts of digestive gland inserted on stomach at distal extremity of gastric pouch; typhlosoles arising from digestive gland ducts and running side by side for several millimetres into intestine. Intestine arising from stomach, producing an anteriorly directed loop which abuts posterior wall of kidney, then passing posteriorly a short distance before running forwards to mantle margin as a rather voluminous rectal duct.

Pallial complex. Fig. 188. Pulmonary cavity extending to about 0.35 of body whorl in active animal, thus about 2x longer than broad. Ventilation of mantle roof distinct but not strongly developed. Kidney triangular, with pericardium extending along left side. Uter? a sigmoid, closed tube arising near anterior apex of kidney extending to top of pulmonary cavity along right side of kidney, and then forwards against rectum to pneumostome.

Free muscle system. Fig. 214. Cephalic retractors, comprising buccal, left tentacular, and right tentacular stems, arising separately from very near origin of columnar muscle. Ocular retractors branching at approximately midway to run to ocular peduncle and inferior tentacle. Buccal retractor bifurcating before its insertion on buccal mass. Main columnar branch a short, broad muscular fan penetrating lateral and pedal tissues of foot.

Central nervous system. Fig. 240. Cerebral ganglia united by a very short but distinct commissure. Left cerebropleural connective slightly longer than the right, its length about 1.2x width of cerebral ganglion. Pleural ganglia close to pedal ganglia, to which they are united by short connectives; right pleural ganglion pressed to right parietal ganglion; left pleural ganglion united to left parietal by a short connective. Visceral ganglion to right of median plane, closely opposed to right parietal ganglion but separated from left parietal by a short connective.

Haploid chromosome number 30.

Type material. The type specimen originates from the environs of Bristol, England, and are presumed to be lost.

Distribution. Widely distributed as a native in northern and western Europe. Introduced into Greenland, North America, St Helena, South Africa, Juan Fernandez, Australia, and New Zealand.

Recommended common name. Garlic glass snail.


History in New Zealand. Musson (1891) recorded Zones nitidus Muller, 1774 (= Zonitoides nitidus) from New South Wales, Australia, and Auckland, New Zealand. In the present study its occurrence here could not be confirmed, and it appears that the New Zealand records of Musson should be referred to O. alliarius, as was done by Taylor (1906–14 (1902–21)). Barker (1982) recognised the error in Musson's identification but wrongly listed this record under O. cellarius (Muller, 1774). Both O. alliarius and Z. nitidus occur in Australia, and it is therefore highly probable that Musson's records of Z. nitidus from that country encompass both species.

The records of Musson (1891) and Taylor (1906–14 (1902–21)) indicate that O. alliarius was well established in the North Island by the early twentieth century. Suter (1913) indicated that it was to be found in conservatories and hothouses.

Biology. In its native range O. alliarius lives in forest and open habitats, among leaf litter and under stones. Chat-
Oxychilus (Oxychilus) cellarius (Müller)

Figures 61, 64, 93, 107, 134, 215, 241, C29, M27, M28, M104, M105, M123, M124; Map 26

cellarius Müller, 1774: 28 (Helix).
licinus of authors (not of Draparnaud, 1801).
mitiata of authors (not of Draparnaud, 1809).
nitens of authors (not of Michaud, 1831).
giaphyra Say, 1816: 8 (Helix).
corneo-fusia Pfeiffer, 1862: 148 (Helix).
sydneyensis Cox, 1864: 37 (Helix).
fariniscus Bourguignat, 1870 (1863–70): 11 (Zonites).
avariccus Bourguignat, 1870 (1863–70): 13 (Zonites).
cersa Bourguignat, 1877: 38 (Hyalinia).
menticeci Fagoi, 1890: 224 (Hyalinia).

Remarks. Taylor (1906–14 (1902–21)) illustrated and described a serrated ectosome on the lateral teeth of specimens of O. alliarius from Britain. In New Zealand material this cusp is not serrate, which is consistent with descriptions of O. alliarius from, for example, Australia (Laws 1966) and Spain (Casellejo 1985). Entry into the literature on O. alliarius is provided by Germain (1930), Pilsbry (1946 (1939–48)), Likharev & Rammel’meier (1952), Grucci (1969), and Casellejo (1985).

Shell (Fig. 61) of mature snails about 5 mm high by 10 mm in diameter, occasionally to 14 mm, strongly depressed, convex above, flattened below, of 5–6 rather rapidly expanding whorls, with suture virtually flush. Coloration translucent brown or yellowish above, paler around umbilicus below, glossy, with faint irregular growth lines. Protoconch (Fig. M27, 28) of about 1.5 whorls, smooth. Umbilicus about 0.15 of shell diameter. Aperture elliptical. Columella not reflected. Peristome thin.

Animal (Fig. 64) blue-grey dorsally, fading to almost white at foot margins; sole pale; mantle edge grey, speckled and spotted grey and brown. Mucus thin, colourless. Tail protruding a short distance in crawling animal. locomotion by muscular pedal waves generated from posterior of sole. Phylacites distributed over most of anterodorsal body wall, borne on tenuosities. Epithelial crypts absent from anterior body wall.

Reproductive system, Fig. 93. Osotestis whitish, composed of acini closely clustered about origin of hemaphrodite duct and embedded amongst lobes of digestive gland. Hemaphrodite duct long, slender, not convoluted, medially distended, ending in a diverticulate talon partially embedded in basal portion of large, Engiform alburnum gland. Spermoviduct multilobate, slender proximally but rather voluminous distally, narrowing abruptly to free oviduct; prostatolic follicles weak or absent in proximal part, but strongly developed distally. Vagina, extending almost to genital atrium. Bursa copulatrix reservoir elongate oval to globulose, on a slender duct that broadens towards its insertion on oviduct. Vasa deferentia slender, arising at distal end of spermoviduct prostate portion, united with epiphallus amongst muscle fibres of phallus sheath. Epiphallus rather short, not twisted, inserted subapically on phallus, broad immediately after origin in vasa deferentia but becoming slender in distal part. Phallus elongate, cylindrical, with a poorly defined medial constriction below which it is enclosed by a thin muscular sheath, extending above insertion of epiphallus as a short flagellum about 0.15–0.18 length of phallus body, internally covered with rather large papillae, which

Field (1975), for example, lists this species as a characteristic element of both grasslands and woodlands in Jersey. It also has been reported as a troglobite species (e.g., Evans & Jones 1973). In New Zealand O. alliarius occurs in a variety of modified habitats, including greenhouses, gardens, roadsides, hedgerows, parks, plantations, and pastures.

O. alliarius is primarily vegetarian, and gregarious. Frequently it attains pest status in greenhouses on tender plants such as ferns, and often occurs together with Zonitoides arboresus, which also damages plants. O. alliarius is also predatory on snails and snail eggs.

When disturbed O. alliarius liberates from gland cells in the mantle near the pneumostome an odour indistinguishable from that of garlic, hence the specific name (Latin: allium = garlic) and the vernacular name garlic snail. Lloyd (1969, 1970a, b) identified the principal volatile in the secretion as propyl mercaptan. In experiments using hedgehogs as predators, Lloyd showed that O. alliarius was rejected but other Oxychilus species, which do not produce the odour, were readily consumed. These results support the widely held opinion that the odour is a defensive adaptation produced on irritation.

The eggs are about 1 mm in diameter and white, owing to a calcareous shell (Fig. M121, 122).
in flagellum and around epiphallus entry fuse to form a series of small pleats, and in distal section tend to coalesce as longitudinal folds. Atrium short.

Spermatophore (Fig. 107) about 3 mm long, in general shape as for O. alliarius.

Phallus retractor as in O. alliarius.

Jaw (Fig. 134) about 0.8 mm wide, of similar shape to that in O. alliarius.

Radular ribbon (Fig. M104, 105) with relatively few teeth, each of the formula 12+3+4+3+4+12. Central tooth tricuspid, narrower and shorter than lateral teeth, with mesocoone shorter than basal plate, and ectocones very weak. Lateral teeth very large, conspicuously tricuspid. Marginal teeth thorn-shaped, without endocones or ectocones, the inner ones very large but diminishing in size rapidly towards edge of radula.

Digestive tract and pallial organs as for O. alliarius.

Free muscle system, Fig. 215. Cephalic retractors comprising buccal, left tentacular, and right tentacular stems, arising separately from dorsal aspect of broad tall fan, very near origin of columellar muscle. Ocular retractors branching anteriorly to run to ocular peduncles and inferior tentacles. Buccal retractor not markedly bifurcate before insertion on buccal mass.

Central nervous system, Fig. 241. Cerebral ganglia united by a very short but distinct commissure. Left cerebropedal connective longer than the right, its length about 1.5× width of cerebral ganglion. Pleural ganglia close to pedal ganglia, linked to pedal and parietal ganglia by short connects. Visceral ganglion closely appressed to right parietal ganglion but separated from left parietal ganglion by a very short but distinct commissure. Left cerebrotentacular connective longer than the right, its length about 1.5× width of cerebral ganglion. Pleural ganglia close to pedal ganglia, linked to pedal and parietal ganglia by short connects. Visceral ganglion closely appressed to right parietal ganglion but separated from left parietal ganglion by a short connective, lying to right of median plane.

Haploid chromosome number 24.

Type material. Miller's type material, collected from wine cellars in Copenhagen, is presumed to be lost.

Distribution. Native to western and central Europe and the western Mediterranean. Introduced to Scandinavia, North America, South America, the Philippines, South Africa, St. Helena, Australia, and New Zealand.

Recommended common name. Cellar glass snail.

History in New Zealand. *O. cellarius* was first recorded in New Zealand by Pfeiffer (1862), who described it as a new species, *Helix corneo-fulva*. Pfeiffer's species, collected from the Bay of Islands, was considered to be an element of the indigenous fauna by several New Zealand malacologists (e.g., Suter 1891, 1893a, Crosse 1893, Hedley & Suter 1893, Suter 1894) although Hutton (1883), Tryon (1886) and later Suter (1904) reduced it to synonymy with *O. cellarius*. The presence of *O. cellarius* in New Zealand was recognised by Musson (1891).

The records of Taylor (1906–14 (1902–21)), Longstaff (1912), Suter (1913), Thomson (1922), and others indicate that this species was widely distributed by the early part of the twentieth century.

**Biology.** In its native range *O. cellarius* occurs in a variety of moist, shaded habitats such as forests, cliffs and rock walls, parks, gardens, and caves (Evans & Jones 1973, Chatfield 1975). In New Zealand it is widely established in most modified habitats, and frequently in native forest adjacent to previous or existing human settlements.

Little information is available on the life cycle of *O. cellarius* in New Zealand but for the occurrence of eggs in spring. For an English population, Rigby (1963) demonstrated an annual cycle of growth and reproduction, with a peak of adults in late winter through to early spring, and juvenile recruitment in summer. In a drought-affected year Cameron (1982) found adults to be most abundant in summer and juveniles in autumn.

The oval eggs (Fig. M123, 124), of approximately 1.5 mm greater diameter, have a whitish calcareous shell, and are deposited in clusters in the soil. Newly hatched snails have a shell diameter of 2.0–2.5 mm.

*O. cellarius* is omnivorous. It preys on slugs and snails and their eggs (Taylor 1902–07 (1902–21); Cotton 1954, von Proschwitz 1994; G.M. Barker, unpubl. data), earthworms (Taylor 1902–07 (1902–21)), and slaters (Cotton 1954). High numbers of *O. cellarius* occur in some native forest habitats, and observations suggest that their predatory activities contribute to decline in indigenous snail populations. The author has observed *O. cellarius* feeding on the following indigenous snails in forest: *Chiacorea cona* (Gray, 1843), *Chiacorea roscoti* Climo, 1985, *Flammochacorea costulata* (Hutton, 1883), *Flammmulina cornea* (Hutton, 1882), *Cavellia buccinella* (Reeve, 1852), *Alloidiscus dimorphus* (Pfeiffer, 1853) and *Lama mariae* (Gray, 1843).

**Remarks.** There has been much confusion in the New Zealand literature regarding the status of *Helix corneo-fulva* Pfeiffer, 1862. Suter (1891) considered it to be a New Zealand indigenous species, in shell form nearer to *Aegopinella nitens* (Michaud, 1831) than to *O. cellarius*. Later, Suter (1904) reduced *H. corneo-fulva* to synonymy of *O. cellarius* (Miller, 1774), a decision confirmed by Climo (1984).


**Oxychilus (Oxychilus) draparnaudi** (Beck)


cellarius of authors (not of Müller, 1774).

*cellid* Draparnaud, 1801: 96 (not of Pultney, 1799) *(Helix, nitida* Draparnaud, 1805: 117 (not of Gmelin, 1791, nor of Müller, 1774); new name for *lucida Draparnaud* (Helix).

*draparnaudi* Beck, 1837 (1837–38): 6, an invalid original spelling for *draparnaudi* [ICZN Opinion 336, 1955]: 87; new name for *nitida Draparnaud* (Helix helicina).

observable of authors (not of Villa & Villa, 1841).

*subglobula* Bourguignat, 1860: 47 (Zonites).

*corneo-fulva* of authors (not of Pfeiffer, 1862).

*septentrionalis* Bourguignat, 1870 (1863–70): 17 (Zonites).

*pictonica* Bourguignat, 1870 (1863–70): 51 (Zonites).

*stechadus* Bourguignat, 1877: 38 (Zonites).

*stechadus* Faget, 1877: 37 (Zonites).

*calabrica* Paulucci, 1879: 44 (as variety of *Helix lucida* Draparnaud) (Hyalinia).

*federa* Bourguignat, 1880: 107 (Hyalinia).

*kraliki* of authors (not *Zonites kraliki* Letourneau, in litter, 1878; Servain, 1880).

*arcadiana* of authors (not *Zonites arcadimana* Servain, 1880).

*raternana* of authors (not *Zonites raternana* Servain, 1880).

*blaneri* Locard, 1882: 37 (not of Smette, 1845) (Hyalinia).

*porroi* Paulucci, 1882 (1882–83): 162 (Hyalinia).

*sectoptile* (not of de Stefani, 1879) var. *nojka* Paulucci, 1886: 11 (Hyalinia).

*sicula* (not *Helix sicula* Benoît, 1857) var. *valencienne* of authors (Montecossato, 1892: 6 (Hyalinia).

*sicula* (not *Helix sicula* Benoît, 1857) var. *melitensis* of authors (Montecossato, 1892: 6 (Hyalinia).

*bareacona* da Silva & Castro, 1894: 46 (Hyalinia).

*gyrocochus* Locard, 1884: 40 (Hyalinia).

*internimma* Locard, 1884: 41 (not *Hyalinia mirabilis* Mousson var. internimma Kobelt, 1879) (Hyalinia).

*macronensis* Locard, 1894: 42 (Hyalinia).

*mucrocutis* Locard, 1894: 46 (Hyalinia).

*hisoldiformis* Locard, 1899: 11 (Hyalinia).

*alganoensis* Locard, 1899: 12 (Hyalinia).

*achryphila* Locard, 1899: 15 (Hyalinia).

*milleriana* Locard, 1899: 16 (Hyalinia).

*chelis* Locard, 1899: 20 (Hyalinia).

*alpina* Suter, 1904: 62 (Flammulina).
Shell (Fig. 62) of mature snails about 6 mm high by 15 mm in diameter, strongly depressed, convex above, flattened below, of 6–7 rather rapidly expanding whorls, with growth lines often rather well defined and giving a slight wrinkled appearance, especially at suture. Coloration translucent, horn brown above, paler around umbilicus below, not very glossy. Protococh of about 1.5 whorls, smooth. Umbilicus about 0.13 of shell diameter. Aperture elliptical. Columella not reflected. Peristome thin.

Animal (Fig. 65) blue-grey, including sole, in which central zone paler than lateral zones; mantle edge dark grey, unspotted. Active animal with tail projecting slightly beyond shell. Locomotion by muscular pedal waves generated at posterior of sole. Mucus colourless. Phylactis distributed over greater part of anterodorsal body wall. Epithelial crypts numerous and conspicuous in skin grooves of right and dorsal aspects of anterior body.

Reproductive system, Fig. 94. Ovotestis elongate, composed of ovicell scattered along proximal hermaphroditic duct, which is embedded in posterior lobe of digestive gland. Hermaphroditic duct scarcely convoluted but medially distended, terminating in a diverticulate talon partially embedded at base of lingiform albumen gland. Spermovide duct narrow proximally, more ample and much folded distally; prostatic follicles weak or absent from proximal region but well developed distally. Free oviduct of moderate length. Bursa copulatrix reservoir small, oval, on a moderately long, slender duct. Vagina moderately long; vaginal gland conspicuous, massed around proximal vagina, concealing base of bursa copulatrix duct. Vas deferens long and very slender, abruptly enlarged to epiphallus after passing through muscular strands of phallus sheath. Epiphallus somewhat twisted, slender at each extremity but medially distended. Phallus elongate, cylindrical, enveloped in muscular sheath distal to pronounced median constriction, abruptly constricted at entry into atrium; above insertion of epiphallus with flagellate extension about 0.15 length of phallus; internally lined with papillae, these small in flagellum, mounded into pleats around entry of epiphallus, then somewhat larger and rounded in proximal phallus and weakly coalescing into longitudinal folds in distal phallus. Atrium short.

Spermatophore (Fig. 108) 3–3.5 mm long, similar in shape to that of <i>O. alliarius</i>.

Phallus retractor long, arising from diaphragm and with fibres from distal part of spermoviduct, inserted at apex of phallus flagellum.

Jaw (Fig. 135) 1.2 mm wide, in general shape like that of <i>O. alliarius</i>.

Radula (Fig. M106, 107) with 30 transverse rows of large teeth, each with the formula 11+2+4+3+2+4+11. Central tooth smaller than lateral teeth, tricuspid, with mesocone elongate and slender and ectocones weak. Lateral teeth, usually 3 in number, tricuspid. Next tooth transitional, lacking ectocone but frequently retaining endocone. Marginal teeth unicusp, aculeate, rapidly decreasing in size towards margin of radula.

Digestive tract and pallial organs as for <i>O. alliarius</i>.

Free muscle system, Fig. 216. Cephalic retractors, comprising buccele, left tentacular, and right tentacular stems, arising separately from very near origin of colomellar muscle. Occular retractors branching anteriorly to run to ocular peduncles and inferior tentacles. Buccal retractor not bifurcating before insertion on buccal mass. A broad, muscular fan arising ventrally from buccal retractor stem and penetrating lateral and ventral pedal tissues.

Central nervous system, Fig. 242. Cerebral ganglia united by a very short but distinct commissure. Left cerebro-pedal connective slightly longer than the right, its length about 1.2X width of cerebral ganglion. Pleural ganglia close to pedal ganglia, linked to pedal and parietal ganglia by short connectives. Visceral ganglion to right of median plane, closely appressed to right parietal ganglion but separated from left parietal by a short connective.

Haploid chromosome number 24.

Type material. Described by Draparnaud (1801), with France as type locality. Syntypes NHMW Acq. No. 1820, xxvi.143 (6 specimens), from unknown locality.

Distribution. Native to western Europe and the Mediterranean. Introduced to Russia, North America, South and North Africa, Asia, Australia, and New Zealand.

Recommended common name. Draparnaud’s glass snail.
History in New Zealand. *O. draparnaudi* has long been established in New Zealand but has generally been overlooked. Barker (1982) reported this species to be widely distributed, especially in the North Island. Climo (1984) showed that the *Flammulina alpina* of Suter (1904) is assignable to *O. draparnaudi*, indicating that the species has been in New Zealand since at least 1884, the year Suter’s material was collected in the Nerger Range.

Biology. In Britain *O. draparnaudi* is strongly synanthropic (Kenney 1966), but little is known of its biology in New Zealand. It is most commonly encountered here in gardens, but populations are also recorded from exotic plantations, grassy wasteland, and disturbed native forest habitats. Observation of populations in gardens confirms the gregarious and strictly geophilous nature of this species, alluded to by Taylor (1906-14 (1902-21)).

Mating and egg laying have been observed during spring at several North Island localities. The eggs are oval, of 1.5 mm greater diameter, with a white calcareous shell. According to Taylor (1906-14 (1902-21)) *O. draparnaudi* in Britain matures in the first few months of its second year, and produces 30–50 eggs during the 6-month period from spring to autumn. Similarly, Frest & Sanders Rhodes (1982) found eggs and young to be present from spring to fall in Iowa, U.S.A. In contrast, Rigby (1963) reported that English *O. draparnaudi* produces eggs during the autumn and winter months, while Rondelaud (1980) reported an annual life cycle in France, with maximum abundance of juvenile snails in spring.

*O. draparnaudi* is omnivorous, but with strong predatory tendencies: molluscs and their eggs can form a significant part of the diet (Rondelaud 1980, Frest & Sanders Rhodes 1982, von Proschwitz 1994). Like *O. cellaria*, this species may be implicated in the decline of indigenous snail populations in some habitats. Impact on native faunas, following introduction of *O. draparnaudi* into Iowa, has been suggested by Frest & Sanders Rhodes (1982).

Remarks. The synonymy of *Flammulina alpina* Suter, 1904 with *O. draparnaudi* (Beck, 1837) was proposed by Climo (1984).


Genus Vitrea Fitzinger

*Helis* of authors. (Not *Helis* et Linnæus, 1758, type species *Helis pomatia* Linnæus, designated by de Montfort (1830); Helicidae.)

*Zonites* of authors. (Not *Zonites* de de Montfort, 1810, type species *Helis alpina* Linnæus, 1758; by original designation; Zonitiidae.)

*Helicella* of authors. (Not *Helicella* d’Aubucourt de Fèresassac, 1821, type species *Helis cricetorum* Müller, 1774 = *Helicella itala* (Linnæus, 1758), designated by Hermannsen (1847) [ICZN Opinion 451, 1956: 350]; Hygromiidae. Not *Helicella* of Gray, 1847, type species *Helis cellaria* Müller, 1774, by original designation - synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae.)


*Oxychilus* of authors. (Not *Oxychilus* de Fitzinger, 1833, type species *Helis cellaria* Müller, 1774, designated by Hermannsen (1847); Zonitiidae.)

*Hyalina* of authors. (Not *Hyalina* de Charpentier, 1837, type species *Helis lucida* Draparnaud, 1821, designated by Bouguignat, 1890 – synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae. Not *Hyalina* of Studer, 1820, listed in synonymy of *Vitrina* Draparnaud, 1801, Vitrinidae, by Zilch (1959-60), type designation act traced. Not *Hyalina* of Schuhmacher, 1817, type species *Hyalina peloucida* Schuhmacher, 1817, by monotypy; Gastropoda, Marginellidae. Not *Hyalina* of Ramsur, 1866, Lepidostega.)

*Polita* of authors. (Not *Polita* of de Held, 1837 (1837-38), type species *Helis cellaria* Müller, 1774, designated by Hermannsen (1847) – synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae.)

*Hyalina* of authors. (Not *Hyalina* de Albers, 1859, type species *Helis cellaria* Müller, 1774, designated by von Martens (1860) – synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae.)

*Crystallina* Lowe, 1855: 178 (as subgenus of *Helis* Linnæus), type species *Helis crystallina* Müller, 1774, by monotypy. *Aplostoma* of authors. (Not *Aplostoma* of Moquin-Tandon, 1855, type species *Helis cellaria* Müller, 1774, designated by Lindholm (1927) – synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae.)

*Discella* Gray, 1837: 98, type species *Helis crystallina* Müller, 1774, by monotypy.

*Lathyrella* of authors. (Not *Lathyrella* of Albers, 1857, type species *Helis cellaria* Müller, 1774, by original designation – synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae.)

*Diaphanella* Clessin, 1880a: 206, type species *Glischrus* (*Helis*) *diaphana* Studer, 1820, by original designation. (Not *Diaphanella* of Hess, 1916, as new name for *Hyalina* Westerlund, 1886 – synonym of *Oxychilus* Fitzinger, 1833; Zonitiidae. Not *Diaphanella* of Thiele, 1912, type species *Bulla fragilis* Vělink – synonym of *Notodiaphana* Thiele, 1917; Gastropoda, Notodiaphanidae.)

type species *Natica fluctuata* Sowerby, 1825, by original designation; Gastropoda, Naticidae.)

Cristallinus Wagner, 1907: 101, emended name for *Crystallus* Lowe.

**Diagnosis.** Animal able to withdraw fully into shell. Shell small, 2.5–4 mm diameter, strongly depressed, with spire slightly raised, colourless, glassy and transparent, umbilicate or imperforate, of numerous very tightly coiled whorls, not flaring towards rounded aperture; peristome thin, often with an internal callus. Animal largely vegetarian, with a tendency to predaceous feeding on snails. Buccal mass spheroidal. Jaw arched, with a broad medial projection. Radula with marginal teeth aculeate. Intestine with a single loop directed forwards. Foot narrow, with a small caudal mucous depression at posterior; sole undivided. Mantle with small shell lobes. Kidney elongate, triangular. Genital orifice near right inferior tentacle. Genitalia characterised by vaginal gland enveloping proximal vagina, and a simple cylindrical phallus containing variously developed frilled or spinose stimulatory pads and a pseudopapilla not traversed by the vas deferens. Bursa copulatrix reservoir vestigial, very small, on a short, simple duct. Epiphallus absent. Right ocular retractor passing between phallus and vagina.

Haploid chromosome number 20.

**Remarks.** *Vitrea* is represented by over 50 species in the region from the Atlantic islands to Scandinavia, Caucasus, and Northern Africa.

**Subgenus Vitrea**

**Diagnosis.** Shell narrowly umbilicate or imperforate; whorls increasing gradually in diameter; aperture narrow, halfmoon-shaped.

**Vitrea (Vitrea) crystallina** (Müller)

Figures 66, 95, 139, 163, 189, 217, 243, C31, M29, M30, M108, M109; Map 28

*crystallina* Müller, 1774: 23 (*Helix*).

*subterraneus* Bourguignat, 1856a: 275 (*Zonites*).

*humicola* Mabille, 1870b: 128 (*Zonites*).

*andreaei* Boettger, 1880: 37 (*Hyalinia (Vitrea)*).

*podolica* Clessin, 1880a: 201 (*Hyalinia*).

*secretus* Bourguignat, 1880: 25 (*Zonites*).

Shell (Fig. 66) to 4 mm in diameter by 2 mm high, strongly compressed, with spire slightly raised, of 4.5–5 closely coiled, rounded whorls, very finely and minutely striate with growth lines, slightly pucker at suture, glassy and transparent, colourless or tinged with green. Umbilicus rather narrow, about 0.12–0.15 of shell diameter, a little eccentric in last whorl. Protoconch (Fig. 29, 30) about 1.5 whorls, smooth except for very fine spiral striae, especially towards periphery. Aperture rounded, in mature specimens with a distinct internal whitish thickening or rib set back a little from sharp peristome.

Animal semi-transparent greyish white, slightly darker dorsally than at sides; mantle collar thin, transparent, finely speckled white; sole whitish; retractor muscles dark grey to black, showing through skin. Tail short, not extending beyond shell in active animal.

**Reproductive system.** Fig. 95. Ovotestis white, composed of acini clustered as an elongate mass embedded in digestive gland. Hermaphrodite duct moderately long, convoluted, distended medially, terminating with a diverticulum in large albumen gland. Spermoviduct rather voluminous; prostatic follicles absent or weakly developed in proximal part but strongly developed as an elongate ribbon over the greater part. Free oviduct very short, slender. Vagina rather long, differentiated into 3 sections: proximal third very slender, like that of free oviduct; medial section broad and somewhat bulbous, its walls heavily invested with glandular tissue; distal section broad, narrowing to atrium. Bursa copulatrix reservoir a very small elliptical vesicle borne on a short, stout duct. Vas deferens long, slender, inserted in apex of phallus adjacent to attachment of phallus retractor. Epiphallus absent. Phallus elongate, cylindrical, without a sheath, internally with a small, conical to bulbous pseudopapilla near entry of vas deferens and a frilled stimulator pad in proximal section. Atrium short; slender.

Spermatophore unknown, probably not produced. Phallus retractor arising as a branch of colunmellar muscle.

Jaw (Fig. 136) about 0.28 mm wide, slightly arched, with medium projection very broad and lateral extremities rounded.

Radular ribbon (Fig. M108, 109) with about 80 transverse rows of teeth, each varying around the formula 16–18+1+2+C+2+1+16–18. Central tooth on a quadrate base, tricuspid, with mesocone strong, elongate, extending beyond basal plate, and ectocones small. Lateral teeth also on quadrate basal plates, the first two tricuspid with prominent mesocone, endocone and ectocone. Third lateral tooth transitional, with a prominent endocone and mesocone, but ectocone very weak or absent. Marginal teeth elongate, unicuspis, aculeate, on slenderly rectangular to triangular basal plates, decreasing in size towards margin of radula.
Digestive tract, Fig. 163. Buccal mass slightly longer than wide. Oesophagus slender, moderately long, running directly to voluminous, cylindrical crop which occupies last third of body whorl and more than half of penultimate whorl. Stomach sacular, not constructed or externally differentiated from crop. Intestine arising from stomach between ducts of digestive gland, passing briefly along inner, columnar wall of crop before turning forwards to produce an anterior loop abutting kidney, then a short posterior loop among lobes of digestive gland, and again turning forwards to run to anus in mantle collar.

Pallial complex, Fig. 189. Pulmonary cavity occupying about 0.65 of body whorl, about 3.5x longer than wide. Kidney large, triangular, its longest axis parallel to pericardium, extending about 0.3 of length of pulmonary cavity. Ureter arising lateral to anterior apex of kidney, extending along anterior margin of kidney and then along rectum, closed to pneumostome. Vascularisation of mantle roof poorly developed. A glandular mass occupying anterior mantle roof adjacent to mantle collar.

Free muscle system, Fig. 217. Cephalic retractors, comprising buccal, left tentacular, and right tentacular stems, arising separately from very near origin of columnar muscle. Ocular retractors branching anteriorly to run to ocular peduncles and inferior tentacles. Buccal retractor bifurcating shortly before its insertion on buccal mass. A broad, muscular fan arising ventrally from buccal retractor to penetrate lateral and ventral pedal tissues.

Central nervous system, Fig. 243. Cerebral ganglia united by a very short but distinct commissure. Left cerebropedal connective markedly longer than the right, its length about 2x width of cerebral ganglion. Pleural ganglia united to pedal and parietal ganglia by short connectives. Visceral ganglion, closely appressed to right parietal ganglion but separated from left parietal by a short connective, lying to right of median plane.

Haploid chromosomes number 20.

Type material. The whereabouts of the type specimens, from near Copenhagen, Denmark, is unknown.

Distribution. Throughout the British Isles, western and central Europe, Scandinavia, and northern Africa. Introduced to South Africa, Australia, and New Zealand.

Recommended common name. Crystal snail.


History in New Zealand. First recorded from New Zealand by Crosse (1893), without a locality. Known only from Auckland in the early part of the twentieth century (Suter 1913, Thomson 1922). Now widely distributed in New Zealand but poorly represented in collections.

Biology. Knowledge of this species, summarised by Taylor (1906-14 (1902-21)) and Kuiper (1964), is very sparse, owing principally to its litter-dwelling and subterranean habit restricting observations of the living animal, but also to its confusion with V. contracta (Westerlund, 1871). In its native European range V. crystallina is characteristic of moist sites such as wet grassland, marshes, stream banks, and woods (e.g., Kerney & Cameron 1979), and caves (Evans & Jones 1973). It is tolerant of oligotrophic conditions such as oceat peat bogs. The snails form a thin, transparent epiphragm to adhere to sand grains and other small particles, and thus close over the shell aperture to conserve moisture.

V. crystallina feeds upon decaying vegetable matter and preys on other small snails.

Remarks. In the older literature V. crystallina had often not been distinguished from V. contracta. Many early authors regarded V. contracta as a variety of V. crystallina or as being synonymous with it. Summaries of characters distinguishing V. crystallina and V. contracta are provided by Kuiper (1964), Kerney & Cameron (1979), and Altonaga (1989a).

Entry into the literature on V. crystallina is provided by Germain (1930), Likharev & Rammel 'meier (1952), Kuiper (1964), Pintor (1968, 1972), and Altonaga (1989a).

Subfamily GASTRODONTINAE

Diagnosis. Zonitidae in which the shell is globulose to strongly depressed, umbilicate, the aperture frequently with barriers or an internal callus. Sole uniform; progression not by muscular waves but arhythmic. Genital orifice...
situated a considerable distance from right ocular peduncle. Phallus with a dart sac containing a dart (sometimes absent in minute forms) and an epiphallus. From a sheath around base of phallus a duct runs to free oviduct, either directly (Gastrodonta, Janulus) or indirectly by way of anterior part of bursa copulatrix duct (Zonitoides, Ventridens). Phallus, ovicinct, and bursa copulatrix duct arising from rather long atrium in close proximity; vagina very short or absent. Right ocular retractor passing to left of genitalia. Radula with lateral teeth lacking endocones, bicuspoid or unicuspid; outer marginal teeth unicuspid; outer marginal teeth unicuspid, aculate.

Remarks. A discussion on the nomenclatural history and generic characteristics of Tryon’s subfamily Gasrodontinae is provided by Pilsbry (1946 (1939–48)).

The subfamily is primarily North American, and comprises the following genera (Zilch 1959–60): Pseudohyalus, Janulus, Ventridens, Oxychilus, and Ochylus. The latter genus was established to accommodate the type species Helix arboreus (Say, 1816).

### Genus Zonitoides Lehmann

_Helix_ of authors. (Not _Helix_ of Linnaeus, 1758, type species _Helix pomatia_ Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

_Zoniotes_ of authors. (Not _Zoniotes_ de Montfort, 1810; type species _Helix alpestris_ Linnaeus, 1758, by original designation; Zoniidae.)

_Omphalina_ of authors. (Not _Omphalina_ of Rafinesque Schmaltz, 1831; type species _Omphalina corniculata_ Rafinesque Schmaltz, 1831, by monotypy; Zoniidae.)

_Ochylus_ of authors. (Not _Ochylus_ of Fitzinger, 1833; type species _Helix collaris_ Müller, 1774, designated by Hermannsen (1847); Zoniidae.)

_Hyalina_ of authors. (Not _Hyalina_ of de Charpentier, 1837 (as subgenus of _Helix_ Linnaeus), type species _Helix lucida_ Draparnaud, 1801, designated by Bourguignat (1890) – synonym of _Ochylus_ Fitzinger, 1833; Zoniidae. Not _Hyalina_ of Studer, 1820, listed in synonymy of _Vitrina_ Draparnaud, 1801, _Vitrinidae_, by Zilch (1859–60), type designation not traced. Not _Hyalina_ of Schmacker, 1817, type species _Hyalina ochylus_ Schmacker, 1817, by monotypy; _Zoniidae_. Not _Hyalina_ of Rumph, 1806; _Lapidotheca_.)

_Poliii_ of authors. (Not _Poliii_ of Helck, 1837 (1837–38), type species _Helix collaris_ Müller, 1774, designated by Hermannsen (1847) – synonym of _Ochylus_ Fitzinger, 1833; Zoniidae.)

**Zonitoides Lehmann, 1862:** 111, type species _Helix nitida_ Müller, 1774, by monotypy [ICZN Opinion 335, 1955a: 59, 59].

**Zonitoides** Baker, 1928: 37, type species _Helix arboreus_ Say, 1816, by original designation.

**Alienitor** Iredale, 1937: 6, type species _Helix lyndhurstensis_ Coxe, 1868 = _Helix arboreus_ Say, 1816, by original designation.

**Diagnosis.** Herbivorous species. Animal able to withdraw fully into shell. Shell small, diameter 4–8 mm, thin, depressed, umbilicate, slightly or distinctly striate above, rarely ribbed, composed of 3.5–4.5 convex, regularly increasing whorls; aperture rounded, lunate, lip thin, with no internal callus or barrier. Foot long and narrow, with distinct pedal grooves and a narrow slit-like caudal pit. Buccal mass spheroidal. Jaw oxygnathic, with a central projection. Radula with marginal teeth elongate, bicuspoid or unicuspid. Intestine with a single loop directed forwards. Genital orifice just above pedal groove, slightly behind anterior edge of visceral stalk. Genitalia characterised by a rather long atrium into which open free oviduct, bursa copulatrix, and phallus. Male genitalia with a short, apical epiphallus and usually a large lateral dart sac bearing 1 or 2 small glands. Bursa copulatrix duct bifurcate, one branch running to atrium, the other to base of phallus. Left cerebropedal connective longer than the right, its length 1.5–2x width of cerebral ganglion. Pleural ganglia close to pedal ganglia, on short but distinct pleural–pedal connectives. Visceral chain compact, but ganglia never fused.

Haploid chromosome number 30.

Remarks. Practically Holartic in distribution. Several species have been widely distributed through the activities of man.

Two subgenera were recognised by Pilsbry (1946 (1939–48)), _Zonitoides_ Lehmann s.s. and _Pseudohyalus_ Baker, 1929.

**Subgenus Zonitoides**

**Diagnosis.** Shell glossy, with only weak sculpture.

**Zonitoides (Zonitoides) arboreus** (Say)

Figures 67, 96, 137, 164, 190, 218, 244, C32, M31, M110–112, M125, M126; Map 29

_arboreus_ Say, 1816: pl. 4, fig. 4 (_Helix_). _tononis_ Pfeiffer, 1840: 251 (_Helix_).

_breweri_ Newcomb, 1864: 218 (_Helix_).

_whitneyi_ Newcomb, 1864: 218 (_Helix_).

_lyndhurstensis_ Coxe, 1868: 18 (_Helix_).

_viridula_ Cockerell, 1888: 257 (as var. of _arboreus_ Say) (_Hyalina_).

_roseni_ Lindholm, 1911: 98 (_Hyalina_ (Polina)).

_lyndhurstoides_ McLaughlan, 1934: 40 (_Alienitor_).
Shell (Fig. 67) up to 3 mm high by 6 mm in diameter, depressed, of about 4.5 moderately convex and regularly increasing whorls, translucent olive buff, glossy in appearance but weakly sculptured with growth wrinkles and extremely faint, minute spiral striac, the base smoother. Protoconch (Fig. M31) of 1.5 whorls, smooth but for microscopic growth lines and spiral striae at periphery. Umbilicus about 0.2 of shell diameter. Aperture deeply lunate, wider than high. Columella scarcely reflected. Peristome thin.

Animal bluish-grey to blackish above and on ocular peduncles and inferior tentacles, paler and often speckled brown or white towards foot edges; mantle collar slate grey flecked with white; sole white or grey. Active animal with tail long, extending beyond posterior limit of shell. Locomotion arhythmic.

Reproductive system, Fig. 96. Ovotestis consisting of 3 groups of clavate acini embedded in digestive gland. Hermaphrodite duct weakly convoluted, terminating in albumen gland with a bulboous diverticular talon. Albumen gland large. Spermoviduct sacculately swollen, particularly at distal end; prostatic gland long, but alveoli absent at proximal end. Free oviduct rather long. Bursa copulatrix reservoir spherical, on a long, slender duct which bifurcates anteriorly to atrium and base of phallus. Vas deferens short, slender, passing directly to slender apex of epiphallus. Phallus retractor arising from fork of bursa copulatrix duct, inserted at apex of dart sac. Lateral teeth bicuspid, with an elongate mesocone and small ectocone, on quadrate basal plates. Marginal teeth elongate, sword-like, unicuspid, on elongate basal plates.

Digestive tract, Fig. 164. Buccal mass spheroidal. Oesophagus long and slender; crop absent. Stomach extending about 0.4 of a whorl, cylindrical, broadening to gastric pouch, with 2 ducts to digestive gland. Intestine with a short, anteriorly directed loop abutting kidney before producing a short posterior loop embedded in digestive gland, then finally running forwards to anus in mantle collar.

Pallial complex, Fig. 190. Pulmonary cavity nearly 3x longer than wide, extending in live animal to about 0.7 of body whorl, with weak but distinct venation. Kidney triangular, its greater axis parallel to lung axis. Ureter sigmoid, considerably distended, closed to pneumostome.

Free muscle system, Fig. 218. Columellar muscle subtending near its origin separate branches to buccal mass and right cephalic region, the latter promptly dividing into tentacular and somewhat heavier lateral retractors; left tentacular retractor branching off more anteriorly from stem which forms combined left lateral retractor and tail retractor. Right ocular retractor crossing over phallus to reach ocular peduncle.

Central nervous system, Fig. 244. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives long, exceeding 1.5x width of cerebral ganglion; right connective shorter than the left. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact, but ganglia neither closely appressed nor fused together. Visceral ganglion lying to right of medium plane.

Haploid chromosome number unknown.

Type material. Described from North America without precise type locality; Baker (1933) thought that Say's material originated from Philadelphia.

Distribution. Z. arboreus appears to be native over the entire Nearctic region, extending to the tropics of Central America. Introduced into Hawaii, Israel, Kenya, South Africa, Madagascar, Mauritius, Hong Kong, South America, Europe, Macao, Scandinavia, Russia, Australia, and New Zealand.

Recommended common name. Orchid snail.


History in New Zealand. Recorded in New Zealand under the name *Zonitoides nitida* (Müller, 1774) by Cotton (1954). The earliest New Zealand collection date for material examined in this study was 1952.  

Biology. In its native range *Z. arboreus* occurs from sea level to altitudes of about 3800 m (Bequaert & Miller 1973). Primarily a woodland or forest snail, *Z. arboreus* has become widely established in cultivated habitats in North America (Goodrich & van der Schalie 1944, Robertson & Blakeslee 1948, Hubricht 1985) and, as a consequence, has been distributed to many parts of the world with plant material. In particular it is associated with greenhouse floricultural crops (Meuse & Hubert 1949, Karlin 1956, Karlin & Naegle 1960, Kerney & Cameron 1979), where it can be a significant pest (Karlin & Naegle 1960, Davidson 1962, Chadwick 1970, Moens 1977, Moran & Katzir 1979, Verdouw 1979, Mioniis 1980, Barker 1986).  

In New Zealand this species is largely confined to greenhouses, where it is frequently found damaging tender plants such as orchids and ferns (Barker 1986, Martin & Workman 1988). In northern areas such as Whangarei, Auckland, and Hamilton *Z. arboreus* has also established outdooors in gardens.  

The biology of *Z. arboreus* has been studied in New Zealand orchid houses and in the laboratory by Dr J. Dymock, who kindly provided the following information. Snails reach sexual maturity at a shell width of 3.6 mm. Fertile eggs can be produced from self-fertilisation. The eggs, about 1 mm in diameter and white, owing to a calcaceous shell (Fig. M125, 126), are laid in clutches of 4–6 in damp litter and bark potting medium. The duration of the egg stage ranges from 5 to 9 days at 25°C. The period from eclosion to egg production for snails reared in a bark medium on lettuce diet ranges from 25 weeks at 15°C, through 8 weeks at 20°C, to 5 weeks at 25°C. The lower threshold for development was estimated to be 12.5°C.  

There were no seasonal trends in age-class distribution (measured by shell width) in snail populations in greenhouse orchids. All sizes of snail were found to be present at any one time, and there was no apparent synchronisation in size distribution from one greenhouse to the next.  

Bartsch & Quick (1926) recorded cross-fertilisation in *Z. arboreus*, where by "... one animal acts as male only and the other as female only. There is, therefore, not a reciprocal fertilization ....".  

Remarks. Entry into the literature on *Z. arboreus* is provided by Pilsbry (1946 (1939–48)), Likharev & Rammel'meier (1952), Waldén (1953), and Bequaert & Miller (1973).  

---  

REFERENCES


Backhuys, W. 1975: Zoogeography and taxonomy of the land and freshwater mollusks of the Azores. Amsterdam, Backhuys & Meesters. xii + 350 pp. 2 pls.


1857: Aménités malacologiques 1: 140–144.


1880: see Servain 1880.


1882: see Locard 1882.


Bruck, J.B. 1960: Some snails and slugs of quarantine significance to the United States. U.S. Department of
Agriculture Agricultural Research Service bulletin no. 82-1. iv + 73 pp.


and their allies.


—— 1891a: Notes on slugs, chiefly in the collection at the British Museum. Annals and magazine of natural history (ser. 6) 7: 97–107, 328–341.


—— 1891c: Notes on Arion hortensis, A. circumscriptus, and their allies. The conchologist 1: 49–52.


—— 1893: A check-list of the slugs, with appendix and notes by Walter E. Collinge. The conchologist 2: 168–176, 185–232.


d'Audebard de Férussac, J.B.L. 1814: Mémoires Géologiques sur les terriers formés sous l'eau douce par les débris fossiles des Mollusques vivant sur la terre ou dans l'eau non salée. Paris. 76 pp, 4 pls.


da Costa, F.M. 1778: Historia naturalis testaceorum Britanniae, or, the British conchology; containing the descriptions and other particulars of natural history of the shells of Great-Britain and Ireland. London, Millan, White & Elmsley. xii + 254 + vii pp., 17 pls.


— 1894: see Locard 1894.


de Cristofori, G.; Jan, G. 1832: Catalogus in quatuor sectiones divisus rerum naturalium in Museo exstantium Josephi De Cristofori et Georgii


Franzen, D.S.; Leonard, A.B. 1947: Fossil and living Pup-1986:
Frest, T.J.; Sanders Rhodes, R. 1982: Notes on the predaceous habits
1976: Die Cochlicellinae
Forcart, L. 1957: Taxonomische Revision paläarktischer
Foord, M. 1990: The New Zealand descriptive animal
Foltz, D.W.; Ochman, H.; Selander, R.K. 1984: Genetic
Foltz, D.W.; Ochman, H.; Jones, J.S.; Evangelisti, S.M.;
1822: Philosophy of zoology, or a general view of
Focardi, S.; Quattrini, D. 1972: Structure of the repro-
Fleming, J. 1813: Conchology.
Flasar, I. 1977: 
Fitzinger, L.J.F. 1833: 
Focardi, S.; Quattrini, D. 1972: Structure of the repro-
Focardi, S.; Quattrini, D. 1972: Structure of the repro-
Foltz, D.W.; Ochman, H.; Jones, J.S.; Evangelisti, S.M.;
189. 
Follminger, E. 1954: Biologie der Mitteleuropäischen
Furey, L. 1982: An archaeological investigation of the Bri-
Garrett, A. 1884: The terrestrial Mollusca inhabiting the
Garido, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Gassies, J.B. 1849: Tableau méthodique et descriptif des
Flehmen, R. 1987: Chemical communication in the social be-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Fleischer, E. 1913: Zur Biologie der Kopulation der Limaciden. II.
Fleming, J. 1813: Conchology.
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Fleischer, E. 1913: Zur Biologie der Kopulation der Limaciden. II.
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Flasar, I. 1977: 
Fitzinger, L.J.F. 1833: 
Focha, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Fleyshmann, B. 1939: Neue biologische Untersuchungen an Lima-
Flasar, I. 1977: 
Fitzinger, L.J.F. 1833: 
Foch, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Fleischmann, B. 1939: Neue biologische Untersuchungen an Lima-
Garrett, A. 1884: The terrestrial Mollusca inhabiting the
Garido, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Gassies, J.B. 1849: Tableau méthodique et descriptif des
Flehmen, R. 1987: Chemical communication in the social be-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Foch, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Fitzinger, L.J.F. 1833: 
Flehmen, R. 1987: Chemical communication in the social be-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Foch, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Fleischer, E. 1913: Zur Biologie der Kopulation der Limaciden. II.
Fitzinger, L.J.F. 1833: 
Fleischer, E. 1913: Zur Biologie der Kopulation der Limaciden. II.
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Foch, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
Foch, C.; Castillejo, J.; Iglesias, J. 1995: The spermato-
Fleming, I. 1977: Helicodiscus (Hebetodiscus) singlynum
della accoppiamento in alcune specie della famiglia Hel-
icidae (Gastropoda, Pulmonata). Atti Accademia della
Giusti, F.; Manganelli, G. 1986: 'Helix' sororcula Benoit
1859 and its relationships to the genera Vallonia Risso
and Planogyra Morse (Pulmonata Pupilloidea). Archiv

Gittenberger, E. 1983: On Iberian Cochlicopidae and the
genus Cryptacea (Gastropoda, Pulmonata). Zoologi-
sche mededelingen 57: 39-130.

Gittenberger, E.; Backhuys, E.; Ripken, Th.E.J. 1984: De
marine molluscs of the Maltese Islands. Museo
tutu 187:

Giusti, F. 1968a: Notulae Malacologicae, II. II genere
Oxychilus nell'Arcipelago Toscano. Atti della Societa
Toscana di Scienze Naturali, Residente in Pisa, Mem-
orie Serie B 75: 218-235, 2 pls.

Giusti, F. 1968b: Notulae Malacologicae, III. II genere
Oxychilus (Ortizius) allarius (Möluz) nuovo reperto per l'Italia
appenninica. Memorie del Museo Civico di Storia
Naturale di Genova 78: 375-978.

Giusti, F. 1970: Notulae Malacologicae, XII. L'isola di Pianosa
e lo scoglio La Scola (Arcipelago Toscano). Annali
del Museo Civico di Storia Naturale di Genova 78:
59-148, 15 pls.

Giusti, F. 1973: Notulae Malacologicae, XVIII. I molluschi
terrestri e salmastri delle isole Eolie. Lavori della
Società Italiana di Biogeografia (n.s.) 3: 113-306, 16
pls.

Giusti, F. 1976: Notulae Malacologicae, XXIII. I molluschi
terrestri, salmastri e di acqua dolce dell'Elba, Giannutri
e scogli minori dell'Arcipelago Toscano. Conclusioni
generali sul popolamento malacologico dell'Arcipel-
ago Toscano e descrizione di una nuova specie (Studi
sulla riserva naturale dell'Isola della Massa \& La说的是


dell'accoppiamento in alcune specie della famiglia Hel-


Getz, L.L. 1959: Notes on the ecology of slugs: Arion
circumscriptus, Deroceras reticulatum and D. laeve.
American midland naturalist 1: 485-498.


Kobelt, W. 1871: Catalog der im europäischen Faunen-Kiauta, B.; Butot, L.J.M. 1969: Contribution to the know-— 1876-81: *Catalog der im europäischen Faunen-*
Koch, C.; Heynemann, D.F. 1874: Neue Nacktschnecken aus Turkestan. *Jahrbücher der Deutschen Malako-
Kuiper, J.G.J. 1951: Soortproblemen. *Correspondentie-
-136-


Likharev, I.M.; Rammel’meyer, E.S. 1952: Nazemnye molljuski fauny SSSR. Akademiya Nauk SSSR, Leningrad. 437 pp., 1 pl.


Manganelli, G.; Giusti, F. 1985: First contribution to the
Mandahl-Barth, G. 1951: 
Madec, L.; Guiller, A. 1994: Geographic variation of distal
Madec, L.; Daguzan, J. 1993: Geographic variation in re-
MacMillan, G.K. 1940: Description of new terrestrial Gas-
Madec, L. 1989: Etude de la differenciation de
1883: Sur Testacellidae. Correspondentieblad van de Nederlandse
Gastropoda).
Manganelli, G.; Giusti, F. 1985: First contribution to the revision of the Oxychilus-species living in the Italian
— 1987: Notulae Malalogicae, XXXVIII. A new Hygromiidae from the Italian Apennines and notes on the genus Cernuella and related taxa (Pulmonata: Hel-
Manganelli, G.; Giusti, F.; Delle Cave, L. 1990: Notulae malalogicae, XLVIII. Laurinae (Gastropoda, Pulmonata, Orculidae/Papillidae) from the Villa-
franchium of peninsular Italy. Basteria 54: 87–103.
Marciano, P. 1986: Growth of Helix aspersa in the presence or absence of adults of the same species or of other species (Helix pomatia). Snail farming research 1: 67–75.
Martin, R.; Angulo, E. 1986: The family Milacidae (Mollusca, Gastropoda) in the Basque country and sur-
McCracken, G.F.; Selander, R.K. 1980: Self-fertilization and monogenic strains in natural populations of ter-


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.


Morse, F.S. 1864: Observations on the terrestrial *Pulmonifera* of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History* 1: 1-63, 10 pls.

Normand, N.A.J. 1852: Description de six limacés nouvelles observées aux environs de Valenciennes. Valenciennes. 8 pp.

Numneley, Th. 1837: A description of the internal structure of various limaces, found in the neighbourhood of Leeds. Transactions of the Leeds Philosophical and Literary Society 1: 41–79.


Perry, G. 1811: Conchology, or the natural history of snails containing a new arrangement of the genera and species. London, Miller. 4 pp., 61 pls.


———. 1858: Breves descriptiones Molluscorum quorundam in America et insulae Cuba. Antw. iv + 303 pp., 16 pls.


in North America. First annual number, for 1820.
Lexington, Smith. 16 pp.
—— 1831: Enumeration and account of some remarkable natural objects of the cabinet of Prof. Rafinesque, in Philadelphia: being animals, shells, plants, and fossils, collected by him in North America, between 1816 and 1831. Philadelphia, Rafinesque Schmaltz.

Scacchi, A. 1836: Catalogus Conchylhoizum Regni Neapolitani que usque adhuc reperit. Neapoli, Scacchi. 18 pp., 1 pl.


—1964: Aminopina, an Australian end land snail. The veliger 6: 115–120.


—1982: A comparison of the life cycles of Deroceras reticulatum (Muller) and Arion intermedius Normand (Pulmonata: Stylommatophora) at different temperatures under laboratory conditions. Journal of molluscan studies 48: 233–244.


—1986c: Experiments on the nutrition of Helix cincta (Kobelt) and Helix aspersa (Muller). Snail farming research 1: 42–49.


1902: Methodus dispositionis Conchyliorum extramarinorum in Regione palaearctica viventium, familias, genera, subgenera et stirpes sistens. Rad Jugoslawenske Akademije znanosti i umjetnosti, u Zagrebu 151: 82–139.


1982: Contributions to the knowledge of the slugs of Yugoslavia (Arionidae, Milacidae, Limacidae,
Agriolimacidae — Gastropoda, Pulmonata. 


1983b: Some data on slugs of Morocco and Algeria with description of a new *Deroceras* species. 

1987a: Spermatophores in Milacidae and their significance for classification (Gastropoda, Pulmonata). 

1987b: Milacidae (Gastropoda, Pulmonata) — systematic monograph. 


1994: Contribution to the knowledge of the slugs of Turkey (Gastropoda terrestria nuda). 
*Archiv für Molluskenkunde* 123: 1–47.


1980: The pallial complex of holarctic terrestrial slugs (Pulmonata, Stylommatophora) and its importance for classification. 

Wiktor, A.; Norris, A. 1982: The synonymy of *Limax maculatus* (Kaleniczenko 1851) with notes on its European distribution. 

1991: *Geomalacus malagensis* sp. n. and some remarks concerning generic level systematics of Arionidae (Gastropoda: Pulmonata). 

*Malakologische Abhandlungen* 17: 1–36.


Winckworth, R. 1926: Notes on nomenclature. 


*Archiv für Molluskenkunde* 89: 175–177.


KEY TO EXOTIC TERRESTRIAL SLUGS AND SNAILS NATURALISED IN NEW ZEALAND

This key provides for species determination of naturalised taxa, and is not systematic. For snails, shells of mature specimens are required for proper function of the key. Indigenous taxa were not taken into account in the development of this key, and hence are unlikely to key out.

1 Animal with an external shell
   — Animal without an external shell  .... 2

2(1) Shell reduced, incapable of housing the retracted animal, auriform, situated at posterior of body. Animal slug-like  .... (p. 98; Fig. 56, 57, C25)  .. Testacella haliotidea
   — Shell capable of housing the retracted animal  .... 3

3(2) Shell conical, cylindrical, elongate-oval or lanceolate, its height clearly greater than its diameter  .... 4
   — Shell flattened or globose, its height equal to or less than its diameter  .... 8

4(3) Shell cylindrical-oval, with apertural teeth  .... 5
   — Shell elongate-oval or lanceolate, lacking apertural teeth  .... 6

5(4) Shell less than 6 mm in height; last whorl less than half shell height; aperture usually with a single lamella; yellowish brown to reddish brown; translucent and glossy, with delicate transverse striaation  .... (p. 95; Fig. 55, C24) .. Lauria cylindracea
   — Shell less than 3 mm in height; last whorl more than half shell height; aperture with 3 to (usually) 5 teeth; yellowish brown to chestnut; glossy to mat, with fine growth lines  .... (p. 103; Fig. 59, C27) .. Vertigo ovata

6(4) Shell conical, 8–12 mm in height, slightly glossy, white to pale brown, generally profusely streaked, flecked, or banded with buff; umbilicus minute, partially closed by reflection of columella  .... (p. 75; Fig. 40, C13) .. Prietocella barbara
   — Shell lanceolate or elongate-oval, less than 8 mm in height, glossy, colourless or brown, without pattern; imperforate  .... 7

7(6) Shell elongate-oval, less than 8 mm in height; apex bluntly pointed; aperture subverbal, oval, with smooth callous rib inside; yellowish conicous  .... (p. 52; Fig. 34, C8) .. Cochlicopa lubrica
   — Shell lanceolate, less than 5 mm in height; apex rounded, blunt; aperture narrow, vertically directed; colourless  .... (p. 59; Fig. 36, C9) .. Cecilioides acicula

8(3) Shell globose – height and diameter about equal  .... 9
   — Shell subglobose to strongly flattened – height clearly less than diameter, less than 1.5 mm  .... 10

9(8) Shell 3–6 mm in height; umbilicus partially closed by reflection of columella; conicous to horn-coloured  .... (p. 56; Fig. 35) .. Coneuplecta calculosa
   — Shell 20–40 mm in height; dull yellow with solid or broken brown bands; imperforate  .... (p. 62; Fig. 37, C10, C11) .. Cantareus aspersus

10(8) Shell subglobose, up to 14 mm in diameter; thick, with coarse radial ribbing; peristome of whorls slightly angled; opaque buff to pale brown with darker continuous or broken bands  .... (p. 73; Fig. 39, C12) .. Candidula intersecta
   — Shell discoidal, rather thin, without coarse radial ribbing  .... 11

11(10) Shell less than 4 mm in diameter  .... 12
   — Shell more than 4 mm in diameter  .... 14

12(11) Shell with an umbilicus less than 0.2× its diameter; transparent, colourless, or tinged green; glossy, with faint growth lines; aperture rounded, with an internal whitish callous rib  .... (p. 117; Fig. 66, C31) .. Vitrea crystallina
   — Shell with umbilicus equal to or greater than 0.2× its diameter; aperture without an internal white callous rib  .... 13

13(12) Shell less than 2.5 mm in diameter; aperture lunate; peristome not thickened or reflected; transparent, pale straw to white; glossy, with faint growth lines  .... (p. 69; Fig. 38) .. Helicodiscus singleyanus
   — Shell less than 2.5 mm in diameter; aperture circular; peristome abruptly thickened but weakly reflected to form a white lip; translucent white to straw coloured; glossy, with faint growth lines  .... (p. 100; Fig. 58, C26) .. Vallonia excentrica

14(11) Shell less than 10 mm in diameter, with 4–5 moderately to strongly depressed whorls  .... 15
   — Shell 10–15 mm in diameter, with 5–7 strongly depressed whorls  .... 16

15(14) Shell whorls strongly depressed, convex above, flattened below; translucent, pale yellowish brown above, paler below; glossy, with faint, rather regular growth lines; Animal with imparute sole and phyllices densely clustered on body wall immediately anterior to mantle collar; (usually) smelling of garlic when disturbed; genitalia lacking dart apparatus  .... (p. 109; Fig. 60, 63, C28) .. Oxychilus alliarius
—Shell whorls slightly compressed, with a hint of keel at periphery; translucent, olive buff; glossy, weakly sculptured with growth wrinkles and microscopic spiral striations. Animal with sole not tripartite and lacking phylacites; not smelling of garlic when disturbed; genitalia with dart apparatus

... (p. 119; Fig. 67, C32) .. Zonitoides arboreus

16(14) Shell with whorls regularly increasing in breadth; translucent yellow or brown, paler below; glossy, with faint irregular growth lines. Animal with phylacites over most of anterodorsal body wall but lacking crypts; phallus divided into proximal and dorsal sections by a poorly defined median constriction

... (p. 111; Fig. 61, 64, C29) .. Oxychilus cellarius

—Shell with last whorl distinctly broader than penultimate whorl; last quarter-whorl often slightly downturned and compressed; translucent brownish-yellow, paler below; not usually very glossy, with well defined growth lines giving wrinkled appearance. Animal with anterodorsal body wall largely covered with phylacites and with numerous crypts in skin grooves on the right; phallus divided into proximal and dorsal sections by a well defined medial constriction

... (p. 114; Fig. 62, 65, C30) .. Oxychilus draparnaudi

17(1) Animal with oval mantle shield situated anterodorsally on body, containing internally granular shell fragments; pneumostome in right anterior margin of mantle shield; caudal mucus gland present

—Animal with elongate-oval mantle shield anterodorsally on body, containing internally an oval shell plate; pneumostome in right posterior margin of mantle shield; caudal mucus gland absent

... 18

18(17) Animal up to 25 mm in extended length; body and mantle shield yellow to pale grey, (usually) with a grey band on either side; sole yellowish grey, with yellow mucus. Genitalia with free oviduct short, not eversible

... (p. 48; Fig. 33, C6, C7) .. Arion intermedius

—Animal 25–50 mm in extended length; body and mantle shield yellowish grey to black, with a band on either side; sole pale yellow to orange, with sticky yellow-orange mucus. Genitalia with free oviduct long

... 19

19(18) Dorsum of body dark brown to (more usually) yellowish grey, with dark lateral bands; band on right side of mantle shield enclosing pneumostome, often with a small break immediately dorsal to pneumostome. Genitalia with free oviduct bipartite or (usually) tripartite, its broad distal section (when present) eversible as a slender process during copulation; entry of epiphallus to atrium with a conical verge; spermatophore slender, with a smooth to weakly serrate longitudinal ridge

... (p. 43; Fig. 31, C4) .. Arion distinctus

—Dorsum of body grey to (more usually) dark brown or black, with a dark lateral band; band on right side of mantle shield arching over pneumostome. Genitalia with free oviduct tripartite, its broadly conical distal section eversible as a slender process during copulation; entry of epiphallus to atrium with an elongate oval verge; spermatophore stout, with a strongly serrate longitudinal ridge

... (p. 45; Fig. 32, C5) .. Arion hortensis

20(17) Mantle shield bearing a horseshoe-shaped groove; dorsal keel of body extending to posterior margin of mantle shield; genitalia with epiphallus well developed, producing elaborately spinose spermatophores

... 21

—Mantle shield lacking a horseshoe-shaped groove; dorsal keel of body not extending to mantle shield posterior margin; genitalia lacking an epiphallus

... 23

21(20) Body with grooves between tubercles mostly unpigmented; pneumostome without a pale border; mucus colourless; genitalia with atrium equipped with accessory glands and housing a long stimulator

... (p. 87; Fig. 49, 52, C20, C21) .. Milax gagates

—Body with grooves between tubercles pigmented; pneumostome with a pale border; mucus yellow or orange; genitalia equipped with accessory glands on distal portion of vagina, but lacking an atrial stimulator

... 22

22(21) Body dull yellow-grey or brown, densely sprinkled and lineolated with black; dorsal keel yellowish or grey; pneumostome with an inconspicuous pale grey border; genitalia with paired, lobate accessory vaginal glands

... (p. 90; Fig. 50, 53, C22) .. Tandonia budapestensis

—Body pale to dark brown, with darker speckling; dorsal keel pale yellow or orange, without speckling of dark pigment; pneumostome with a pale border; genitalia with numerous tubular accessory vaginal glands and several folds in atrium

... (p. 92; Fig. 51, 54, C23) .. Tandonia sowerbyi

23(20) Body speckled, flecked, mottled, or nearly unpatterned, but never with bands; tail obliquely truncated; posterior of mantle shield rounded; right ocular retractor to left of terminal genitalia; intestine with 1 forward-directed loop
—Body banded or spotted; tail pointed but not truncated; posterior margin of mantle shield obtusely angled; right ocular retractor passing over phallus; intestine with 2 forward-directed loops

24(23) Animal up to 50 mm long, stout, generally whitish or creamy with darker markings; mucus normally colourless, but milky when animal disturbed; rectum with a caecum

... (p. 38; Fig. 27, 30, C3) Deroceras reticulatum

—Animal up to 30 mm long, slim, generally dark grey or brown, finely speckled or flecked with black; mucus colourless; rectum without a caecum

... 25

25(24) Pneumostome without a pale border. Phallus elongate, its proximal apical part with several small papillae, its distal part internally with a small hemispherical to conical sarcobelum; phallus often reduced or absent... (p. 32; Fig. 25, 28, C1) Deroceras laeve

—Pneumostome with a conspicuous pale border. Proximal phallus with 4-6 slender flagella located in a shallow recess between phallus lobe and digitiform caecum; distal phallus bulbous, internally with a large conical sarcobelum

... (p. 35; Fig. 26, 29, C2) Deroceras panormitanum

26(23) Mantle shield with 2 lateral bands and a more-or-less conspicuous central band

—Mantle shield spotted or mottled, but never with longitudinal bands

... 27

27(26) Animal 40-60 mm long. Body pale greyish yellow to greyish brown, overprinted with brown or black bands; mantle shield with lateral bands and a diffuse central band; back with 1 or 2 pairs of more-or-less visible lateral bands. Phallus cylindrical, elongate, lacking an appendix... (p. 78; Fig. 41, 45, C14, C15) Lehmannia nyctelia

—Animal 60-75 mm long. Body pale greenish yellow, brown, or reddish, overprinted with brown bands and mottling; mantle shield with a median band, 2 conspicuous lateral bands, and a spotted or mottled lateral and anterior margin; back usually with a band on either side and, below this, either spotted or with diffuse lower bands. Phallus cylindrical, short, with a lateral appendix

... (p. 79; Fig. 42, 46, C16) Lehmannia valentiana

28(26) Animal 100-120 mm long; back and mantle shield greyish or greenish with paler spots. Rectum with a long caecum. Duct of bursa copulatrix opening to free oviduct

... (p. 81; Fig. 43, 47, C17, C18) Limacus flavus

—Animal 100-200 mm long; back pale brown or grey with 4-6 more-or-less interrupted dark bands; mantle shield spotted. Rectal caecum absent. Duct of bursa copulatrix opening to base of phallus

... (p. 84; Fig. 44, 48, C19) Limax maximus
Fig. 1, 2 Generalised lateral habitus of Stylommatophoran snail and slug.

Fig. 3, 4 Schematic longitudinal sections of Stylommatophoran snail and slug, showing extent of general body cavity and pulmonary cavity.
Fig. 5-7 Generalised stylommatophoran shell, in lateral, dorsal, and ventral aspect, illustrating features useful in taxonomy. Key: d, diameter; h, height; 1-5, shell whorls.

Fig. 8, 9 Shell aperture from two stylommatophoran species, illustrating terminology applied to apertural barriers.

---155---
Fig. 10–14 Variation in arrangement of pulmonary and excretory organs in the stylommatophoran pulmonary cavity (semi-schematic), representative of taxa referred to Orthurethra (10, 11), Mesurethra (12), and Sigmurethra (13, 14).
Fig. 15, 16 Generalised layout of digestive system in stylommatophoran snails and slugs. Fig. 17, 18 Stylommatophoran buccal mass: (17) generalised lateral view; (18) schematic longitudinal section, showing features of radula.
**Fig. 19, 20** Features of stylommatophoran buccal mass: (19) variation in jaw morphology; (21) generalised radular teeth (central tooth and first lateral tooth).

**Fig. 21** Generalised stylommatophoran reproductive system, with cross-section through oviducal and prostatic glands.
Fig. 22, 23 Generalised layout of reproductive system and cephalic part of columnar retractor muscle system in stylommatophoran snails and slugs. Fig. 24 Generalised stylommatophoran central nervous system.
Fig. 25–27 Habitus, lateral and dorsal: (25) Deroceras laeve; (26) D. panormitanum; (27a–e) D. reticulatum, showing variation in body pigmentation. Fig. 28–30 Shell: (26) Deroceras laeve, lateral and dorsal; (29) D. panormitanum, dorsal; (30) D. reticulatum, dorsal. Fig. 31–33 Habitus: (31) Arion distinctus; (32) A. hortensis; (33) A. intermedius.
C1 AGRICLIMACIDAE: Deroceras laeve

C2 AGRICLIMACIDAE: Deroceras panormitanum

C3 AGRICLIMACIDAE: Deroceras reticulatum

C4 ARIONIDAE: Arion distinctus
C5 ARIONIDAE: Arion hortensis

C6 ARIONIDAE: Arion intermedius

C7 ARIONIDAE: Arion intermedius

C8 COCHLICOPIDAE: Cochlicopa lubrica
C10 HELICIDAE: *Cantareus aspersus*

C12 HYGROMIIDAE: *Candidula intersecta*
C13 HYGROMIIDAE: *Prietocella barbara*

C14 LIMACIDAE: *Lehmannia nyctelia*

C15 LIMACIDAE: *Lehmannia nyctelia*

C16 LIMACIDAE: *Lehmannia valentiana*
MILACIDAE: Milax gagates

MILACIDAE: Tandonia budapestensis

MILACIDAE: Tandonia sowerbyi

PUPILLIDAE: Lauria cylindracea
C25 TESTACELLIDAE: *Testacella halotidea*

C26 VALLONIIDAE: *Vallonia excentrica*

C27 VERTIGINIDAE: *Vertigo ovata*

C28 ZONITIDAE: *Oxychilus allarius*
Fig. 34-40 Shell: (34) Cochlicopa lubrica, from mature animal and 3 juveniles; (35) Conguipeda calcicola, from mature animal and 2 juveniles; (36) Coelioidea adoula, from mature animal and 2 juveniles; (37) Cantareus aspersus, from mature animal and a juvenile; (38) Helicodiscus singleyanus, from mature animal; (39) Candidula intersecta, from mature animal and 2 juveniles; (40) Prietocella barbara, from mature animal and a juvenile.
Fig. 41–44 Habitus, showing variation in body pigmentation: (41a–c) *Lehmannia nyctelia*, (42a–c) *L. valentiana*, (43a–c) *Limacus flavus*, (44) *Limax maximus*, adults (a–c) and juveniles (d–f).
Fig. 45–47 Shell, dorsal: (45) Lehmannia nyctelia; (46) L. valentiana; (47) Limacus flavus. Fig. 48 Limax maximus, shell, dorsal and lateral. Fig. 49–51 Habitus: (49) Milax gagates; (50) Tandonia budapestensis; (51) T. sowerbyi. Fig. 52–54 Shell, dorsal and lateral: (52) Milax gagates; (53) Tandonia budapestensis; (54) T. sowerbyi. Fig. 55 Lauria cylindracea, shell, from mature animal and 3 juveniles. Fig. 56, 57 Testacella halistoides: (56) habitus, dorsal and lateral of extended animal, and lateral of contracted animal; (57) shell, dorsal and ventral.
Fig. 58-62 Shell, from mature animal and juveniles: (58) Vallonia excentrica; (59) Vertigo ovata; (60) Oxychilus allarius; (61) O. ocellarius; (62) O. draparnaudi.
Fig. 63-65 Habitus, anterior lateral, showing phylactes and glandular crypts: (63) *Oxychilus alliarius*; (64) *O. cellarius*; (65) *O. draparneudi*. Fig. 66, 67 Shell, from mature animal and 2 juveniles: (66) *Vitrea crystallina*; (67) *Zonitoides arboreus*.

-173-
Fig. 68 Reproductive system, *Deroceras laeve*: (a) entire system; (b) phallus of euphallic individual, opened to show longitudinal folds and stimulator; (c–f) distal part of system, showing variation in reduction of male genitalia.

Fig. 69 Reproductive system, *Deroceras panomitanum*: (a) entire system; (b) phallus, opened to show conical stimulator; (c, d) distal part of system, showing variation in form of phallus glands, appendix, and flagellum.
Fig. 70 Reproductive system, *Deroceras reticulatum*: (a) entire system; (b) phallus, opened to show folds and stimulator; (c–f) variation in phallus gland.

Fig. 71 Reproductive system, *Arion distinctus*: (a) entire system; (b) terminal part of system, opened to show conical verge penetrated by epiphallus and thickened openings of bursa copulatrix and free oviduct.
Fig. 72 Reproductive system, *Arion hortensis*: (a) entire system; (b) terminal part of system, opened to show verge overhanging epiphallus opening, and thickened free oviduct opening.

Fig. 73 Reproductive system, *Arion intermedius*: (a) entire system; (b) terminal part of system, opened to show raised, nodulate verge and tongue-like overhang to bursa copulatrix opening.
Fig. 74 Reproductive system, Cochlicopa lubrica: (a) entire system; (b) phallus, opened to show small vergic papilla, terminal part of phallus appendix, and fleshy stimulatory pads.

Fig. 75 Reproductive system, Coneuplecta calculosa.

Fig. 76 Reproductive system, Cecilioides acicula: (a) entire system; (b) male genitellia, opened to show epiphALLus and phallic pilasters.
Fig. 77 Reproductive system, Cantarbus aspersus: (a) entire system; (b) terminal part of system, with phallus opened to show nodulate vergic papilla, pseudopapilla, and stylophore opened to show dart; (c) dart.

Fig. 78 Reproductive system, Helicodiscus singleyanus: (a) entire system; (b) phallus, opened to show vergic papilla and weak longitudinal folds.
Fig. 79 Reproductive system, *Candidula intersecta*: (a) entire system; (b) terminal female genitalia, opened to show dart in stylophore and stimulatory shield on vaginal walls; (c) dart; (d) phallus, opened to show elongate epiphallic papilla.

Fig. 80 Reproductive system, *Priestocella barbara*: (a) entire system; (b) terminal part of female genitalia, showing stylophore and mucus glands; (c) phallus, opened to show epiphallic papilla; (d) epiphallic papilla from phallus, showing nodulate surface.
Fig. 81 Reproductive system, *Lehmannia nyctelia* (a) entire system; (b) phallus, opened to show longitudinal folds.

Fig. 82 Reproductive system, *Lehmannia valentiana* (a) entire system; (b) phallus, opened to show internal folds; (c) terminal part of hermaphrodite duct, with talon.

Fig. 83 Reproductive system, *Limacus flavus* (a) entire system; (b) phallus, opened to show longitudinal folds.
Fig. 84 Reproductive system, *Limax maxinus*: (a) entire system; (b) phallus, opened to show longitudinal folds.

Fig. 85 Reproductive system, *Milax gagates*: (a) entire system; (b) terminal part of system, with epiphallus opened to show finely papillate walls, phallus opened to show epiphallic papilla, and atrium opened to show stimulator.

Fig. 86 Reproductive system, *Tandonia budapestensis*: (a) entire system; (b) terminal part of system, with epiphallus opened to show finely papillate walls, phallus opened to show epiphallic papilla, and vagina opened to show entry of accessory glands.
Fig. 87 Reproductive system, *Tandonia sowerbyi*: (a) entire system; (b) terminal part of system, with epiphallus opened to show finely papillate wall, and phallus opened to show epiphallinic verge and fine longitudinal folcis.

Fig. 88 Reproductive system, *Lauria cylindracea*: (a) entire system; (b) terminal part of male genitallia, with epiphallus opened to show finely papillate lumen, and phallus opened to show caecum with spinate papillae and thick wall of bulbous terminus of appendix.
Fig. 89 Reproductive system, *Testacella haliotidea*.

Fig. 90 Reproductive system, *Vallonia excenrica*: (a) entire system of euphallic individual; (b) entire system of aphallic individual; (c) phallus, opened to show epiphallic papilla.
Fig. 91 Reproductive system, *Vertigo ovata*: (a) entire system; (b) phallus, opened to show small epiphallus papilla and low longitudinal folds.

Fig. 92 Reproductive system, *Oxychilus alliiarius*: (a) entire system; (b) phallus, opened to show flagellum above entry of epiphallus, weakly papillate folds in proximal part, and rather smooth folds in distal part.
Fig. 93  Reproductive system, *Oxychilus cellarius*: (a) entire system; (b) terminal part of system, with phallus opened to show very short flagellum above entry of epiphallus, and longitudinal folds in proximal part bearing large papillae.

Fig. 94  Reproductive system, *Oxychilus draparnaudi*: (a) entire system; (b) terminal part of system, with phallus opened to show very short flagellum above entry of epiphallus, papillate folds in proximal part, and weakly papillate or smooth folds in distal part.
Fig. 95 Reproductive system, *Vitreo crystallina*: (a) entire system; (b) phallus, opened to show pseudopapilla near entry of vas deferens, and frilled stimulator pad. Fig. 96 Reproductive system, *Zonitoides arboreus*: (a) entire system; (b) male genitalia, opened to show large epiphallic papilla invested with a calcareous plate, and dart sac containing dart; (c) dart. Fig. 97–99 Spermatophores: (97) *Arion distinctus*; (98) *A. hortensis*; (99) *A. intermedius*. 
Fig. 100–108 Spermatophores: (100) *Cantareus aspersus*; (101) *Candidula intersecta*; (102) *Prietoecilla barbara*; (103) *Milax gagates*; (104) *Tandonia budapestensis*; (105) *T. sowerbyi*; (106) *Oxychilus allarius*; (107) *O. cellarius*; (108) *O. draparnaudi*. 

-187-
Fig. 109–124 Jaws: (109) Deroceras laeve; (110) D. panormitanum; (111) D. reticulatum; (112) Arion distinctus; (113) A. hortensis; (114) A. intermedius; (115) Cochlicopa lubrica; (116) Corenoplecta calcutta; (117) Cecilioides acicula; (118) Cantareus aspersus; (119) Helicodiscus singleyanus; (120) Candidula intersecta; (121) Prietocella barbara; (122) Lehmannia nycteii; (123) L. valentina; (124) Limacus flavus.
Fig. 125–137 Jaws: (125) Limax maximus; (126) Milax gagates; (127) Tardonua budapestensis; (128) T. sowerbyi; (129) Lauria cylindracea; (130) Vallonia excentrica; (131) Vertigo ovata with (132) radular teeth; (133) Oxychilus alliarius; (134) O. cellarius; (135) O. drapamaudi; (136) Vitrea crystallina; (137) Zonitoides arboreus.
Fig. 138–147 Layout of digestive tract (schematic): (138) Deroceras laeve; (139) D. panormitanum; (140) D. reticulatum; (141) Arion distinctus; (142) A. hortensis; (143) A. intermedius; (144) Cochlicopa lubrica; (145) Coneuplecta calculosa; (146) Cacilioides acicula; (147) Cantareus aspersus.
Fig. 148–158 Layout of digestive tract (schematic): (148) Helicodiscus singleyanus; (149) Candidula intersecta; (150) Prietocella barbara; (151) Lehmannia nyctelia; (152) L. val-entiana; (153) Limacus flavus; (154) Limax maximus; (155) Milax gagates; (156) Tandonia budapestensis; (157) T. sowerby; (158) Lauria cylindracea.
Fig. 159–164 Layout of digestive tract (schematic): (159) Testacella haliotidea; (160) Vattonia excentrica; (161) Vertigo ovata; (162) Oxychilus alliarius; (163) Vitrea crystallina; (164) Zonilites arboreus. Fig. 165–169 Layout of pallial organs: (165) Deroceras laeve, dorsal and ventral; (166) D. panormitanum, ventral and dorsal; (167) D. reticulatum, dorsal and ventral; (168) Arion distinctus, ventral and dorsal; (159) A. intermedius, dorsal and ventral.
Fig. 170–176 Pallial organs, ventral: (170) Cochlicopa lubrica; (171) Coneuplecta calciososa; (172) Cecilioides acicula; (173) Cantareus aspersus; (174) Helicodiscus singleyanus; (175) Candidula intersecta; (176) Prailocella barbara.
Fig. 177-183 Layout of pallial organs: (177) *Lehmannia nyctolea*, ventral and dorsal; (178) *L. valentiana*, dorsal and ventral; (179) *Limacus flavus*, dorsal and ventral; (180) *Limax maximus*, dorsal and ventral; (181) *Milax gagates*, dorsal and ventral; (182) *Tardonia budapestensis*, ventral and dorsal; (183) *T. sowerbyi*, dorsal and ventral.

-194-
Fig. 184–190 Pallial organs: (184) *Lauria cylindracea*, ventral; (185) *Testacella haikolidea*, dorsal and ventral; (186) *Valonia excentrica*, ventral; (187) *Vertigo ovata*, ventral; (188) *Oxychilus alliarius*, ventral; (189) *Vitra crystallina*, ventral; (190) *Zonitoides arboreus*, ventral.
Fig. 191–199 Layout of free muscle system (schematic): (191) Deroceras laeve; (192a,b) D. panormitanum, with variation in derivation of buccal and right tentacular retractors; (193a-c) D. reticulatum, ditto; (194) Aön distinctus; (195) A. intermedius; (196) Cochlicopa lubrica; (197) Coneplecta calcillosa; (198) Cecilioides acicula; (199) Cantareus aspersus.
Fig. 200–210 Layout of free muscle system (schematic): (200) Helicodiscus singleyanus; (201) Candidula intersecta; (202) Prietocella barbara; (203) Lehmannia nyctolepis; (204) L. valentina; (205) Limacus flavus; (206) Limax maximus; (207) Mithax gagates; (208) Tandonia budapestensis; (209) T. sowerbyi; (210) Lauria cylindracea.
Fig. 211–218 Layout of free muscle system (schematic): (211) Testacella haliotidea; (212) Vallonia excentrica; (213) Vortigo ovata; (214) Oxychilus allianus; (215) O. cellarius; (216) O. draparnaudi; (217) Vitrea crystallina; (218) Zonitoides arboreus.
Fig. 219–222a Central nervous system: (219) *Deroceras laeve*, posterior; (220a,b) *D. panormitanum*, posterior and left posterolateral; (221a,b) *D. reticulatum*, posterior and left posterolateral; (222a) *Arion distinctus*, posterior.
Fig. 222b–227 Central nervous system: (222b) Arion distinctus, left posterolateral; (223) A. intermedius, posterior; (224) Cochlicopa lubrica, posterior; (225) Coneuptacta calculosa, left posterolateral; (226) Cecilioides acica, posterior; (227) Centareus aspersus, posterior.
Fig. 228–233 Central nervous system: (228) Candidula intersecta; (229) Prietoecilia barbara; (230) Lehmannia nyctelia; (231) L. valentina; (232) Limax maximus; (233) Milax gagates.
Fig. 234–238 Central nervous system: (234) Tandonia budapestensis, posterior; (235) T. sowerbyi, posterior; (236) Lauria cylindracea, posterior; (237a,b) Testacella hallotidea, posterior and left posterolateral; (238) Vallonia excentrica, posterior.
Fig. 239–244 Central nervous system, posterior: (239) Vertigo ovata; (240) Oxychilus alliarius; (241) O. cellarius; (242) O. draparnaudi; (243) Vitrea crystallina; (244) Zonitoides arboreus.
Fig. 245 Courtship and mating behaviour, *Deroceras panormitanum.*

Fig. 246 Courtship and mating behaviour, *Deroceras reticulatum.*
Fig. 247 Courtship and mating behaviour, *Arion hortensis*.

Fig. 248 Courtship and mating behaviour, *Cantareus aspersus*.
Fig. 249  Courtship and mating behaviour, *Limacus flavus*.

Fig. 250  Courtship and mating behaviour, *Limax maximus*. 
Fig. 251 Courtship and mating behaviour, *Milax gagates.*
Fig. 252, 253 Mating posture, *Tandonia budapestensis* and *Vailonia excentrica.*
Fig. 254 Courtship and mating behaviour, *Vertigo ovata.*
Fig. M1, 2 Shell granules, *Arian distinctus* and *A. intermedius*, ventral. Fig. M3 Protocoonch, *Cochlicopa lubrica* taken from egg, lateral. Fig. M4 Shell apex, *C. lubrica*, dorsolateral. Fig. M5, 6 Protocoonch, *Coneuplecta calculesa*, shell apex, lateral and dorsolateral.
Fig. M7, 8 Protoconch, Coneuplecta calciosra, surface sculpture of early and late protoconch whorls. Fig. M9-12 Teleoconch, C. calciosra: surface sculpture: (9, 10) dorsal surface; (11) at peripheral thread; (12) ventral surface.
Fig. M13–18 Protoconch: (13, 14) Cecilloides acicula, lateral and dorsal; (15) Cantarea aspersus, dorsal; (16) Helicodiscus singleyanus, dorsal; (17) Candidula intersecta, dorsal; (18) Prietocella barbara, dorsolateral.
Fig. M19 Protoconch, *Lauria cylindracea*, dorsolateral.  
Fig. M20 Shell aperture, *L. cylindracea*, showing parietal lamella.  
Fig. M21, 22 Shells, *L. cylindracea* juveniles, showing columellar and parietal lamellae.  
Fig. M23, 24 Protoconch: (23) *Vallonia excentrica*, dorsal; (24) *Vertigo ovata*, dorsolateral.
Fig. M25 Shell aperture, *Vertigo ovata*, showing barriers. Fig. M26-30 Protoconch: (26) *Oxychilus allarius*, dorsal; (27, 28) *O. cellarius* taken from egg, lateral and dorsal; (29, 30) *Vitrea crystallina*, dorsolateral, and surface sculpture.
Fig. M31 Protoconch, *Zonitoides arboreus*, dorsolateral.

Fig. M32-36 Radular teeth: (32-34) *Deroceras laeve*; (35, 36) *D. panormitanum*.
Fig. M37-42 Radular teeth: (37) *Deroceras panormitanum*, (38-40) *D. reticulatum*, (41, 42) *Arion distinctus*.
Fig. M43-48 Radular teeth: (43, 44) *Arion distinctus*; (45-47) *A. hortensis*; (48) *A. intermedius*.
Fig. M49-54 Radular teeth: (49, 50) Arion intermedius; (51-53) Cochlicopa lubrica; (54) Coneuplecta calculosa.
Fig. M55–60 Radular teeth: (55) Conopecta calculosa; (56, 57) Cecilioides acicula; (58–60) Cantareus aspersus.
Fig. M61-66 Radular teeth: (61-63) Helicodiscus singleyanus; (64, 65) Candidula intersecta; (66) Priocella barbara.
Fig. M67-72 Radular teeth: (67, 68) Prietocella barbara; (69-72) Lohmannia nyctelia.
Fig. M73-78 Radular teeth: (73-76) *Lehmannia valentiana*; (77, 78) *Limacus flavus*.
Fig. M79–84 Radular teeth: (79) Limacus flavus; (80–82) Limax maximus; (83, 84) Milax gagates.
Fig. M85–90 Radular teeth: (85, 86) Milax gagates; (87–90) Tandonia budapestensis.
Fig. M91–96 Radular teeth: (91–94) Tandonia sowerbyi; (95, 96) Lauria cylindracea.
Fig. M97–102 Radular teeth: (97–99) Testacella halotidea; (100, 101) Vallonia excentrica; (102) Oxychilus alliarius.
Radular teeth: (103) Oxychilus alliarius; (104, 105) O. cellarius; (106, 107) O. drapernaudi; (108) Vitrea crystallina.
Fig. M109-112 Radular teeth: (109) Vitrea crystallina; (110-112) Zonitoides arboreus.

Fig. M113 Cross-section of egg shell, Cochlicopa lubrica. Fig. M114 Surface of egg shell, Conuspecta callosa.
Fig. M115, 116 Cross-section of egg shell, *Coneuplecta calculosa* and *Cantareus aspersus.
Fig. M117-120 Surface and cross-section of egg shell: (117, 118) *Prietoella barbara*; (119, 120) *Vallonia excentrica.*
Fig. M121-124 Surface and cross-section of egg shell: (121, 122) *Oxychilus alliarius*; (123, 124) *O. cellarius*. Fig. M125, 126 Egg and cross-section of shell, *Zonhoides arboreus*.
Map 1 Collection localities, Deroceras laeve.

Map 2 Collection localities, Deroceras panormitanum.

Map 3 Collection localities, Deroceras reticulatum.

Map 4 Collection localities, Arion distinctus.
Map 5 Collection localities, *Arion hortensis*.

Map 6 Collection localities, *Arion intermedius*.

Map 7 Collection localities, *Cochlicopa lubrica*.

Map 8 Collection localities, *Coneuplecta calculosa*.
Map 9 Collection localities, Ceciellodes acicula.

Map 10 Collection localities, Cantareus aspersus.

Map 11 Collection localities, Helicodiscus singleyanus.

Map 12 Collection localities, Candidula intersecta.
Map 13 Collection localities, *Prietocella barbara*.

Map 14 Collection localities, *Lehmannia nyctelia*.

Map 15 Collection localities, *Lehmannia valentiana*.

Map 16 Collection localities, *Limax maximus*.
Map 17 Collection localities, *Limacus flavus*.

Map 18 Collection localities, *Milax gagates*.

Map 19 Collection localities, *Tandonia budapestensis*.

Map 20 Collection localities, *Tandonia sowerbyi*.
Map 21 Collection localities, *Lauria cylindracea*.

Map 22 Collection localities, *Testacella haliotidea*.

Map 23 Collection localities, *Vallonia excentrica*.

Map 24 Collection localities, *Vertigo ovata*.
OFFSHORE ISLANDS
Kermadecs
Three Kings
Chathams
Snares
Bounty
Antipodes
Aucklands
Campbell

Map 25 Collection localities, *Oxychilus allarius*.

OFFSHORE ISLANDS
Kermadecs
Three Kings
Chathams
Snares
Bounty
Antipodes
Aucklands
Campbell

Map 26 Collection localities, *Oxychilus cellarius*.

OFFSHORE ISLANDS
Kermadecs
Three Kings
Chathams
Snares
Bounty
Antipodes
Aucklands
Campbell

Map 27 Collection localities, *Oxychilus draparnaudi*.

OFFSHORE ISLANDS
Kermadecs
Three Kings
Chathams
Snares
Bounty
Antipodes
Aucklands
Campbell

Map 28 Collection localities, *Vitrea crystallina*. 

-235-
Map 29 Collection localities, *Zonitoides arboreus*. 
TAXONOMIC INDEX

This index covers the nominal taxa mentioned in the text, regardless of their current status in taxonomy. In the case of synonyms, the combinations of generic and specific names listed are those originally published by authors, and may differ from combinations implicit in current usage. Taxa in bold indicate valid taxa which have a description in this publication, and page numbers in bold indicate the start page of a description. The letter “k” after a page number indicates the page of the key to the taxon. The Figures, Colour plates (prefixed “C”), SEM micrographs (prefixed “M”), and Maps are located on the following pages: Figures, pages 154–160 and 169–207; Colour plates, pages 161–168; SEMs, pages 208–228; Maps, pages 229–236.

Abidia Turton, 1831 94, 95, 104
academia Clime, 1970, Laema (Prixgnathus) 59
Acaudiae 51, 58, 61, 75, 94
Acaus of authors 61
Achathia of authors 51, 58
Achathella of authors 51, 58
Achaitinelidae 51
Achaitinonesiae 51, 58
achyophia Locard, 1899, Hyalinia 114
acciula(Mùller, 1774), Cecilioides(Cecilioides) 59, 151k, Figures 35, 76, 117, 148, 172, 198, 226, C9, M13, M14, M56, M57, Map 9
Accula eburnea Risso, 1826 58
Accula Risso, 1826 58
Acciculidae 58
Acciculoidea Westariund, 1886 58
acciolum de Cristofor & Jan, 1832, Columna 59
accicum Müller, 1774, Buccinum 59
Acteonidae 94, 104
acta Company, 1837, Achatina 59
acta of authors 75
aetnes Sacchi, 1857, Oxychilus 114
Agardha Gude, 1911 84
agiena Bourguignat, 1857, Caciciaanella 59
agrestis of authors 32, 35, 38
agrestis var. nigra of authors 35
agrestis var. violacea of authors 36
AGRIOMACIDAE 20, 28, 31, 77, 84
Agrofrax of authors 77
Aleta Jeffreys, 1830 104
Aleta pakestris Locash, in Turton, 1831 104
alta Brown, 1837–49, Achatina 59
algovarsis Locard, 1899, Hyalinia 114
Ailenitor Iredale, 1937 119
aflaria Miller, 1822, Heilx 109
aliiarius (Miller, 1822), Oxychilus(Oxychilus) 105, 151k, Figures 60, 63, 92, 106, 133, 162, 188, 214, 240, C28, M26, M102, M103, M121, M122; Map 25
alpina Suter, 1804, Flammulina 114
alteral Lulu, 1976, Deroceras 38
Amalia badenensis Simroth, 1910 90
Amalia cepria Simroth, 1906 87
Amalia maculata Collinge, 1896 92
Amalia marginata Draperiand, 1805 67
Amalia Moquin-Tandon, 1855 87
Amalia of authors 90
Amalia robic Simroth, 1885 90
Ambigolimax Pollonera, 1887 77
amoticana Tate, 1870, Krynokia 32
amoestatum Dohrn, 1869, Caciciaanella 59
Amphiboleidae 26
Amphidoxa costumata Hutton, 1882 108
Amphilocidae of authors 108
Amplexis Brown, 1827 109
anconostoma Lowe, 1831, Helix (Coclitodon) 95
anconostoma var. cristula Mousson, 1856, Pupa 95
Anchyliidae 28
anococela d'Orbigny, 1837, Limax 32
andraser Boitger, 1880, Hyalinia (Vitrea) 117
anglia Bourguignat, 1856, Caciciaanella 59
anomalata Torres Mincue, 1924, Testafacca 98
Anomphala Westariund, 1886 116
anipodarum Grey, 1855, Milax 67
aniquorum Cockearl, 1891, Pupa ovata 105
antiquorum d'Audebard de Férussac, 1819 84
antiquorum Sowerby, 1828, Limax 81
apennina Pollonera, 1899, Arion intermedius 48
Aplolostoma Moquin-Tandon, 1855 109
Apleosina of authors 116
araneeus Gassiat, 1857, Limax 32
arboresus (Say, 1816), Zonitoides(Zonitoides) 119, 152k, Figures 67, 68, 117, 164, 190, 216, 244, C32, M31, M110–112, M125, M126; Map 29
arbores Say, 1818, Helix 119
arborum of authors 78, 79
arcasianus of authors 114
Arctolimax Westariund, 1894 32
argentinus Strael & Pfeffer, 1874, Limax 32
argilaceus Gassiat, 1856, Limax 92
Argininae 94
Arion bourguignatii Mabilic, 1868 42
Arion circumscriptus Johnston, 1828 42
Arion d'Audebard de Férussac, 1819 42
Arion distinctus Mabilic, 1868 43, 152k, Figures 31, 71, 97, 112, 141, 168, 194, 222, C4, M1, M41–44; Map 4
Arion empirorum d'Audebard de Férussac, 1819 42
Arion hortensis d'Audebard de Férussac, 1819 45, 152k, Figures 32, 72, 98, 113, 142, 247, C5, M45–47, Map 5
Cecilioides (Cecilioides) d'Audebard de Férussac, 1814 59

Cecilioides (Cecilioides) acicula (Müller, 1774) 59, 151k, Figures 33, 76, 117, 146, 172, 198, 226, C9, M13, M14, M25, M57, Map 9

Cecilioides acicula (Müller, 1774) 58

Cecilioides d’Audebard de Férussac, 1814 58
cellar glass snail 111
cellaria Müller, 1774, Helix 111
cellarius (Müller, 1774), Oxychilus (Oxychilus) 111, 152k, Figures 61, 64, 93, 107, 121, 215, 241, C29, M27, M28, M104, M105, M123, M124; Map 26
cellaria Müller, 1774, Helix 111
cellarius of authors 114
Cerion Röding, 1798 94, 104
Cerionidae 94, 104
Cernuella Schlüter, 1838 72
Charadriiformes of authors 95
Charopidae 20, 98, 106
Chelina d’Audebard de Férussac, 1814 114
Chersa Bourguignat, 1877, Helix 111
Chilinidae 29
Chiliomotora Fitzinger, 1833 100
Chiostoma of authors 100
Chondrinidae 26, 94, 95, 104
Chorolimax Westerlund, 1894 38
Chromolimax Pini, 1876 84
chrysalis snail 95
cibicides von Kimakowicz, 1884, Amalia 90
chionea Müller, 1774, Limax 84
Cliona Jeffreys, 1830 51
Cliona of authors 59
Cinaria Beck, 1837 100
cirtensis Koch, 1903, Helix aspersa 62
Clavella of authors 94, 95
Clausiliidae 28, 84
Cochea of authors 61
Cochlicella of authors 75
Cochlicopa (d’Audebard de Férussac, 1814) 51 51
Cochlicopa lubrica (Müller, 1774) 52, 151k, Figures 34, 74, 115, 144, 170, 196, 224, C8, M3, M4, M51-53, M113; Map 7
Cochlicopa of authors 58
COCHLICOPIDAE 51, 58
Cochlodonta Lowe, 1831 94
Cochlodonta d’Audebard de Férussac, 1821 94
Coenastoria of authors 82
cornuensis Collinge, 1897, Arion 43
cottage Hesse, 1826, M10 93
? columna Cleesin, 1875, Cliona lubrica 52
Columna of authors 51, 58
companyoi Bourguignat, 1863, Limax 81
Coneuplecta calculosa (Gould, 1852) 58, 151k, Figures 35, 75, 118, 145, 171, 197, 226, M5-6, M6-12, M64, M55, M114, M115; Map 8
Coneuplecta Möllendorff, 1893 56
Conibycus dehli Theilea, 1828 56
Conilus circumenestus Reinhardt, 1893 59
copa a von Born, 1776, Conus 62
conoëdula Pfeffer, 1862, Helix 111
conoëdula of authors 114
Coneola of authors 100
Cornu von Born, 1776 61
cornicolea Amelin, 1791, Serpula 62
cothanus Pollonera, 1899, Arion 43
? erassula Fagot, 1679, Zia 52
? cristallina Bercot, 1862, Cacicianella 59
Cryptoleca de Folin & Bérillon, 1877 51
Cryptophalus de Charpentier, 1837 61
crystal snail 117
crystallina (Müller, 1774), Vitrea (Vitreus) 117, 151k, Figures 66, 95, 139, 153, 189, 217, 243, C31, M29, M36, M108, M109; Map 28
crystallina Müller, 1774, Helix 117
Crystallinus Wagner, 1907 116
Crystallus Lowe, 1856 116
cylindracea (da Costa, 1778), Laura 99, 151k, Figures 55, 88, 129, 158, 164, 210, 236, C24, M19-22, M35, M96; Map 21
cylindracea da Costa, 1778, Turbo 95
cypraea Simroth, 1910 67
danica Schlasch, 1906, Stenogyra octona 50
Danubiana of authors 97
Daudebard Auction 57
debilis Mousson, 1882, Pupa 95
deferens Bourguignat, in Locard, 1882, Helix 73
depressa Paulucci, 1879, Helix aspersa 62
Deroceras (Agriolimax) Mörch, 1865 31, 38
Deroceras (Agriolimax) reticulatum (Müller, 1774) 38, 153k, Figures 27, 30, 71, 110, 140, 157, 167, 221, 245, C3, M36-40; Map 3
Deroceras (Deroceras) laeve (Müller, 1774) 32, 153k, Figures 25, 28, 68, 109, 136, 165, 191, 219, C1, M32-34; Map 1
Deroceras (Deroceras) pannormitanum (Lessona & Pollonera, 1882) 95, 153k, Figures 26, 29, 69, 100, 139, 166, 192a, b, 220a, b, 245, C2, M35-37; Map 2
Deroceras (Deroceras) Rafinesque Schmaltz, 1820 32
Deroceras Rafinesque Schmaltz, 1820 31
deshayes/Bourguignat, 1861, Limax 81
Desmothea Stüble, 1884 104
diastole Pilsbry, 1319, Vertigo ovela 105
Diplomella Cassin, 1890 116
Disphaniella Hesse, 1916 109
Diaphanella 29, 109
Diastole Gude, 1879 105
Discidae 68
distinctus Mabille, 1868, Arion 43, 152k, Figures 31, 71, 97, 112, 141, 168, 194, 222, C4, M1, M41-44; Map 4
dohri Pfeffer, 1877, Pupa 95
Draspara's glass snail 114

*Draspara* (Beck, 1837), *Oxychilus (Oxychilus)* 114, 122k, Figures 62, 65, 94, 106, 135, 216, 242, C30, M106, M107; Map 27

*Draspara* Beck, 1837, *Halix (Heliacella)* 114
*Draspara* Leach, 1831, *Pupilla* 95
*Duba* Pallonera, 1888, *Testacella* 98
*Dubius* Hoffmann, 1941, *Agiolimax* 35
*Durgella Thiele, 1928* 56
*Durgella vitrina Thiele, 1928* 56

eburnes Risso, 1826, *Acicula* 59

ecentric grass snail 100

ehrenbergi Bourguignat, 1853, *Limax* 81

*Elloidae* 27, 29

elongatus Collinge, 1894, *Arion* 45
**emarginatus** Hutton, 1879, *Milax* 88

*Endodontidae* 28, 68, 108
**eninsula** Bourguignat, 1860, *Caecilianella* 59
*Enneogoppa Boettger, 1889* 94
*Entelula* de Maria de Montecosato, 1894 62
*Eucha Swainson, 1840* 95
**esserana** Fagot, 1832, *Testacella* 98
*etruscus Iseel, 1858, Limax* 92
*cubitus* Bourguignat, 1845c, *Limax* 81
**eucharis** Sorvain, 1880, *Caecilianella* 59

*EUCONULIDAE* 28, 55
**Eugoniostoma** Mabille, 1870 42
*Euhyalinella* Albers, 1857 108
*Euhyalinella* of authors 116
*Euhyalinella* Taylor, 1907 108
*Euhyalinella* Moquin-Tandon, 1855 84
**eutecta** of authors 32, 77
*Eurolax Boettger, 1881* 77
*Europaea de Rossy, 1805, Testacella* 98
*eutaca* de Maria de Montecosato, 1892, *Halix* 62
*Euxinolauria Lindholm, 1924* 84

**excavata** Sterki, 1893, *Valtonia* 100, 151k, Figures 58, 90, 130, 160, 196, 212, 228, 253, C26, M23, M100, M101, M119, M120; Map 28
**excavatoides** Weise, 1894, *Valtonia pulchella* 100
**exiguia** Menke, 1830, *Achatina* 52
**expedenta** Locard, 1889, *Halix* 73

*fagotii* Westarfund, 1894, *Pupa* 95
? *falkii* Sterki, 1892, *Arion* 45
*fenalensis* Lowe, 1852, *Pupa* (Gastrodon) 65
*fannesiensis* Bourguignat, 1870, *Zonites* 111
*fasciatus* Moquin-Tandon, 1855, *Arion fascius* 43
? *fasciata* Poiret, 1801, *Halix* 73
*Férrussac's orange snail* 45
*Férrussac's gonomova Risso, 1825* 51, 58
*Férrussac's of authors 51, 58

*FERUSSACIIDAE* 28, 51, 58
*Fiemmulina* Doll, 1852 20
*Fiemmulina van Marton, 1873* 108

*flavus* (Linnaeus, 1758), *Milax* 81, 152k, Figures 48, 47, 53, 124, 153, 179, 205, 249, C17, C18, M77–79; Map 17
*flavus* Linnaeus, 1758, *Milax* 81
*flavus* Müller, 1774, *Milax* 48
*foederana* Bourguignat, 1880, *Hyelina* 114
*foedrica* Brown, 1827, *Halix* 109
*Folliculitis de Charpentier, 1837* 51
*fuliginosa* Gould, 1852, *Limax* 87
*funa* Paulucci, 1879, *Amaia margaritans* 92
*Furocopenia Castillejo & Wiktor, 1993* 31
*fuscosus* Morelet, 1845, *Arion* 48
*fuscus* of authors 45, 48

*gagates* (Draspara, 1801), *Milax* 87, 152k, Figures 49, 52, 95, 103, 125, 155, 161, 207, 253, 251, C20, C21, M53–66; Map 18
*gelatodes Draspara, 1801, Limax* 87
*gelatodes* Menegazza, 1856, *Milax* 90
*gelatodes Mabille, 1883, Milax 88
*gelati* von Oken, 1816, *Testacella* 98
*gelatodes* Mabille, 1883, *Milax* 88
*gelatodes* of authors 108
*Gelatodes panteina* Hutton, 1882 108
*Gelatodes von Oken, 1816* 72
*Gastrodon* Pini, 1876 84
*Gigantamia* Boettger, 1885 77
*glabesca Costa, 1778* Turbo 52
*glade slug* 48
*Glandina* of authors 51, 58
*Glandina olivaee Schumacher, 1817 51, 58
*glaphyra* Say, 1816, *Halix* 111
*Gephyra Albers, 1850* 100
*Glischrus* Hecker, *candidula* Studer, 1820 72
*Glischrus* (Hecker) *diaphana* Studer, 1820 107, 109, 116
*gorgonanus* Guisti, 1868, *Oxychilus* 114
*gracilis* Leydig, 1876, *Milax* 90
*gracilis* Rafinesque Schmaltz, 1820, *Milax* 32
*grassland snail* 105
*grey field slug* 38
*grisea Gmelin, 1791, Halix* 62
*guatemalensis* Crossa & Fischer, 1870, *Milax* 32
*gundlachi* Pfeiffer, 1850, *Achatina* 59
*gyrocurtopsis* Locard, 1889, *Hyelina* 114
Helix lucida
Helix lubrica
Helix
Helix lineata
Helix infula
Helix hydatina
Helix haemastomus
Helix fuscosa
Helix fatua
Helix explanate
Helix ericetorum
Helix crystallina
Helix cretica
Helix cornea
Draparnaud, 1801 100
Helix conoidea
Helix citrina
Helix cheilogona
Helix cellaria
Helix calculosa
Helix aspersa
Helix carthusiana
Helix arboreus
Helix aperta
Helix algira
Helix (Zenobia) binarginata
Helix (Jacosta) albella
Helix (Isthmia) cylindrica
Helix (Cochlodon) anconostoma
Heliomanes
Helicodiscus
Helicodiscus (Hebetodiscus) singleyanus inermis
Helicodiscus parallelus
Helicodiscus (Hebetodiscus) singleyanus
HELICODISCIDAE 68
HELICINAE
Helicodiscus Morse, 1864 68, 69
Helicodiscus peraleus (Say, 1821) 69
Helicodiscus fontana d'Audebard de Férussac, 1819 107
Helicogena of authors 61
Helicopsis Fitzinger, 1833 72
Heliocones of authors 72
Heliocones of authors 72
Helix
Helix (Cochlodon) enconostoma Lowe, 1831 94
Helix (Lithium) cylindrica Gray, 1821 104
Helix (Jaccotta) albella Draparnaud, 1801 72
Helix (Zenobia) binaerigata Gray, 1821 72
Helix aigua Linnaeus, 1758 56, 69, 104, 107, 116, 119
Helix aperta von Born, 1778 61, 62
Helix arboreus Say, 1816 119
Helix aspersa Müller, 1774 61
Helix calcicola Gould, 1852 56
Helix carthusaiana Müller, 1774 72
Helix cellaria Müller, 1774 55, 69, 107, 108, 116, 119
Helix chellogona Lowe, 1831 95
Helix citrina Linnaeus, 1758 56
Helix coroidea Draparnaud, 1801 75
Helix cornea Draparnaud, 1801 100
Helix cretica Pfeiffer, 1841 75
Helix crystallina Müller, 1774 116
Helix ericetorum Müller, 1774 72, 75, 108, 116
Helix explanata Müller, 1774 72
Helix tatus Hutton, 1880 69
Helix tuscosa Roessmaessler, 1838 109
Helix haemastomus Linnaeus, 1758 61
Helix hyalina Roessmaessler, 1838 108
Helix intuia Benson, 1848 56
Helix lineata Say, 1817 69
Helix Linnaeus, 1758 12, 61
Helix lubrica Müller, 1774 51, 58
Helix lucida Draparnaud, 1801 103, 116, 119
Helix
Helix tyndhustensis Cox, 1868 119
Helix marmorea Pfeiffer, 1845 106
Helix mazzulifera de Cristolori & Jan, 1832 62
Helix melanostoma Draparnaud, 1801 61
Helix mortillii "Stabile" Pfeiffer, 1859 108
Helix mozambicensis Pfeiffer, 1855 56
Helix Müller, 1774 51
Helix naticodis Draparnaud, 1801 81
Helix nita Müller, 1774 108, 119
Helix octona Gmelin, 1799 58
Helix of authors 51, 56, 58, 69, 72, 75, 94, 97, 100, 107, 116, 119
Helix olivetorum Müller, 1774 109
Helix olvietorum Gmelin, 1799 109
Helix paludosus da Costa, 1778 100
Helix pisana Müller, 1774 72, 75
Helix pomatia Linnaeus, 1758 56, 69, 72, 75, 94, 97, 100, 107, 116, 119
Helix pulchella Müller, 1774 100
Helix rufa Draparnaud, 1801 97
Helix rubra Müller, 1774 55
Helix setubalensis Pfeiffer, 1850 72
Helix striata Müller, 1774 72
Helix univalvata Poiret, 1801 72
Helix ventricosa Draparnaud, 1801 75
Helix villae Mortillet in Strobl, 1853 106
Helminthoglyptidae 20
hemiptyli Binney, 1890, Limax 32
hacaracensis Westerlund, 1893, Hyalina (Pellia) 111
herbarum Sarsvik, 1860, Helix 73
hespertium Pillsbury, 1844, Deroceras 32
hessei Boatger, 1892, Amalia 92
hessei Simroth, 1894, Arion 48
hewstoni Cooper, 1872, Limax (Amalia) 98
Hemynannia Malm, 1868 84
hibbardi Baker, 1928, Vulturco 105
hibernica Kennard, 1907, Vitrea (Hyalina) 111
hiemens Drouet, 1867, Geomalacus 48
H. hufeliformis Locard, 1899, Hyalina 114
hortensis d'Audebard de Férussac, 1819, Arion 45
1526, Figures 32, 72, 68, 113, 142, 247, C5, M45–47; Map 5
hortensis of authors 45, 48
hortensis Pennant, 1777, Helix 62
? hortensis var. alpha d'Audebard de Férussac, 1819, Arion 43
humbleo Mabil, 1870, Zonites 117
Hyalina Bielu, 1860, Acicula 59
Hyalina (Pellia) heveliana Blum, 1881 109
Hyalina de Charpentier, 1837 108
Hyalina of authors 113, 119
Hyalina pellucida Schumacher, 1817 108, 115, 119
Hyalina Albers, 1850 108
Hyalina of authors 56, 69, 116
Hyalina fulgida di Maria di Montereale, 1892 103
Hydatina Perrays, 1849 51
Hydatina Westerlund, 1886 108, 109, 116

- 241 -
Laconia Pollonera, 1855, Zool. 52
Lochea Moquin-Tandon, 1855 42
Iubrica (Müller, 1774), Cochlicopa 52, 151k, Figures 34, 74, 115, 144, 170, 196, 224, C8, M3, M4, M51-53, M113; Map 7
Iubrica Müller, 1774, Helix 52
Iubricoides Stimpson, 1851, Bulimus 52
Lucina Gray, 1840 100
Lucilia Draparnaud, 1801, Helix 114
Lucilius of authors 111
Lucilla Lowe, 1855 106
Lucorum de Ruzoumowsky, 1789, Helix 62
Lusitanica Locard, 1899, Hyalinia 111
Lychnothusensis Cox, 1868, Helix 119
Lymphurttoides McLachian, 1854, Akement 119
Lythosce Adams & Adams, 1855 20
Lytopsche Boettiger, 1886 31
Mabille's orange snail slug 43
Mabille Baudon, 1868, Geomalace 43
Mabillianus Baudin, 1894, Arion 48
Macrochevrenamala Simroth, 1891 84
Macrospira Swainson, 1840 58
Macrothyacous Wagner, 1930 90
Maculata Collinge, 1895, Amalia 92
Maculatus Nurseney, 1637, Limax 84
Maculents Morelet, 1873, Gandina 52
Magaeoneusi Locard, 1894, Hyalinia 114
Malacolimax Malm, 1868 77
Malacolimax of authors 31, 77
Maino Gray, 1855 32
Mamelonensis Bourguignat, 1869, Krynikillus 84
Margari Caziot, 1903, Lauria umbilicata 95
Margirata of authors 78, 87
Marginatensis of authors 79, 92
Margirinae Ie, 116, 119
Mariposa Pilsbray, 1919, Vertigo ovata 105
Marsh slug 32
Maugei of authors 99
Maugiana Bourguignat, 1870, Caecilianella 58
Mauriciell Locard, 1894, Hyalinia 114
Maurocy Quoy & Gaimard, 1824, Limax 87
Maximus Linnaeus, 1758, Limax (Limax) 84, 153k, Figures 44, 48, 84, 125, 154, 180, 205, 222, 250, C18, M80-82; Map 16
Mazzulopsis Pilsbray, 1893, Helix (Pourisia) 82
Mediterranea Ciesini, 1850 108
Megalobium Miller, 1789 51, 58, 75, 94
Megalodontes Quoy & Gaimard, 1824, Limax 81
Megalopeltich Lindholm, 1914 31
Megapetala Möch, 1857 31
Megastoma of authors 62
Meliorisdi Maria di Monterosato, 1892, Hyalinia sica 114
Melitia Westfall, 1882, Chiorea (Caecilianella) 59
Melitofax Pollonera, 1851 77
Mentonicus Nevill, 1880, Krynichillus 32
Menidionara Heygrobelati, 1968, Deroceras 35
Merisoma Bourguignat, 1870, Caecilianella 58
Mesolimax brauni Pollonera, 1868 77
Mesolimax of authors 77
Mesolimax Pollonera, 1858 31
Metalimax Simroth, 1896 77
Microcanus Hesse, 1926 42
Microcoris of authors 50
Microcystinidae 50
Microlimax Hesse, 1926 87
MILACIDAE 20, 87, 90
Milax brandii von Martens, 1880 82
Milax gigeates (Draparnaud, 1801) 87, 152k, Figures 49, 52, 95, 103, 126, 135, 151, 207, 233, 251, C20, C21, M83-86, Map 18
Milax Gray, 1855 87, 90
Milax jahabanacensis Wagner, 1860 90
Milax of authors 90
Milax gracilis de Cristofori & Jan, 1832, Colubmia 59
Milax Dohn, 1869, Pupa 95
Minima von Siebold, 1847, Agathina 52
Minimus Simroth, 1885, Arion 48
Minor Paulucci, 1870, Helix aspersa 62
Minutos de Kalamensky, 1851, Krynichillus 38
Misia Paulucci, 1882-83, Pupa cydatraeus 95
Mollusca Mauritaniae Mabille, 1867, Geomalace 48
Molestus Hutton, 1879, Limax 36
Molifera Locard, 1899, Hyalinia 114
Mollona Pollonera, 1889, Arion 48
Momantophopous Pilsbray, 1944, Deroceras 32
Monaganensis Paulucci, 1879, Amalia marginata 92
Monodonta seminigra de Monet de Lamarck, 1822 51, 58
Montanus Ingersoll, 1875, Limax 32
Monticola Faget, 1860, Hyalinia 111
Moestaquenius Cockerell, 1914, Agrofimax guatemalensis 32
Mouescusia Gassies, 1871, Limax 32
Muscum of authors 95
Muscum Perrault, 1777, Turbo 52
Nanina of authors 56
Nanina of authors 56
Naninia Sowerby, 1842 56
Natica fluctuata Sowerby, 1825 116
Naticidae 116
Navonianus Bourguignat, 1870, Zonites 111
Neglecta Faget, 1890, Hyalinia 111
Nicensis Nevill, 1880, Krynichillus 36
Niger Morelet, 1845, Limax agrestis 38
Nigrifustulus Tate, 1881, Milax 88
Nitens of authors 109, 111
Nikda Draparnaud, 1805, Helix 114
Nikula of authors 111
Nikulas of authors 109
Notha Paulucci, 1886, Hyalinia scotophila 114
Notodiaphana Thiele, 1917 109, 116
Notodiaphadamidae 116
Vertigo bidens Montagu, 1803 - 94
Turbo bidens Ström, 1765 - 94
Turbo cylindracea da Costa, 1778 - 94 - 95
Turbo marmoratus Linneaus, 1758 - 94
Turbo muscorum Linneaus, 1758 - 94
Turbo of authors 51 - 94
Turbo patholatus Linneaus, 1758 - 51
Turbo picatus Montagu, 1803 - 94
Turbo uva Linneaus, 1758 - 104
Turcomalix Simroth, 1901 - 77

? Turrisitala Iredale, 1933 - 56
Turrisitala normalis Iredale, 1933 - 56

Tyrena Lessona & Pollonera, 1862, Amalia 92
umbikata Draparnaud, 1801, Pupa 95
umbrosus Philippi, 1844, Limax 81
ungulatus Brand, 1815, Limacella 81
unicentatus Vallot, 1801, Bulimus 95
uniplicata Bourguignat, 1864, Caecilianella 59
Urocoptidæ 21
Uroculidae 28

? vagans Hutton, 1882, Testacellidae 88
Vaginulidae 23
valachicus Grossu & Lupu, 1961, Milax gracilis 90
valvatus Philippi, 1858, Limax 32
Valencia slug 79

valentiana (d’Audebard de Férussac, 1823), Loehmannia 79, 153k, Figures 42, 46, 82, 123, 152, 178, 204, 221, C16, M73-76; Map 15
valentianus d’Audebard de Férussac, 1823, Limax 79

Vallonia excentrica Sterki, 1893 100, 151k, Figures 58, 90, 130, 160, 196, 212, 238, 253, C26, M23, M100, M101, M119, M120; Map 23
Vallonia pulchella (Müller, 1774) 100
Vallonia Risso, 1826 100
Vallonia rosalia Risso 100
Vallonia zaru Almuhembetova, 1979 100

VALLONIIDAE 28, 99
vernegisca Gmelin, 1791, Helix 82
vernegatus Draparnaud, 1801, Milax 81
veldovskiyi Dabor & Kostel, 1983, Arion 46
vendeanus Lenoueux, 1969, Geomalacæ 48
ventricosus Draparnaud, 1801, Bulimus 75
Ventridens Binney & Bland, 1869 118
ventricosa d’Audebard de Férussac, 1821, Helix (Cochlicella) 75
vernexui Meblei, 1863, Milax 88
vernucosus Breière, 1881, Arion 46

VERTIGINIDAE 21, 28, 103

VERTICINIDAE 104
Vertigo antivertigo (Draparnaud, 1801) 104
Vertigo daillanae Sterki, 1890 104
Vertigo Müller, 1774 104

Vertigo ovata (Say, 1822) 105, 151k, Figures 59, 91, 131, 132, 161, 187, 239, 254, C27, M24, M26, Map 24
Vertigo pusilla Müller, 1774 104

- 246 -
Vertigo pygmea (Draparnaud, 1801) 104
Veru Benson, 1856, Achatina 59
violacea Gassies, 1849, Limax 38
virens d'Audebard de Férussac, 1819, Limax 81
vinctula Cockerell, 1886, Hyalina arboreus 119
Vitrea (Vitrea) crystallina (Müller, 1774) 117, 151k, Figures 66, 85, 139, 163, 189, 217, 243, C31, M29, M30, M108, M109; Map 28
Vitrea (Vitrea) Fitzinger, 1833 117
Vitrea Fitzinger, 1833 109, 116
Vitrea of authors 107
vitrina Thiele, 1828, Durgelfina 56
Vitrina Draparnaud, 1801 119
Vitrina zebra Le Guillou, 1842 108
Vitrinidae 28, 119
Voluta soto finger Linnaeus, 1758 94, 104
Vortex of authors 107
vulcanica di Maria di Monterosato, 1892, Hyalinia sicula 114
vulgaris da Costa, 1778, Cochlea 62
generis Moquin-Tandon, 1835 84
weinlandi Heynemann, 1862, Limax 32
whitneyi Newcomb, 1864, Helix 119
wrinkled snail 73
Xerocrusta of authors 75
Xerocrassa di Maria di Monterosato, 1892 75
Xerophila of authors 72, 75
Xeroplex of authors 72
Xerovaga di Maria di Monterosato, 1892 72
yellow cellar slug 81
Zenobia of authors 72
Zenobiella Gude & Woodward, 1921 72
zonatipes Cockerell, 1892, Agriolimax campestris 32
Zonitellus Baker, 1928 119
Zonites of authors 56, 69, 104, 107, 116, 119
ZONITIDAE 28, 56, 69, 104, 107
ZONITINAE 107
Zonitoides (Zonitoides) arboreus (Say, 1816) 119, 152k, Figures 67, 96, 137, 164, 190, 218, 244, C32, M31, M110–112, M125, M126, Map 29
Zonitoides (Zonitoides) Lehmann, 1862 119
Zonitoides Lehmann, 1862 118, 119
Zonitoides of authors 108
Zua Leach, in Turton, 1831 51
Zurama Leach, 1819 100
Area codes and boundaries used to categorise specimen locality data (after Crosby et al. 1976)

Base map for plotting collection localities; this may be photocopied without copyright release
THE NEW ZEALAND SUBREGION
(excludes Lord Howe, Norfolk, and Macquarie islands except in the context of extralimital zoogeography)
TITLES IN PRINT / PUNA TAITARA TAA

1 Terebrantia (Insecta: Thysanoptera) • Laurence A. Mound & Annette K. Walker
ISBN 0-477-06687-9 • 23 Dec 1982 • 120 pp. .................................................. $29.95

2 Osoriinae (Insecta: Coleoptera: Staphylinidae) • H. Pauline McColl
ISBN 0-477-06688-7 • 23 Dec 1982 • 96 pp. .................................................. $18.60

3 Anthribidae (Insecta: Coleoptera) • B.A. Holloway
ISBN 0-477-06703-4 • 23 Dec 1982 • 272 pp. ................................................. $41.00

4 Eriophyoidea except Eriophyinae (Arachnida: Acari) • D.C.M. Manson
ISBN 0-477-06745-X • 12 Nov 1984 • 144 pp. ................................................. $29.95

5 Eriophyinae (Arachnida: Acari: Eriophyoidea) • D.C.M. Manson
ISBN 0-477-06746-8 • 14 Nov '84 • 128 pp. ............................................... $29.95

6 Hydraenidae (Insecta: Coleoptera) • R.G. Ordish
ISBN 0-477-06747-6 • 12 Nov 1984 • 64 pp. .................................................. $18.60

7 Cryptostigmata (Arachnida: Acari) – a concise review • M. Luxton
ISBN 0-477-06762-X • 8 Dec 1985 • 112 pp. ................................................ $29.95

8 Calliphoridae (Insecta: Diptera) • James P. Dear
ISBN 0-477-05736-6 • 24 Feb 1986 • 88 pp. .................................................. $18.60

9 Protura (Insecta) • S.L. Tuxen

10 Tubulifera (Insecta: Thysanoptera) • Laurence A. Mound & Annette K. Walker
ISBN 0-477-06784-0 • 22 Sep 1986 • 144 pp. ............................................... $34.65

11 Pseudococcidae (Insecta: Hemiptera) • J.M. Cox
ISBN 0-477-06791-3 • 7 Apr 1967 • 232 pc. ................................................ $49.55

12 Pompilidae (Insecta: Hymenoptera) • A.C. Harris

13 Encyrtidae (Insecta: Hymenoptera) • J.S. Noyes
ISBN 0-477-02517-X • 9 May 1988 • 192 pp. .............................................. $44.95

14 Lepidoptera — annotated catalogue, and keys to family-group taxa • J. S. Dugdale

15 Ambositrinidae (Insecta: Hymenoptera: Diapriidae) • J.D. Naumann

16 Nepticulidae (Insecta: Lepidoptera) • Hans Donner & Christopher Wilkinson

17 Mymaridae (Insecta: Hymenoptera) • J.S. Noyes & E.W. Valentine
ISBN 0-477-02542-0 • 28 Apr 1989 • 100 pp. .............................................. $24.95

18 Chalcidoidea (Insecta: Hymenoptera) – introduction, and review of smaller families

19 Mantodea (Insecta), with a review of aspects of functional morphology and biology • G.W. Ramsay
ISBN 0-477-02581-1 • 13 Jun 1990 • 96 pp. .............................................. $24.95

20 Bibionidae (Insecta: Diptera) • Roy A. Harrison

21 Margarodidae (Insecta: Hemiptera) • C.F. Morales
ISBN 0-477-02607-9 • 27 May 1991 • 124 pp. .............................................. $34.95

- 250 -
Taxonomic groups covered in the
Fauna of New Zealand series

Insecta

Coleoptera
Family-group review and keys to identification (J. Klimaszewski & J.C. Watt, FNZ 37, 1997)
Anthribidae (B.A. Holloway, FNZ 3, 1982)
Anthicidae (F.G. Werner & D.S. Chandler, FNZ 34, 1995)
Curculionidae: Cryptorrhynchinae (C.H.C. Lyal, FNZ 29, 1993)
Curculionoidea larvae: a systematic overview (Brenda M. May, FNZ 2, 1982)
Hydraenidae (R.G. Ordish, FNZ 6, 1884)
Staphylinidae: Osoriinae (H. Pauline McColl, FNZ 2, 1982)
Tenebrionidae: catalogue of types and keys to taxa (J.C. Watt, FNZ 26, 1992)

Diptera
Bibionidae (Roy A. Harrison, FNZ 20, 1990)
Caliphoridae (James P. Dear, FNZ 8, 1986)
Dolichopodidae: Sciapodinae, Medeterinae with a generic review (D.J. Bickel, FNZ 23, 1992)
Therevidae (L. Lyneborg, FNZ 24, 1992)

Ephemeroptera
Leptophlebiidae (D.R. Towns & W.L. Peters, FNZ 38, 1996)

Hemiptera
Cercopidae (K.G.A. Hamilton & C.F. Morales, FNZ 25, 1992)
Cynidae, Acanthosomatidae, and Pentatomidae (M.-C. Lariviére, FNZ 35, 1995)
Margarodidae (C.F. Morales, FNZ 21, 1991)
Pseudococcidae (J.M. Cox, FNZ 11, 1987)

Hymenoptera
Diapriidae: Ambrosiinae (J.D. Naumann, FNZ 15, 1988)
Encyrtidae (J.S. Noyes, FNZ 13, 1988)
Myrmaridae (J.S. Noyes & E.W. Valentine, FNZ 17, 1989)
Pompilidae (A.C. Harris, FNZ 12, 1987)
Pteromalidae: Eunotinae: Moranini (J.A. Barry, FNZ 33, 1995)
Sphecidae (A.C. Harris, FNZ 32, 1994)

Lepidoptera
Annotated catalogue, and keys to family-group taxa (J.S. Dugdale, FNZ 14, 1988)
Hepialidae (J.S. Dugdale, FNZ 30, 1994)
Nepaliculidae (Hans Donner & Christopher Wilkinson, FNZ 16, 1989)

Mantodea, with a review of aspects of functional morphology and biology (G.W. Ramsay, FNZ 19, 1990)

Plecoptera
Antarctoperlinae (I.D. McLellan, FNZ 27, 1993)
Notonemouridae (I.D. McLellan, FNZ 22, 1991)

Protura (S.L. Tuxen, FNZ 9, 1986)

Thysanoptera
Terebrantia (Laurence A. Mound & Annette K. Walker, FNZ 1, 1982)
Tubulifera (Laurence A. Mound & Annette K. Walker, FNZ 10, 1986)

Arachnida

Acarina
Cryptostigmata - a concise review (M. Luxton, FNZ 7, 1985)
Eriophyoidea except Eriophyinae (D.C.M. Manson, FNZ 4, 1984)
Eriophyinae (D.C.M. Manson, FNZ 5, 1985)

Crustacea

Amphipoda
Talitridae (K.W. Duncan, FNZ 31, 1994)

Mollusca

Gastropoda
Naturalised terrestrial Stylommatophora (G.M. Barker, FNZ 38, 1999)
NOTICES

This series of refereed occasional publications has been established to encourage those with expert knowledge to publish concise yet comprehensive accounts of elements in the New Zealand fauna. The series is professional in its conception and presentation, yet every effort is made to provide resources for identification and information that are accessible to the non-specialist.

Fauna of N.Z. deals with non-marine invertebrates only, since the vertebrates are well documented, and marine forms are covered by the series Marine Fauna of N.Z.

Contributions are invited from any person with the requisite specialist skills and resources. Material from the N.Z. Arthropod Collection is available for study.

Contributors should discuss their intentions with a member of the Invertebrate Systematics Advisory Group or with the Series Editor before commencing work; all necessary guidance will be given.

Subscribers should address inquiries to Fauna of N.Z., Manaaki Whenua Press, Landcare Research, P.O. Box 40, Lincoln 8152, New Zealand.

Subscription categories: ‘A’ — standing orders; an invoice will be sent with each new issue, as soon after publication as possible; ‘B’ — promotional fliers with order forms will be sent from time to time.

Retail prices (see ‘Titles in print’, page 250) include packaging and surface postage. Subscribers in New Zealand and Australia pay the indicated amount in $NZ; GST is included in the price. Other subscribers pay the listed price in $US, or its equivalent.

Back issues are available, and new subscribers wishing to obtain a full set or a selection may request a discount. Booksellers and subscription agents are offered a trade discount of ten percent.

NGA PANUI

Kua whakatūria tēnei rārangi pukapuka hou whakahauhau ki nga tohunga whai mātāuranga kia whakātū i nga mea e pā ana ki nga kararehe o Niutireni. He āhua tohunga tēnei rārangi pukapuka, engari, ko te hiāria kia mārama ai te tuhituhi, kia mōhio ai te mara ki nga tohu o ia ngaarara, o ia ngaarara, ā, kia whakāri i te mātāuranga e pā ana ki a rātou.

Ko e nei pukapuka Fauna of New Zealand kāore e pā ana ki nga kararehe moana, arā, ki nga ika, ki nga mātai tānei. E tino mōhio tia ana nga kararehe. Kei roto i nga pukapuka e kia ana Marine Fauna of New Zealand nga tuhituhi e pā ana ki nga kararehe moana nga ika me nga mātai tānei, hoki.


Me whāki ē koutou whakārō ki te mema o te kāhui tohutuho o Fauna e tika ana, ki te Etta rānei, i mua i te timatanga tuhituhi.

Nga kai-hoko pukapuka. Me tuhi ki te Fauna of N.Z., Manaaki Whenua Press, Landcare Research, P.O. Box 40, Lincoln 8152, New Zealand.

E rua nga tūmomo kai-hoko: ‘A’ — Kai-hoko tūmāu; ka tukua ia pukapuka, ia pukapuka, me te kaute, i muri tonu i te tānga o laua pukapuka. ‘B’ — ka tukua nga pānui anake, a tōna wā, a tōna wā.

Te utu (tirohia te whārangi 250): Ko te kōpakitanga me te pane kuini kei roto i te utu. Me tuhoutou e nohu ana i Niutireni me Ahiterenira ki nga tāra o Niutireni. Ko ētahi atu me tuhoutou te whakaretenga i nga tāra Markena.

E toe ana nga pukapuka o mua. Me he mātai te hiahia ena ko te katoa o nga pukapuka, tona mai kia heke iho te utu. E tekau pai hēnēte heke iho te utu ki nga toa hoko pukapuka.
Fauna of New Zealand
Ko te Aitanga Pepeke o Aotearoa

Number 38

Naturalised terrestrial Stylommatophora
(Mollusca: Gastropoda)

Gary M. Barker