ISSN 0136-0027

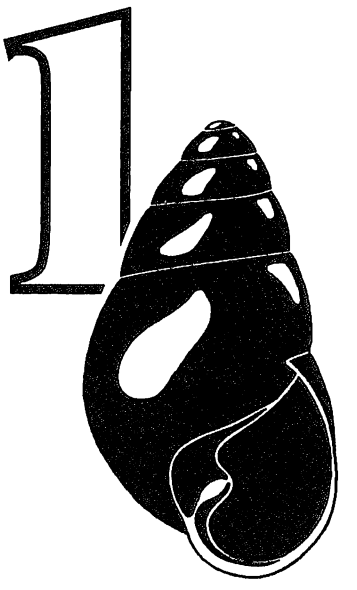
A. A. SCHILEYKO

TREATISE

ON

RECENT TERRESTRIAL PULMONATE MOLLUSCS

RUTHENICA
SUPPLEMENT 2



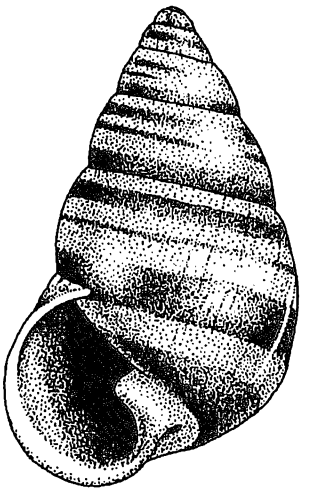
Suppl.2
Pt.1
1998

A. A. Schileyko

TREATISE ON RECENT TERRESTRIAL PULMONATE MOLLUSCS

Part 1

Achatinellidae, Amastridae, Orculidae, Strobilopsidae, Spelaeodiscidae, Valloniidae, Cochlicopidae, Pupillidae, Chondrinidae, Pyramidulidae



Ruthenica, Supplement 2
Moscow ✦ 1998

CONTENTS

Editors of the volume: A. V. Sysoev, D. L. Ivanov,
Zoological museum of Moscow State University

Preface

Any comprehensive research has at least two main goals: to generalize the main results of investigations conducted since last analogous work (in this case — the admirable monograph by Dr. Adolf Zilch, 1959-1960), and to give some fresh impetus for next researches. Besides, in the course of preparation of this book I have got some new ideas on the phylogeny of various groups; these ideas will be discussed in the concluding part.

I tried to examine personally as many type species of genera (subgenera) as possible; otherwise I used illustrations and/or descriptions from original or later publications. In total, type species (or, at least, similar to type species) of about 2600 taxa of genus group are described and illustrated in the book; the figures of more than 2000 shells are original. As concerns anatomical drawings, there are altogether over 800 figures; about 450 of them are based on my own dissections.

In systematic and phylogenetic parts I have used traditional both conchological and anatomical characters, except radular ones: on the one hand, because of numerous cases of convergence in radular teeth shape in many unrelated taxa, and, on the other hand, because of no less numerous cases when species of the same families have quite different shape of radular teeth (in particular, in Chondrinidae, Clausiliidae, endodontoid, helicoid and helicarionoid taxa, carnivorous pulmonates, etc.) (see Gittenberger, 1973; Likharev, 1962; Schileyko, 1972d; Solem, 1973c, 1974, 1976, 1982; Solem & Van Goethem, 1974, and many others).

Indeed, a book of this kind could not be written without cooperation with numerous colleagues and institutions who helped me in countless ways — starting from invitations to come and assistance in my work with collections, and ending by financial support. Some problems of taxonomy and phylogeny were discussed with many colleagues, particularly with Dr. George Davis, Dr. Edmund Gittenberger, Dr. Folco Giusti, Dr. Walter Miller, Dr. Igor Muratov, Dr. Barry Roth, Dr. Alan Solem, Dr. Yaroslav Starobogatov, Dr. Andrzey Wiktor. In addition, I managed to collect some very interesting material in arid Southwest of the United States due to efforts of my friends Dr. Eric Hochberg, Dr. Walter Miller and Dr. James Hoffman, and in Alps owing to friendly assistance of colleagues from Austria and Switzerland (Drs. Anette, Bruno, and Martin Baurs, Dr. Trudi Meier, Dr. Helmut Sattmann, Margarete and Ludwig Sattmanns, Drs. Hans, Mädi, and Renate Kothbauers, Dr. Olivier Paget, Dr. Karl Edlinger, Dr. Helmut Baminger, Dr. Ilse Wenger, Dr. Anita Eschner, Dr. Gabriele Baumgartner and many others). Dr. George Davis supported my visiting the Academy of Natural Sciences in Philadelphia. Dr. Edmund Gittenberger helped me to come and to examine the very rich collection of the Nationaal Natuurhistorisch Museum in Leiden. Dr. Mary Seddon kindly invited me to work with collection of the National Museum of Wales and to collect some material in Wales. Dr. Philippe Bouchet helped me to visit the Museum National d'Histoire Naturelle in Paris, to study the collection of this Museum and to collect mollusks in environs of Paris; in this work the assistance of Dr. Theodorus Ripken was priceless. Dr. Trudi Meier, Prof. Dr. Bruno Baur, and Dr. Ives Finet gave me a lucky possibility to work in museums of Switzerland. Dr. Andrey Kuznetsov has gathered a vast collection and kindly permitted me to use it. Dr. Hiroshi Minato kindly sent me a number of Japanese Clausiliidae. Dr. Dmitri Ivanov, Dr. Yuri Kantor and Dr. Alexander Sysoev did their utmost to improve the text and prepared the book for publication. The stuff of my laboratory (Laboratory of soil zoology and experimental entomology of A.N. Severtzov Institute of Problems of Evolution), and its head — Dr. Bella Striganova — kindly gave me a possibility to spend most of my time for writing of this book. I am deeply obliged to all of them.

Through the courtesy of the following institutions and colleagues it was possible to study collections:

A.N. Severtzov Institute of Problems of Evolution of Russian Academy of Sciences, Moscow (Dr. Yuri Kantor);

Academy of Natural Sciences, Philadelphia (Dr. George Davis, Dr. David Robinson, Dr. Coryl Hesterman, Dr. Robert Robertson, Dr. Gary Rosenberg, Miss Willa Mae Harvey);

Bernice Bishop Museum, Honolulu (Dr. Robert Cowie, Dr. B.K.Kawamoto);

Field Museum of Natural History, Chicago (Dr. Rudiger Bieler, Dr. Alan Solem, Dr. Jonn Slapcinsky, Miss Margaret Baker);

Florida Museum of Natural History, Gainesville (Dr. Fred Thompson, Dr. Kurt Auffenberg);

Forschungsinstitut Senckenberg, Frankfurt am Main (Dr. Ronald Janssen);

Muséum d'Histoire naturelle, Genève (Dr. Yves Finet, Dr. Claude Vaucher);

Museum National de l'Histoire Naturelle, Paris (Dr. Philippe Bouchet, Dr. Simon Tillier, Madame Virginie Heros, Dr. Bernard Metivier);

Nationaal Natuurhistorisch Museum, Leiden (Dr. Edmund Gittenberger, Dr. Theo Keppermann, Dr. Henk Menkhorst, Dr. Adolf Cornelis van Bruggen, Dr. Jaab Vermeulen, Dr. Antonius De Winter);

National Museum Wales, Cardiff (Dr. Mary Seddon, Dr. P. Graham Oliver);

Naturhistorisches Museum, Basel (Dr. Christoph Oberer and Frau Suzanne Oberer, Dr. Birgit Krumscheid);

Naturhistorisches Museum, Bern (Dr. Margrit Gosteli);

Naturhistorisches Museum, Wien (Dr. Erhard Wawra, Dr. Helmut Sattmann, Dr. Karl Edlinger, Dr. Oliver Paget, Dr. Anita Eschner, Dr. Gabriele Baumgartner, Frau Helga Ognar);

Santa Barbara Musem of Natural History (Dr. Erik Hochberg, Dr. Walter Miller, Dr. Barry Roth, Dr. Paul Scott);

Staatliches Museum für Tierkunde, Dresden (Dr. Katrin Schniebs);

The Natural History Museum, London (Dr. Jonh Taylor, Dr. Joan Mulrooney, Dr. Fred Naggs, Dr. Kathie Way);

Zoological Institute of Russian Academy of Sciences, Sanct-Petersburg (Dr. Ilia Likharev, Dr. Yaroslav Starobogatov, Mrs. Lidia Yarohnovich);

Zoological Museum of Moscow State University (Dr. Olga Rossolimo, Dr. Dmitri Ivanov, Dr. Alexander Sysoev, Dr. Michail Heptner, Dr. Arkady Schileyko);

Zoologischen Museum, Berlin (Prof. Dr. Rudolf Kilias);

Zoologisches Museum der Universität Zürich (Dr. Trudi Meier, Dr. Georg Ribi).

Some comments on the text

Descriptions of taxa include the dimensions of shells; they are followed by actual size of the illustrated shell indicated in brackets.

In the end of synonymy, after point, sometimes are indicated publications containing the most recent revision or a good analysis (or redescription) of the taxon, even if they do not contain descriptions of new taxa or changes in nomenclature.

In captions to figures, an exclamation mark (!) before the species name indicates that it is not a type species.

Abbreviations "OD" and "SD" mean "type species by original designation" and "type species by subsequent designation of..." correspondingly.

Some contradictions in understanding the terms "distal" and "proximal" exist in current literature. As reproductive apparatus "begins" from the gonade I designate as "distal" the section farthermost from the hermaphroditic gland, i.e. I consider the genital atrium to be the distalmost section of genitalia.

I have got a number of specimens from various museums as gifts or by exchange; all of them are deposited in the Zoological Museum of Moscow State University and have collection numbers of this Museum. However, I indicate in brackets the collection numbers of series from which the given specimen came: e.g., the indication "**Moscow** No. Lc-12345 (**Phil.** No. 15070)" means that the depicted shell is now stored in the Zoological Museum of Moscow University, but the original series is in Academy of Natural Sciences in Philadelphia.

The use of abbreviation of museum names by the first letters is generally accepted; however majority of names contain the same letters H, M, N (Museum, National, Natural History, Histoire Naturelle, Naturhistorisches, etc.) and abbreviations often differ in just a single letter or in the order of the

same letters. To make the abbreviations more understandable, I decided to use the location of the respective museum, namely:

Basel — Naturhistorisches Museum, Basel;

Berlin — Zoologischen Museum, Berlin;

Bern — Naturhistorisches Museum, Bern;

Cambridge — Harvard University, Cambridge, U.S.A.;

Cardiff — National Museum Wales, Cardiff;

Chicago — Field Museum of Natural History, Chicago;

Dresden — Staatliches Museum für Tierkunde, Dresden;

Gain. — Florida Museum of Natural History, Gainesville;

Geneva — Museum d'Histoire Naturelle, Genève;

Honolulu — Bernice Bishop Museum, Honolulu;

Leiden — Nationaal Natuurhistorisch Museum, Leiden;

London — The Natural History Museum, London;

Moscow — Zoological Museum of Moscow State University, Moscow;

Paris — Museum National d'Histoire Naturelle, Paris;

Phil. — Academy of Natural Sciences, Philadelphia;

StB — Santa Barbara Museum of Natural History, Santa Barbara;

Senck. — Forschungsinstitut Senckenberg, Frankfurt am Main;

SPb — Zoological Institute of Russian Academy of Sciences, Sanct-Petersburg;

Vienna — Naturhistorisches Museum, Wien;

Zürich — Zoologisches Museum der Universität, Zürich.

Abbreviations in figures

A — genital atrium
AA — atrial appendix
A-1...A-5 — divisions of penial appendix
AG — albumen gland
App — penial appendix
AR — atrial retractor
AS — additional sac
AtG — atrial gland
CF — carrefour
CS — circular slit in epiphallus
DSt — diverticle of spermatheca
E — epiphallus
EC — epiphallic caecum
Em — embryo in uterus
EP — epiphallic pore
F — flagellum
FO — free oviduct
GL — glandular layer
GS — gland of sarcobelum
HD — hermaphroditic duct
HG — hermaphroditic gland
K — kidney
MG — mucus gland
ML — muscular layer
N — neophore
OR — ommatophoran retractor
Ov — egg(s) in uterus
OVD — orifice of vas deferens or of epiphallus
P — penis
PA — papilla in penial appendix
PC (PC-1, PC-2) — penial caecum
PG — penial gland
Pil — pilaster
PR — penial retractor
Pro — prostate
PS — penis sheath
PSb — papilla of sarcobelum
PU — primary ureter
PVG — perivaginal gland
RS — reservoir of spermatheca
Sb — sarcobelum
SG — gland on spermathecal stalk
SOD — spermoviduct
SP — spermatophore
Sph — sphincter
SS — spermathecal stalk
St — stylophore
Sti — stimulator
SU — secondary ureter
T — talon
Ut — uterus
V — verge (penial papilla)
Va — vagina
Vap — vaginal appendix
VD — vas deferens
Vel — velum
VP — vaginal papilla

SYSTEMATICS

Class GASTROPODA

Subclass PULMONATA Cuvier, 1817

= Limaciones Golikov & Starobogatov, 1988: 69.

Operculum absent (only exception — freshwater family Amphibolidae). Respiratory organ is lung.

Superorder STYLOMMATOPHORA A. Schmidt, 1855

Schmidt A., 1855: 8.

= Limaciformii Férussac, 1801 (cf. Golikov & Starobogatov, 1988: 69).

Tentacles four in number (rarely, in small snails, lower pair absent). Eyes located on tips of upper tentacles.

Order GEOPHILA Férussac, 1812

= Limaciformes Férussac, 1801 (cf. Golikov & Starobogatov, 1988: 69).

Animals live and lay their eggs not in water.

Suborder PUPILLOIDEI Schileyko, 1979

Schileyko, 1979: 56 (as Pupillina).

Shell bulimoid, rarely depressed or microhelicoid, primarily with a long columellar lamella which appears in embryogenesis and persists at all later stages. Presence of parietal lamellae is characteristic. Palatal teeth often present.

Foot holopodous, without caudal horn or foss.

Excretory apparatus of orthurethral type: kidney nearly as long as lung or twice shorter, ureters open, having appearance of ciliary grooves, or closed.

Jaw, when present, thin, delicate, of aulacognathous, sometimes of polyplacognathous type.

Prostate consists of separate acini. Distal part of female division of genitalia without appendages. Penis primarily has caecum and appendix consisting of 5 sections. With exception of Sagdoidea, there are no obligatory predators in suborder.

Oviparous, rarely ovoviviparous.

Herbivorous or detrivorous.

Infraorder PUPILLOINEI Schileyko, 1979

Shell pupilloid, buliminoid, or microhelicoid.

Excretory apparatus typical orthurethral: kidney long, straight, ureters incompleted, or only partially completed.

ACHATINELLOIDEA Gulick, 1873

Gulick, 1873: 497 (pro fam.).

Shell dextral or sinistral, small to medium-sized, primarily turrited. Embryonic whorls smooth or with delicate spiral striae. Postembryonic whorls nearly smooth to radially ribbed. Among elements of aperture armature, long entering parietal and columellar lamellae primarily distingished. Aperture margins simple to reflexed and/or thickened. Inner lip, with rare exceptions, absent. Umbilicus closed to narrowly open.

Head with two pairs of tentacles.

Prostate consisting of few to numerous digitate or simple acini situated at base of albumen gland or stretched out along uterus. Penis generally without episphallus. Caecum absent. Inner walls of penis mostly with characteristic "achatinellid" pilaster or its modification. Penial appendix primarily present, sometimes modified, reduced, or absent. Penial retractor mostly biramous, rarely simple. Spermathecal stalk without diverticle.

Oviparous or ovoviviparous animals.

DISTRIBUTION. Predominantely Pacific islands in tropical and subtropical zones.

ACHATINELLIDAE Gulick, 1873

Gulick, 1873: 497

— Helicterinae Pease, 1869: 6 (Helicidae subf.).

Cooke, Kondo, 1960: 50.

Shell dextral or sinistral, elongate, ovate to turrited; small to medium sized. Coloration varies from uniformly dark-brown to bright, spirally banded or variegated. Aperture primarily with a complex armature, but in most advanced taxa much simplified. Parietal lamella and long, spirally ascending columellar lamellae very characteristic. Umbilicus usually closed, rarely narrowly open.

Jaw weakly developed or absent.

Genital orifice nearer to tentacle base than to mantle collar.

Hermaphroditic gland unilobate to multilobate, with duct usually swollen and convoluted. Talon mostly small (one exception). Albumen gland minute to large. Female and male divisions separated very early, so common division (spermoviduct) unusually short. Prostate either small, with few acini, or large, with many acini; acini strongly elongated. Vas deferens following vagina to atrium, hence recurving and following penis upward; entering penis terminally or subterminally, often adherent to penis from atrial area or at some distance above it. Penis well developed to small, reduced or occasionally lacking. Epiphallus absent (one exception). Internally penis as a rule with longitudinal recurved pilaster or with its modification. Penial appendix primarily present, rarely lacking. Penial retractor biramous.

DISTRIBUTION. Islands of Pacific Ocean; three species (of genus *Elasmias*) known from Lombok and Java in East Indies and from Mauritius and Reunion in Indian Ocean (introduced).

PITYSINAE Cooke et Kondo, 1960

Cooke & Kondo, 1960: 51.

Shell dextral, of various shape.

Right ocular retractor free of peni-oviducal angle.

Penis innervated by pedal ganglion.

Hermaphroditic gland multilobate. Albumen gland either minute, often absent in adults and large in juveniles, or large in adults and minute, often absent, in juveniles. Talon small, carrefour hidden among acini of albumen gland or of prostate. Prostate large if albumen gland minute or small, and vice versa. Epiphallus absent. Penis with or without appendix, with reflexed or modified achatinellid pilaster. Appendix, when present, with retractor; internally with secretory-ejaculatory apparatus. Spermathecal stalk entering spermoviduct above uterus, reservoir lying on surface of albumen gland and/or prostate.

Oviparous or viviparous animals.

DISTRIBUTION. Highest diversity in Austral Islands.

Pitysini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 53.

Shell strongly varying in shape, mostly aciculate and many-whorled; one group with subglobose shell; one genus with pagodiform, umbilicate shell.

Albumen gland minute in adult snails. Internally penis with recurved pilaster ending in semi-pendent papilla (stimulator). Penial appendix present.

Oviparous animals.

DISTRIBUTION. French Polynesia (Austral Islands) (Rapa, Raivavae, Tubuai, Rurutu).

Strobilus Anton, 1839

Anton, 1839: 46 (*Clausilia* subg.).

— *Elasmatina* Petit, 1843: 2 (t.-sp. *Elasmatina subulata* Petit, 1843; SD Gray, 1847).

— *Strombilus* Gray, 1847: 175 (nom. err. pro *Strobilus* Anton, 1839).

TYPE SPECIES — *Strobilus turritus* Anton, 1839; SD Pilsbry & Cooke, 1915.

Shell aciculate to elongated-ovate, thin, subtransparent to translucent, glossy or somewhat dull, of 8-11 nearly flat to convex whorls. Outlines of spire straight to slightly convex. Embryonic whorls smooth or with extremely fine crowded spiral striae, which sometimes slightly oblique. Postapical sculpture of irregular very fine radial striae. Aperture subvertical, relatively small, with thin to slightly thickened non-reflexed margins. Parietal lamella long, rather strong, entering about 1.5 whorls. Columella simple or with one or two minute oblique lamellae. Palatal wall

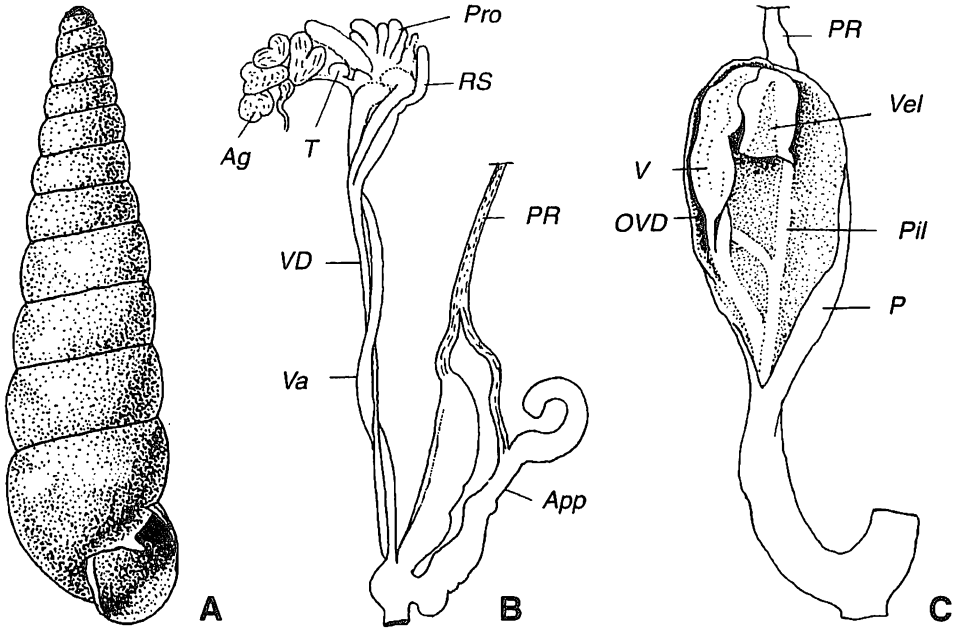


Fig. 1. ***Strobilus (Strobilus) turritus*** Anton, 1839.
A — shell: Tumu valley, Rapa. **Phil.** No. 180903; B — reproductive tract; C — interior of penis. B,C — after Cooke & Kondo, 1960.

smooth in adults; juvenile shell sometimes with palatal folds. Umbilicus absent.

DISTRIBUTION. French Polynesia (Rapa).

Strobilus (*Strobilus* s.str.) Fig. 1

Cooke, Kondo, 1960: 56.

Shell turrited or aciculate, of 8-12 whorls. Juveniles with or without a single palatal plica, usually with two (rarely three) columellar lamellae and moderate to strong parietal lamella. Height 3.06-7.04, diam. 1.00-2.36 mm (5.51 × 1.52 mm).

Talon small. Prostate small, of about 8 digitate acini. Vas deferens entering penis subapically under tip of verge. Penis internally with ascending narrow, Y-shaped arm of pilaster; velum comparatively large, campanulate; "verge" a simple elongate, high, fleshy ridge, apex diminishing in size into low ridge descending into basal portion of penis. Penial appendix fairly large, entering adatrial section of penis. Atrium short. Penial arm of retractor attached apically, arm of appendix inserted onto junction of short united A-3+A-4 and A-5.

DISTRIBUTION. Rapa Island. 7 spp. & subspp.

Strobilus (*Tautautua* Cooke et Kondo, 1960) Fig. 2

Cooke, Kondo, 1960: 68.

TYPE SPECIES — *Strobilus perfragilis* Cooke et Kondo, 1960; OD.

Shell turrited to acutely conic, of 9 whorls; differs from those of *Strobilus* s.str. in much reduced apertural armature: parietal lamella very low, columellar lamella absent at juvenile stage. Height 5.08, diam. 1.91 mm.

DISTRIBUTION. Rapa Island. 1 sp.

Strobilus (*Tanga* Cooke et Kondo, 1960) *Fig. 3*

Cooke & Kondo, 1960: 70.

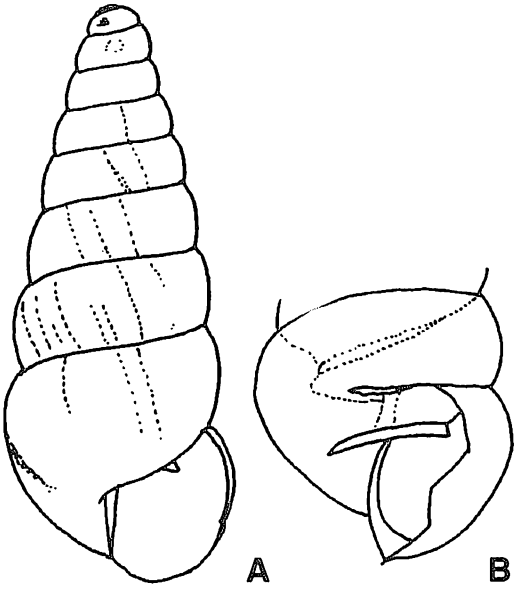


Fig. 2. ***Strobilus (Tautautua) perfragilis*** Cooke et Kondo, 1960.
A — adult shell, holotype; B — latero-oblique view of aperture. After Cook & Kondo, 1960.

TYPE SPECIES — *Strobilus brevis* Cooke et Kondo, 1960; OD.

Shell elongated, differing from *Strobilus* s.str. in fewer whorls (7 in number); whorls slightly flatter and increase more rapidly, parietal lamella higher and shorter, with sinuous ridge. In juveniles 3 columellar plates much stronger; 2 rather short palatal plicae entering about 0.3 whorl. Umbilicus absent. Height 3.01-2.87, diam. 1.18-1.28 mm.

Albumen gland large, multifollicular. Prostate not seen. Vas deferens entering penis well below apex. Penis large, clavate. Structure of appendix and retractor typical. Atrium long. Uterus enlarged, folded. Spermathecal shaft short, slender. Reservoir of spermatheca subglobular; Cooke and Kondo (1960) have found remnants of spermatophore in it.

DISTRIBUTION. Rapa Island. 1 sp. with 3 subspp.

Apopitys Cooke et Kondo, 1960
Fig. 4

Cooke & Kondo, 1960: 92.

TYPE SPECIES — *Apopitys andersoni* Cooke et Kondo, 1960; OD.

Shell subulate, thin, translucent, of 9.25 rather convex whorls. Outline of spire nearly straight. Color uniformly brown. Embryonic sculpture of fine but quite distinct spiral striation. Postapical whorls distinctly, closely, evenly ribbed. Aperture more or less ovate, with thin, sharp, straight margins. Parietal lamella in mature shells moderately developed, somewhat oblique, more than one whorl in length; in juveniles strong, with sinuous and flaring outward edge. Columella with 3 obligue plates. Palatal wall with rather long plica. Umbilicus closed. Height 6.49, diam. 2.45 mm.

Hermaphroditic gland 10-lobate. Albumen gland minute. Acini of prostate rather large. Vas deferens unusually broad. Penis with greatly enlarged apical portion and narrowed neck. Penial appendix well developed. Both arms of penial retractor short and heavy.

DISTRIBUTION. Rapa Island. 1 sp.

Pukunia Cooke et Kondo, 1960
Fig. 5

Cooke & Kondo, 1960: 73.

TYPE SPECIES — *Pukunia acuta* Cooke et Kondo, 1960; OD.

Shell sublanceolate, thin, glossy, translucent, of 8-10 slightly convex whorls. Spire tapering gradually to apex. Color cinnamon. Embryonic whorls smooth, later very finely radially striate. Aperture small, subvertical, with thin margins. Parietal lamella moderately developed, simple, obliquely seated, about 1.3 whorls in length. Columella in adult shells nearly straight, its inner face with thickened, almost straight lamella. In juveniles columella with strong, spirally ascending lamella and minute, nearly vertical, deeply seated supracolumellar plate. Palatal wall unarmed; in juveniles a low, continuous lower plica present. Umbilicus closed. Height 3.43-4.68, diam. 1.64-1.78 mm (4.31 × 1.62 mm).

Hermaphroditic gland 10-lobate; duct thick, convoluted, swollen. Albumen gland small. Prostate large, of digitate acini. Vas deferens narrow, entering penis apically through simple pore situated just below velum. Penis relatively long, clavate, with lower portion partly twisted, internally with

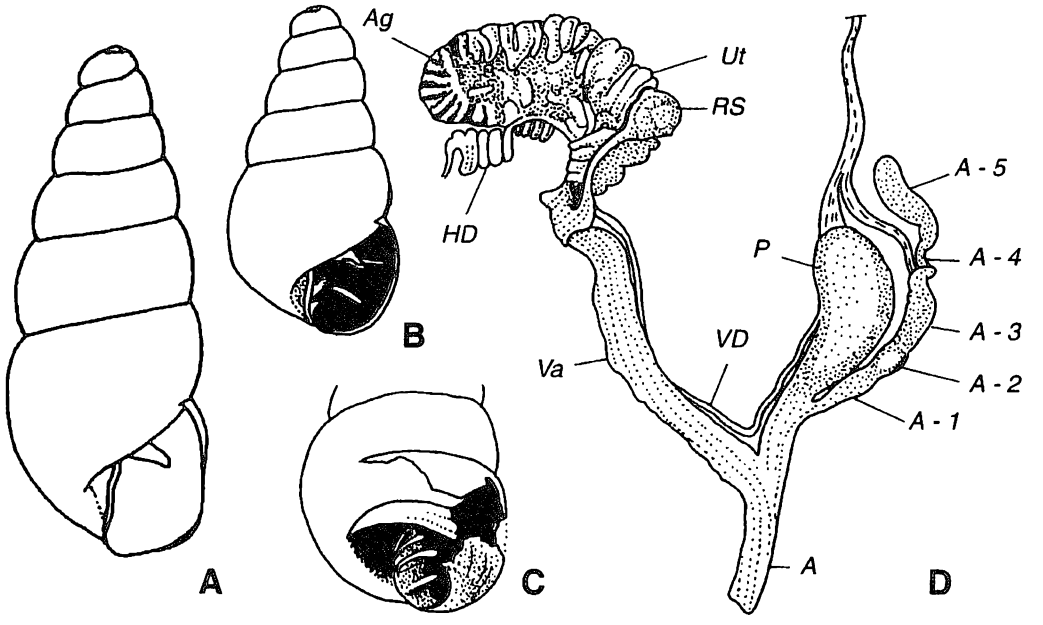


Fig. 3. ***Strobilus (Tanga) brevis*** Cooke et Kondo, 1960.
A — adult shell, holotype; B — juvenile; C — juvenile, latero-oblique view of aperture; D — reproductive tract. After Cooke & Kondo, 1960.

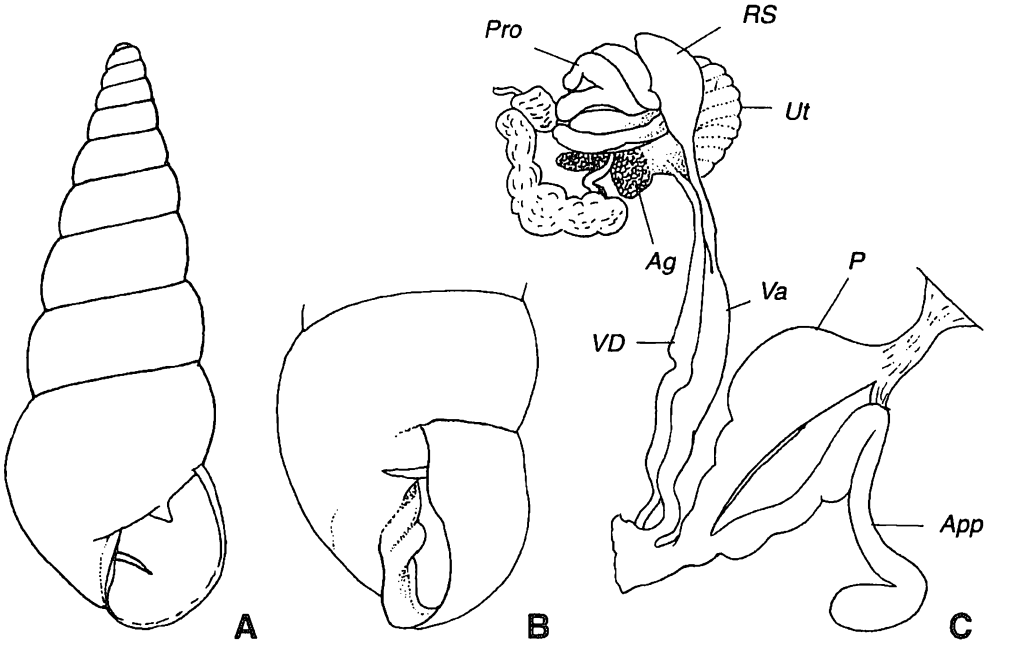


Fig. 4. ***Apopitys andersoni*** Cooke et Kondo, 1960.
A — adult shell, holotype; B — adult, latero-oblique view of aperture; C — reproductive tract. After Cooke & Kondo, 1960.

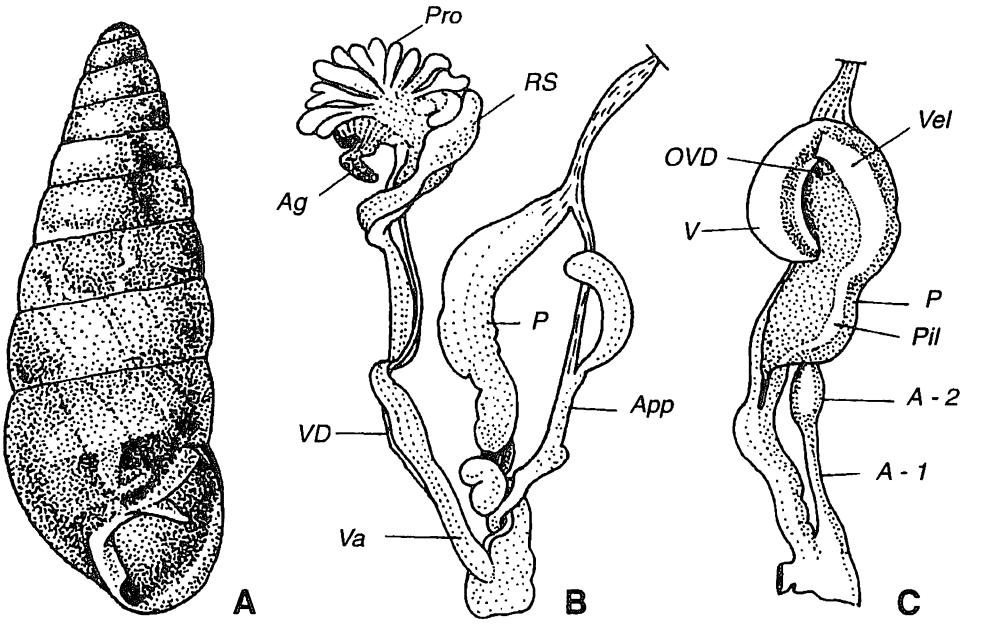


Fig. 5. ***Pukunia acuta*** Cooke et Kondo, 1960.
A — shell: Perahu Mt., Rapa Island. Paratype. **Phil.** No. 180927. B — reproductive tract; C — interior of penis. B,C — after Cooke & Kondo, 1960.

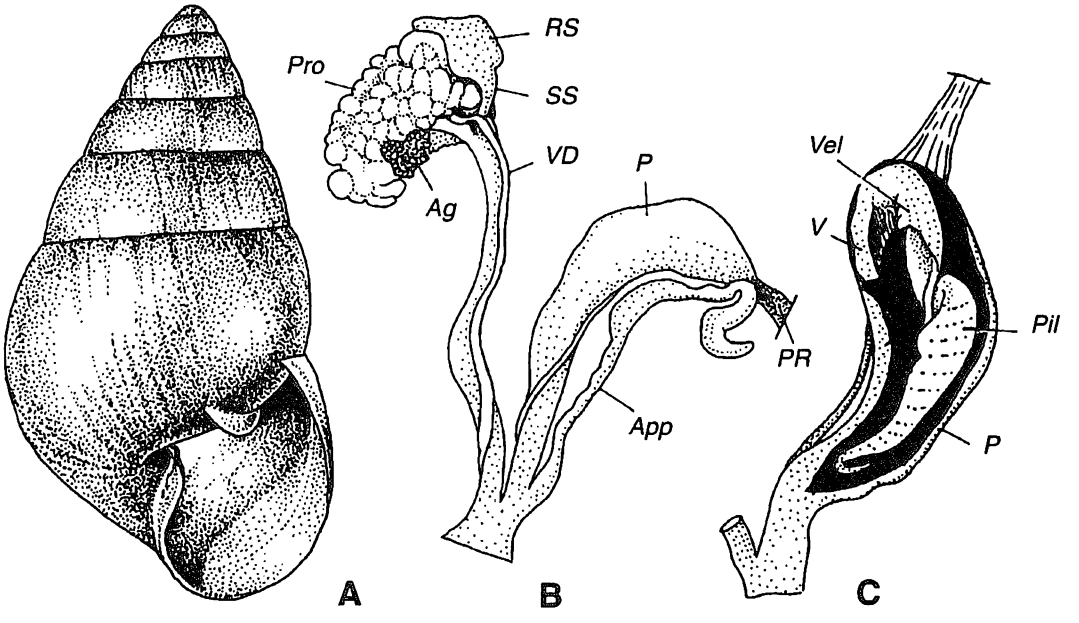


Fig. 6. ***Mitiperua simplex*** Cooke et Kondo, 1960.
A — shell: Makiki, Oahu Island. **Phil.** No. 163336. B — reproductive tract; C — interior of penis. B,C — after Cooke & Kondo, 1960.

low pilaster ascending from half-way point, forming small velum at apex, and descending as banana-shaped, semi-pendent verge with inner margin somewhat raised. Appendix in adult specimens rather small, shorter than penis. United portion of penial retractor and very short penial arm are thick, appendical branch slender, inserting onto base of A-5. Atrium shallow. Vagina fairly broad, long. Spermathecal shaft short, reservoir large, elongated-ovate.

DISTRIBUTION. Rapa Island. 3 sp.

Mitiperua Cooke et Kondo, 1960
Fig. 6

Cooke, Kondo, 1960: 79.

TYPE SPECIES — *Mitiperua simplex* Cooke et Kondo, 1960; OD.

Shell nearly conic to ovately conic, rather thin, slightly translucent, of 7-7.25 flattened whorls. Color more or less light- olive. Spire narrowly conic, with only slightly convex sides. Embryonic whorls nearly smooth or microscopically spirally striated. Later whorls with fine radial striation; striae somewhat closely and evenly spaced, not sharp or periostracal. Aperture subvertical, higher than broad, with indistictly thickened margins. Parietal lamella low, slightly oblique, entering about a half whorl. Columella more or less sigmoid, with two oblique, rather low, nearly equal lamellae. Palatal wall smooth at all stages of growth. Umbilicus closed. Length 5.16-6.57, diam. 2.86-3.84 mm (6.22 × 3.75 mm).

Hermaphroditic duct and albumen gland typical. Prostate large, of many subglobular acini. Vas deferens entering penis subapically; orifice not determinable because of transparent penial wall. Penis bulky, internally with heavy longitudinal pilaster, with strong apical velum, ending as short verge. Appendix relatively small. Penial retractor stout, unbranched, inserting onto penis apex. Vagina very long. Spermathecal shaft very short, reservoir large, with pointed apex.

DISTRIBUTION. Rapa Island. 1 sp. with 3 subspp.

Taitaa Cooke et Kondo, 1960

Cooke & Kondo, 1960: 82.

TYPE SPECIES — *Taitaa dacryma* Cooke et Kondo, 1960; OD.

Shell subulate to globosely conic, thin to somewhat thickened, of 5.25-6.25 rather convex whorls. Color very light to brown, practically monochromate. Embryonic whorls smooth, sculpture of rest whorls very delicate, of indistinct radial striae. Aperture ovate, with thin or a little thickened margins. Parietal lamella strong, oblique, entering 0.5-1 whorl. Columella slightly twisted, bearing 1 or 2 oblique lamellae in mature specimens and 3 in juveniles. Palatal wall unarmed in adults, with 1 or 2 short plicae in juveniles. Umbilicus closed.

DISTRIBUTION. Tubuai Archipelago (Tubuai, Rurutu and Raivavae).

Taitaa (*Taitaa* s.str.)
Fig. 7

Cooke & Kondo, 1960: 84.

Shell globosely conic. Juveniles with 2 columellar lamellae, persisting in adults. Palatal wall with single, high fold. Height 2.13-3.77, diam. 1.42-2.55 mm.

Hermaphroditic gland 6-lobate, duct convoluted. Talon small. Albumen gland minute in adults. Prostate large, of few elongated acini. Vas deferens slender, entering bulky penis laterally. Internally penis with modified pilaster: remains of ascending pilaster invertedly Y-shaped; verge large, cup-shaped, semi-pendent, fleshy, covering a small flap or valve; latter small, semi-ovate, pendulous or curled upward against orifice of vas deferens. Penial appendix large; three lower divisions (A-1 + A-2 + A-3) modified into voluminous thin-walled sac, in which a sperm mass may be found. Penial retractor biramous, short, stout. Atrium short. Vagina fairly broad. Spermathecal stalk short, reservoir small in adults and rather large in juveniles.

DISTRIBUTION. Tubuai Island. 2 spp.

Taitaa (*Taireva* Cooke et Kondo, 1960)
Fig. 8

Cooke & Kondo, 1960: 87.

TYPE SPECIES — *Taitaa striatula* Cooke et Kondo, 1960; OD.

Shell elongated-ovate. Juveniles with 3 columellar lamellae, subcolumellar persisting in adults. Palatal wall with a single high plica. Height 1.93-2.31, diam. 1.03-1.13 mm.

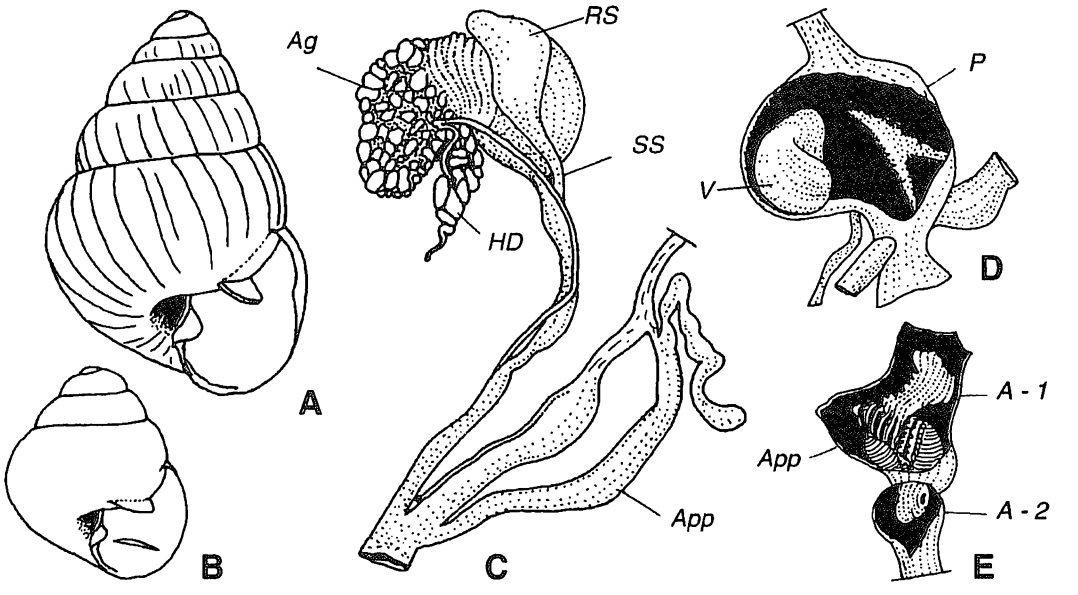


Fig. 7. ***Taitaa (Taitaa) dacryma*** Cooke et Kondo, 1960.
A — adult shell, holotype; B — juvenile shell; C — reproductive tract; D — interior of penis; E — interior of penial appendix. After Cooke & Kondo, 1960.

Anatomy similar to that of *Taitaa* s.str.

DISTRIBUTION. Tubuai and Rurutu Islands. 2 spp.

Taitaa (*Taraia* Cooke et Kondo, 1960)
Fig. 9

Cooke & Kondo, 1960: 89.

TYPE SPECIES — *Taitaa neanica* Cooke et Kondo, 1960; OD.

Shell elongately conic to nearly subulate. Juvenile shells with three columellar lamellae, middle somewhat more prominent; upper two persisting as low, thick ridges in adults. Palatal wall furnished with one or two plicae. Height 2.5-3.8, diam. 1.1-2.0 mm.

DISTRIBUTION. Raivavae Island. 2 spp. based on subfossil shells only.

Maitua Cooke et Kondo, 1960
Fig. 10

Cooke, Kondo, 1960: 108 (*Lamellovum* subg.).

TYPE SPECIES — *Lamellovum auriculella* Cooke et Kondo, 1960; OD.

Shell subturbinate to elongated-conic, thin to somewhat thickened, of 7-8 flattened to moderately convex whorls. Color uniformly corneous. Columella with 3 lower lamellae that not united into prominent protruding callus plate. Palatal fold(s) continuous, not interrupted. Height 3.30-7.04, diam. 1.65-3.85 mm.

Hermaphroditic gland 8-10-lobate. Albumen gland minute. Vas deferens entering penis subapically, wide above, narrowing below, still more along penis, entering penis terminally or nearly so. Ascending penial pilaster reflexed, terminating in semi-pendent verge (papilla). Velum one, campanulate.

DISTRIBUTION. Rapa Island. 4 spp.

Lamellovum Pilsbry, 1910
Fig. 11

Pilsbry, 1910: 123. Cooke & Kondo, 1960: 103.

TYPE SPECIES — *Elasmatina globosa* Petit, 1843; OD.

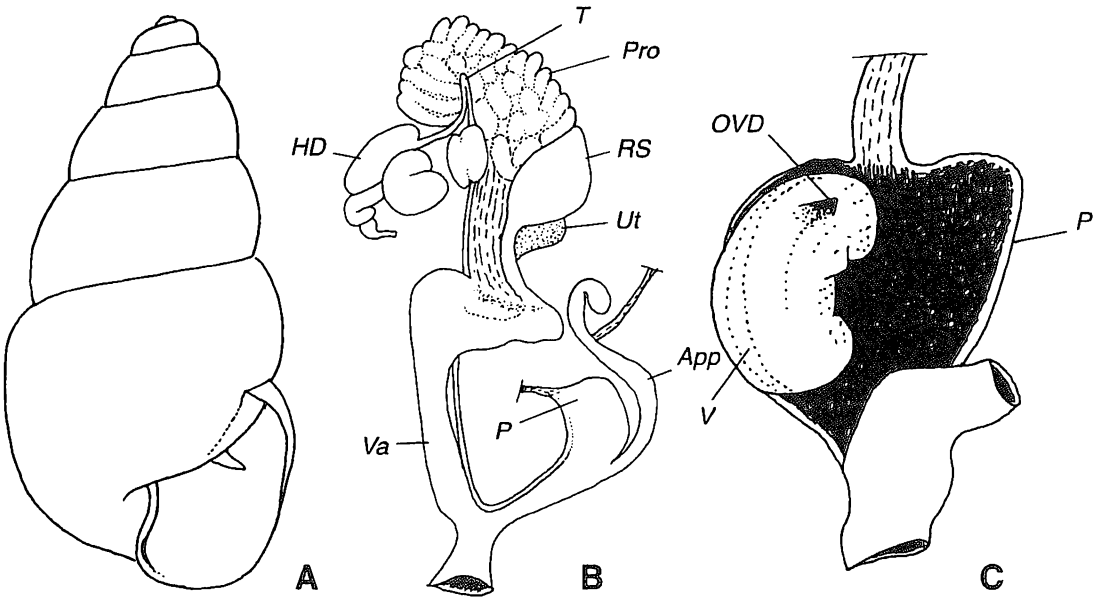


Fig. 8. ***Taitaa (Taireva) striatula*** Cooke et Kondo, 1960.
A — adult shell, holotype; B — reproductive tract of subadult specimen; C — interior of penis. After Cooke & Kondo, 1960.

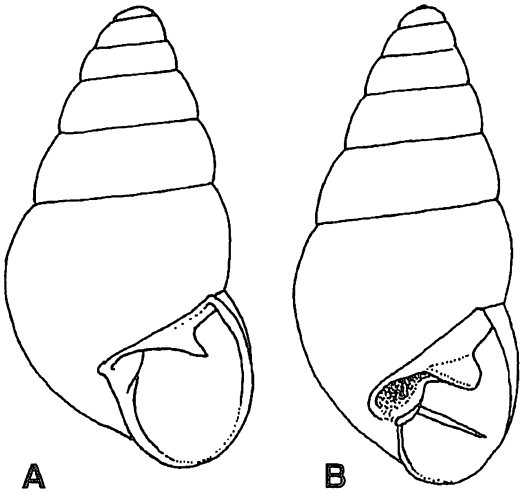


Fig. 9. ***Taitaa (Taraia) neanica*** Cooke et Kondo, 1960.
A — adult; B — not completely mature. After Cooke & Kondo, 1960.

Shell broadly ovate, subconic or elongated, thin to moderately solid, of 6.5-8 flattened or slightly convex whorls. Color whitish to corneous, sometimes with dark peripheral band. Nuclear whorls smooth, postembryonic sculpture of radial irregular striation to fine ribbing. Aperture of irregular shape because of strong development of armature. Aperture margins thin, sometimes with heavy palatal lip inside; lip ridge ornamented with tubercles. Parietal lamella strong and long, its edge bent more or less outward. Columella more or less thickened, with 3 or 4 lamellae, that united into prominent protruding callus plate. Palatal margin in adults with or without longitudinal folds. Umbilicus closed. Height 3.5-3.7, diam. 2.3-3.2 mm (3.5 × 2.3 mm).

Hermaphroditic gland 8-9-lobate. Albumen gland very small. Vas deferens entering penis at short distance from apex. Ascending arm of penial pilaster long, with fleshy, terminally truncate verge (papilla); velum broad. There is an additional velum between orifice of vas deferens and ascending pilaster.

DISTRIBUTION. Rapa Island. 1 sp.

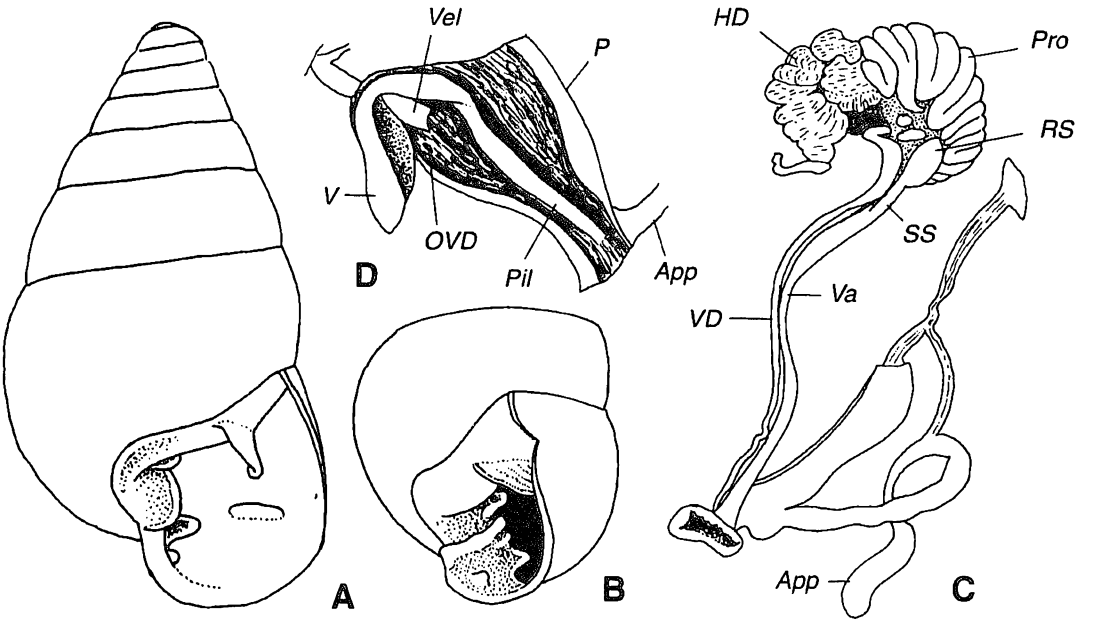


Fig. 10. ***Maitua auriculella*** (Cooke et Kondo, 1960).
A — adult shell, holotype; B — adult, columellar view; C — reproductive tract; D — interior of penis. After Cooke & Kondo, 1960.

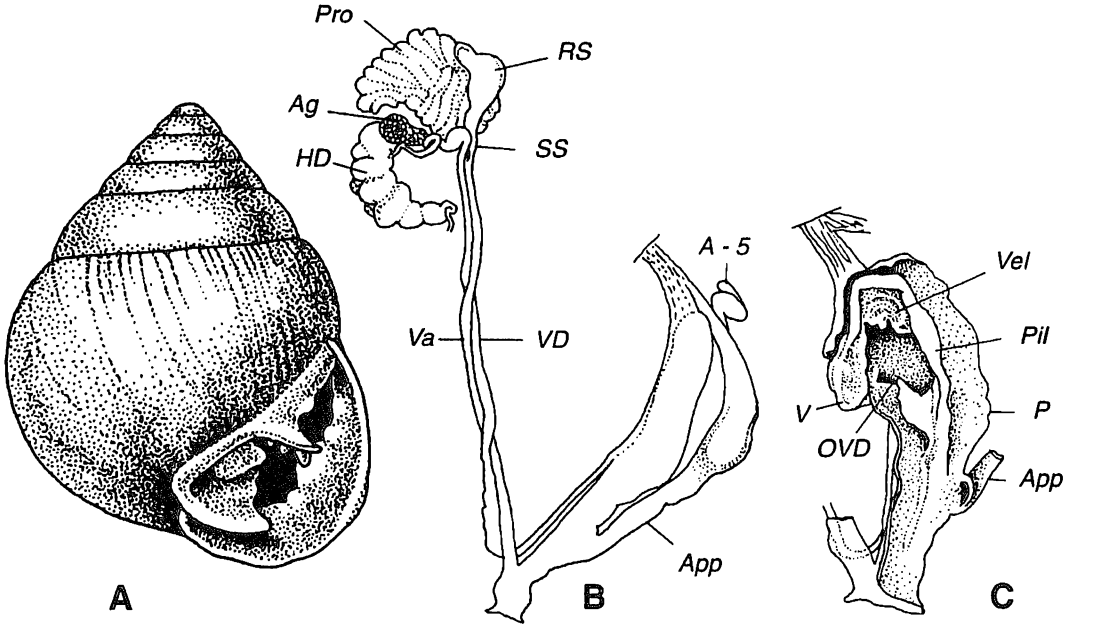


Fig. 11. ***Lamellovum globosum*** (Petit, 1843).
A — shell: Tepiahu Mt., Rapa Island. **Phil.** No. 180894; B — reproductive tract; C — interior of penis. B,C — after Cooke & Kondo, 1960.

Pitys Mörch, 1852
Fig. 12

Mörch, 1852: 6.

— *Diaglyptus* Pilsbry, 1892 (1892-1893): 86 [*Patula* (*Endodonta*) sect.; t.-sp. *Helix bilamellata* L.Pfeiffer, 1845; OD].

— *Diglyptus* Pilsbry, 1893 (1892-1893): 22 (nom err. pro *Diaglyptus* Pilsbry, 1892).

Cooke & Kondo, 1960: 94.

TYPE SPECIES — *Helix bilamellata* L.Pfeiffer, 1845 (non Sowerby, 1825; = *Patula pagodiformis* E.Smith, 1892); monotypy.

Shell turbinate to elongated, thin, somewhat translucent, of 7-9 flattened whorls. Outline of spire conic or a little concave. Color uniformly corneous. Embryonic sculpture, a fine spiral striation. Remaining whorls with strong, regular, periostracal ribs, extended near and at periphery. Aperture ovate to subquadrate, with straight and thin peristome; basal margin sometimes hardly thickened. Parietal lamella strong, entering about one whorl. Columella somewhat oblique, calloused, with 3 lamellae; upper two approached, parallel, coalescing near their outer ends and forming a slightly raised nodule or narrow plate. Subcolumellar lamella weak, deeply located, not visible at standard position of shell. Palatal wall smooth or with low, rather short fold. Umbilicus relatively wide, subcylindrical, or absent. Height 3.62-4.50, diam. 2.02-3.65 mm (4.00 × 3.65 mm).

Hermaphroditic gland 6-lobate. Talon small, recurved. Albumen gland minute or externally non visible. Prostatic acini large. Vas deferens large, entering penis well below apex. Penis enlarged, subfusiform, internally with reflexed pilaster terminating in semi-pendent, spoon-shaped verge, furrowed in inner surface; few short folds along midbody. Penial appendix of approximately same length as penis, vaguely differentiated into sections. Penial retractor thick, with very short penial and much longer appendical arms. Atrium short, broad. Vagina long, rather narrow. Spermathecal shaft very short, ending just below exit of vas deferens; reservoir large, bluntly pointed.

DISTRIBUTION. Rapa Island. 3 spp., one of them represented by 5 conchological forms.

Mangaoa Cooke et Kondo, 1960
Fig. 13

Cooke & Kondo, 1960: 78.

TYPE SPECIES — *Mangaoa perissa* Cooke et Kondo, 1960; OD.

Shell elongated, subfusiform, very thin, translucent, of 5.75 loosely coiled convex whorls. Color brownish. Embryonic sculpture complex: first whorl glossy, with exceptionally fine spiral threads; second whorl faintly but distinctly, radially closely striatulate. Postnuclear whorls with thin, lamellar, widely spaced, radial, slightly flexuous periostracal riblets. Aperture large, subovate, vertical, with very delicate fragile margins. Parietal lamella absent. Columella nearly straight, slightly sigmoid, with 1-2 indistinct lamellae bordering inner margin and uniting with peristome. No palatal plicae. Umbilicus absent. Height 4.55, diam. 2.34 mm.

Hermaphroditic gland swollen, 4-lobate. Albumen gland large. Prostate large, of numerous, swollen acini. Vas deferens enlarged, adherent to penis from half way and above, entering penis subapically through simple pore below verge. Penis of moderate size, internally with well-defined ascending pilaster; velum semitransparent, verge tongue-shaped with thickened inner marginal ridge, and free near tip, with few narrow, longitudinal secondary pilasters. Appendix rather short, with weakly defined divisions. Both arms of penial retractor stout and short. Vagina long, enormously wide. Spermathecal shaft short, reservoir voluminous, ovate.

DISTRIBUTION. Rapa Island. 1 sp.

Tubuaiini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 131.

Adult shell not clearly distinguishable from that of some of other tribes. Whorls 5.25-7.75. In juveniles, parietal lamella weak, moderate, or strongly sinuous. Columella with 2 or 3 lamellae, some predominantly bilamellate with vestigial third, others predominantly trilamellate with a few bilamellate forms among them.

Albumen gland well developed in adults. Penis internally with simple pilaster ending in semipendent verge. Penial appendix present.

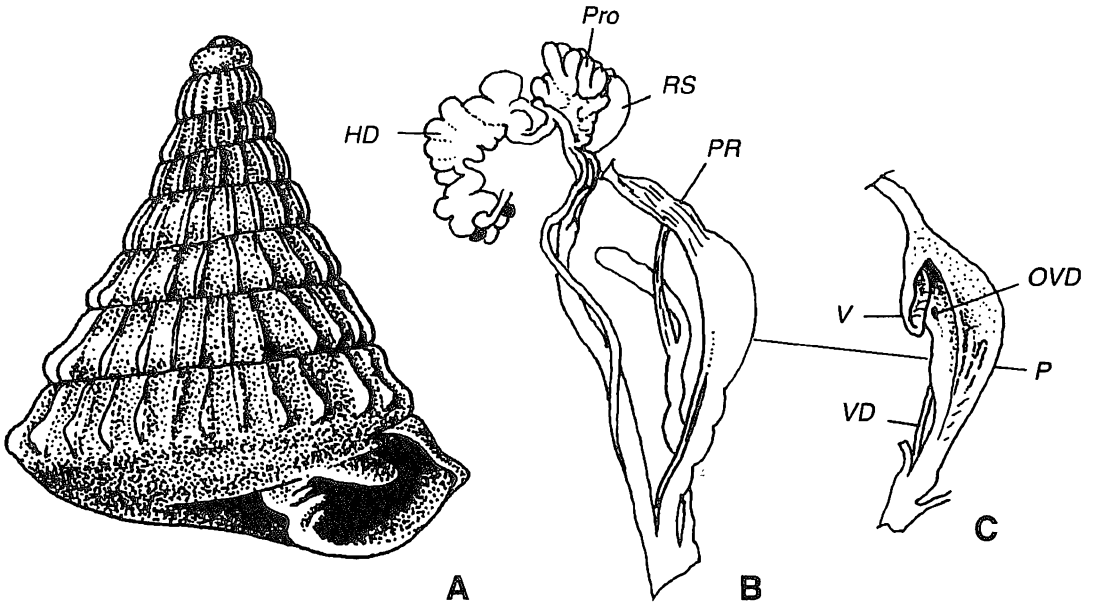


Fig. 12. ***Pitys pagodiformis*** E. Smith, 1892.
A — shell: Rapa Island. **Chicago** No. 159261; B — reproductive tract; C — interior of penis. B,C — after Cooke & Kondo, 1960.

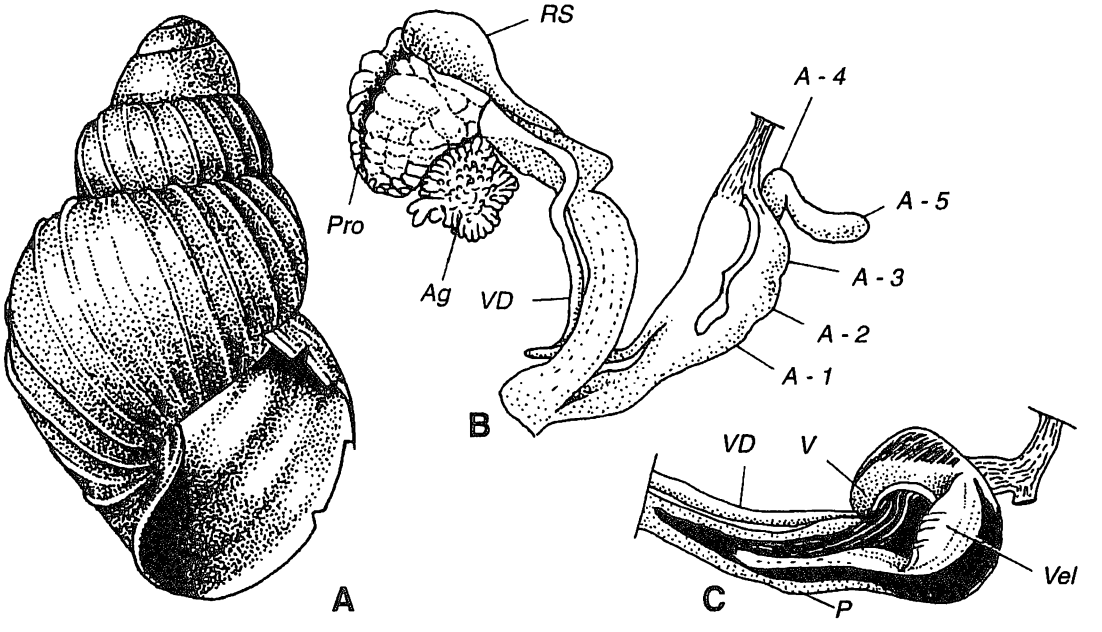


Fig. 13. ***Mangaoa perissa*** Cooke et Kondo, 1960.
A — shell: Perahu Mt., Rapa Island. Paratype. **Phil.** No. 180915; B — reproductive tract; C — interior of penis. B,C — after Cooke & Kondo, 1960.

DISTRIBUTION. Kermadec, Cook, Society, Tubuai and Tuamotu Islands.

Celticola Cooke et Kondo, 1960

Cooke & Kondo, 1960: 131.

TYPE SPECIES — *Celticola pilsbryi* Cooke et Kondo, 1960; OD.

Shell elongated to conic, rather thin, translucent. Embryonic whorls smooth or finely spirally striated, rest with distinct radial striae. Parietal lamella weak to strong (usually moderate). Columella mostly with 3 (rarely 2) plates, upper two stronger than deeply situated lowest; sometimes columella without lamellae in adults. Palatal plicae 2, or one plus vestigial upper, or none.

DISTRIBUTION. Rapa Island.

Celticola (*Celticola* s.str.)
Fig. 14 A-D

Cooke & Kondo, 1960: 132.

Shell ovate-turrited, glossy, of 6.5-7.75 slightly convex whorls. Postembryonic whorls irregularly striated. Parietal plate moderately to strongly developed; in juveniles more or less sinuous. Columellar lamellae 3, conspicuously developed in young shells, upper 2 strong. Height 4.33-5.84, diam. 2.06-2.75 mm.

Albumen gland relatively large. Prostate small or hidden. Vas deferens slender, entering penis subapically. Penis rather long. Penial appendix long, slender, vaguely externally differentiated into divisions; inside A-2 + A-3 an eversible papilla present. Atrium short. Uterus contains few embryos. Spermathecal stalk long, branching off oviduct below lowest embryo; reservoir small.

DISTRIBUTION. Rapa Island. 1 sp. with 4 subspp.

Celticola
(*Nesonoica* Cooke et Kondo, 1960)
Fig. 14 E, F

Cooke & Kondo, 1960: 140.

TYPE SPECIES — *Celticola conoides* Cooke et Kondo, 1960; OD.

Shell conic to elongated-conic, of 7-7.5 convex whorls. Apical whorls densely spirally striated. Sculpture of rest whorls of delicate but quite distinct, widely spaced radial striae. Parietal lamella strong. Columellar lamellae in juveniles 3, low, blunt, rapidly ascending. Palatal wall unarmed at all stages. Height 4.00-6.40, diam. 2.28-2.98 mm.

DISTRIBUTION. Rapa and Raivavae Islands. 2 spp.

Celticola
(*Meryticola* Cooke et Kondo, 1960)
Fig. 15

Cooke, Kondo, 1960: 137.

TYPE SPECIES — *Celticola arborea* Cooke et Kondo, 1960; OD.

Shell oblong, subcylindrical, slender, of 5-5.5 rather convex whorls. Postembryonic whorls finely but distinctly striated; striae stronger just below suture. In adults parietal lamella rather weak, nearly one whorl long; columella slightly sigmoid, without lamellae. In juveniles parietal plate proportionately slightly, if at all, stronger than at adult stage; columella with 2 weak thread-like rapidly ascending lamellae. Palatal wall smooth. Height 2.25-3.22, diam. 1.00-1.45 mm.

Albumen gland large. Prostate minute. Vas deferens thin, entering penis medially. Penis rather large. Appendix long; A-3 markedly swollen. Both arms of penial retractor long, slender. Spermathecal duct thin, reservoir small, ovate.

DISTRIBUTION. Rapa Island. 1 sp. with 2 or 3 subspp.

Tubuaia Cooke et Kondo, 1960
Fig. 16

Cooke, Kondo, 1960: 143.

TYPE SPECIES — *Tornatellina perplexa* Garrett, 1879; OD.

Shell oblong-conic, rather thin, translucent, of 5-7 somewhat convex whorls. Embryonic whorls smooth and glossy, rest surface delicately sculptured with radial striae. Parietal lamella rather strong (weak in one species), slightly oblique, from one-half to a full whorl long. Columella in adults twisted, generally unarmed (in one species with short lamella), forming a projecting obtuse

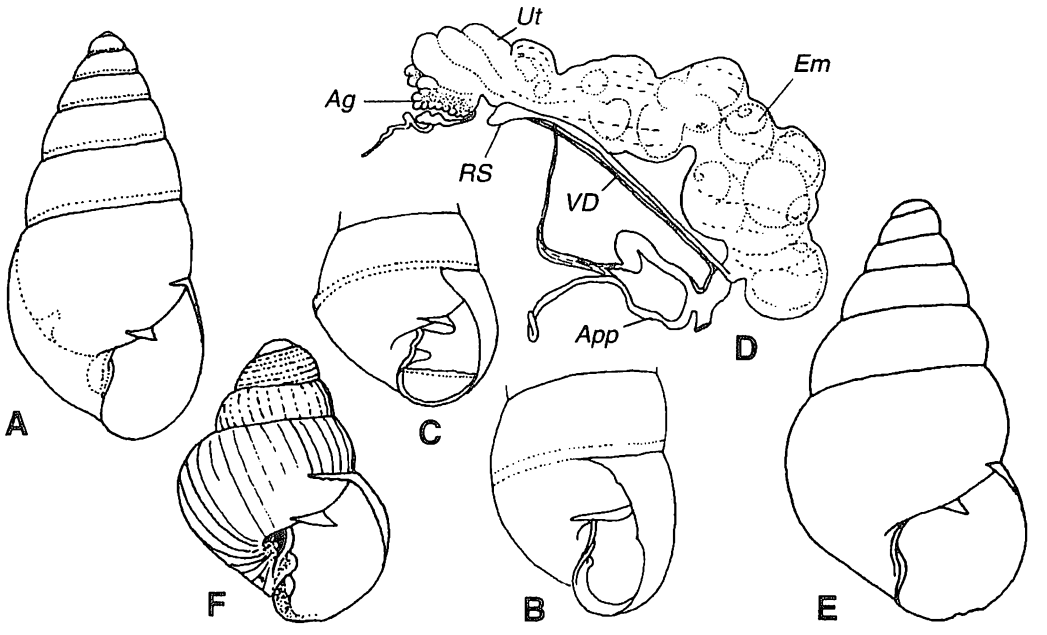


Fig. 14. ***Celticola (Celticola) pilsbryi*** Cooke et Kondo, 1960 (A-D; A — holotype, B — columellar view; C — fragment of juvenile shell, D — reproductive tract), and ***Celticola (Nesonoica) conoides*** Cooke et Kondo, 1960 (E, F; E — holotype, F — juvenile shell). After Cooke & Kondo, 1960.

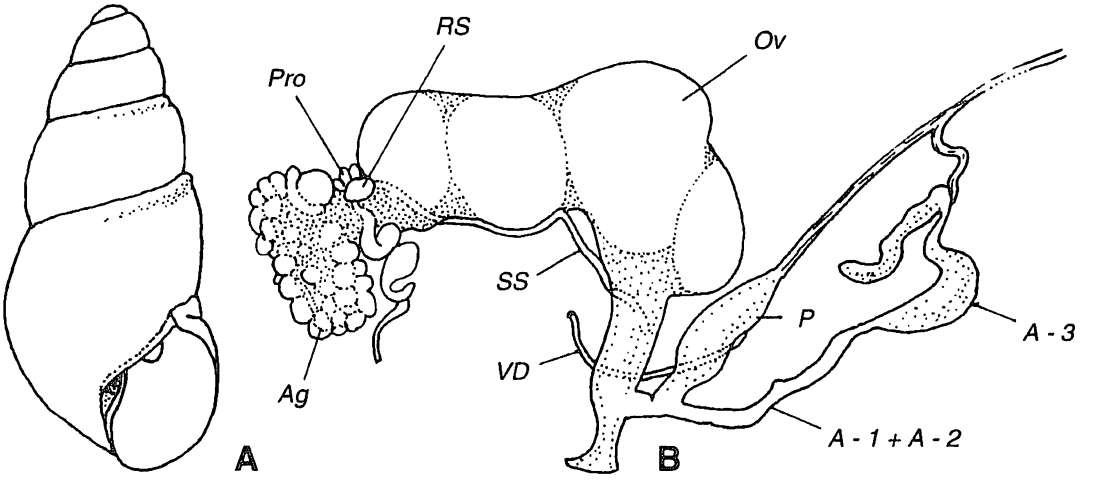


Fig. 15. ***Celticola (Meryticola) arborea*** Cooke et Kondo, 1960.
A — holotype; B — reproductive tract. After Cooke & Kondo, 1960.

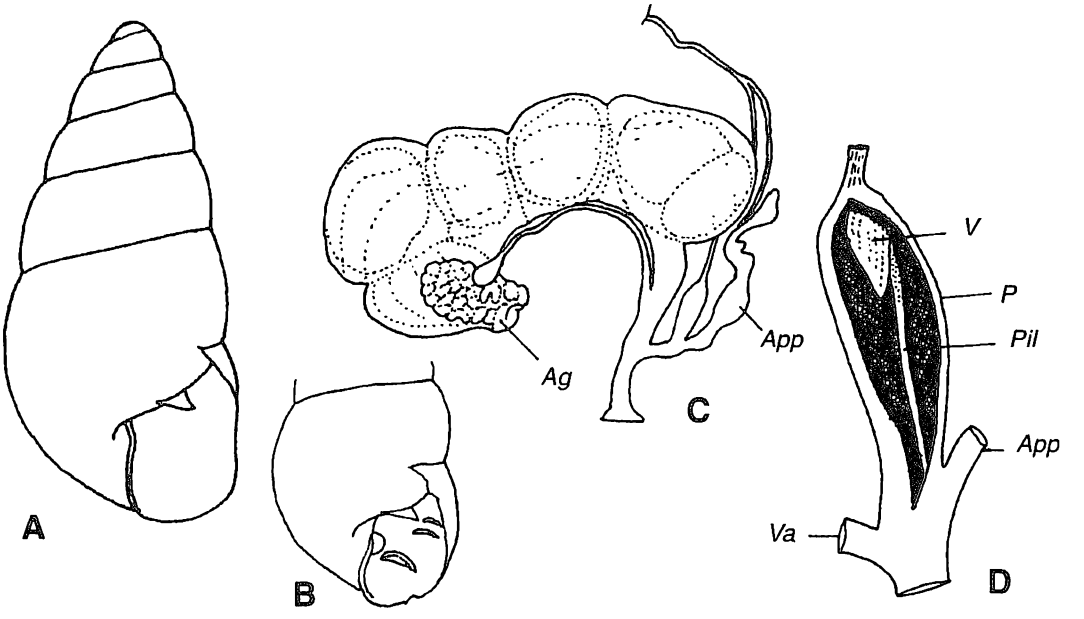


Fig. 16. *Tubuaia perplexa* (Garrett, 1879).
A — adult shell; B — juvenile; C — reproductive tract; D — interior of penis. After Cooke & Kondo, 1960.

angle at edge of columella; at juvenile stages there are 2, rarely 3 columellar plates, of which lower is stronger. Palatal wall smooth in adults; with two rows of spirally entering tubercles, nearly united by very fine thread-like callus in young shells. Besides, thickened lip may be present at some distance from margin. Umbilicus absent. Height 2.03-3.78, diam. 1.06-2.20 mm.

Hermaphroditic gland 3-6-lobate; its duct short, convoluted. Albumen gland relatively large. Prostate small. Vas deferens thin, adherent to penis, entering it subapically. Penis short, subfusiform or of irregular shape, internally with modified pilaster: narrow, ascending fleshy ridge, recurved at apex into relatively large, triangular, semipendent, fleshy verge, below which a pore of vas deferens opens. Penial appendix rather long, slightly enlarged at middle, with secretory-ejaculatory apparatus. Penial retractor thin, long. Atrium short to medium, narrow. In subadult animals penis and appendix proportionately larger. Spermathecal shaft long, narrow, entering oviduct below lowest embryo; reservoir small, ovate.

DISTRIBUTION. Kermadec (Raoul), Cook (Mauke, Mangaia), Society (Huahine), Tubuai (Rimatara, Rurutu, Tubuai, Raivavae), Rapa, Tuamotu (Mangareva, Henderson, Pitcairn) islands. 11 spp. & subspp.

Antonellini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 116.

Shell fusiform or nearly so, of 6.5-7.5 whorls. Surface macroscopically smooth. Parietal wall with or without a small lamella. Columella with 2 simple lamellae.

Albumen gland minute. Prostate large. Penis internally with recurved longitudinal pilaster. Penial appendix absent. Free oviduct comparatively broad.

Oviparous animals.

DISTRIBUTION. Rapa Island.

Antonella Cooke et Kondo, 1960
Fig. 17

Cooke & Kondo, 1960: 117.

TYPE SPECIES — *Tornatellina trochlearis* L. Pfeiffer, 1842; OD.

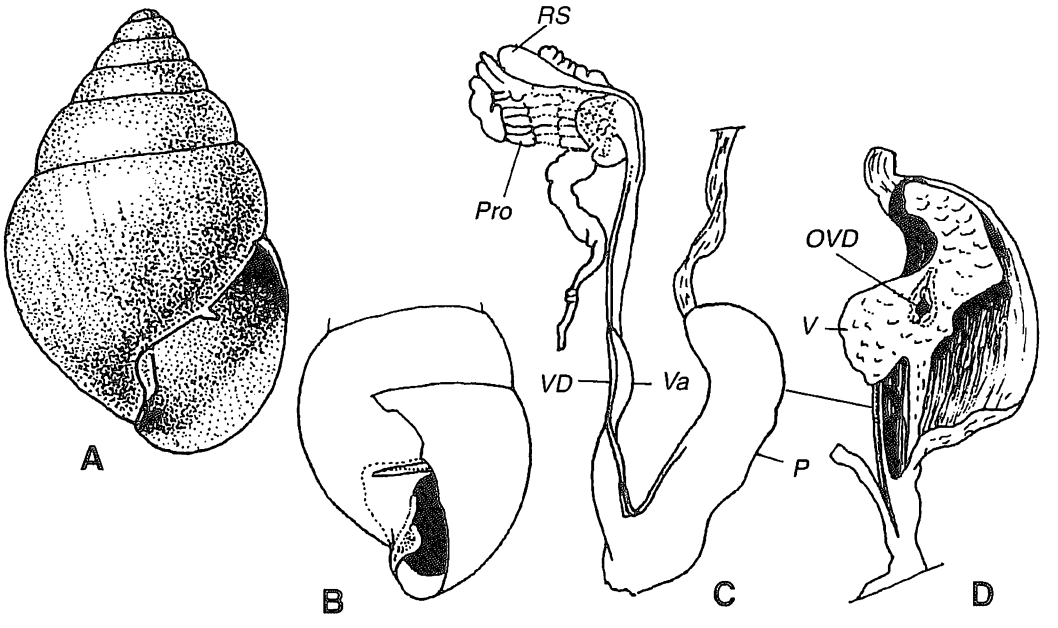


Fig. 17. *Antonella trochlearis* (L.Pfeiffer, 1842).
A — shell: Maitua, Rapa Island. **Phil.** No. 145412. B — columellar view; C — reproductive tract; D — interior of penis. C,D — after Cooke & Kondo.

Shell ventricose-fusiform to elongated-ovate, very thin and fragile, of 6-7.5 flattened to slightly convex whorls. Color uniformly yellowish to corneous. Embryonic whorls smooth, remaining nearly so, with only fine radial irregular striation. Aperture ample, pointed ovate, with sharp thin margins. Parietal wall bears lamella about one whorl long. Columella vertical, nearly straight; columellar plates terminate at acute angle at outer margin near its base. Long uninterrupted palatal plica may be present. Umbilicus absent. Height 3.30-6.86, diam. 1.60-3.70 mm (3.31 × 1.60 mm).

Hermaphroditic gland multilobate. Vas deferens narrow, entering penis midway but its pore subterminal in position. Penis swollen, of moderate length; pilaster narrow below, broadening above, enlarged at apex into semi-pendent stimulatory verge. Penial retractor thick, attached apically. Spermathecal shaft short, entering oviduct at summit or halfway below; reservoir large, oval, bluntly pointed, lies on prostate or nearby.

DISTRIBUTION. Rapa Island. 3 spp., one consisting of 3 subspp.

Perahua Cooke et Kondo, 1960
Fig. 18

Cooke & Kondo, 1960: 125.

TYPE SPECIES — *Perahua grandis* Cooke et Kondo, 1960; OD.

Shell elongated-conic to subfusiform, thin, subtransparent, of 7-7.5 moderately convex whorls. Color grayish-yellow to olive. Embryonic whorls with microscopic spiral incised lines. Postnuclear sculpture of very fine irregular radial striation. Aperture acutely- ovate, with thin erected margins. Parietal lamella absent at all growth stages. Columella sigmoid, internal surface margined with strong, long lamella entering about 2 whorls, terminating near base and projecting outward over columella. Palatal wall toothless. Height 5.95-9.05, diam. 2.95-5.40 mm (8.60 × 5.12 mm).

Hermaphroditic duct 8-10-lobate. Vas deferens entering penis a little below its apex. Penis vermiform, long, convoluted, twisted around vas deferens two or three times, of nearly equal diameter throughout except for slightly larger summit and narrower neck. Interior of penis with pilaster

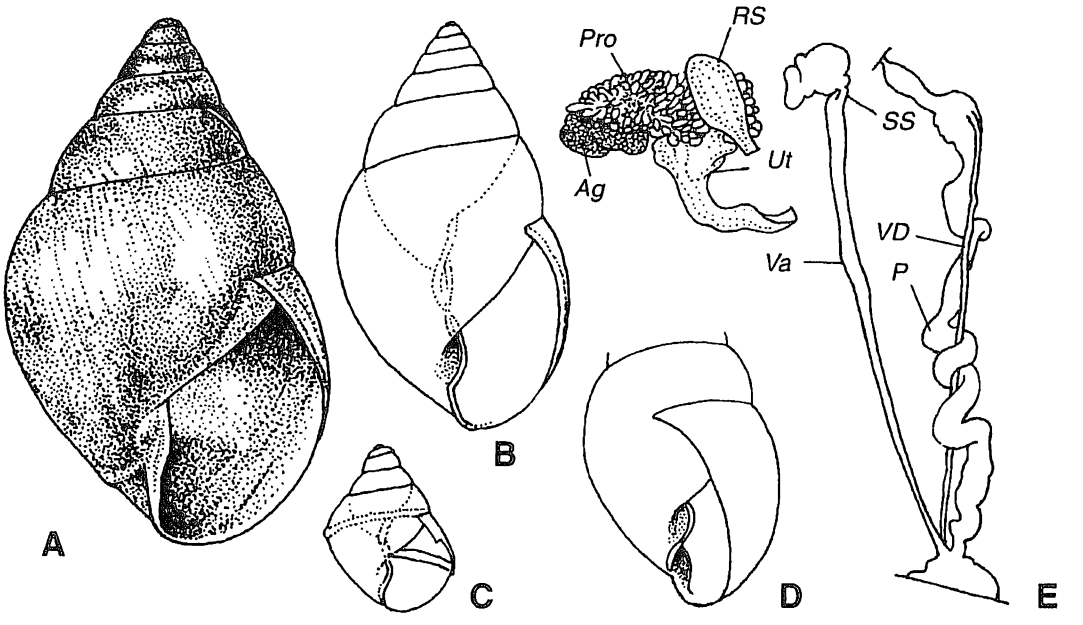


Fig. 18. ***Perahua grandis*** Cooke et Kondo, 1960.
Shells: A — Perahua Mt., Rapa Island. Paratype. **Phil.** No. 180900; B — holotype, C,D — juvenile shells; E — reproductive tract. B-E — after Cooke & Kondo, 1960.

enlarging at apex, recurved, without velum; verge similar to pilaster, both ending soon as very narrow ridges. Spermathecal shaft very short, entering oviduct almost immediately; reservoir large, ovate.

DISTRIBUTION. Rapa Island. 2 spp.

LAMELLIDEINAE Cooke et Kondo, 1960

Cooke & Kondo, 1960: 162.

— Pacificellidae Steenberg, 1925: 195 (based upon praeoccupied name *Pacificella* Odhner, 1922).

Shell dextral, minute to medium-sized, elongate, elongated-conic, turrited, or ovate-conic. Palatal wall with or without plica.

Right ommarophoral retractor free of peni-oviducal angle.

Penis innervated by cerebral ganglion.

Hermaphroditic gland unilobate. Albumen gland variable in size, well developed. Prostate small. Penis with or without appendix, internally with modified pilaster; aphallic specimens known. Appendix, when present, with retractor, internally with secretory-ejaculatory organ. Spermathecal stalk entering spermoviduct above uterus, reservoir free.

Oviparous or viviparous.

DISTRIBUTION. Widely distributed throughout tropical and subtropical islands of Pacific.

Tornatellinoptini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 162.

Penial appendix present.

Viviparous animals.

DISTRIBUTION. As in subfamily.

Tornatellinops Pilsbry et Cooke, 1915 Fig. 19

Pilsbry & Cooke, 1915 (1914-1915): 169 (Tornatellina sect.).

— *Pacificella* Odhner, 1922: 249 (t.-sp. *Pacificella variabilis* Odhner, 1922; monotypy).

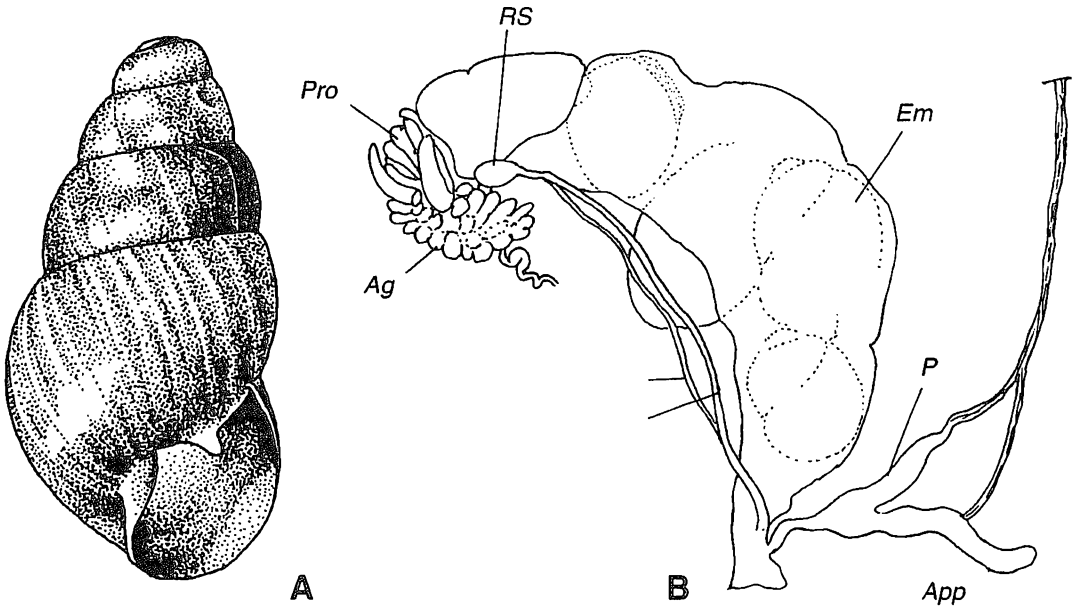


Fig. 19. ***Tornatellinops novoseelandica*** (L. Pfeiffer, 1852).
A — shell: Waitakere Range, Auckland, New Zealand. **Phil.** No. 220749.
! ***Tornatellinops variabilis*** (Odhner, 1922), B — reproductive tract, after Cooke & Kondo, 1960.

— *Tornelasmias* Iredale, 1944: 308 (t.-sp. *Tornelasmias capricorni* Iredale, 1944; OD).

Cooke & Kondo, 1960: 162.

TYPE SPECIES — *Tornatellina novoseelandica* L. Pfeiffer, 1852; OD.

Shell oblong-conic, ovate-conic to ovate, thin, shining, of 3.5-6.0 (mostly 5-5.5) moderately convex whorls. Color corneous. Embryonic whorls smooth or finely spirally striate, surface of postapical whorls also nearly smooth, with only fine radial striae; sometimes very fine spiral lines may be present on body whorl. Parietal lamella weak to moderate (at juvenile stages proportionately stronger), entering less than one whorl. Columella more or less twisted, thickened near its middle. No palatal folds; juveniles rarely with 1-2 weak plicae. Umbilicus absent. Height 2.20-4.00, diam. 1.30-2.10 mm (2.51 × 1.42 mm).

Albumen gland relatively large. Prostate composed of several long acini. Vas deferens entering penis subterminally. Penis small, tapering, internally with modified pilaster: thick longitudinal fleshy ridge recurved at apex to long, digitate, semi-pendent verge, adherent at one edge to penial wall, terminating just below curvature. Penial appendix short, broad, bluntly pointed, indistinctly differentiated. Penial retractor attached by one arm to penis apex, by the other — to middle portion of appendix. Atrium short. Spermathecal shaft slender, entering oviduct just below lowest embryo; reservoir small, ovate.

DISTRIBUTION. The most widespread genus in the family: the Philippines; Ryukyu, Izu and Ogasawara (Bonin) Islands; the Marianas, the Carolines, Hawaiian Islands; Easter Island, Pitcairn, Tuamotu, Mangareva Islands; the Marquesas; Tubuai, Society, Line, Cooke, Tonga, Samoa, Fiji, Ellice Islands; the Kermadecs, New Zealand, Lord Howe Island, New Caledonia, North Australia (New South Wales and Queensland) with some islets in Torres Strait; Amboina in the East Indies. 24 spp. & subspp.

Lamellideini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 178.

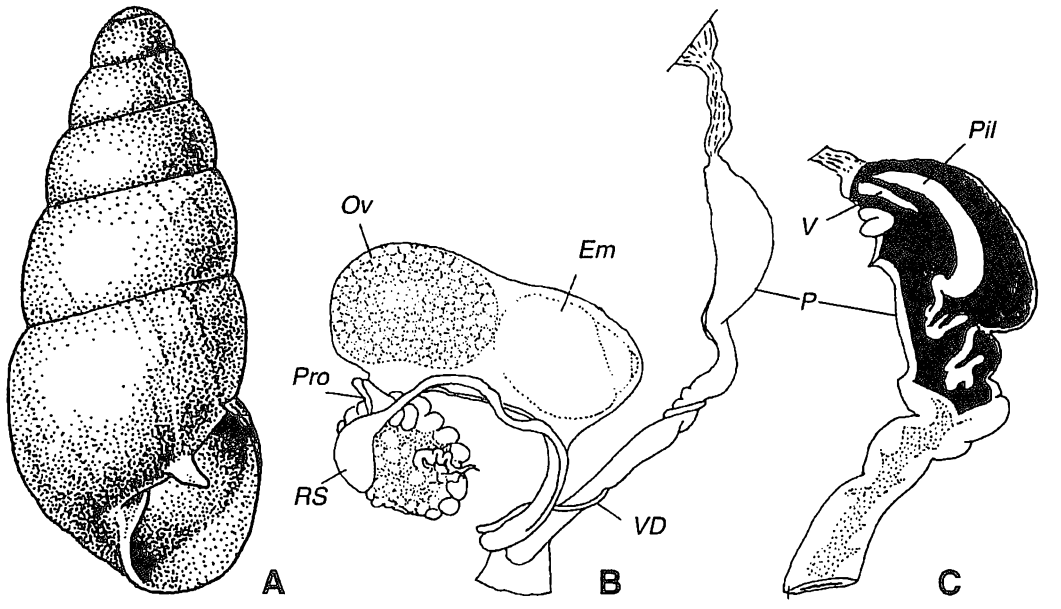


Fig. 20. ***Lamellidea (Lamellidea) peponum*** (Gould, 1847).
A — shell: Waikii, Hawaii Islands. **Phil.** No. 162609.
! ***Lamellidea (Lamellidea) oblonga*** (Pease, 1864), B — reproductive tract; C — interior of upper portion of penis. B, C — after Cooke & Kondo, 1960.

Penial appendix absent.
Viviparous animals.
DISTRIBUTION. Western Pacific, Polynesia, Hawaii.

Lamellidea Pilsbry, 1910

Pilsbry, 1910: 123 (Tornatellina sect.).

— *Lamellina* Pease, 1860: 439 [nom. praeocc., non Bory de Saint Vincent, 1826; t.-sp. *Lamellina serrata* Pease, 1860 (= *Partula pusilla* Gould, 1847); monotypy].

Cooke & Kondo, 1960: 178.

TYPE SPECIES — *Pupa peponum* Gould, 1847; SD Pilsbry & Cooke, 1933.

Shell slender, turrited, of 5-9 whorls. Parietal lamella moderate to strong. Columella vertical or somewhat sinuous, with or without distinct lamella. Palatal plica absent.

DISTRIBUTION. Western Pacific (Gilbert to Bonin Islands), Polynesian islands (Ellice to Marquesas, westward to New Hebrides and Solomon Islands), and Hawaiian Islands.

Lamellidea (*Lamellidea* s.str.)
Fig. 20

Cooke & Kondo, 1960: 181.

Shell elongated-ovate, elongated-conic or nearly cylindrical, of 5-6.75 moderately convex whorls. Body whorl convex or flattened dorsally and sometimes with broad shallow depression on distal half, extending to and modifying palatal margin of aperture. Embryonic whorls smooth, later silky radially striatulate. Aperture rather small, slightly oblique, with simple, thin margins. In adult shell parietal lamella moderate to prominent. Columella nearly straight to distinctly sigmoid, somewhat thickened internally at middle, but without clearly defined lamella. In young shells parietal lamella proportionately stronger, with edge ranging from simple to strongly sinuous; columella with 2-3 lamellae; palatal wall mostly with 1-3 lips. Height 2.07-4.50, diam. 0.88- 2.20 mm (3.81 × 1.53 mm).

Prostate small, of fairly large acini. Vas

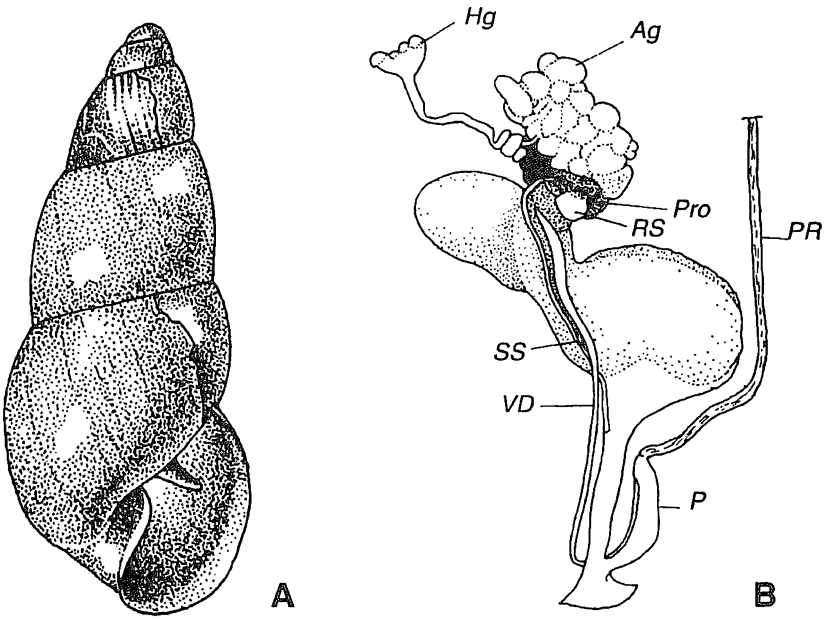


Fig. 21. ***Lamellidea (Elamellidea) tantalus*** Pilsbry et Cooke, 1915.
A — shell: outside SW ruin of Tantalus bowl, Oahu. Lectotype. **Phil.** No. 108025a; B — reproductive tract, after Cooke & Kondo, 1960.

deferens narrow, looping around penis 1.5 times, entering penis almost apically. Penis club-shaped, internally with short but strong fleshy recurved pilaster; principal pilaster terminating in small muscular cord below; verge short, pointed; remainder of penis a mixture of thin portions plus irregular hardened areas. Penial retractor short, stout. Aphallic specimens known. Spermathecal shaft long, large; reservoir ovate, capacious.

DISTRIBUTION. As in genus. About 20 spp. & forms.

Lamellidea (*Elamellidea* Cooke et Kondo, 1960) Fig. 21

Cooke & Kondo, 1960: 211.

TYPE SPECIES — *Tornatellina tantalus* Pilsbry et Cooke, 1915; OD.

Shell slightly smaller than most species of Lamellidea s. str.; parietal lamella in adults proportionately much stronger and more oblique, its length not much more than a half whorl. In juveniles edge of parietal lamella not undulate, columella thickened, almost plate-like, with strong, spirally ascending lamella. Upper columellar lamella absent or indistinct. No palatal lips at any age stage. Height 2.4-3.0, diam. 0.9-1.2 mm.

Albumen gland large. Prostate small, of few large acini. Vas deferens relatively broad, entering penis subapically. Penis rather small, subcylindrical. Penial retractor long, rather thin. Spermathecal duct narrow, moderately long, branching off the oviduct quite high; reservoir rather large, ovate, lying among acini of prostata.

DISTRIBUTION. Hawaiian Islands (Oahu). 1 sp. Cooke & Kondo (1960, p. 213) point out that there are 3 more undescribed species from Ponape, Truk and Fiji.

Lamellidea (*Auhea* Kondo, 1962) Fig. 22

Kondo, 1962: 125 (nom. nov. pro *Atea* Pilsbry et Cooke, 1933).

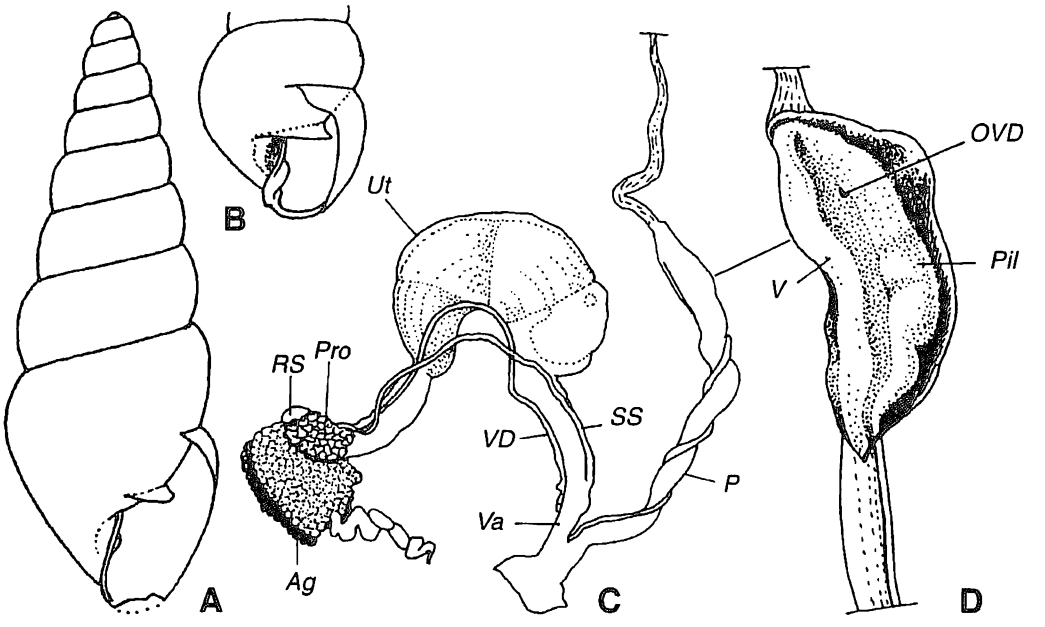


Fig. 22. ***Lamellidea (Auhea) adamsoni*** Pilsbry et Cooke, 1933.
A — lectotype (subadult); B — subadult, columellar view; C — reproductive tract; D — interior of penis. After Cooke & Kondo, 1960.

— *Atea* Pilsbry et Cooke, 1933: 62 [nom. praeocc., non Koch, 1837 (Arachnida); *Lamellidea* subg.; t.-sp. *Lamellidea adamsoni* Pilsbry et Cooke, 1933; OD].

Cooke & Kondo, 1960: 213.

TYPE SPECIES — *Lamellidea adamsoni* Pilsbry et Cooke, 1933; OD.

Shell slender, subfusiform to elongated conic, of 6.5-9 moderately to strongly convex whorls. Postnuclear whorls finely radially striated to costulate. Parietal lamella strongly extends anteriorly, its length about 1.5 whorls. In juvenile shells columella bears two equal plates. No palatal lips at any stage. Height 4.08-7.04, diam. 1.47-1.82 mm.

Albumen gland quite large. Prostate small, of rather numerous acini. Vas deferens narrow, twisted around penis 2-3 times, entering penis nearly apically. Penis long, more or less cylindrical, internally with modified pilaster: fat, fleshy, ascending arm recurved at apex, descending a short distance as smaller non-pendent arm, soon fading into penial wall. Penial retractor long, rather thick. Vagina short. Spermathecal stalk slender, long; reservoir small, ovate, hidden partially among prostate acini.

DISTRIBUTION. Marquesas Islands. 3-4 spp.

TORNATELLININAE Sykes, 1900

Sykes, 1900: 380 (pro fam.). Cooke & Kondo, 1960: 217.

Shell dextral, semiglobous, ovate, or turrited-conic, usually with parietal and columellar lamellae. Umbilicus absent.

Right ommatophoral retractor free of peni-oviducal angle.

Penis innervated by cerebral ganglion.

Hermaphroditic gland uni- or multilobate. Albumen gland small to relatively large. Carrefour with small and short or long and large talon apically attached to columellar muscle. Prostate small, recessive. Epiphallus absent. Penis much reduced, internally with or without pilaster. Penial appendix present, either with verge or with complex copulatory mechanism composed of rugae and pilasters. Penial retractor biramous. Sper-

mathecal stalk entering above uterus; reservoir free.

Viviparous snails.

DISTRIBUTION. Many islands of tropical and subtropical Pacific Ocean.

Elasmiatini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 218.

Shell globose-conic to rotund-ovate, thin, fragile, of 3-5.5 rather convex whorls. Embryonic whorls with fine spiral striation (in one species apex smooth), postnuclear sculpture of delicate radial striation and spiral incised lines. Aperture large; parietal lamella in adults present or absent, columella calloused, in form of wide or narrow vertical plate, bilobate or angular, but without deeply entering lamellae, truncated or excavated below plate. Umbilicus absent.

Hermaphroditic gland unilobate. Talon small. Penis without interior musculature. Penial appendix with internal secretory-ejaculatory apparatus, without complex copulatory mechanism.

DISTRIBUTION. Widespread throughout islands of tropical and subtropical zones of Pacific.

Elasmias Pilsbry, 1910
Fig. 23

Pilsbry, 1910: 122. Cooke & Kondo, 1960: 218.

TYPE SPECIES — *Tornatellina aperta* Pease, 1864; OD.

Shell as in tribe. Height 1.19-4.06, diam. 1.67-3.06 mm.

Albumen gland rather small. Prostate small to rather large, of 2-8 acini. Talon not expressed superficially or modified. Vas deferens entering base of rudimentary penis. Appendix bulky, basally enlarged, with bulge above penis; divisions of appendix indistinct; rarely there is a process at bulge. Internally appendix with specialized apparatus probably used as stimulator during mating. Common portion of penial retractor thin, penial branch thinner, appendical arm attached to midway of appendix. Vagina short. Spermathecal shaft long, thin; reservoir small, ovate, lying on albumen gland or at its base.

DISTRIBUTION. Pacific islands: Hawaiian, Marquesas, and Mangarevan to the east; Eastern coastal Australia, Java, Philippines, Izu to the west; Lord Howe, Kermadec, Tubuai to the south; besides, some species have been reported from Java, Sumatra and islands of the Indian Ocean: Maldives, Reunion and Mauritius (obviously introduced). 20-22 spp. & subspp.

Tornatellinini Sykes, 1900

Sykes, 1900a: 380 (pro fam.). Pilsbry, 1910: 122 (Achatinellidae subfam.). Cooke & Kondo, 1960: 233.

Shell ovate-conic to bulimoid, conic or turrited-cylindrical. Aperture either unarmed at all age stages or with parietal and/or palatal elements at some stages; in latter case columellar lamellae present.

Hermaphroditic gland multilobate. Talon large, conspicuous. Penis with vestigial pilaster. Penial appendix complexly plicose.

DISTRIBUTION. Juan Fernandez Islands.

Tornatellina L. Pfeiffer, 1842
Fig. 24

Pfeiffer L., 1842: 5, 55, 130. Beck, 1837: 80 (*Achatina* subg.; nom. nud.).

— *Strobilus* Anton, 1839: 46 (part.).

Cooke & Kondo, 1960: 234.

TYPE SPECIES — *Tornatellina clausa* L. Pfeiffer, 1842 [= *Clausilia (Strobilus) bilamellata* Anton, 1839]; SD Gray, 1847

Shell elongated-conic to ovate-conic, glossy, translucent, of 5-10 whorls. Color yellowish to corneous. Embryonic whorls smooth, postnuclear whorls with fine irregular radial wrinklets. Aperture ovate, with simple margins. Parietal lamella and/or palatal plicae present at some stages of postembryogenesis. Columellar lamella very long. Height 2.8-7.2, diam. 1.5-3.5 mm (5.0 × 2.5 mm).

Right ocular retractor free of peni-oviducal angle.

There is a large talon arising from carrefour. Penis rudimentary. Penial appendix well developed.

DISTRIBUTION. Juan Fernandez Islands. 7 spp.

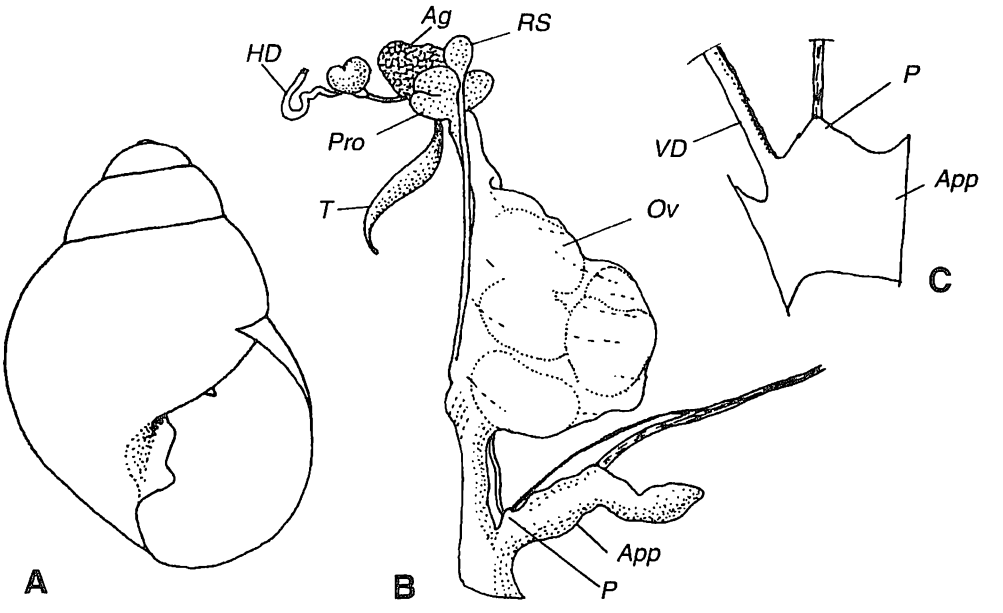


Fig. 23. ***Elasmias apertum*** (Pease, 1864).
A — shell; B — reproductive tract; C — closeup of rudimentary penis. After Cooke & Kondo, 1960.

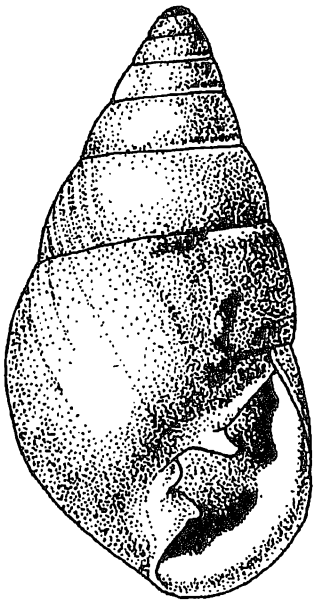


Fig. 24. ***Tornatellina bilamellata*** (Anton, 1839). Puertezuello, Juan Fernandes Islands. **Phil.** No. 130435.

Fernandezia Pilsbry, 1911
Fig. 25

Pilsbry, 1911: 93. Cooke & Kondo, 1960: 237.

TYPE SPECIES — *Fernandezia wilsoni* Pilsbry, 1911; OD.

Shell ovate to oblong-turrited and turrited-conic, thin, somewhat translucent, glossy, of 5-11.5 weakly to moderately convex whorls. Color yellow, corneous or pale-brown. Embryonic whorls smooth or very delicately spirally striated. Rest whorls radially striated or weakly wrinkled. Aperture irregularly ovate, subvertical, with a little thickened peristome. Parietal and palatal walls always smooth; columella usually simple or with weak lamella. Umbilicus closed. Height 3.5-12.0, diam. 2.0-6.5 mm (10.4 × 5.5 mm).

Hermaphroditic gland of 10-12 lobes. Albumen gland rather large. Talon enormously long, descending to, and terminally embedded in columellar muscle. Prostate well developed, of many acini. Vas deferens nar-

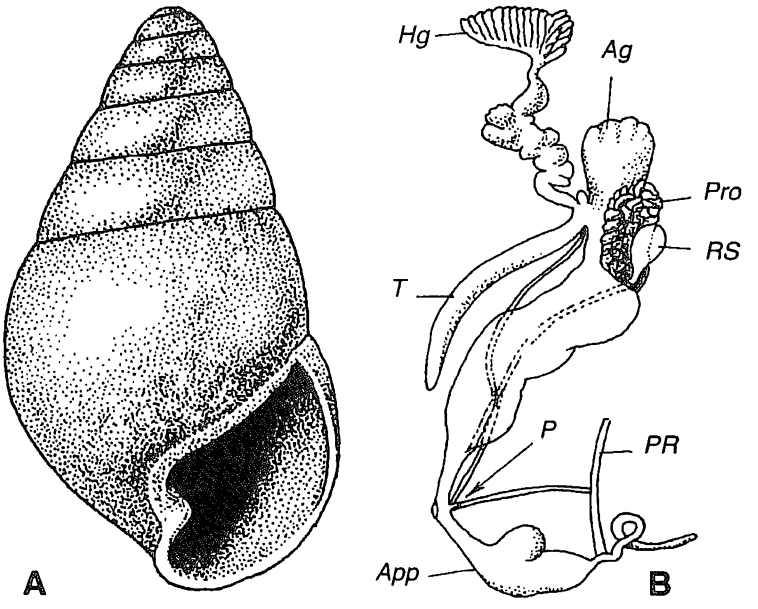


Fig. 25. *Fernandezia wilsoni* Pilsbry, 1911.
A — shell: Juan Fernandez Island. Holotype. **Phil.** No. 10166.
! *Fernandezia bulimoides* (L. Pfeiffer, 1846), B — reproductive tract, after Cooke & Kondo, 1960.

row, entering penis base. Penis vestigial, containing very weak pilaster or muscular tissue. Penial appendix large, of copulatory type, interior complexly rugose, with muscular cords. Penial retractor forked. Spermathecal shaft long, reservoir small, ovate.

DISTRIBUTION. Juan Fernandez Islands. 12 spp.

TORNATELLIDINAE Cooke et Kondo, 1960

Cooke & Kondo, 1960: 242.

Shell dextral, ovate, ovate-conic, oblong, or pyramidal-conic, of 3.5-9.5 flat to convex whorls. Parietal lamella weak to strong. Columella in adults simple or with 1-2 short lamellae; in juveniles usually with 2 lamellae. Palatal wall smooth (except two species of *Tornatellides*). Umbilicus, a minute perforation to narrow, cylindrical.

Right ommatophoral retractor usually free of peni-oviducal angle but sometimes passes through.

Penis innervated by cerebral ganglion.

Hermaphroditic gland 2-7-lobate. Albumen gland relatively large. Prostate small, fan-shaped. Epiphallus absent. Penis with or without appendix, internally with reflexed or modified straight pilaster. Appendix, when present, without retractor, internally without secretory-ejaculatory apparatus, its cavity simple, plain. Spermathecal shaft entering oviduct either above youngest embryo at junction of oviduct and carrefour or below oldest embryo or egg; reservoir free or partially embedded into albumen gland or prostate.

Oviparous or viviparous animals.

DISTRIBUTION. Widespread throughout tropics and subtropics of Pacific Ocean.

Tornatellidini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 242.

Shell composed of 3.75-8 (usually about 6) more or less convex whorls. Periphery of body whorl evenly rounded.

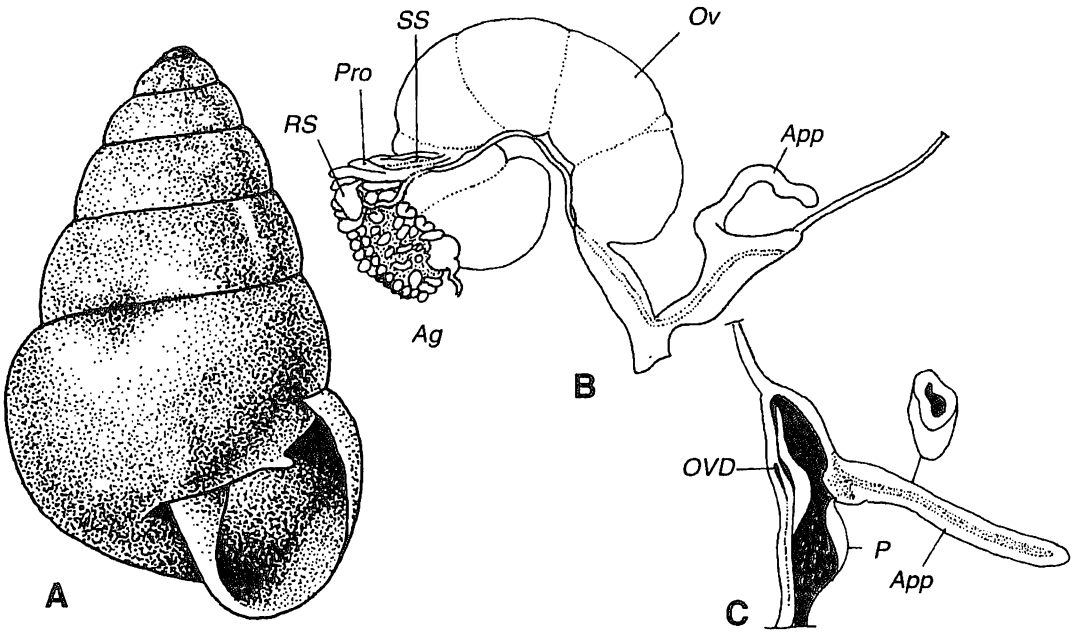


Fig. 26. *Tornatellides (Tornatellides) oblongus* (Anton, 1839).
A — shell: "Tahiti, Tal von Tiirahu bei Teahupoo" **Basel** No. 4976-b; B — reproductive tract; C — interior of penis. B, C — after Cooke & Kondo, 1960.

Viviparous.

DISTRIBUTION. Hong Kong, Taiwan, Ryukyu, Izu and Ogasawara (Bonin) islands; Hawaii; Revillagigedos, Galapagos, and Marquesas; from Pitcairn and Henderson through Mangarevan islands to Rapa and through all of the high islands of Tubuai, Society Islands, Cook Islands, and the Kermadecs to New Zealand (North Island).

Tornatellides Pilsbry, 1910

Pilsbry, 1910: 123. Cooke & Kondo, 1960: 243.

TYPE SPECIES — *Tornatellina simplex* Pease, 1864 (= *Strobilus oblongus* Anton, 1839); OD.

Shell ovate-conic to oblong, thin, of 4.5-7.5 fairly convex whorls. Aperture ovate; parietal lamella 1, columellar 1-2 (often absent in adult shells); palatal wall simple. Umbilicus point-like or narrow, cylindrical.

Hermaphroditic gland of 2-3 lobes. Albumen gland relatively large. Prostate small, composed of a few digitate acini. Vas deferens slender, entering penis subapically. Penis thin, narrowed below, slightly enlarged above, internally bearing simple longitudinal pilaster. Penial appendix short, vaguely differentiated into sections, inserting subterminally or at some distance from penis summit; internally without tubular structure, plain, apex sometimes contains a small papilla. Penial retractor unbranched, attached to penis apically. Atrium short. Uterus contains 2-8 embryos. Spermathecal stalk very short, hidden by acini, entering female side at its junction with carrefour above embryos; reservoir small, lying on lower part of albumen gland.

DISTRIBUTION. See Tornatellidini.

Tornatellides (*Tornatellides* s.str.) Fig. 26.

Cooke & Kondo, 1960: 248.

Shell as in genus. Postembryonic whorls finely radially striated or wrinkled. Height

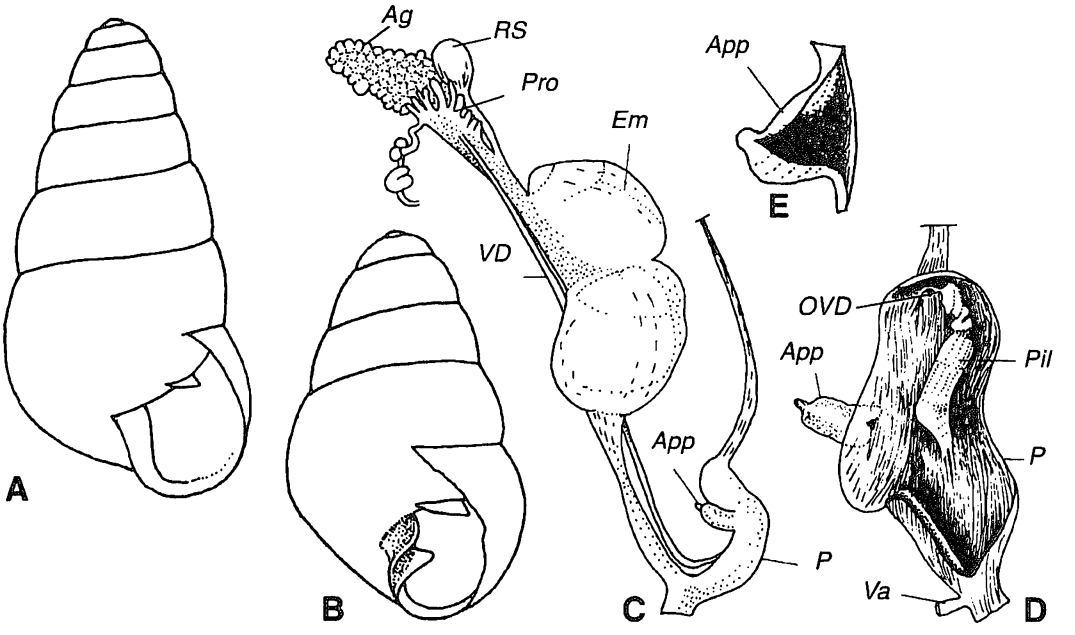


Fig. 27 ***Tornatellides (Aedituans) neckeri*** Cooke et Kondo, 1960.
A — holotype; B — columellar view; C — reproductive tract; D — interior of penis; E — interior of rudimentary appendix. After Cooke & Kondo, 1960.

2.29-3.68, diam. 1.58-2.32 mm (3.20 × 1.61 mm).

Penial appendix normally developed. Pilaster in penis simple.

DISTRIBUTION. Japan, Taiwan, Polynesia, Australia, Galapagos Islands, Hawaii. Over 60 spp.

Tornatellides (*Aedituans* Cooke et Kondo, 1960) Fig. 27.

Cooke, Kondo, 1960: 258.

TYPE SPECIES —*Tornatellides neckeri* Cooke et Kondo, 1960; OD.

Shell does not differ materially from that of *Tornatellides* s.str. Height 4.55, diam. 2.29 mm.

Penial appendix rudimentary. Pilaster in penis with vestiges of recurvature and descending arm.

DISTRIBUTION. Hawaiian Islands (Necker Island). 1 sp.

Tornatellides (*Ambrosiella* Odhner, 1963) Fig. 28.

Odhner, 1963: 208 (pro gen.).

TYPE SPECIES — *Ambrosiella kuscheli* Odhner, 1963; OD.

Shell turrited-conic, thin, fragile, of 6-7 convex whorls. Spire with slightly convex outlines. Color dark chestnut-brown with faint paler and darker radial streaks. Embryonic whorls nearly smooth; postnuclear sculpture of crowded fine radial riblets, most distinct and sinuated below suture; in some specimens with faint traces of incised spiral lines. Aperture ovate, with erect slightly thickened margins. Parietal lamella absent in adults but developed in juveniles. Columella subvertical, broadly sinuous below, without marked lamella at adult stage, but young shells with faint tuberculiform plate. Palatal wall smooth. Umbilicus closed. Height up to 6.0, diam. up to 2.6 mm.

DISTRIBUTION. Desventuradas Archipelago (San Ambrosio Island). 1 sp.

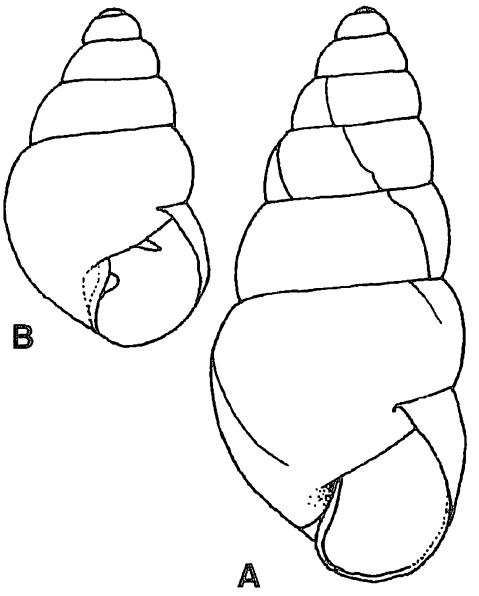


Fig. 28. *Tornatellides (Ambrosiella) kuscheli* (Odhner, 1963).
Syntypes. A — adult shell, B — juvenile. After Odhner, 1963 (drawings made from photos).

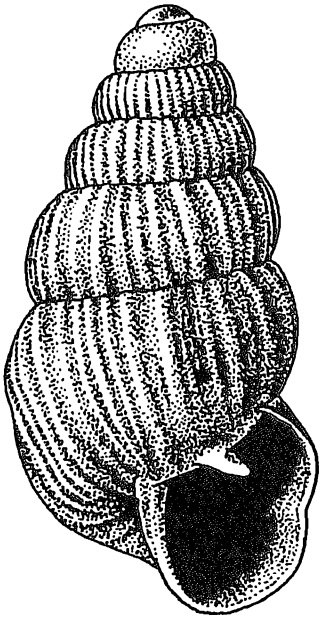


Fig. 29. *Tornatellides (Waimea) rudicostatus* Ancey, 1904.
Waimea, Hawaii. **Phil.** No. 112763.

Tornatellides (*Waimea* Pilsbry et Cooke, 1915) Fig. 29

Pilsbry & Cooke, 1915 (1914-1915): 250. Cooke & Kondo, 1960: 261.

TYPE SPECIES — *Tornatellides rudicostatus* Ancey, 1904; OD.

Shell pointed-ovate, thin, of 6-6.5 convex whorls. Last whorl with broad, shallow, spiral depression. Color brownish. Embryonic whorls with delicate spiral threads. Later whorls irregularly radially ribbed, ridges of riblets lighter than background. In adult shells aperture ovate, palatal margin slightly concave; ridge of parietal lamella directed toward palatal wall. Aperture margins slightly thickened, columellar margin subvertical, slightly reflexed. Juvenile shells with two columellar lamellae and rather long, low, palatal fold. Umbilicus minutely open. Height 2.5-3.5, diam. 1.3-1.8 mm (3.5 × 1.8 mm).

DISTRIBUTION. Hawaiian Islands (Hawaii, Maui). 1 sp. (subfossil shells only).

Tornatellariini Cooke et Kondo, 1960

Cooke & Kondo, 1960: 262.

Shell of 6.25-9.3 flattened whorls. Periphery of body whorl usually more or less angular.

Right ommatophoral retractor passes through peni-oviducal angle.

Penial appendix absent.

Oviparous or viviparous animals.

DISTRIBUTION. Hawaiian Islands.

Philopoa Cooke et Kondo, 1960 Fig. 30

Cooke, Kondo, 1960: 262.

TYPE SPECIES — *Philopoa singularis* Cooke et Kondo, 1960; OD.

Shell elongated-conic, rather thin, translucent to subtransparent, of 7 flattened whorls. Coloration: upper portion of spire tawny, lower whorls of isabella colour. Embryonic whorls spirally striated, striae fine, consisting of closely spaced minute points; rest surface somewhat glossy, with very fine radial lines. Aperture obliquely truncated-

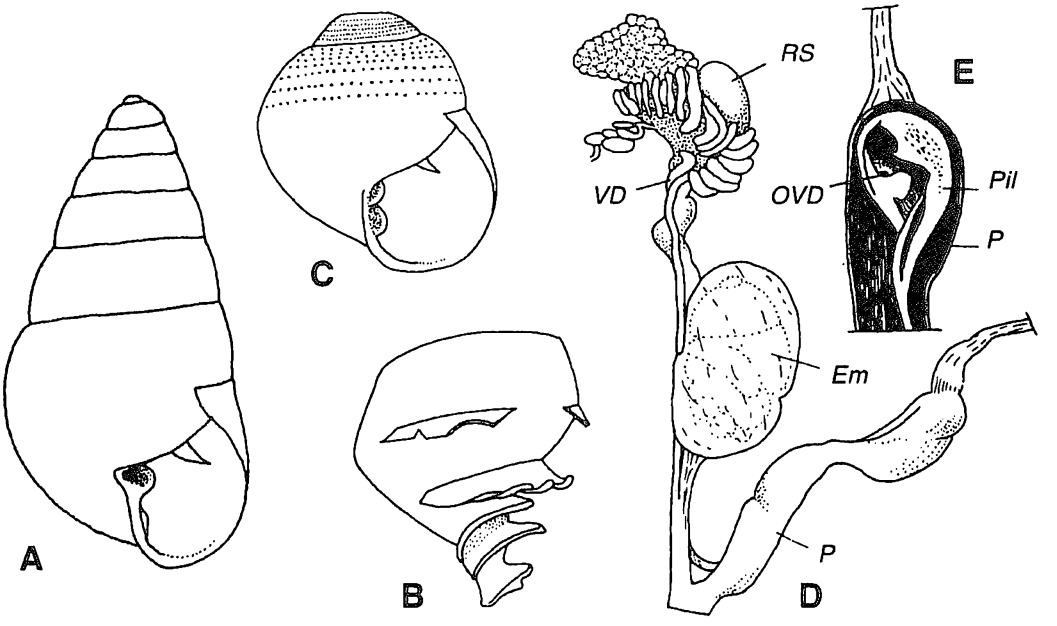


Fig. 30. ***Philopoa singularis*** Cooke et Kondo, 1960.
A — holotype, B — elements of aperture armature, C — early postembryonic shell to show embryonic sculpture, D — reproductive tract; E — interior of penis. After Cooke & Kondo, 1960.

ovate, with straight, sometimes indistinctly thickened margins; upper portion slightly flattened just below its insertion. Parietal lamella strong, entering slightly more than a half whorl; its edge flaring outward. Columella narrowly triangular, upper portion of its ridge bent downward to form an angle when viewed laterally; two slightly oblique lamellae, upper strong, rib-like, extending nearly to margin; lower weaker, more deeply seated. Umbilicus shallow, rather narrow. Height 3.97, diam. 2.00 mm.

Hermaphroditic gland of 7 lobes. Albumen gland large. Prostate large, of many acini. Vas deferens branched off lower part of carrefour below prostate, loosely adnate to penis, entering nearly apically. Penis large, long, internally with small recurved pilaster; verge low, very weak, not pendent. Atrium short. Vagina rather long. Spermathecal shaft slender, passing through prostatic acini, entering oviduct shortly below embryo; reservoir large, ovate, lying on prostate.

DISTRIBUTION. Hawaiian Islans (Nihoa). 1 sp.

Tornatellaria Pilsbry, 1910
Fig. 31

Pilsbry, 1910: 123. Cooke & Kondo, 1960: 265.

TYPE SPECIES — *Tornatellina newcombi* L. Pfeiffer, 1856; OD.

Shell ovate to ovate-turrited and pyramidal-conic, thin, of 6.5-9.5 more or less flattened whorls. Embryonic whorls with fine spiral striation; rest surface weakly sculptured with radial lines. Aperture ovate, with simple and sharp margins. Parietal lamella entering shell from two-thirds to entire whorl. Columellar lamellae 2 in juveniles, one or both more or less emerging in adults. Height 2.75-4.00, diam. 1.22-2.30 mm (4.00 × 2.10 mm).

Hermaphroditic gland of 3-5 lobes. Albumen gland large. Prostate small to large, of 12-30 acini. Vas deferens enlarged, strongly adherent to penis from near atrium, entering penis well below apex. Penis large, crooked-clavate, internally with typical recurved pilaster. Penial retractor attaching terminally. Vagina long. Spermathe-

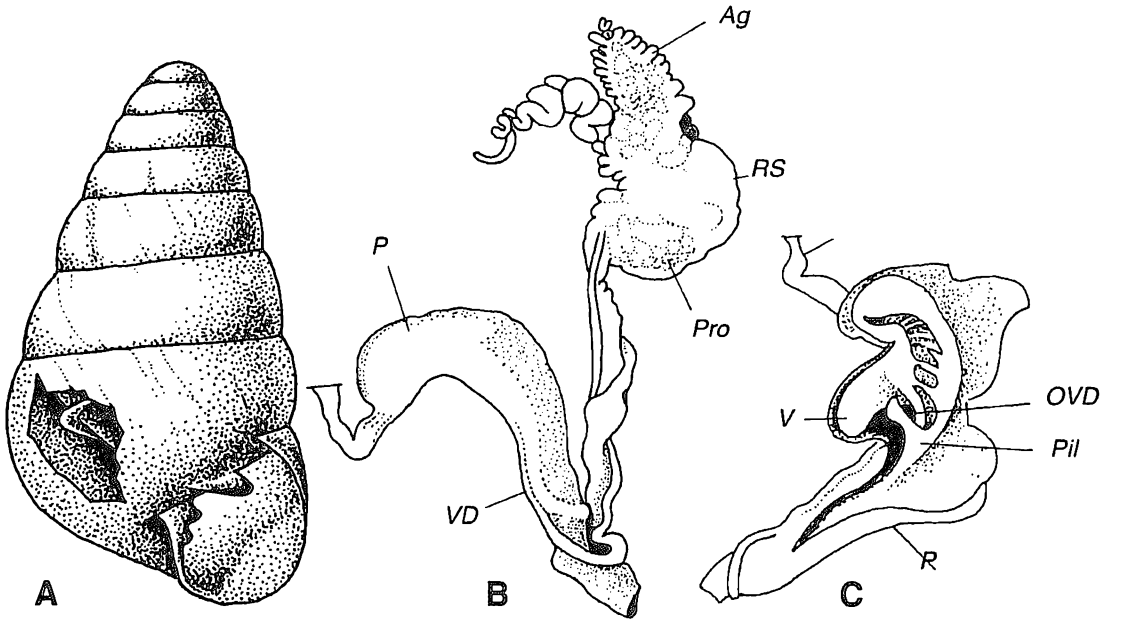


Fig. 31. *Tornatellaria newcombi* (L.Pfeiffer, 1856).
A — shell: Makaua (Weliweli), Oahu. **Phil.** No. 376297; B — reproductive tract; C — interior of penis. D, C — after Cooke & Kondo, 1960.

cal stalk of medium length, tapering upwards, entering female side 0.25-0.5 way down oviduct; reservoir large, ovate, lying on albumen gland or somewhat below.

DISTRIBUTION. Hawaiian Islands (Oahu, Kauai, Molokai). 18 spp. & subspp.

TEKOULININAE Solem, 1972

Solem, 1972: 97.

Shell dextral, rather large, subcylindrical or turrited. Palatal wall with strong longitudinal plica.

Right ocular retractor free of peni-oviducal angle.

Penis innervated by cerebral ganglion.

Hermaphroditic duct multilobate. Albumen gland minute in adults, very small in subadults. Prostate of many long branched acini. Vas deferens entering penial appendix through sphincter pilaster just above penial junction. Epiphallus absent. Penis somewhat reduced, internally with low rounded pilaster extending from atrium to penial apex and then down to appendix margin. Spermathecal shaft long, entering oviduct to form short vagina; reservoir free, lying next to prostate acini.

Viviparous.

DISTRIBUTION. Cook Islands.

Tekoulina Solem, 1972
Fig. 32

Solem, 1972: 98.

TYPE SPECIES — *Tekoulina pricei* Solem, 1972; OD.

Shell thin, fragile, of 9.5-11.5 slightly convex whorls. Outlines of upper spire conic, usually somewhat concave. Color brownish yellow. Embryonic whorls with vague radial riblets becoming only slightly more prominent on later whorls. Aperture moderately elongated in adults by downward expansion of columella; margins thin, not expanded. Parietal lamella high, thin, with microdenticulation on ridge, extending one whorl. Columellar lamella more prominent in juveniles than in adult shells. Palatal plica long, with ridge having same denticles found on parietal. In adult shells a low to medium lip developed at some distance

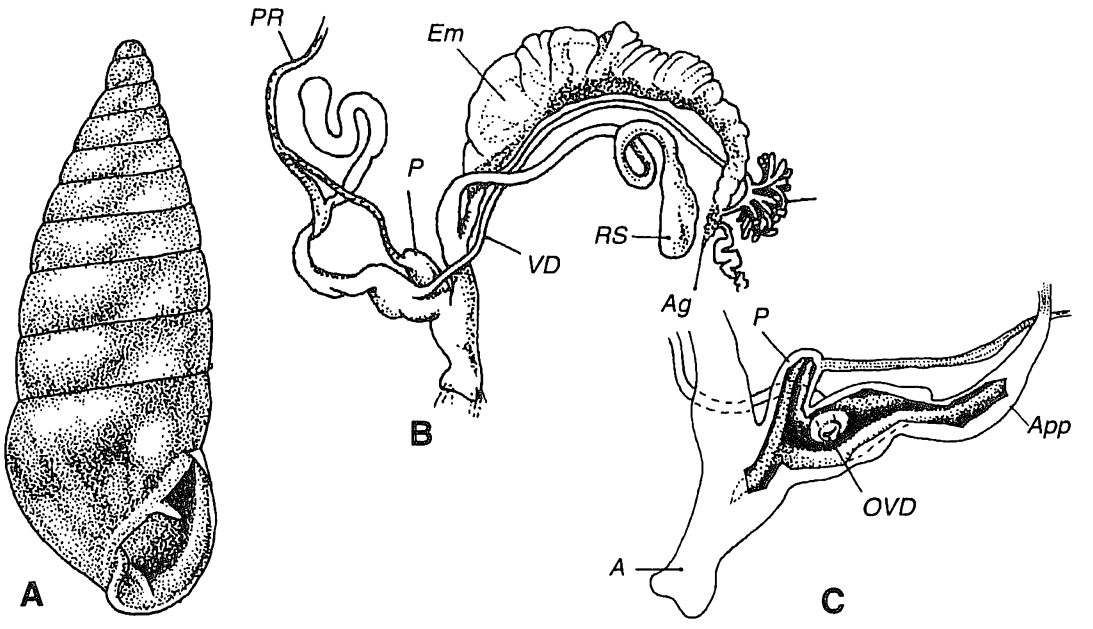


Fig. 32. ***Tekoulina pricei*** Solem, 1972.
A — shell: Summit of Mt. Te Kou, head of Takuvaine Valley, Rarotonga, Cook Islands. Paratype. **Chicago** No. 153389; B — reproductive tract; C — interior of penis. B, C — after Solem, 1972.

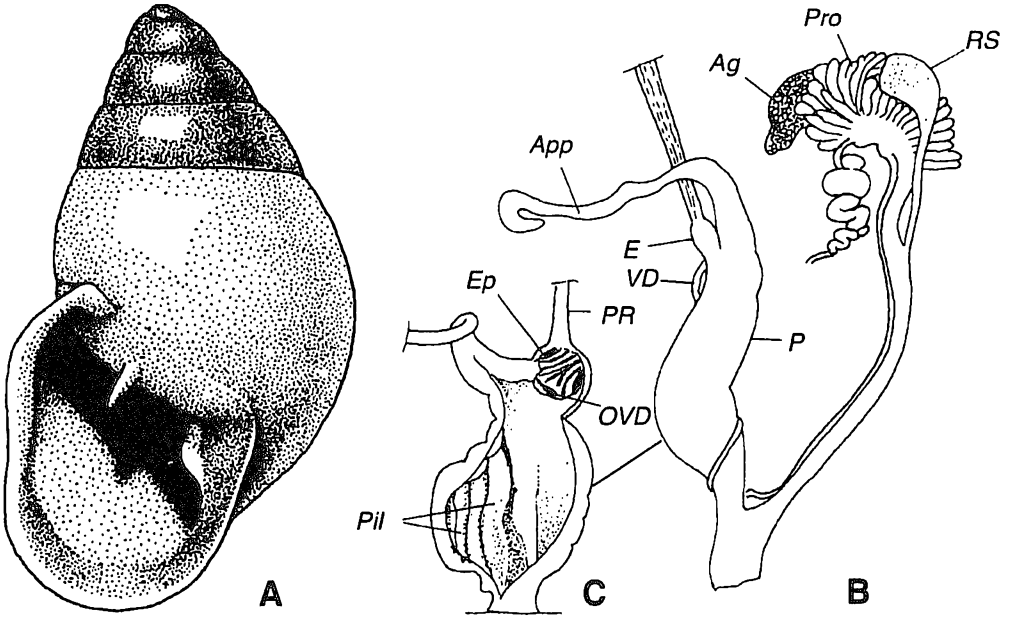


Fig. 33. ***Auriculella auricula*** (Férussac, 1821).
A — shell: Koolau Range, Oahu. **Honolulu**; B — reproductive tract; C — interior of penis. B, C — after Cooke & Kondo, 1960.

from aperture edge. Height 6.54-9.08, diam. 2.48-3.20 mm (8.02 × 2.73 mm).

Vas deferens entering penial appendix through sphincter pilaster just above penial junction. Penis much shorter than A-1 of appendix. This section internally with two low pilasters, A-2 + A-3 united. Penial retractor biramous, penial arm inserted subapically, appendical arm attached to base of A-4.

DISTRIBUTION. Cook Islands (Rarotonga Island). 1 sp.

AURICULELLINAE Odhner, 1922

Odhner, 1922: 234. Cooke & Kondo, 1960: 268.

Shell dextral or sinistral, more or less elongated, of 5-9.5 whorls. Parietal lamella well developed. Columella with 1 or 2 lamellae. Palatal plicae absent at all stages of postembryonic development.

Ommatophoral retractor passes through peni-oviducal angle.

Penis innervated by cerebral ganglion.

Hermaphroditic gland multilobate. Albumen gland large, well developed. Prostate large, fan-shaped. Talon and carrefour small, hidden. There is short epiphallus, containing small verge. Penis internally without achatinellid pilaster. Penial appendix present but lacking its own branch of penial retractor; interior with tubular secretory-ejaculatory apparatus. Spermathecal stalk entering above or below uterus; reservoir free.

Viviparous or oviparous.

DISTRIBUTION. Hawaiian Islands (Oahu, Maui).

Auriculella L. Pfeiffer, 1855
Fig. 33

L. Pfeiffer, 1855a: 1 (*Achatinella* Gruppe).

— *Frickella* L. Pfeiffer, 1855: 2 (*Achatinella* Gruppe; t.-sp. *Achatinella amoena* L. Pfeiffer, 1855; monotypy).

— *Trickella* Nevill, 1878: 159 (nom. err. pro *Frickella* L. Pfeiffer, 1855).

Cooke & Kondo, 1960: 268.

TYPE SPECIES — *Helix auricula* Férussac, 1821; SD Sykes, 1900.

Shell dextral or sinistral, oblong-conic to ovate-pyramidal, rather solid, of 5-6 weakly convex whorls. Color yellow to chestnut; if dark, a light peripheral band sometimes present; upper whorls may be darker than body whorl. Both apical and postapical whorls practically smooth, highly polished. Aperture ovate, with somewhat expanded, blunt, usually thickened margins; parietal lamella somewhat oblique, rather short. Columella slender, simple or with 1 or 2 plates, that always present in juvenile shells; lower lamella much stronger than upper. Umbilicis closed or narrowly open. Height 5-10, diam. 3-6 mm (8.7 × 5.2 mm).

Talon small, recurved. Carrefour small. Vas deferens free, entering penis through small epiphallus. Penis large, long, internally with low longitudinal secondary pilasters. Epiphallus short, containing minute verge. Appendix slender, rather long. Penial retractor unbranched, attached to summit of epiphallus. Atrium short. Oviduct long, narrow; uterus occasionally saccate near prostate. Spermathecal shaft moderately short, slender; reservoir voluminous, ovate to oblong, lying on prostate.

DISTRIBUTION. Hawaiian Islands. 34 spp. & subspp.

Gulickia Cooke, 1915
Fig. 34

Cooke in Pilsbry & Cooke, 1915 (1914-1915): 112, 228. Cooke & Kondo, 1960: 273.

TYPE SPECIES — *Gulickia alexandri* Cooke, 1915; OD.

Shell sinistral, rather thin, translucent to semitransparent, of about 6 flattened whorls. Last whorl not descending. Surface nearly colourless. Embryonic whorls microscopically spirally striated, subsequent whorls with very fine, silky, radial striation. Aperture ovate, with thin, straight margins. Parietal lamella subhorizontal, deeply entering, its ridge unevenly, weakly serrate. Columellar margin slightly sigmoid, furnished with two almost equal, rather strong, oblique lamellae. Umbilicus, a minute perforation. Height 3.5-4.0, diam. 1.8-2.0 mm (3.6 × 1.9 mm).

Vas deferens thin, entering penis apically. Penis long, inner surface covered with short, vermiform, chaotically arranged, folds. Penial appendix well developed; three basal sections united, A-4 slender, long, cylindrical, piercing through A-1+A-2+A-3 as thin tube. Space between this tube and outer walls of this section filled with loose tissue.

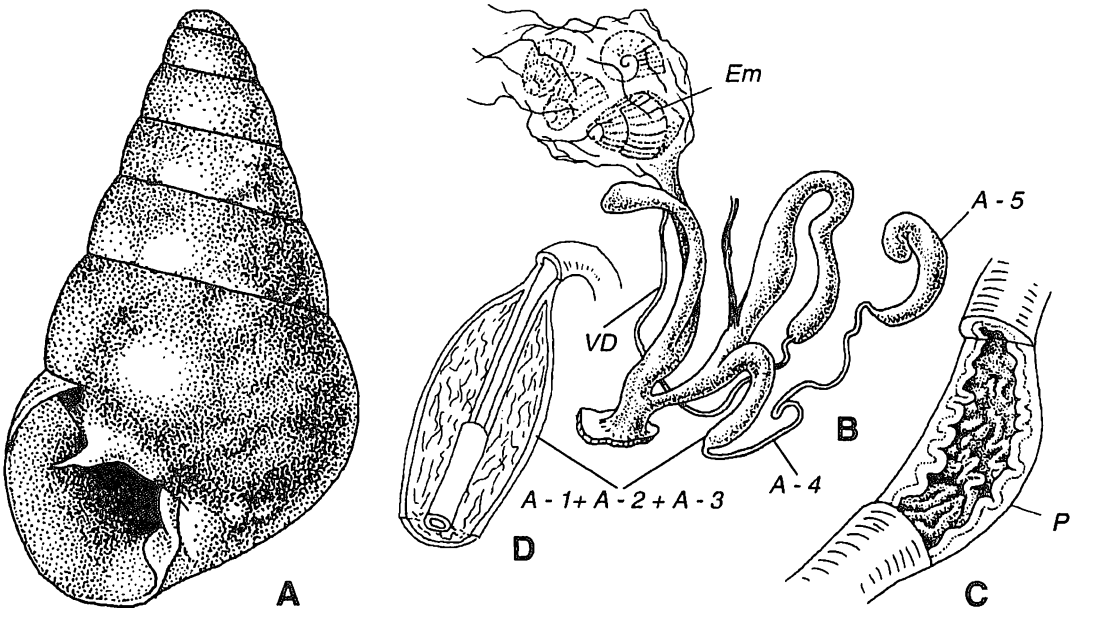


Fig. 34. *Gulickia alexandri* Cooke, 1915.
A — shell: Maunahooma, western Maui. Paratype. **Phil.** No. 111919; B — reproductive tract; C — interior of penis; D — structure of basal section of penial appendix. B-D — Maui. **Phil.** No. 1780-A.

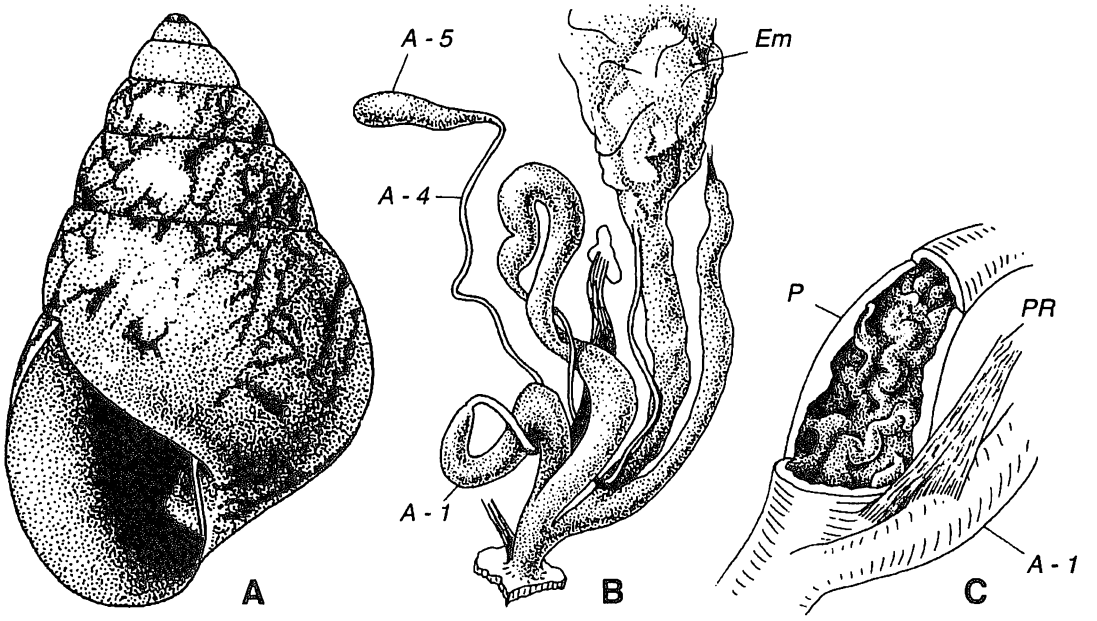


Fig. 35. *Laminella gravida* (Férussac, 1824).
A — shell: Oahu. **Moscow** Lc-23215; B — reproductive tract; C — interior of penis. B-C — Waialaenui, Oahu. **Honolulu** No. 184114.

A-5 of moderate length. Penial retractor uniramous, inserts onto penis somewhat above base of appendix. Vagina rather short. Spermathecal stalk rather enlarged, slightly longer than free oviduct. In uterus a number of embryos with well developed shells are found.

DISTRIBUTION. Hawaiian Islands (Maui). 1 sp.

? *Laminella* L. Pfeiffer, 1854
Fig. 35

Pfeiffer L., 1854: 126.

TYPE SPECIES — *Helix gravida* Férussac, 1824; SD Martens in Albers, 1860.

Shell mostly sinistral, high conic, rather thin, slightly translucent, of 6 somewhat flattened whorls. Last whorl rounded at periphery, outlines of spire conic, apex pointed. Color pattern consists of yellowish background and irregular brown network; first 2-3 whorls yellowish-pink. Embryonic sculpture of radial wrinkles; rest whorls practically smooth, with only irregular smoothed radial wrinkles. Aperture somewhat oblique, pointed-ovate, margins sharp, not reflexed. Parietal wall smooth. Columellar lamella thin, sharp. Umbilicus closed. Height 10-26, diam. 4.5-13.5 mm (21.1 × 12.0 mm).

Distal portion of penis (below appendix insertion) very short; penis without distinct subdivision into sections, although with alternation of narrowings and enlargings. Internally penis with irregularly spaced tubercles and vermiform folds. There are 3 externally visible sections of penial appendix: basal section is result of fusion A-1, A-2 and A-3, internally with sharp longitudinal folds but without tube. A-4 long, A-5 comparatively small. Broad base of penial retractor attached to both penis and appendix. Atrial retractor weak. Spermatheca inserts just above atrium, without visible subdivision into shaft and reservoir, with terminal ligament.

DISTRIBUTION. Hawaian Islands (Oahu, Molokai, Maui, Lanai). 25 spp. & subspp.

REMARK. Hyatt & Pilsbry in Pilsbry (1911) and Zilch (1959) attribute this genus to Amastridae; Cooke & Kondo (1960) did not consider it in their book on Achatinellidae. However the anatomy of type species is very similar to that of *Gulickia* (compare Figs. 34 and 35), including inner structure of penis; the only serious anatomical difference of *Laminella gravida* from *Gulickia alexandri* seems to consist in different inner structure of basal portion of penial appendix. In addition, I do not know the jaw structure of *Laminella*, therefore I provisionally place the genus in Achatinellidae.

ACHATINELLINAE Gulick, 1873

Pilsbry & Cooke, 1914 (1914-1915): IX. Cooke & Kondo, 1960: 274.

Shell dextral or sinistral, oblong to ovate, rather to quite solid, of 5-7 whorls. Coloration variable, often bright, uniformly white or yellowish or with dark band(s). Embryonic whorls smooth or with delicate spiral cording; postnuclear whorls usually weakly sculptured, rarely with coarse spiral ribbing. Aperture ovate, with margins expanded a little. No entering lamella or tooth on parietal wall. Columella usually with strong, oblique lamella. Umbilicus, a minute perforation or closed.

Ocular retractor passes through peni-oviducal angle.

Penis innervated by cerebral ganglion.

Hermaphroditic gland of 3-10 lobes. Albumen gland usually minute. Prostate large, not fan-shaped, composed of many elongated acini. Epiphallus absent. Vas deferens fairly large, free or adherent to penis, entering penis apically or nearly so. Penis large, clavate, internally with reflexed and recurved pilaster, either with semipendent fleshy verge or with simple fleshy ridge. Penial appendix large, variable in length, supplied with retractor, containing straight tubular secretory-ejaculatory apparatus. Spermathecal stalk entering vagina usually not far from atrium; reservoir hidden among acini of prostate.

Viviparous animals.

DISTRIBUTION. Hawaiian Islands (except Kauai, Niihau, and perhaps Kahoolawe).

REMARK. Two largest generally accepted genera of Achatinellinae (*Partulina* and *Achatinella*) are distinguished, in essence, mainly by two features: the presence of internal lip within the aperture in species of *Achatinella* (in *Partulina* the lip is absent) and the development of spiral engraved lines in *Partulina* (in *Achatinella* the spiral sculpture is absent or extremely weak); but even these weak distinctions are not absolute. At the same time I was not able to find any constant anatomical differences between these taxa. Perhaps, only the genus *Achatinella*

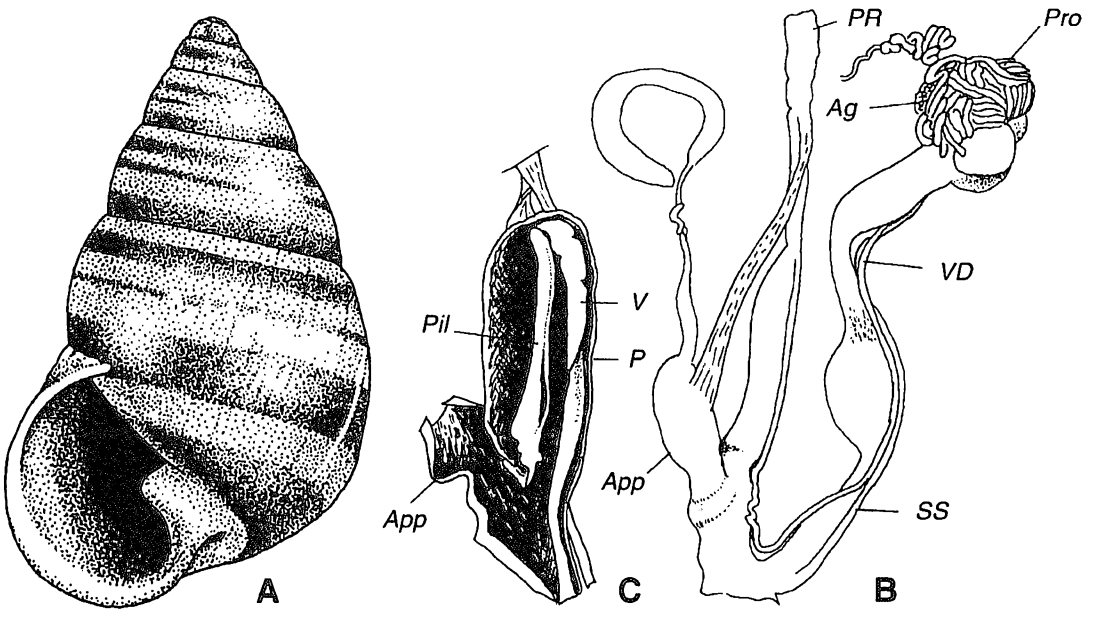


Fig. 36. ***Partulina (Eburnella) variabilis*** (Newcomb, 1854).
A — shell: Lanai Island. **Phil.** No. 10501.
! ***Partulina (Eburnella) mighelsiana*** (L.Pfeiffer, 1847): B — reproductive tract; C — interior of penis. B, C — after Cooke & Kondo, 1960.

with a number of subgenera exists. However, as I had no sufficient material on Achatinellidae, I prefer to refrain from definite decision and tentatively retain both taxa as genera.

Partulina L. Pfeiffer, 1854

Pfeiffer L., 1854: 114. Cooke & Kondo, 1960: 280.

TYPE SPECIES — *Partula virgulata* Mighels, 1845; SD Martens in Albers, 1860.

Shell ovate-conic, inflated, moderately solid, of 5-6 slightly convex whorls. Coloration usually consists of yellowish or whitish background and oblique stripes or dark spiral bands developed to various degree. First embryonic whorl smooth, next 1-1.5 embryonic whorls microscopically spirally striated, postnuclear sculpture of distinct spiral incised lines. Aperture widely ovate, with more or less expanded, slightly thickened margins. Columella nearly simple or with weak plate.

DISTRIBUTION. Hawaiian Islands.

Partulina (*Eburnella* Pease, 1870) Fig. 36

Pease, 1870: 647. Cooke & Kondo, 1960: 284.

TYPE SPECIES — *Achatinella variabilis* Newcomb, 1854; SD Gulick, 1873.

Shell dextral or sinistral, solid, shining, of about 6 moderately convex whorls. Color uniformly white, yellow, or brown, or consisting of yellowish background and several brownish or greenish bands. Both embryonic and postembryonic whorls with distinct spiral striae. Aperture ovate, with slightly thickened margins. Columella with strong, tuberculiform, entering lamella. Height 14-20, diam. 8-12 mm (17.2 × 10.0 mm).

Vas deferens adherent to penis. Penis internally with normal achatinellid pilaster. A-1 + A-2 united, A-3 indistinctly differentiated, A-4 relatively short. Appendical arm of penial retractor much longer than penial arm.

DISTRIBUTION. Hawaiian Islands (Molokai, Maui, Lanai). About 15 spp. & forms.

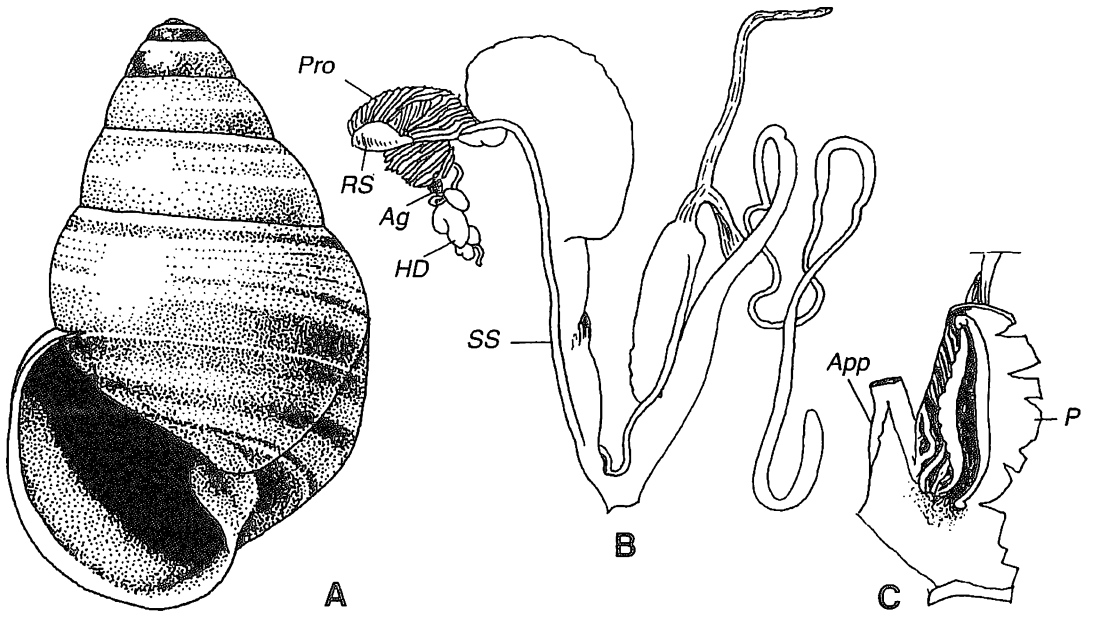


Fig. 37 ***Partulina (Partulina) virgulata*** (Mighels, 1845).
A — shell: Molokai. **Moscow** Lc-23199; B — reproductive tract; C — interior of penis. B, C — after Cooke & Kondo, 1960.

Partulina (*Partulina* s.str.)
Fig. 37

Shell dextral or sinistral, inflated, glossy, solid, of about 6 rather convex whorls. Coloration consists of white background and a number of brown spiral bands of various width and intensity. Embryonic whorls vaguely spirally striated; on next whorls this striation becomes stronger, and fine irregular radial wrinkles added. Aperture ovate, somewhat oblique, with thin and erected margins; wide, low lip sometimes lies at some distance from aperture edges. Columellar lamella well calloused, occupies upper part of columellar margin. Umbilicus absent. Height 15-26, diam. 9-15 mm (25.8 × 14.7 mm).

Anatomically differs from *Eburnella* mainly by much longer penial appendix which poorly differentiated into divisions.

DISTRIBUTION. Hawaiian Islands (Molokai, Maui, Lanai). Around 40 spp. & subspp.

Partulina (*Partulinella* Hyatt, 1914)
Fig. 38

Hyatt in Pilsbry, 1914 (1914-1916): 391.

TYPE SPECIES — *Achatinella marmorata* Gould, 1847; SD Pilsbry, 1914 (p. 392, Footnote)

Shell very similar to *Partulina* s.str., differs in having rather distinct oblique striation on last embryonic whorl which also persist throughout later whorls. Coloration consists of white or cream background and zigzagged brown markings. Parietal tooth developed variously. Height 15-25, diam. 9-13 mm (21.5 × 12.0 mm).

Albumen gland hidden among acini of prostate. Vas deferens entering penis subapically through a simple pore. Penis internally with a typical Y-shaped pilaster; one of arms shorter than the other. Penial appendix long. Penial branch of retractor very short, appendical markedly longer.

DISTRIBUTION. Hawaiian Islands (Molokai, Maui). About 10 spp.

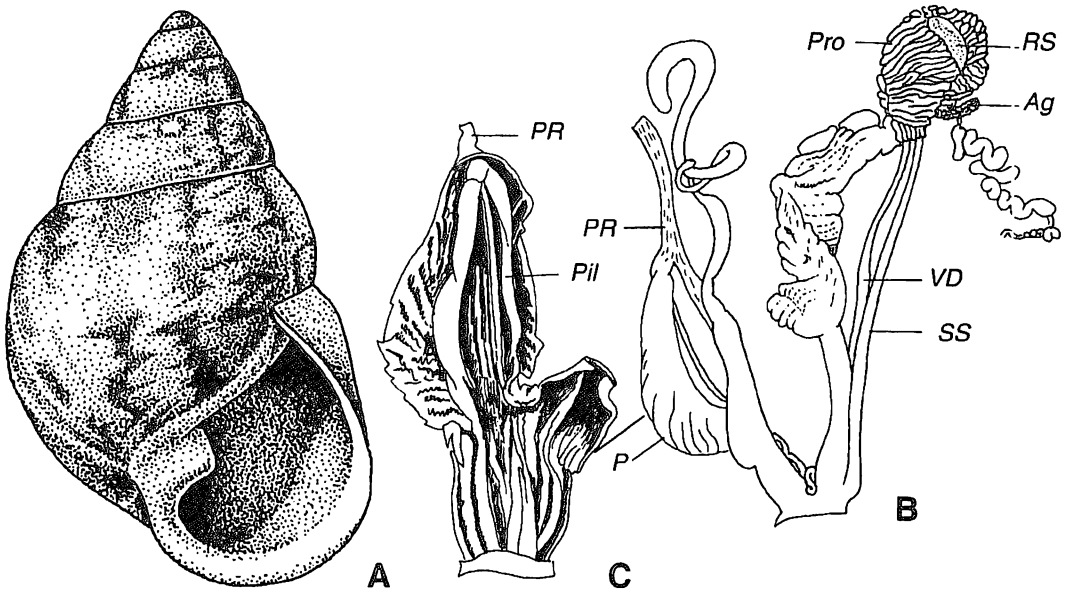


Fig. 38. ***Partulina (Partulinella) marmorata*** (Gould, 1847).
A — shell: Huelo, eastern Maui. **Phil.** No. 204741.
! ***Partulina (Partulinella) redfieldii*** (Newcomb, 1853). B — reproductive tract; C — interior of penis. After Cooke & Kondo, 1960.

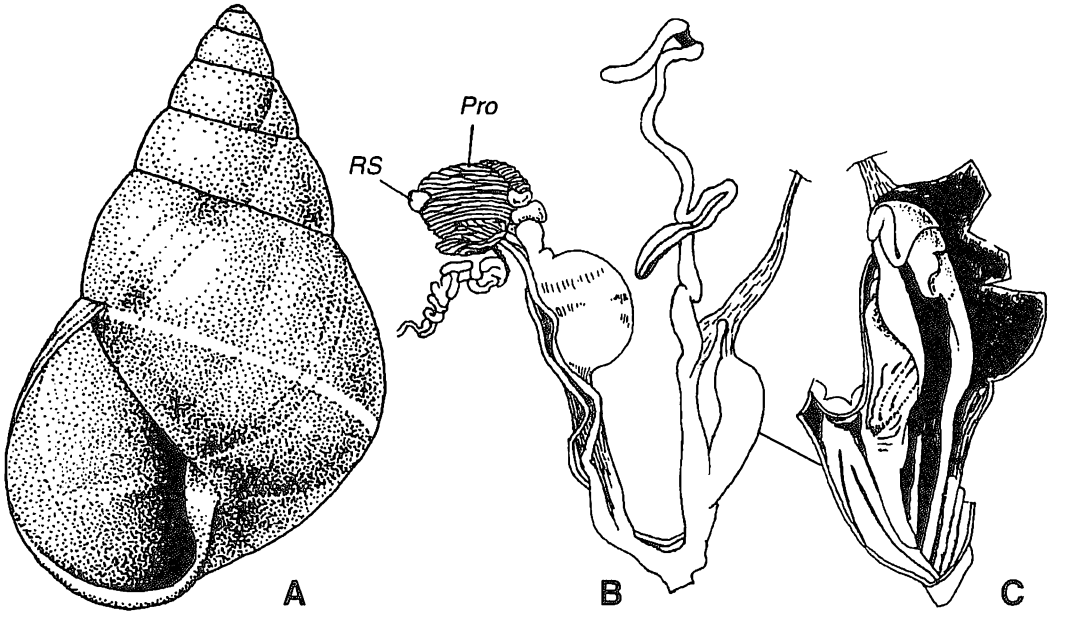


Fig. 39. ***Partulina (Baldwinia) confusa*** (Sykes,. 1900).
Shell — Mauna Kea, Hawaii (Big Id.). **Moscow** No. Lc.-20956 (**Phil.**).
! ***Partulina (Baldwinia) dubia*** (Newcomb, 1853). B — reproductive tract; C — interior of penis. After Cooke & Kondo, 1960.

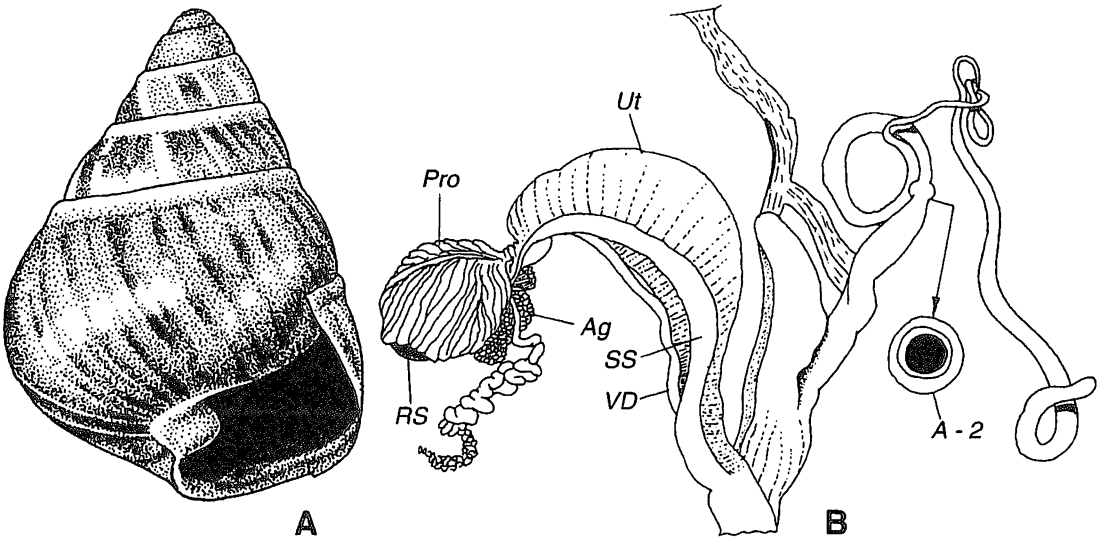


Fig. 40. ***Achatinella (Achatinella) seminigra*** Lamarck, 1822.
Shell — Right Branch, North Gulch junction of branches of North Poamoho, in Ravine Bed Poamoho, Oahu. Phil. No. 383657.
! ***Achatinella (Achatinella) concavospira*** L. Pfeiffer, 1859. B — reproductive tract. After Cooke & Kondo, 1960.

Partulina (*Baldwinia* Ancey, 1899)
Fig. 39

Ancey, 1899: 270 (*Achatinella* subg.). Cooke & Kondo, 1960: 281.

TYPE SPECIES — *Achatinella physa* Newcomb, 1855 [= *Achatinella (Partulina) confusa* Sykes, 1900; nom. nov. pro *Achatinella physa* Newcomb, 1855, non *A. physa* Newcomb, 1854]; OD.

Shell sinistral (except for one species), pointed-ovate or ovate-conic, thin, somewhat glossy, of 5.5-6 flattened whorls. Color yellowish to brownish, usually with light narrow peripheral band. Embryonic whorls smooth, later weakly sculptured with fine irregular radial striae. Aperture acutely-ovate, toothless, with thin margins; columellar margin subvertical, somewhat thickened, without calloused plate or tooth. Umbilicus, a minute perforation. Height 16-22, diam. 9.0-13.5 mm (22.0 × 13.5 mm).

Hermaphroditic gland of 8-10 lobes. Vas deferens entering at and below apical recurvature of pilaster. Penis rather large, internally with modified achatinellid pilaster and diagonal folds at middle portion, heavily ridged below by numerous longitudinal fleshy pilasters. Principal pilaster flat, wide, starting at penial base as a low ridge, widening dorsally, heavily wrinkled at middle, with free folded velum on inner face near apex. Spermathecal shaft long, reservoir hidden among acini of prostate.

DISTRIBUTION. Hawaiian Islands (Oahu, Manui). 7 spp.

Achatinella Swainson, 1828

Swainson, 1828: 83 (*Achatina* subg.).

— *Helicteres* Beck, 1837: 51 (t.-sp. *Helix vulpina* Férussac, 1824; SD Gray, 1847).

— *Apex* Martens in Albers, 1860: 248 (*Achatinella* subg.; t.-sp. *Achatinella lugubris* Chemnitz, 1795; OD).

— *Helicter* Pease, 1862: 3 (t.-sp. *Monodonta seminigra* Lamarck, 1822; here des.).

TYPE SPECIES — *Monodonta seminigra* Lamarck, 1822 (=*Turbo Apex Fulva* Dixon, 1789); OD.

Shell oblong, ovate, or globose-conic. Color whitish, with spiral bands or radial

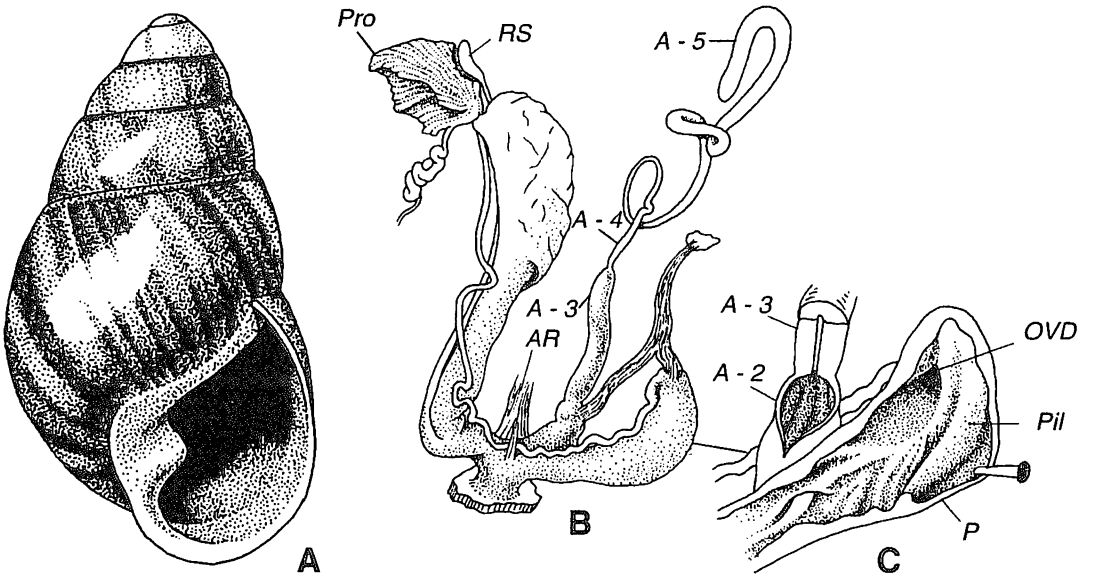


Fig. 41. *Achatinella (Achatinellastrum) producta* Reeve, 1850.
A — shell; B — reproductive tract; C — interior of distal part of male division: slopes of Mt. Tantalus, Koolau Range, Oahu, August 23, 1961. **Chicago** No. 155357.

streaks, never in forwardly descending strikes. Embryonic whorls smooth, rest surface nearly smooth or radially corrugated, with only minute and weak traces of spiral striation. Aperture broadly ovate, margins erected or slightly expanded, sometimes with wide, low lip inside. Columella with strong callous tooth-like lamella.

DISTRIBUTION. Hawaiian Islands (Oahu).

Achatinella (*Achatinella* s.str.)
Fig. 40

Shell dextral or sinistral, generally ovate-conic or pyriform, of about 6 slightly to moderately convex whorls. Coloration mostly banded, with brown or chestnut-violet streakes. Embryonic whorls practically smooth, later whorls smooth, with only vague radial wrinklets. Aperture margins simple or only slightly expanded, more or less thickened within. Umbilicus tiny or absent. Height 14-24, diam. 9-15 mm (18.0 × 12.5 mm).

Hermaphroditic gland of 9-10 lobes. Talon absent or not seen. Albumen gland minute, closely adherent to lower wall of carrefour. Prostate large, acini very long, tubular, closely packed. Vas deferens not strongly adherent, emerging from upper wall of carrefour and entering penis subapically. Penis large, long, internally with large recurved pilaster, ascending from below as narrow fleshy ridge, recurving at apex, descending as semi-pendent verge. Latter with groove formed by free edge curving inward. Appendix very long, narrow, all its five divisions well defined; interior with narrow tubular secretory-ejaculatory apparatus. Common portion of penial retractor heavy, long; penial branch short; appendical arm much longer. Spermathecal shaft somewhat expanded, entering female side at short distance above atrium; reservoir entirely enclosed within prostatic acini, except tip.

DISTRIBUTION. Hawaiian Islands (Oahu). Around 200 spp. with numerous forms.

Achatinella (*Achatinellastrum* L. Pfeiffer, 1854)
Fig. 41

Pfeiffer L., 1854: 133. Cooke & Kondo, 1960: 291.

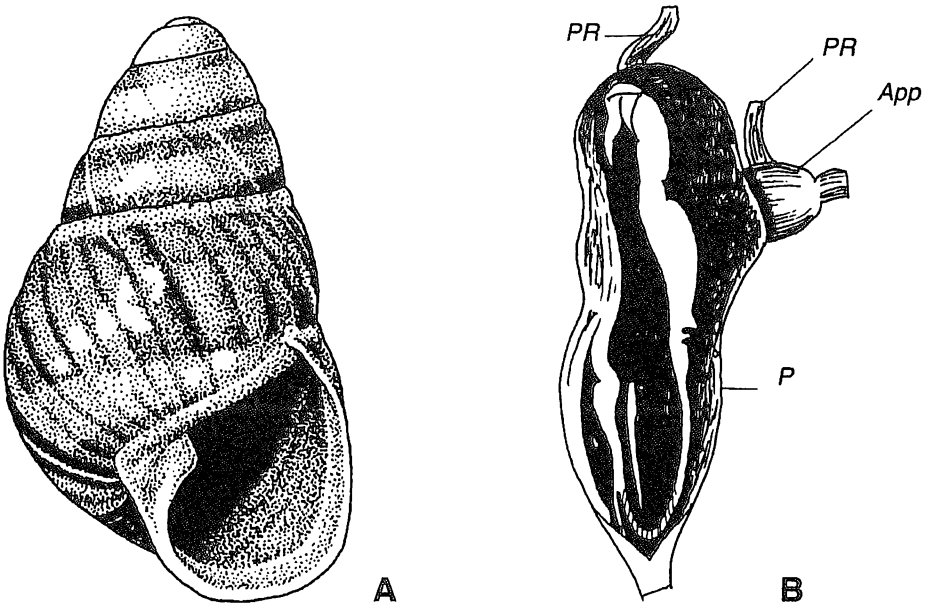


Fig. 42. ***Achatinella (Bulimella) rugosa*** Newcomb, 1853.
A — shell: Waiawa, Oahu. **Phil.** No. 92227.
! ***Achatinella (Bulimella) viridans*** Mighels, 1845. B — interior of penis After Cooke & Kondo, 1960.

TYPE SPECIES —*Achatinella producta* Reeve, 1850; SD Pease, 1869.

Shell dextral or sinistral, ovate-conic or elongated-ovate, fairly solid, shining, of about 6 slightly convex whorls. Color greenish-olive, with irregular brown radial stripes of various width. Embryonic whorls smooth, rest with very fine spiral striae, stronger on early spire; radial striation fine, irregular. Aperture ovate, only slightly oblique, margins not expanded, thickened a little, with vague lip inside. Columellar lamella large. No umbilicus. Height 15-30, diam. 6-13 mm (21.8 × 11.5 mm).

Albumen gland tiny, hidden among acini of prostate. Vas deferens entering penis laterally very close to penis apex through simple pore. Penis internally with very low modified principal pilaster, starting below at termination of single low secondary pilaster, with short, fleshy, ventrally pointed piece at apex. One of lower pilasters entering penial appendix. All sections of appendix quite distinct. A-1 very short, much expanded basally; A-2 globular, A-3 unusually long, A-4 and A-5 normal. Penial retractor forked, one branch attached to penis apically, the other (much longer) — to A-2. Atrial retractor well developed. Vagina very short. Spermathecal shaft slender, small reservoir lies on prostate.

DISTRIBUTION. Hawaiian Islands (Oahu). About 35 spp. and forms.

Achatinella (*Bulimella* L. Pfeiffer, 1854) Fig. 42

Pfeiffer L., 1854: 119. Cooke & Kondo, 1960: 289.

TYPE SPECIES — *Achatinella byronii rugosa* Newcomb, 1853; SD Martens in Albers, 1860.

Shell dextral or sinistral, ovate-conic or slightly pyramidal, of about 6 whorls. Apex obtuse, rounded. Early whorls only slightly flatter than rest. Color greenish to brownish, with darker radial strikes and a few lighter bands. Embryonic whorls finely, regularly, spirally striatulate; later whorls with irregular radial wrinkles and, in places, spiral striae. Aperture margins often slightly ex-

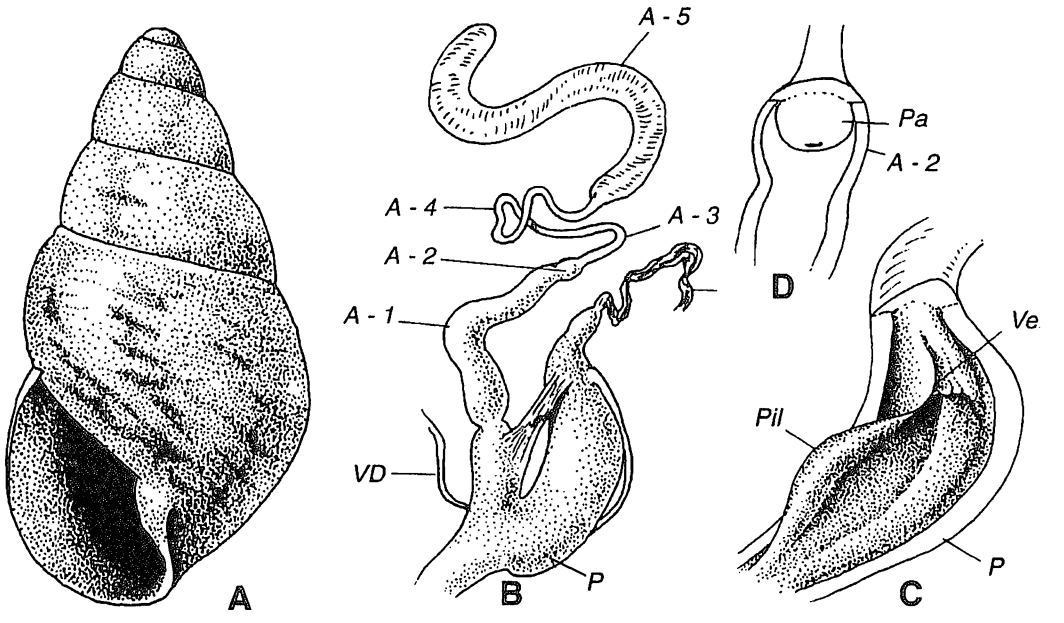


Fig. 43. ***Perdicella helena*** (Newcomb, 1853).
A — shell: Kahanui, Molokai Island. **Phil.** No. 204780. B — male division of reproductive tract; C — interior of penis; D — interior of basal portion of appendix: Puunea, Molokai Island. **Phil.** No. A 1766.

panded, with wide lip inside. Height 15-23, diam. 6.6-12.5 mm (18.5 × 10.5 mm).

Penis internally smooth except for principal pilasters plus a few wide ridges formed by inner surface of penis. Ascending arm of pilaster starts below as low, irregular folds, continues upward as low flat ridge. Apex complicated by accessory free outgrowth. Penial verge rounder than ascending arm, decreasing in size below appendical opening, thence descending as narrow fold. Penial retractor biramous.

DISTRIBUTION. Hawaiian Islands (Oahu). 25-30 spp. & subspp.

Perdicella Pease, 1869
Fig. 43

Pease, 1869: 648. Cooke & Kondo, 1960: 278.

TYPE SPECIES — *Achatinella helena* Newcomb, 1853; SD Sykes, 1900.

Shell dextral or sinistral, rather thin, of 5-5.5 slightly convex whorls. Color whitish, striped or spotted with dark; a light peripheral band often present. Embryonic whorls practically smooth, postnuclear sculpture of distinct wavy spiral lines. Aperture pointed ovate; peristome thin, simple. Columella nearly straight, or, if columellar lamella present, somewhat sinuated, not truncated or scarcely truncated. Umbilicus, a narrow slit or absent. Height 11-16, diam. 6-8 mm (12.0 × 6.5 mm).

Hermaphroditic gland of 2-3 lobes. Albumen gland minute. Vas deferens thin, entering penis laterally at some distance from apex through simple pore. Penis large, bulky, attenuated at apex, internally with two pilasters; one of them high, lamellar, the other low. At upper ends both pilasters connected by thin velum, under which pore of vas deferens situated. All sections of penial appendix normally developed. A-1 unusually long,A-2 subglobular, minute, with tiny closed papilla inside; A-3 and A-4 not not differentiated markedly from each other, A-5 heavily muscularized. Penial arm of retractor attached terminally; appendical branch independent, wide, connecting A-1

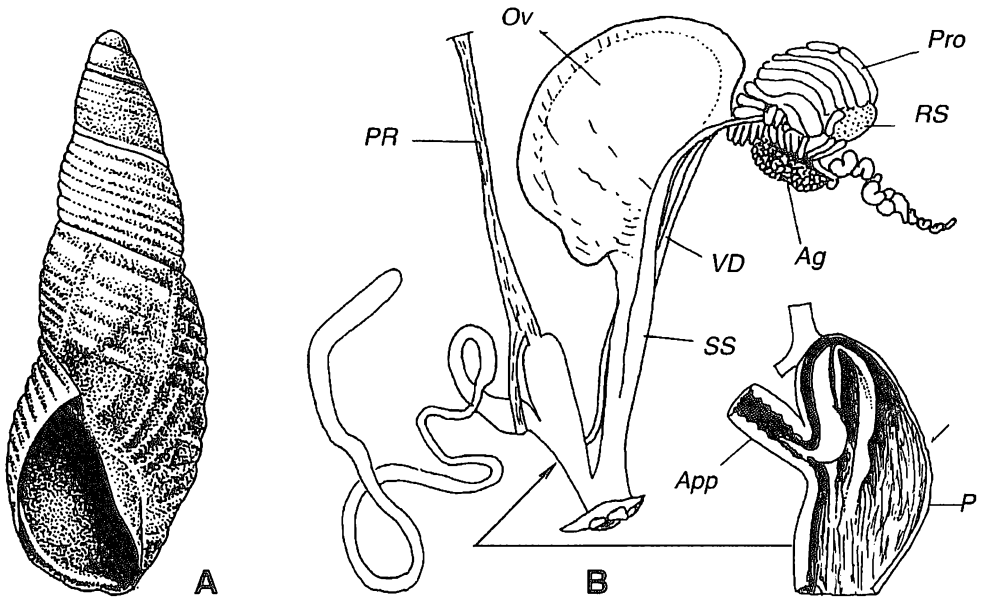


Fig. 44. ! *Newcombia cumingi* (Newcomb, 1853).
A — shell: Hawaiian Islands, Maui. **Leiden.**
! *Newcombia canaliculata* (Baldwin, 1905). B — reproductive tract and interior of penis. After Cooke & Kondo, 1960.

with penis at level of vas deferens insertion. Uterus contains a few very large embryos.

DISTRIBUTION. Hawaiian Islands (Molokai, Manui). 8-9 spp.

Newcombia L. Pfeiffer, 1854
Fig. 44

Pfeiffer L., 1854: 117.

— *Newcombiana* Thwing, 1907: 138 (nom. err. pro *Newcombia* L. Pfeiffer, 1854).

Cooke & Kondo, 1960: 277.

TYPE SPECIES — *Achatinella plicata* L. Pfeiffer, 1848; SD Martens in Albers, 1860.

Shell sinistral (one species dextral), oblong-turrited, moderately solid, of 5-6 slightly convex whorls. Color whitish, monochromate. Embryonic sculpture of distinct spiral cords; last embryonic whorl usually radially striped. Postnuclear whorls with similar spiral cords, but here sculpture much coarser (8-12 cords on last whorl). Peristome slightly expanded or simple. Parietal lamella absent; columella straight or with weak lamella. Umbilicus absent. Height 12.5-25.0, diam. 6.0-12.2 mm (12.5-6.1 mm).

Hermaphroditic gland of 5-6 lobes. Vas deferens free. Internally penis with only principal U-shaped pilaster that starts as low fold at middle, descends as relatively large fold with one shallow furrow at its upper part, terminating at orifice of appendix, continuing into appendix as short branch but also descending to small, narrow ridge and terminating here. Penial appendix long. Common trunk of penial retractor long, penial arm very short, appendical somewhat longer. Uterus contains single large egg. Spermathecal shaft long, reservoir rounded, partially embedded into prostate.

DISTRIBUTION. Hawaiian Islands (Molokai, Maui). 12 spp. & subspp.

AMASTRIDAE Pilsbry, 1910

Pilsbry, 1910: VIII (Achatinellidae subf.).

Shell subcylindrical, high conic, ovate, or

nearly flat, mostly of medium size. Aperture primarily with columellar lamella; parietal and palatal walls never armed. Umbilicus closed to widely open.

Jaw strong, well developed, very opaque and smooth or irregularly vertically striated, plaited or ribbed.

Genital orifice nearer to mantle collar than to tentacle base.

Hermaphroditic gland multilobate, with duct more or less distended and strongly convoluted. Talon small, hidden. Albumen gland well developed. Female and male divisions separated at some distance from albumen gland. Prostate moderately long, of many acini; acini more or less elongated. Vas deferens entering penis strictly terminally, never adherent to penis. Penis well developed. Epiphallus present. Internally penis with various relief, but achatinellid pilaster absent. Penial appendix always normally developed. Penial retractor unbranched and attached to penis at base of appendix or splitted at the very insertion to penis and basal section of appendix.

Oviparous or viviparous animals.

DISTRIBUTION. Hawaiian Islands.

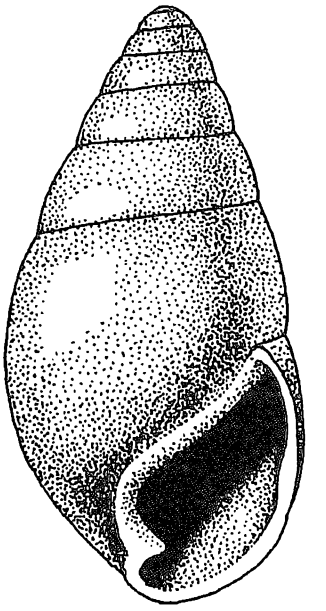


Fig. 45. ***Labiella labiata*** (Newcomb, 1853). Makaha, Waianae Mts., Oahu. Honolulu No. 185188.

LEPTACHATININAE Cockerell, 1913

Cockerell, 1913: 256 (pro trib.). Pilsbry & Cooke, 1914 (1914-1915): 256 (as Leptachatinini).

Shell elongated-ovate, thin, often translucent, uniformly yellowish or brownish; rarely with radial streaks, but spiral bands absent. Umbilicus closed.

Oviparous animals.

DISTRIBUTION. Hawaiian Islands.

Labiella L. Pfeiffer, 1854
Fig. 45

Pfeiffer L., 1854: 142 (*Achatinella* sect.).

TYPE SPECIES — *Achatinella labiata* Newcomb, 1853; monotypy.

Shell ovate-conic, moderately thin, somewhat glossy, of 6.5-7 slightly convex whorls; last whorl not descending. Apex a little pointed. Color uniformly ivory or yellowish. Nuclear whorls smooth, postembryonic with weak but rather regular radial wrinkles and extremely fine, locally expressed spiral striation; as all sculpture elements are weak, surface looks nearly smooth. Aperture acutely-ovate, places of peristome insertion remoted; parietal callus well developed. Parietal wall sometimes with light thickening, columellar lamella horizontal, thin and sharp. Umbilicus absent. Height 8-16, diam. 3.5-6.8 mm (11.8 × 5.4 mm).

DISTRIBUTION. Hawaiian Islands (Oahu, Maui). 4 spp.

Leptachatina Gould, 1847
Fig. 46

Gould, 1847: 201 (*Achatinella* group).

TYPE SPECIES — *Achatinella acuminata* Gould, 1847; OD.

Shell acuminate, more or less solid, glossy, of 6-7 flattened whorls. Color yellowish to chestnut, often with darker radial strikes, especially on lower whorls. Embryonic whorls finely radially wrinkled, subsequent nearly smooth. Aperture ovate, pointed above; columella truncate below

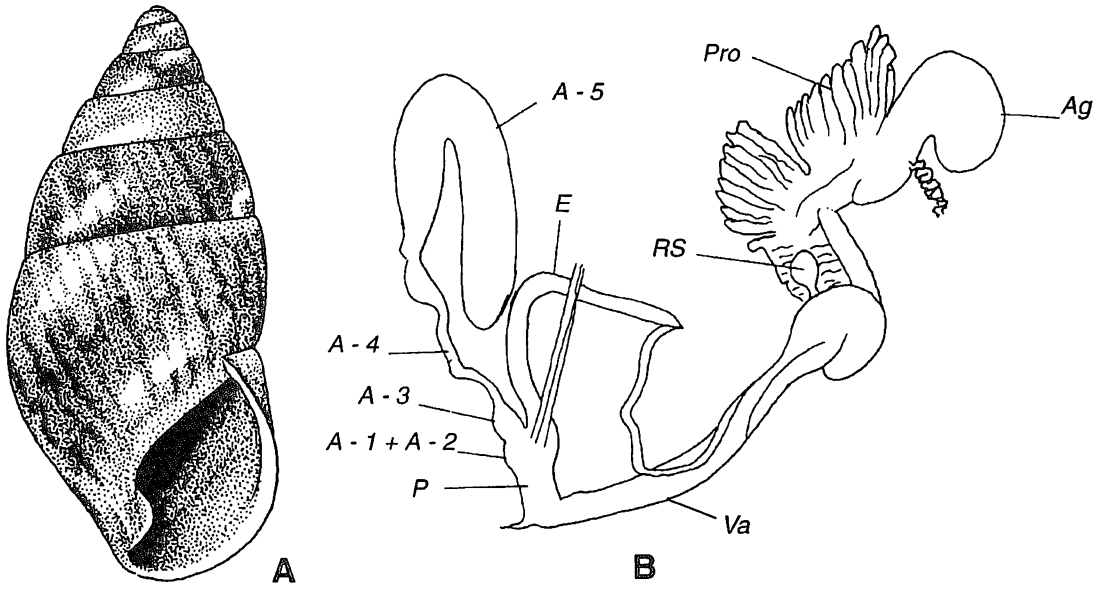


Fig. 46. ***Leptachatina acuminata*** (Gould, 1847).
A — shell: Lualualei, Waianae Mts., Oahu. **Phil.** No. 161353
! ***Leptachatina corneola*** (L. Pfeiffer, 1846). B — reproductive tract. After Pilsbry, 1916.

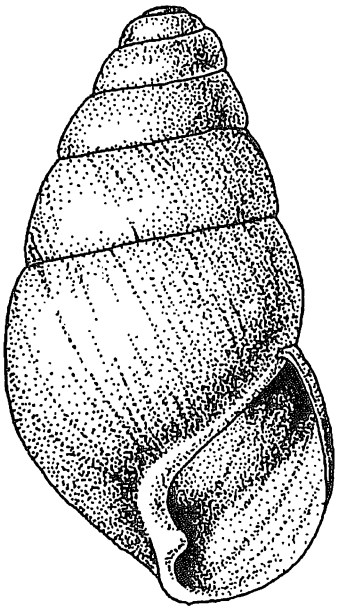


Fig. 47. ***Ilikala fusca*** (Newcomb, 1853).
Oahu. Syntype. **Phil.** No. 57793.

and furnished with low entering lamella. Height 6-19, diam. 3.0-8.5 mm (19.0 × 8.5 mm).

Prostate of many elongated acini. Vas deferens entering epiphallus apically. Penis very short. Penial retractor inserted to penis at base of penial appendix. A-1+A-2 very small, A-3 short, globose-conical, A-4 of moderate length, A-5 bulky and massive. Spermathecal stalk not long, reservoir small, lying below prostate.

DISTRIBUTION. Hawaiian Islands. More than 110 spp., subspp. & forms.

Ilikala Cooke, 1911
Fig. 47

Cooke in Pilsbry, 1911: 89 (*Leptachatina* subg.).

TYPE SPECIES — *Achatinella fusca* Newcomb, 1853; OD.

Shell elongated ovate, thin, translucent, of 5.5-6 flattened whorls. Last whorl evenly rounded. Color corneous to whitish. Embryonic whorls delicately radially wrinkled; subsequent whorls finely irregularly costate.

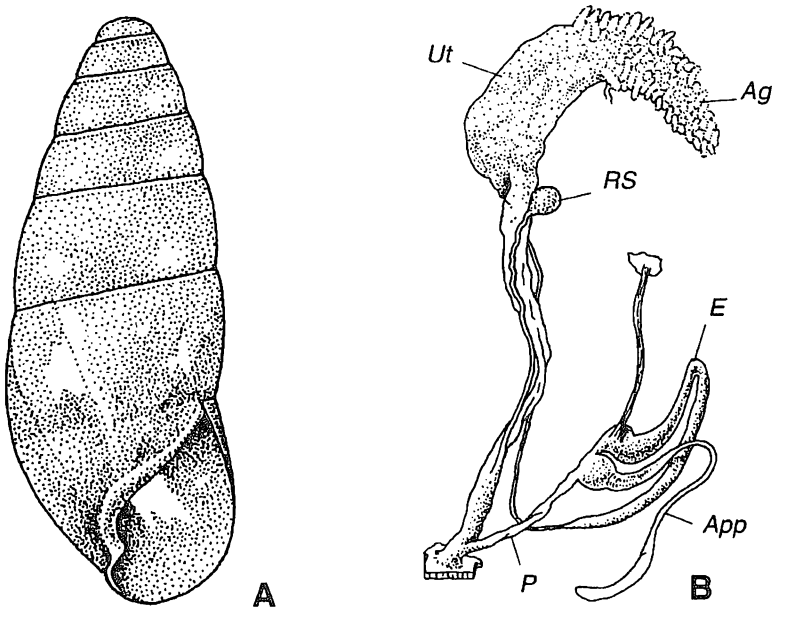


Fig. 48. *Pauahia* aff. *artata* (Cooke, 1911).
Mts. Kualoa, Oahu. **Honolulu** No. 93575. A — shell; B — reproductive tract.

Aperture pointed-ovate, with thin margins; columellar margin somewhat thickened, with rather weak, short lamella. Umbilicus minute or absent. Height 7-10, diam. 3.8-5.0 mm (8.6 × 4.3 mm).

DISTRIBUTION. Hawaiian Islands (Kauai, Oahu). 3 spp.

Pauahia Cooke, 1911
Fig. 48

Cooke in Pilsbry, 1911: 80 (*Labiella* subg.).

TYPE SPECIES — *Labiella artata* Cooke, 1911; OD.

Shell elongated-ovate, thin, fragile, shining, translucent, of 7-8 slightly convex whorls, body whorl straight. Apex narrowly rounded. Almost colorless, with light yellowish tint. Embryonic whorls smooth, rest with much smoothed, rather regular, radial wrinkles. Aperture pointed-ovate, places of its insertion broadly remoted; margins thin, sharp. Parietal callus variously developed. Columellar lamella weak, but always noticeable. Umbilicus closed. Height 5.4-9.0, diam. 2.4-3.5 mm (7.6 × 2.5 mm).

Penis slender, fairly long, thin-walled. Epiphallus rather thin, cylindrical, longer than penis, enlarged above appendix insertion. A-1+A-2 nearly spherical, A-3 relatively long, A-4 and A-5 comparatively thin. Internally both penis and A-1+A-2 without special structures. Basal portion of spermathecal shaft nearly not expanded; reservoir well defined, globular, rather small, lying just below uterus.

DISTRIBUTION. Hawaiian Islands (Oahu). 3 spp.

Angulidens Pilsbry et Cooke, 1914
Fig. 49

Pilsbry & Cooke, 1914 (1914-1915): 8 (*Leptachatina* sect.).

TYPE SPECIES — *Leptachatina subcylindracea* Cooke, 1910; OD.

Shell ovate-conic or cylindrical-conic, thin, semitransparent, very shining, of 5-6 slightly convex whorls. Last whorl not descending. Below suture shallow spiral depression may present. Surface colourless or with light yellowish tint. Embryonic whorls

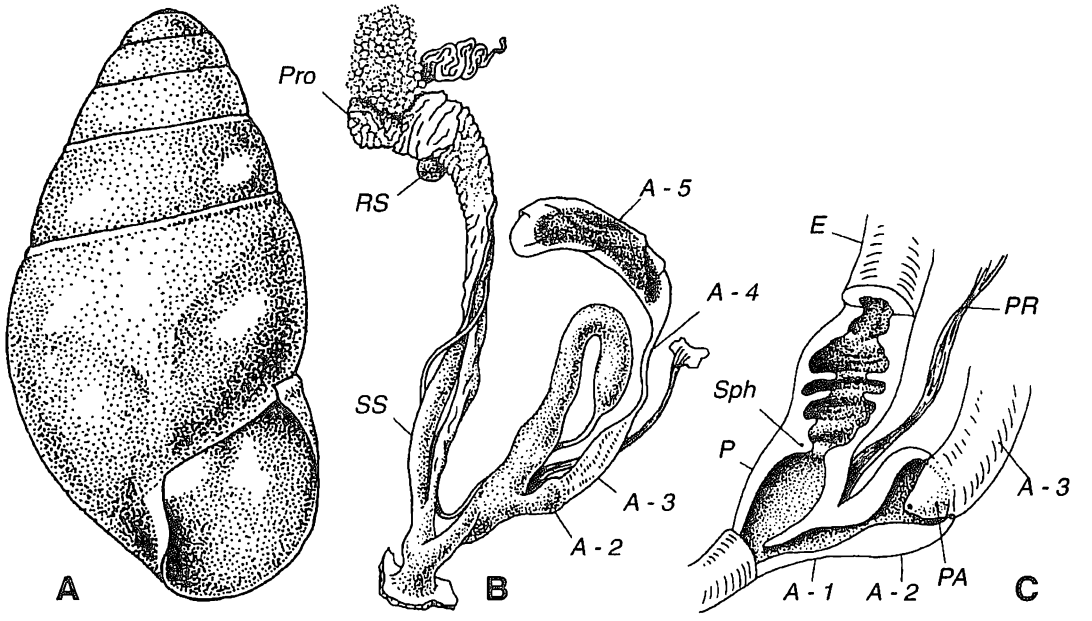


Fig. 49. ***Angulidens*** aff. ***subcylindracea*** Cooke, 1910.
Kaaawa, Oahu. **Honolulu** No. 92081. A — shell; B — reproductive tract; C — interior of distal part of male division.

nearly smooth (very vaguely microgranulate); postnuclear sculpture of rather regular but much smoothed radial wrinkles (nevertheless surface looks glabrous). Aperture contracted, rounded-ovate, markedly oblique, with only slightly thickened, non-reflexed margins, except upper portion of columellar. Peristome insertions remoted, parietal callus developed to various degree, often bearing angular tubercle. Columellar lamella small, but markedly developed. Umbilicus nearly closed to shortly drop-like. Height 5-11, diam. 2.6-4.2 mm (6.0 × 2.8 mm).

Vas deferens thin. Epiphallus somewhat swollen, its distal portion with a few thin, high circular folds. Penis relatively short, internally smooth, separated from epiphallus by a sphincter. A-1 weakly pronounced, A-2 subglobular, containing short conic papilla. A-3 long, highly muscularized, A-4 short, A-5 voluminous, with thin transparent walls. Vagina very short. Expanded portion of spermathecal shaft of about same length as slender part. Reservoir small, globular, not reaching albumen gland.

DISTRIBUTION. Hawaiian Islands. 5 spp.

Thaanumia Ancey, 1899
Fig. 50

Ancey, 1899: 269.

TYPE SPECIES — *Thaanumia omphalodes* Ancey, 1899; OD.

Shell ovate-conic, thin, fragile, dull, of 5.5-6 moderately convex whorls; body whorl scarcely ascending in front. Apex narrowly rounded. Color brownish. Embryonic sculpture of fine distinct radial riblets and wavy spiral threads. Postnuclear whorls with fine, sharp, irregular radial riblets. Aperture generally ovate, places of peristome insertion remoted, margins thin, shortly reflexed. Parietal callus variously developed. Columellar lamella rudimentary, located on posterior face of columellar margin. Umbilicus minute or closed. Height 6-9, diam. 3.0-3.5 mm (7.0 × 3.2 mm).

Penis long, slender, ramified in upper part into two subequal enlarged arms — epiphallus and basal portion of appendix. Epiphallus markedly swollen basally, gradually passing into vas deferens. Interior of penis with very indistinct relief of folds of

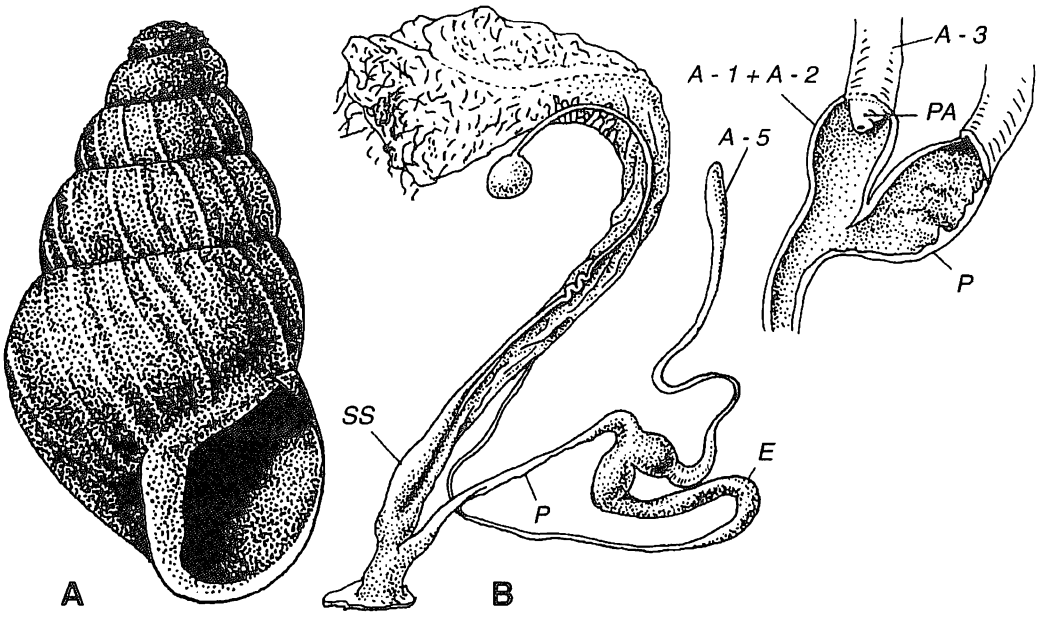


Fig. 50. *Thaanumia omphalodes* Ancey, 1899.
Waianae Mts., Nanakuli, Oahu. **Honolulu** No. 211344. A — shell; B — reproductive tract and interior of distal part of male division.

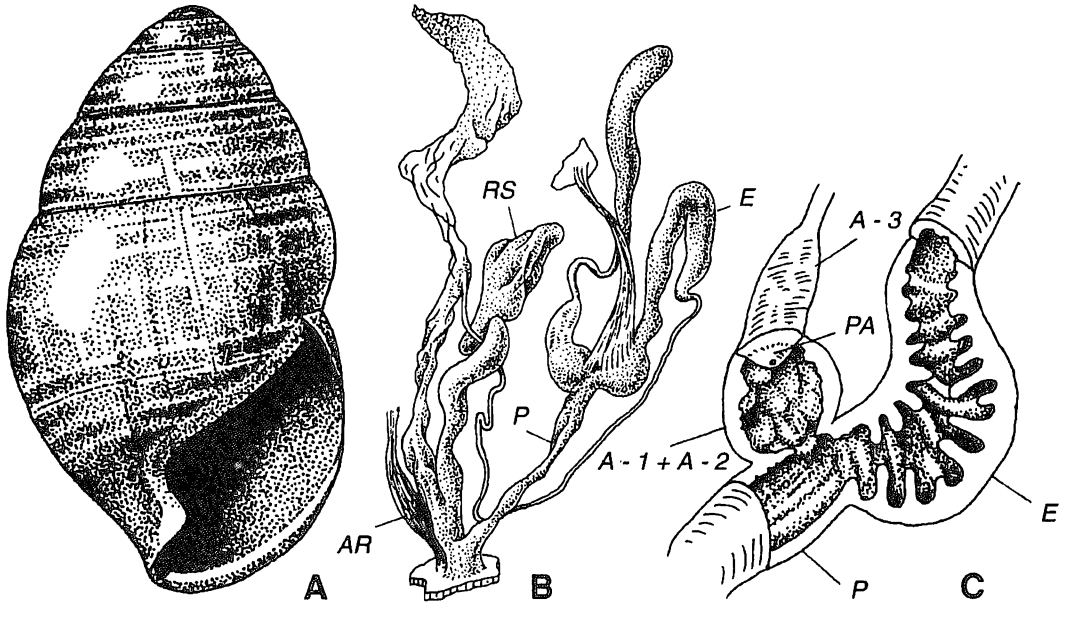


Fig. 51. *Metamastra reticulata* (Newcomb, 1853).
Napepeolelo, Waianae Mts., Oahu. **Honolulu** No. 127026. A — shell; B — reproductive tract; C — interior of distal part of male division.

annular orientation. A-1+A-2 globular, internally with short conic papilla. A-3 moderately long, boundary between A-4 and A-5 not visible. Penial retractor not found. Base of spermathecal stalk enlarged; reservoir small, globular.

DISTRIBUTION. Hawaiian Islands (Kauai, Oahu, Molokai, Maui, Hawaii). 8 spp.

AMASTRINAE Pilsbry, 1910

Pilsbry, 1910: VIII.

Shell high conic to flat, moderately thin to solid and opaque, variously colored, sometimes banded. Umbilicus closed to broadly open.

Ovoviviparous animals.

DISTRIBUTION. Hawaiian Islands.

Metamastra Hyatt et Pilsbry, 1911
Fig. 51

Hyatt & Pilsbry in Pilsbry, 1911: 162 [*Amastra* (Amastra); sect.].

TYPE SPECIES — *Achatinella reticulata* Newcomb, 1853; OD.

Shell dextral, ovate to elongated-ovate, comparatively thin, moderately shining, of about 6 somewhat convex whorls. Body whorl straight, evenly rounded at periphery. Color pattern composed of brownish or chestnut background and lighter irregularly spaced narrow bands; on upper spire light spots and marks may present. Embryonic whorls with very dense and fine radial ribbing, rest whorls almost smooth, with only fine irregular radial wrinklets. Aperture pointed-ovate, places of peristome insertion remoted; margins thin, straight. Parietal callus variously developed. Columellar lamella represented by lower end of columella. Umbilicus absent. Height 10-20, diam. 6-11 mm (18.2 × 9.2 mm).

Penis long, slender, internally with vague longitudinal folds. Distal portion of epiphallus much swollen, internally with strong circular folds. Slit-like cavity in penial or epiphallic walls absent. Penial appendix inserts onto penis/epiphallus junction. Penial retractor attached mainly to swollen part of epiphallus, but small branch inserts onto base of A-1 + A-2; this section thick-walled, with tuberculate inner surface; at boundary between it and A-3 there is a sphincter, modified into very short conic papilla. A-3 conic, A-4 short, markedly shorter than A-5. Spermathecal shaft sinuous, thick, branched off a little above atrium; reservoir voluminous, sac-like.

DISTRIBUTION. Hawaiian Islands (Oahu). About 25 spp. & subspp.

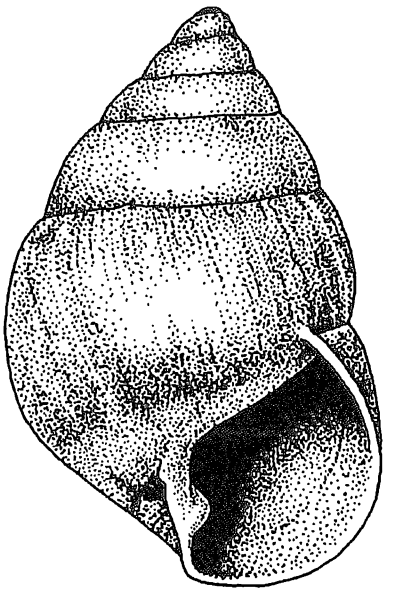


Fig. 52. ***Amastrella rugulosa*** (Pease, 1869). Kipu, Kauai. Holotype of ***A. rugulosa normalis*** Pilsbry, 1911. **Phil.** No. 104685.

Amastrella Sykes, 1900
Fig. 52

Sykes, 1900: 352 (*Amastra* subg.).

TYPE SPECIES — *Amastra rugulosa* Pease, 1869; OD.

Shell dextral, pointed-ovate, solid, shining, of 5-6 slightly convex whorls. Last whorl not descending, evenly rounded at periphery. Color rich reddish-brown, with narrow yellow subsutural band, that sometimes badly defined; aperture inside bluish-white. Embryonic whorls with spaced spiral engraved lines; same sculpture continues, gradually weakening, on subsequent whorls. Radial sculpture very faint. Aperture ovate, pointed above, margins thin,

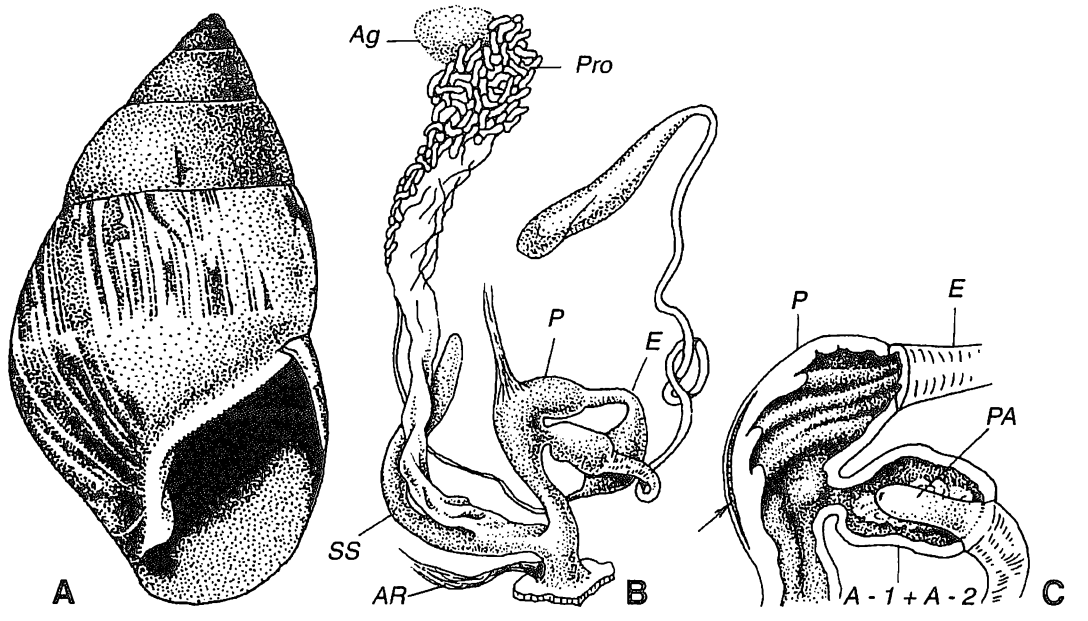


Fig. 53. *Amastra magna* (C. Adams, 1850).
A — shell: Oahu. **Moscow** Lc-23209.
! *Amastra inflata* (L. Pfeiffer, 1856). Kahana, Oahu. **Honolulu** No. 92223. B — reproductive tract; C — interior of distal part of male division. Arrow indicates slit-like cavity in wall of penis.

sharp, not reflexed. Parietal callus weak. Columellar lamella well developed, white. Umbilicus closed or in form of a narrow slit. Height 9-23, diam. 7-13 mm (19.0 × 11.0 mm).

DISTRIBUTION. Hawaiian Islands (Kauai, Oahu, Maui, Molokai, Hawaii). About 30 spp. & subspp.

Amastra H. Adams et A. Adams, 1855
Fig. 53

Adams H. & Adams A., 1855 (1853-1858): 137 (*Achatinella* subg.).

TYPE SPECIES — *Achatinella magna* C.Adams, 1850; SD Gulick, 1873.

Shell mostly dextral, acutely-ovate, solid, slightly shining, of 6-7 weakly convex whorls (upper flattened), last whorl evenly rounded at periphery or with indistinct angle. Color of upper spire nearly black, then becoming brownish (sometimes with pinkish tint); last whorl covered with dark brown periostracum. Aperture inside brown or yellowish-brown. Embryonic whorls smooth, postnuclear

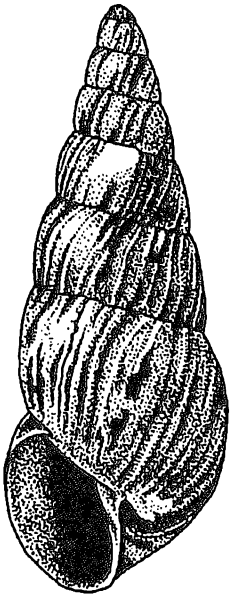


Fig. 54. *Heteramastra hutchinsoni* (Pease, 1862). Makawao, Maui. **Phil.** No. 71268.

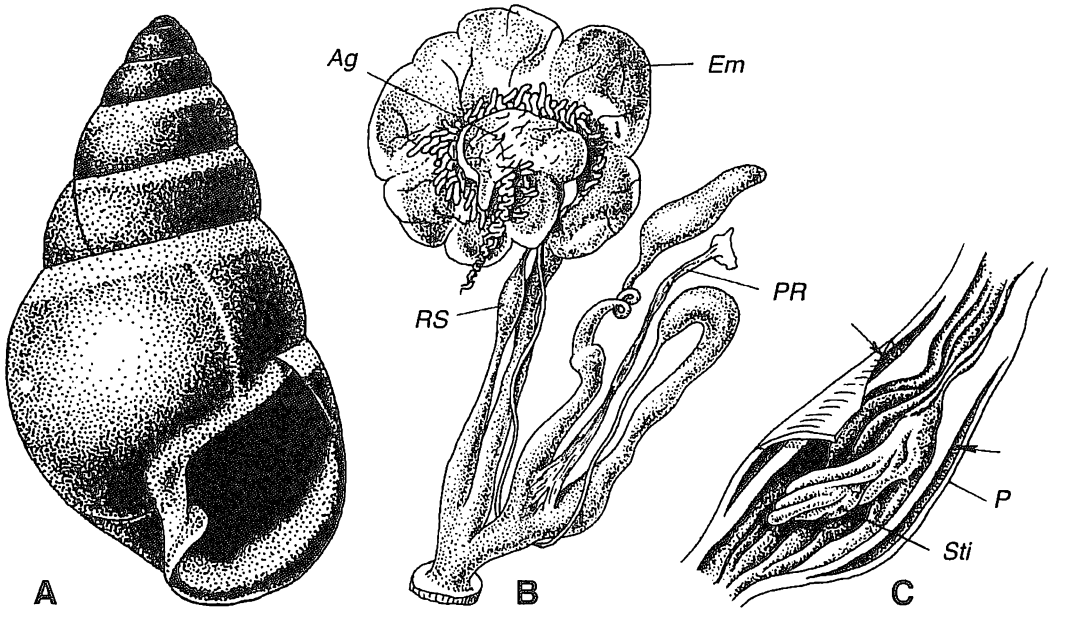


Fig. 55. ***Paramastra spirizona*** (Férussac, 1824).
Napepeolelo, Waianae Mts., Oahu. **Honolulu** No. 126912. A — shell; B — reproductive tract; C — interior of penis. Arrows indicate circular cavity in wall of penis.

whorls with irregular, fine, radial wrinkles. Aperture pointed-ovate, with thin, erected margins. Parietal callus variously developed. Columellar lamella is present from later embryonic stages, thin, sharp, high, occupying lower edge of columella; above this plate another, very light lamella may present. No umbilicus. Height 9-36, diam. 4-16 mm (30.0 × 15.5 mm).

Distal portion of penis short, nearly cylindrical, internally with vague longitudinal folds; proximal part expanded, shortly fusiform. There is a narrow slit-like cavity in wall of penis. A-1 + A-2 attached to penis by narrowed "neck"; this division contains slender cylindrical papilla and uneven glandular smoothed pad. A-3 short, conical, A-4 slender, very long. A-5 thin-walled. Penial retractor inserts only on penis — to side opposite to base of appendix. Length of spermatheca approximately equal to length of free oviduct; spermatheca branched off rather low, without visible demarcation into shaft and reservoir.

DISTRIBUTION. Hawaiian Islands (Lanai, Molokai, Maui). More than 50 spp. & forms.

Heteramastra Pilsbry, 1911
Fig. 54

Pilsbry, 1911: 141, 230 [*Amastra* (*Amastra*); sect.].

TYPE SPECIES — *Helicter hutchinsoni* Pease, 1862; OD.

Shell sinistral, turrited, moderately solid, dull, with thick, easily detached periostracum. Color dark corneous to greyish-brown, sometimes with indistinct light radial strikes and dark marks. Embryonic whorls delicately costulate, subsequent whorls with irregular coarse radial wrinkles. Aperture rather small, ovate, somewhat oblique, with simple margins. Columellar margin with weak lamella which enters about one whorl. Umbilicus very narrow, more or less covered up. Height 12-24, diam. 5-9 mm (19.0 × 7.1 mm).

DISTRIBUTION. Hawaiian Islands (Lanai, Molokai, Hawaii, Maui, ?Oahu). About 18 spp.

Paramastra Hyatt et Pilsbry, 1911
Fig. 55

Hyatt & Pilsbry in Pilsbry, 1911: 208 (*Amastra* sect.).

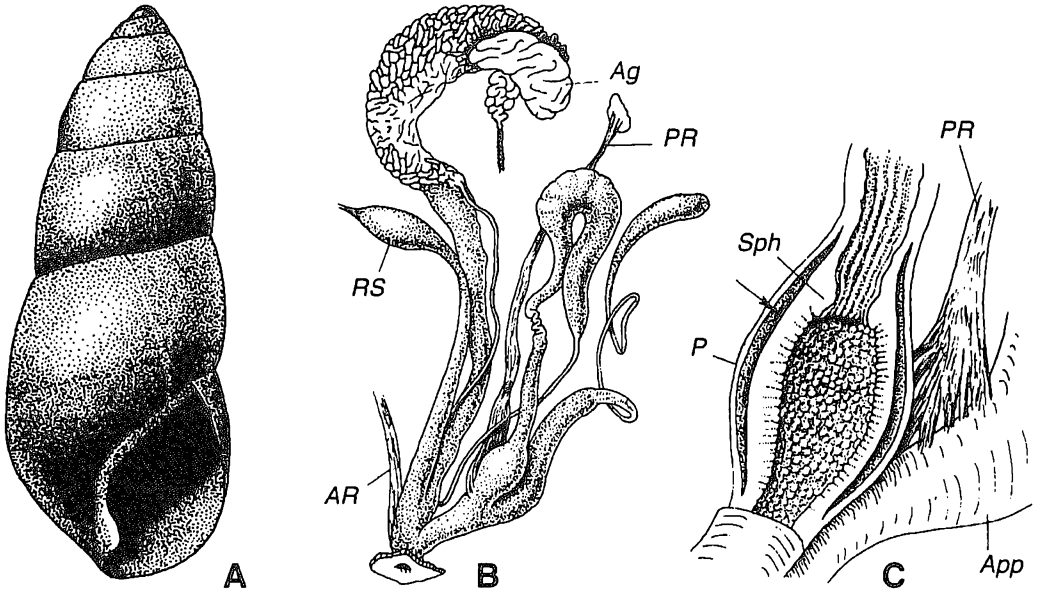


Fig. 56. ***Carelia bicolor*** (Jay, 1839).
Limahuli Valley, Kauai. **Honolulu** No. 86066. A — shell; B — reproductive tract; C — interior of penis. Arrow indicates circular cavity in penial wall.

TYPE SPECIES — *Helix (Cochlogena) spirizona* Férussac, 1824; OD.

Shell dextral, conic, solid, silky glossy, of 6-8 moderately convex whorls; last whorl not descending, evenly rounded at periphery. Apex black, lower whorls reddish-chestnut with lighter (yellow to yellowish-brown) subsutural band; interior of aperture porcelainy-white. Embryonic whorls with extremely fine radial ribbing. Sculpture of postnuclear whorls of irregular fine radial wrinkles (but macroscopically surface looks smooth). Aperture subvertical, acutely ovate, places of peristome insertion not approached, margins thin, straight, very upper part of columellar margin dilated. Parietal callus weak or absent. Columellar lamella thin, high. Umbilicus, a very short and narrow crack. Height 15-24, diam. 11-12 mm (21.4 × 11.7 mm).

Albumen gland lacks (at least in dissected specimen) usual alveolar structure, its upper end extended as a slender tongue. Distal portion of penis very short. Proximal portion expanded, internally with sharp longitudinal folds and pivot-like stimulator, bearing deep furrow and strong longitudinal folds. Walls of this portion contain circular cavity. Penial appendix inserted near atrium. A-1 relatively very long, internally with same folds as in penis; at boundary between A-1 and A-2 there is a simple sphincter. A-3 conic. A-4 short. Penial retractor scarcely forked at base. Uterus contains few embryos. Vagina very short. Spermatheca shorter than free oviduct, stalk enlarged basally, reservoir with apical ligament.

DISTRIBUTION. Hawaiian Islands (Oahu). 12-15 spp., subspp. & forms.

Carelia H. Adams et A. Adams, 1855
Fig. 56

Adams H. & Adams A., 1855: 132 (*Achatina* subg.).

TYPE SPECIES — *Achatina bicolor* Jay, 1839; SD Martens in Albers, 1860.

Shell dextral, high, turrited-conic, solid, dull, of 6-7.5 moderately convex whorls. Last whorl straight, rounded at periphery. Color of upper whorls yellowish-corneous, then becoming darker; interior of aperture very dark, with pearl tint. Embryonic whorls

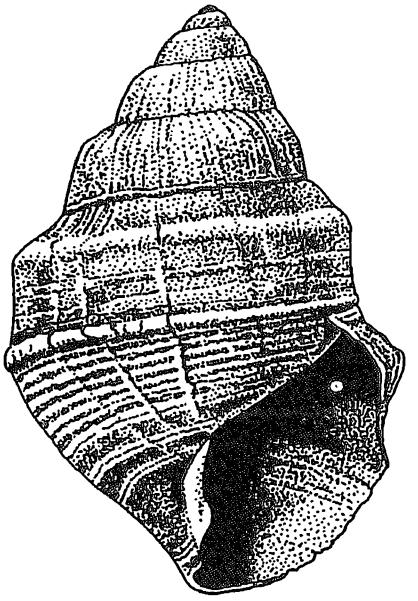


Fig. 57. *Armiella knudseni* (Baldwin, 1895). Haleamanu, Kauai. Syntype. **Phil.** No. 65725.

nearly smooth or with very fine malleate sculpture; rest surface with crowded delicate irregular wrinkles and has somewhat chagreen appearance. Aperture subvertical, ovate, with straight sharp margins. Parietal callus weak. Columellar lamella occupies lower end of columella. No umbilicus. Height 32-85, diam. 13-16 mm (33.2 × 13.1 mm).

Albumen gland coarsely folded, without visible alveolar structure. Distal portion of penis short; just above base of appendix penis forms nearly globular extension, inner surface of which densely covered with numerous, high, minute, pustules. Wall of this section containing well developed circular slit. This section separated from epiphallus by sphincter; epiphallus internally with longitudinal folds. Then strongly narrowed thin-walled section comes, and proximal portion expanded again, internally usually with semicircular folds. Inner surface of A-1+A-2 also with fine pustules; at junction with A-3 there is a weak sphincter; no papilla. Penial retractor very long, inserting by several very short branches to globular portion of penis and basal part of A-1. Vagina very short. Atrial retractor rather weak. Spermathecal shaft almost cylindrical, without basal extension; reservoir with terminal ligament.

DISTRIBUTION. Hawaiian Islands (Kauai, Niihau). About 30 spp., subspp. & forms.

Armiella Hyatt, 1911
Fig. 57

Hyatt & Pilsbry in Pilsbry, 1911: 145 [*Amastra* (*Kauaia*); sect.].

TYPE SPECIES — *Amastra knudseni* Baldwin, 1895; OD.

Shell dextral, high conic, moderately thin but rather solid, dull, of 5.5-6 shouldered whorls. Last whorl with blunt angle below suture and peripheral thick cord-like keel. Color chestnut. Embryonic whorls smooth, early postnuclear whorls with dense radial striation, body whorl bears coarse, widely spaced spiral cords, especially below peripheral keel. Aperture rather narrow, irregularly ovate, moderately oblique, with thin and simple margins. Columella subvertical, with weak entering lamella. Umbilicus closed or nearly so. Height 31-34, diam. 20-22 mm (31.2 × 20.0 mm).

DISTRIBUTION. Hawaiian Islands (Kauai). 1 sp.

Kauaia Sykes, 1900
Fig. 58

Sykes, 1900: 355 (nom. nov. pro *Carinella* L. Pfeiffer, 1875).

— *Carinella* L. Pfeiffer, 1875: 116 (nom. praeocc., non Sowerby, 1839; *Achatinella* Gruppe; t.-sp. *Achatinella kauaiensis* Newcomb, 1860; OD).

TYPE SPECIES — *Achatinella kauaiensis* Newcomb, 1860; OD.

Shell dextral, turbinate, solid, not shining, of 6-6.5 whorls; upper nearly flat, last rounded, but bears smoothed keel which traced above suture on preceding whorls. Distal part of body whorl below keel with broad shallow depression, occupying most of upper surface of whorl. Outlines of spire somewhat concave, apex narrowly pointed. Color nearly uniformly brownish. Embryonic whorls almost smooth, postnuclear with crowded, coarse, irregular, radial wrinkles. Aperture rounded-quadrangular, places of peristome insertion widely remoted. Parie-

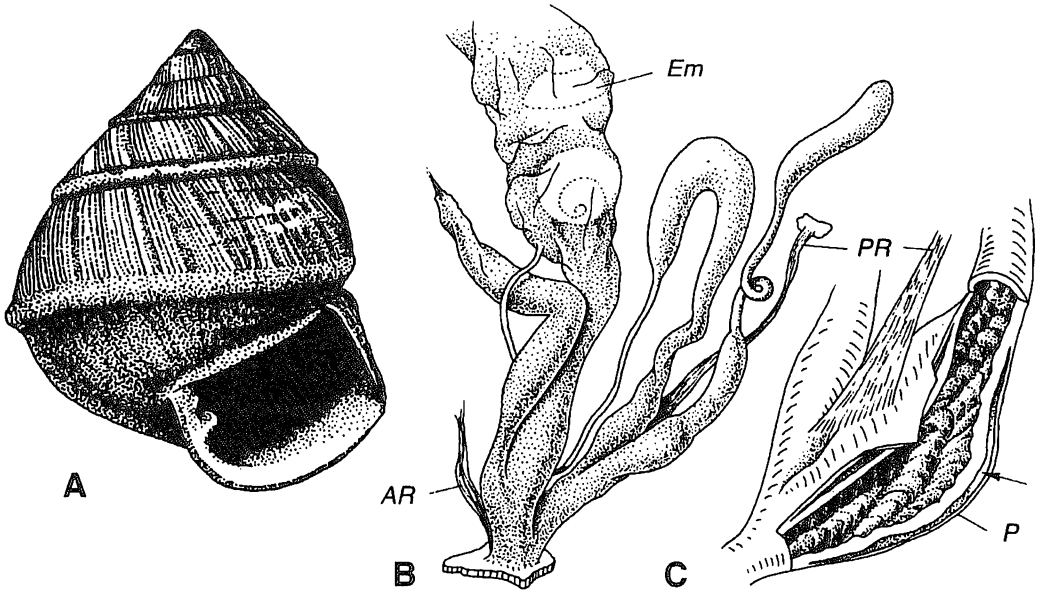


Fig. 58. ***Kauaia kauaiensis*** (Newcomb, 1960).
Haleamanu, Kauai. **Honolulu** No. 48147. A — shell; B — reproductive tract; C — interior of penis. Arrow indicates circular cavity in wall of penis.

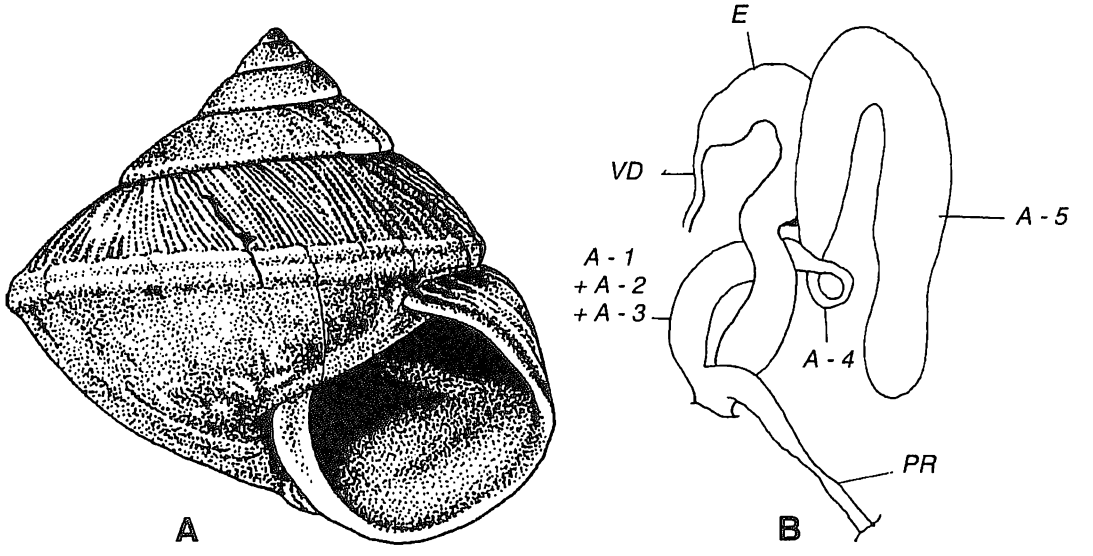


Fig. 59. ***Cyclamastra cyclostoma*** (Baldwin, 1895).
A — shell: Makaweli, Kauai. Syntype. **Phil.** No. 65724. B — male division of reproductive tract. After Pilsbry, 1916 (1914-1916).

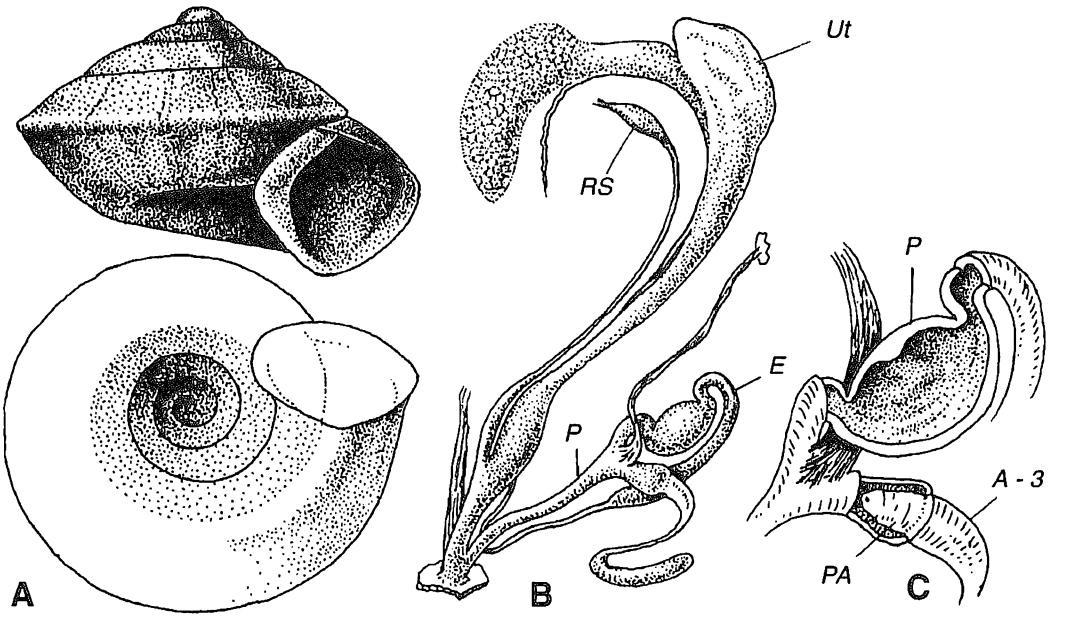


Fig. 60. *Armsia petasus* (Ancey, 1899).
Kanehoa, Waianae Mts., Oahu. **Honolulu** No. 217342. A — shell; B — reproductive tract; C — interior of distal part of male division.

tal callus weak. Margins sharp, not reflexed. Columellar lamella rather low, but quite distinct; above it a rudiment of supracolumellar lamella may be seen. No umbilicus. Height 22-23, diam. 15-16 mm (22.0 × 16.0 mm).

Distal section of penis very short, proximal somewhat enlarged, both contains longitudinally oriented pilasters subdivided into series of rounded tubercles. Circular slit-like cavity in penial walls well developed. Penial retractor attached to penis and A-1+A-2. This part of appendix internally with longitudinal folds; papilla absent. A-3 strongly developed, A-4 and A-5 as usual. Short atrial retractor present. Spermatheca branched off just above atrium, with an apical ligament; reservoir as such not expressed; lower part of spermathecal stalk narrowed.

DISTRIBUTION. Hawaiian Islands (Kauai). 1 sp.

Cyclamastra Pilsbry et Vanatta, 1905
Fig. 59

Pilsbry & Vanatta, 1905: 570 (*Amastra* sect.).

TYPE SPECIES — *Amastra cyclostoma* Baldwin, 1895; OD.

Shell dextral, turbinate, thin, of 5-6 flattened whorls; last whorl keeled at periphery, directed or a little descending. Spire pointed, conically protruded. Color corneous to dark brown. Embryonic whorls smooth, postnuclear whorls sharply radially striated above and nearly smooth below peripheral keel. Aperture irregularly subcircular, with a little thickened margins; columellar margin slightly expanded and reflexed, without trace of lamella. Umbilicus narrow. Height 10-18, diam. 9-19 mm (17.0 × 18.0 mm).

Penial appendix branched off penis near atrium; A-1, A-2, and A-3 fused, superficially not differentiated; A-4 very short, A-5 massive. Atrial retractor present.

DISTRIBUTION. Hawaiian Islands (Kauai, Oahu, Molokai, Maui). 5-7 spp.

Armsia Pilsbry, 1911
Fig. 60

Pilsbry, 1911: 132.

TYPE SPECIES — *Pterodiscus petasus* Ancey, 1899; OD.

Shell depressedly conic, with protruded apex, rather thin, not shining, of 4-4.5 slightly convex whorls. Last whorl a little and gently

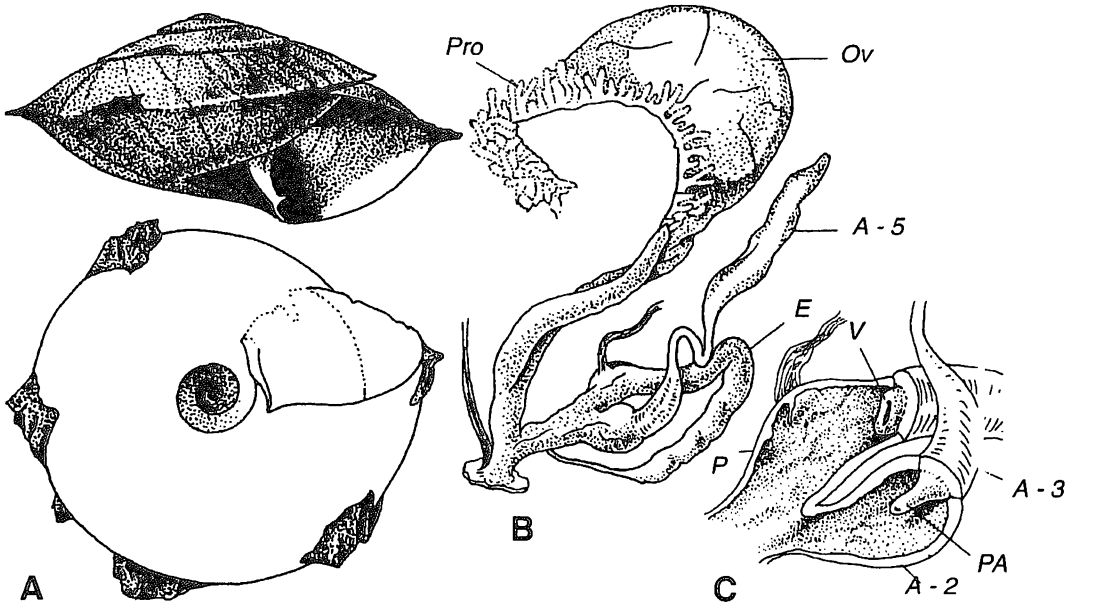


Fig. 61. ***Tropidoptera alata*** (L. Pfeiffer, 1856).
Nanakuli, Waianae Mts., Oahu. Honolulu No. 183430. A — shell; B — reproductive tract; C — interior of distal part of male division.

descending in front. Embryonic whorls convex, projecting. Periphery of body whorl occupied by smoothed keel; another keel or angle encircles umbilicus. Color uniformly brown. Embryonic whorls with fine distinct spiral threads; sculpture of rest whorls consists of irregularly spaced wrinkles or riblets. Aperture rounded-quadrangular, slightly oblique, margins thin, well expanded; places of perisrome insertion somewhat approached and connected by thin, light callus. No teeth in aperture. Umbilicus broad. Height 3.0-3.5, diam. 4.0-5.8 mm.

Distal portion of penis slender, proximal shortly cylindrical to globular, internally nearly smooth. Penial appendix branched off distal section of penis noticeably below expanded part. Penial wall solid, without circular cavity. United A-1 + A-2 short, containing minute but quite distinct tubular papilla. A-3 well developed, A-4 and A-5 relatively very short. Penial retractor attached to angle between penis and appendix. Free oviduct 2.5-3 times longer than vagina. Spermathecal shaft narrow, its basal part slightly expanded; reservoir rather small, with apical ligament.

DISTRIBUTION. Hawaiian Islands (Oahu). 1 sp.

Tropidoptera Ancey, 1889
Fig. 61

Ancey, 1889: 191. — *Pterodiscus* Pilsbry, 1893 (1892-1893): 36 [nom. emend. pro *Tropidoptera* Ancey, 1889, non *Tropidopterus* Blanchard, 1845 (Coleoptera)].

— *Helicamastra* Pilsbry et Vanatta, 1905: 570 [*Amastra* sect.; t.-sp. *Amastra discus* Pilsbry et Vanatta, 1905; OD].

TYPE SPECIES — *Helix alata* L. Pfeiffer, 1856; OD.

Shell lenticular, thin, fragile, of 4-4.5 flattened slightly shouldered above suture whorls. Body whorl straight, sharply angled at periphery. Color uniformly yellowish-brown to chestnut; soil particles usually adhere to shell surface. Early embryonic whorls smooth, subsequent with extremely fine radial striation. Postapical sculpture of widely spaced irregular radial wrinkles. Aperture angled, light-colored internally; places of peristome insertion not approached. Margins thin, erect; columellar margin dilated, with depression, corresponding to thin columellar lamella. Umbilicus moderately broad, nearly cylindrical to conic. Height 4-6, diam. 8-11 mm (6.0 × 11.0 mm).

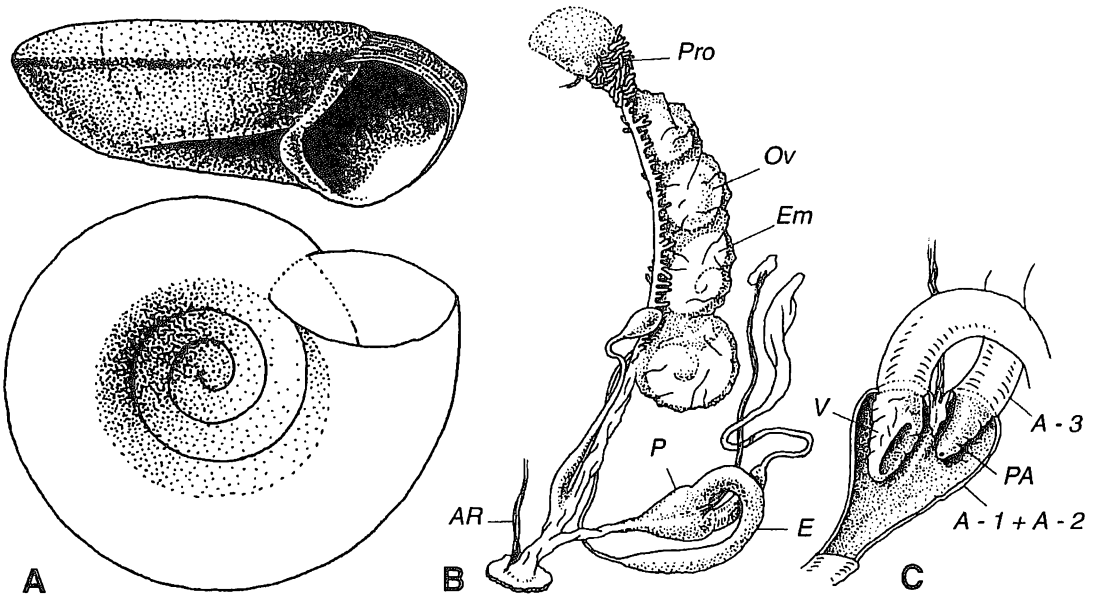


Fig. 62. *Planamastra* cf. *digonophora* (Ancey, 1889).
Kaawa, Waianae Mts., Oahu. **Honolulu** No. 133374. A — shell; B — reproductive tract; C — interior of distal part of male division.

Penis short; immediately behind appendix base with a light extension, containing vague relief of tubercles and folds. Boundary between penis and epiphallus superficially not demarcated, but internally with sphincter, modified into short closed vergic papilla. Penial appendix not long, A-1 + A-2 globular, with slender papilla; A-3 normally developed; A-4 relatively very short, A-5 of nearly same length as all preceding divisions in sum, with very thin, subtransparent walls. Penial retractor inserted onto swollen part of penis. Atrial retractor weak. Spermatheca sleeve-shaped, short, without visible subdivision into stalk and reservoir.

DISTRIBUTION. Hawaiian Islands (Lanai, Oahu). 9 spp. & subspp.

Planamastra Pilsbry, 1911
Fig. 62

Pilsbry, 1911: 129.

TYPE SPECIES — *Patula digonophora* Ancey, 1889; OD.

Shell flat or nearly so, sometimes even with sunken apex; not glossy, of about 4 flat whorls. Last whorl not descending, angled or keeled at periphery. Color uniformly grey to brownish, sometimes with darker band just below peripheral angle or keel. Embryonic sculpture of crowded, extremely fine radial riblets; similar, although not so regular sculpture retained on next whorls. Aperture subvertical, rounded, angled at palatal and basal sides. Margins thin, not reflexed except columellar; places of their insertion nearly not approached. Umbilicus broadly open, encircled by smoothed ridge. Height 3.0-3.5, diam. 5.0-8.5 mm (3.4 × 8.5 mm).

Distal part of penis slender, thin-walled, proximal somewhat expanded. This expansion includes both swollen part of penis and basal portion of appendix (A-1 + A-2). Inner surface of this part nearly smooth; penial side of expansion with papilla having wide lumen and orifice, directed toward lumen of appendix. Appendical side also contains conic papilla with very narrow lumen. A-3 rather large, A-4 short. Penial retractor attached by single band between penis and base of appendix. Atrial retractor weak. Spermatheca short, consisting of shaft with slightly enlarged base and small ovate reservoir.

DISTRIBUTION. Hawaiian Islands (Oahu). 6 spp. & subspp.

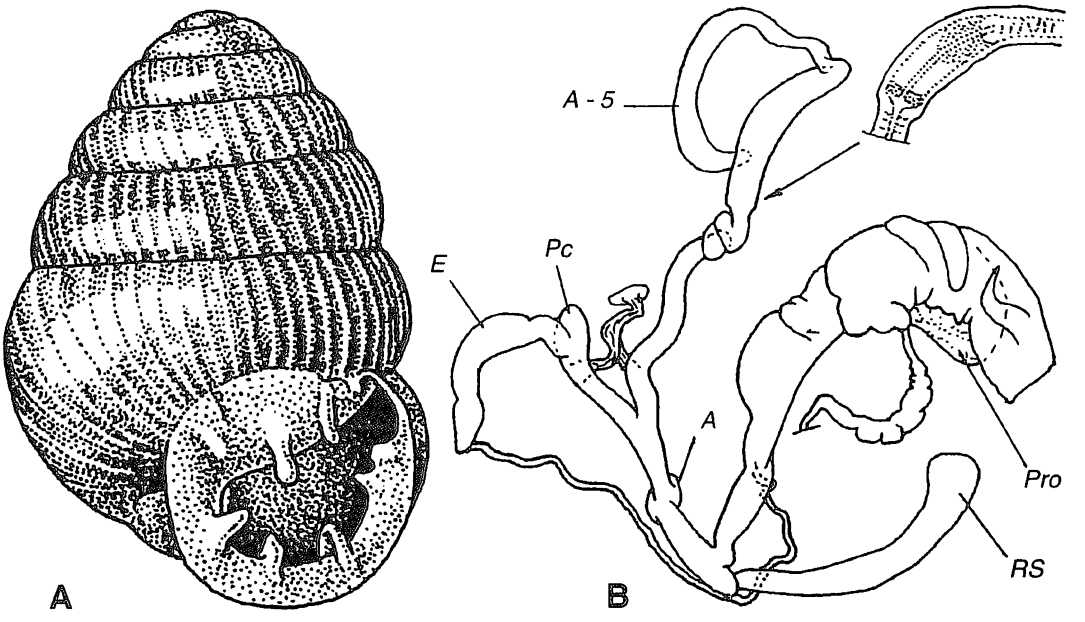


Fig. 63. *Walklea rossmaessleri* (Rossmaessler, 1838).
A — shell: Italy, Carnian Alps. Moscow No. Lc-7683; B — reproductive tract. After Gittenberger, 1978.

ORCULOIDEA Steenberg, 1925

Steenberg, 1925: 201 (pro fam.). Schileyko, 1984: 116.

Shell small to medium-sized, primarily cylindrical or ovate-cylindrical. Embryonic whorls smooth, microgranulate or with fine spiral threads; postnuclear sculpture of weak radial striation to ribbing. Among aperture teeth long parietal and columellar lamellae distinguished. Aperture margins thin or a little thickened, reflexed; lip weak or absent. Umbilicus dot- or drop-like or (rarely) somewhat widened, perspective.

Head with two pairs of tentacles.

Prostate of few acini at base of albumen gland. Penis with epiphallus and caecum of various shape (mostly conic). Inner walls of penis furnished with somewhat spirally directed folds. Penial appendix present. Penial retractor biramous; penial arm inserted near base of caecum. Spermathecal stalk with or without diverticle.

DISTRIBUTION. Western Palearctic and South Africa.

ORCULIDAE Steenberg, 1925

Steenberg, 1925: 201. Schileyko, 1984: 116. Hausdorf, 1996: 1.

Shell with distinct fine radial sculpture, sometimes with membraneous periostracal riblets. Embryonic whorls finely granulate or with distinct spiral threads. Aperture with lamellar teeth. Margins of aperture widely, evenly reflexed and expanded. Umbilicus, a narrow perforation.

Prostate band-like. Penial verge absent. Penial appendix and penial caecum initially present, but both tending to considerable transformations or reduction. Flagellum absent or rudimentary, in latter case it may be seen after dissection of epiphallus. Diverticle of spermathecal stalk present or absent.

DISTRIBUTION. Mediterranean countries, Crimea, Caucasus, Middle Europe, Central Asia, South Africa.

ODONTOCYCLADINAE Hausdorf, 1996

Hausdorf, 1996: 10.

Shell dextral or sinistral, cylindrical to subglobose, radial sculpture mostly well developed. Aperture often free or nearly so, with parietal, columellar, and palatal teeth; parietal wall always with at least two well-developed lamellae.

Penial caecum short to long. Penial appendix initially present, but retained in only one genus. Spermathecal duct without morphologically expressed gland. Diverticle of spermathecal stalk present or absent.

DISTRIBUTION. South and South-western Africa, Madagascar, eastern Alps.

Walklea Gittenberger, 1978
Fig. 63

Gittenberger, 1978: 11.

TYPE SPECIES — *Pupa rossmaessleri* Rossmaessler, 1938; OD.

Shell dextral, pointed-ovate, moderately thin, of 5-5.5 moderately convex whorls. Last whorl slightly and gradually ascending in front. Outlines of spire convex. Color uniformly corneous. Embryonic whorls nearly smooth, rest surface rather regularly ribbed. Aperture rounded, subvertical, margins shortly but sharply reflexed. Due to strong development of parietal callus, aperture nearly free. Teeth 9-10. Angular lamella short, connected with place of insertion of palatal margin. Parietal lamella vertical, with thickened ridge, starting at some distance from edge of parietal callus. Between parietal and angular lamellae there is an aditional plate, running from edge of callus. Angle between parietal and columellar margins occupied by low longitudinal thickening. Columellar lamella short, nearly horizontal; one vertical plate on columella stands deeply. Basal margin with short tooth. There are 3-4 short palatal plicae. Umbilicus comma-like. Height 4.5-4.7, diam. 3.7-3.8 mm (4.7 × 3.8 mm).

Vas deferens entering epiphallus apically. Penial caecum very short. Penial appendix well developed, of more or less typical structure. Free oviduct and vagina of about equal length. Spermatheca sleeve-shaped, without distinct demarcation between stalk and reservoir.

DISTRIBUTION. Alps of Italy (Udine) and of Slovenia. 1 sp.

Odontocyclas Schlüter, 1838
Fig. 64

Schlüter, 1838: 10.

— *Scopelophila* Albers, 1850: 206 (*Pupa* subg., t.-sp. *Pupa kokeilii* Rossmaessler, 1837; SD Martens in Albers, 1860).

TYPE SPECIES — *Pupa kokeilii* Rossmaessler, 1837; monotypy.

Shell dextral, short-conic, moderately thin, slightly translucent, of 6 rather convex whorls; body whorl a little ascending in front. Outlines of spire nearly conic. Color corneous. Embryonic whorls vaguely finely granulate, rest surface with thin but sharp oblique irregular striation. Aperture rounded, with well developed parietal callus, sometimes providing impression of adnate aperture. Aperture margins slightly thickened and a little reflexed. Parietal wall with several teeth: angular, supraparietal and parietal lamellae; latter is strongest. Additional superficial plate located in angle between parietal and columellar margins, same plate may present as a local thickening of parietal callus. Columellar lamella 1. Small rounded tubercle at baso-columellar angle. Basal fold long, well developed; farther a small tubercle sits, followed by elongated palatal fold; upper palatal plica tubercle-like. Third tubercle situated between these two palatal plicae. Umbilicus open, fairly wide, cylindrical. Height 3.0-4.0, diam. 2.4-2.5 mm (3.8 × 2.5 mm).

Talon small, external. Vas deferens entering epiphallus subapically. Epiphallus markedly narrowed near penis. Penis internally with fine longitudinal folds. Penial caecum unusually long. Penial appendix lacking. Penial retractor attached to penis at base of caecum. Vagina markedly shorter than free oviduct. Diverticle of spermathecal stalk well developed.

DISTRIBUTION. Eastern Alps: Italy (Udine), Austria (Carintia), Slovenia, Croatia. 1 sp.

Fauxulella Pilsbry, 1917
Fig. 65

Pilsbry, 1917 (1916-1918): 235 (*Fauxulus* sect.).

TYPE SPECIES — *Pupa pamphorodon* Benson, 1864; OD.

Shell sinistral, elongate-ovate, moderate-

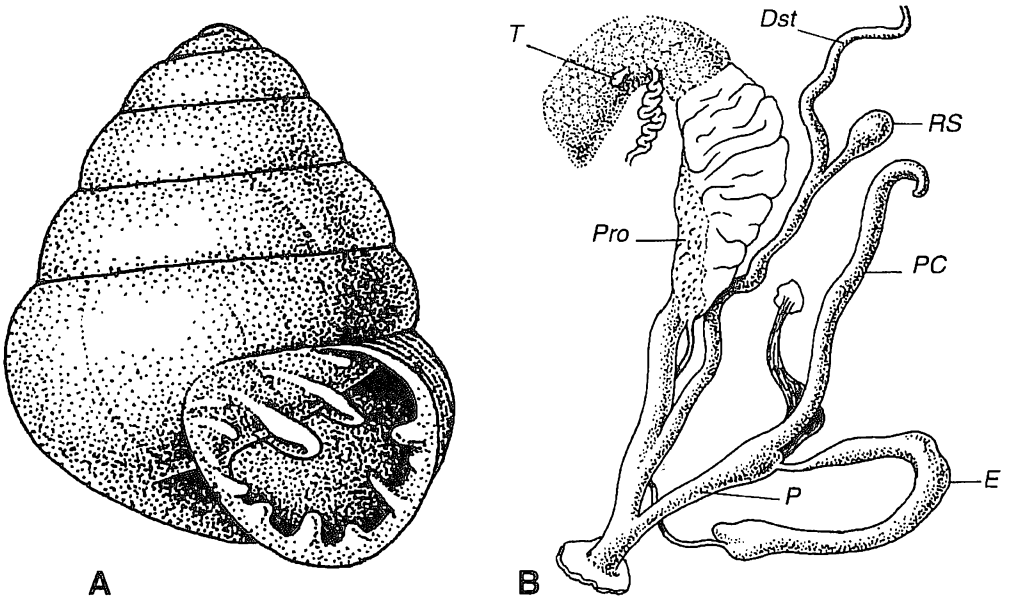


Fig. 64. *Odontocyclas kokeilii* (Rossmaessler, 1837).
A — shell: Abbrovazzo, Udine, Italy. **Moscow** No. Lc-3512; B — reproductive apparatus: Slovenia, Kamniska Planina, valley Kamniska Bela, September 1970. **Leiden**.

ly solid, of 8-9 strongly flattened whorls. Color corneous. Embryonic whorls smooth, later whorls with regular radial rib-striation to fine ribbing. Aperture subcircular, slightly oblique, places of peristome insertion approached. Aperture margins well reflexed and expanded. Both parietal lamellae strong, tuberculiform. Columellar lamella subhorizontal, sometimes with tiny subcolumellar lamella. Upper part of palatal wall occupied by small tubercle; rest 3-4 palatal teeth lamellate, lying at some distance from aperture edge, but not entering deeply. Height 7.5-9.0, diam. 3.6-4.0 mm (7.8 × 3.7 mm).

DISTRIBUTION. South Africa. 1 sp.

Anisoloma Ancey, 1901
Fig. 66

Ancey, 1901: 141. Gittenberger, 1978: 8.

TYPE SPECIES — *Pupa (Faula) ponsonbyana* Morelet, 1889; SD Pilsbry, 1917.

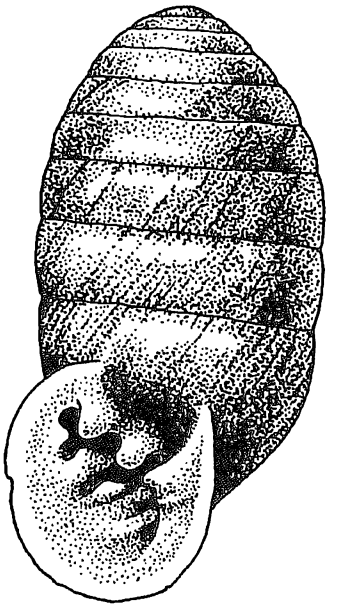


Fig. 65. ***Fauxulella pamphorodon*** (Benson, 1864). Kalkbaai, S Africa. **Leiden**.

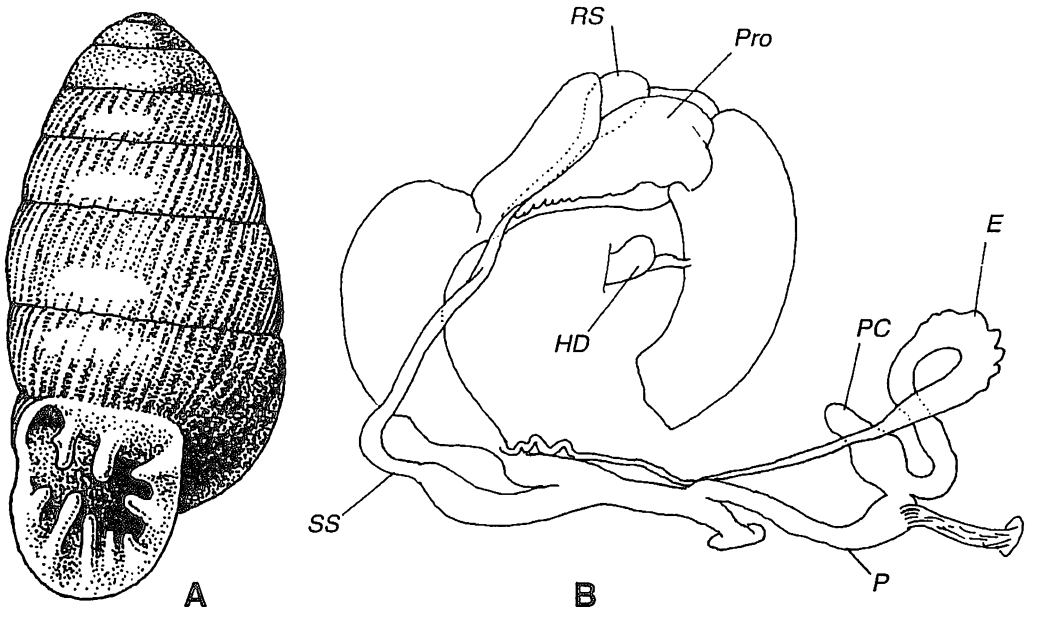


Fig. 66. *Anisoloma ponsonbyana* (Morelet, 1889).
A — shell: Hilton Road, Natal, S Africa. **Leiden.**
! *Anisoloma grayi* Van Bruggen et Meredith, 1983. B — reproductive tract. After Van Bruggen & Meredith, 1983.

Shell sinistral, ovate to acuminate-ovate, moderately solid, of 6.25-8 flattened to flat whorls. Last whorl sometimes a little ascending. Color pale to rufous brown. Embryonic whorls with more or less distinct spiral striae. Subsequent whorls with radial rib-striation to fine ribbing. Aperture ovate or subquadrate, adnate or nearly so, often with palatal depression. Teeth number up to 9, most of them protruded from aperture plane. Parietal lamellae 2, columellar 2, rest teeth shortly lamellar or tuberculiform, not entering. Umbilicus very narrow, semicovered. Height 2.4-7.0, diam. 1.7-3.0 mm (2.4 ×1.7 mm).

Vas deferens entering apically. Epiphallus rather long, its external surface bears more or less distinct tubercles. Penial caecum moderately long, blunt or pointed. Penial retractor attached to penis at base of caecum. Penial appendix absent. Spermathecal stalk long, enlarged basally, without a diverticle.

DISTRIBUTION. SE Africa, Madagascar. 9 or 10 spp.

Fauxulus Schaufuss, 1869
Fig. 67

Schaufuss in Paetel & Schaufuss, 1869: 15 (nom. nov. pro *Faula* H. & A. Adams, 1855).

— *Faula* H. & A. Adams, 1855: 171 (*Pupa* subg.; nom. praeocc., non Blanchard, 1850; t.-sp. *Pupa capensis* Küster, 1841; SD Martens in Albers, 1860).

TYPE SPECIES — *Pupa capensis* Küster, 1841; SD Martens in Albers, 1860.

Shell usually sinistral, clavate to ovate-conic, moderately solid, of 9-10 weakly convex whorls. Body whorl just behind aperture strongly ascending in front. Color light-grey or creamy; below periphery of last whorl a narrow dark band may present. Embryonic whorls nearly smooth or with fine spiral striae, rest surface covered with fine, silky, radial riblets and, locally, spiral striation. Aperture vertical, ovate, with palatal depression; its margins thin, somewhat reflexed. Aperture armed with 5 teeth: slender, high, angular lamella; parietal lamella with thickened ridge, beginning markedly deeper

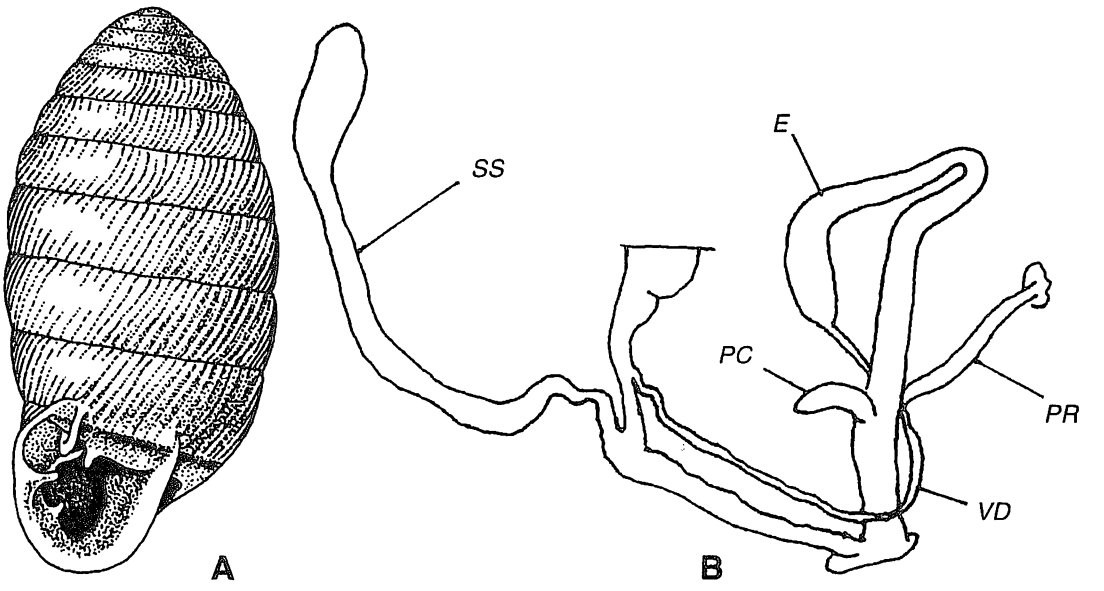


Fig. 67 ***Fauxulus capensis*** (Küster, 1841).
A — shell: Cape Agulhas, Cape Province, S Africa. **Moscow** No. Lc-19638 (**Leiden**).
! ***Fauxulus ovularis*** (Küster, 1841). B — reproductive tract. After Gittenberger, 1978.

than angular lamella; tubercle-like (as seen through aperture) columellar lamella; palatal plica thin, entering, its edge turned to ridge of angular plate; lower palatal plica lower and shorter than palatal. Umbilicus narrowly cylindrical or slit-like. Height 5-12, diam. 2.2-3.8 mm (5.2 × 2.2 mm).

Vas deferens entering epiphallus terminally. Epiphallus long, penis short. Penial caecum short. Penial retractor inserting to penis/epiphallus junction just opposite to base of caecum. Spermathecal stalk not enlarged basally, without diverticle.

DISTRIBUTION. South Africa, Malawi, Madagascar, Namibia. 2 spp. & several subspp.

Tomigerella L. Pfeiffer, 1878
Fig. 68

Pfeiffer L., 1878 (1878-1881): 347.

TYPE SPECIES — *Pupa soluta* L. Pfeiffer, 1863 (=*Pupa layardi* Benson, 1856); monotypy.

Shell dextral, ovate-fusiform to subturri-

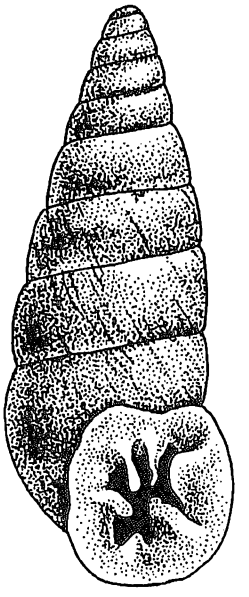


Fig. 68. ***Tomigerella layardi*** (Benson, 1856).
Cape Point, S Africa. **Phil.** No. 106495.

form, rather thin, somewhat glossy, of about 9 weakly convex whorls. Last whorl scarcely ascending in front. Color uniformly brown. Embryonic whorls smooth, later with fine irregular radial striae, crossed on 2-3 last whorls by microscopic spiral incised lines. Aperture free, irregularly subcircular, slightly oblique, with reflexed and broadly expanded margins. Parietal wall bears two subequal well-developed lamellae; columellar lamella subhorizontal, there is a minute, often almost evanescent tubercle in or near parieto-columellar angle; basal tooth small, tuberculiform; two palatal plicae strong, lamellate, shortly entering. Umbilicus, a minute perforation. Height 5.4-9.2, diam. 2.0-3.3 mm (8.8 × 3.2 mm).

DISTRIBUTION. South Africa (Cape Province). 3 spp.

? *Afriboysidia* Zilch, 1939
Fig. 69

Zilch, 1939: 221.

TYPE SPECIES — *Afriboysidia buchmanni* Zilch, 1939; OD.

Shell conic, thin but solid, lustrous, of 5-6 flattened whorls; last whorl moderately ascending in front, a little obtusely angled at periphery. Color corneous. Embryonic whorls smooth, postnuclear sculpture of very weak and irregular radial striation. Aperture subvertical, rounded-subquadrate, adnate, with strongly reflexed and expanded margins. Parietal and supraparietal lamellae subequal, approached; latter somewhat bent toward palatal margin; columellar lamella horizontal, one basal and one palatal folds rather short. Umbilicus narrowly open. Height 3.1-4.5, diam. 1.8-2.4 mm (4.2 × 2.2 mm).

DISTRIBUTION. SW Africa. 3 spp.

ORCULINAE Steenberg, 1925

Steenberg, 1925: 201 (pro fam.). Schileyko, 1984: 117.

Shell mostly dextral, elongate ovate, cylindrical, or clavate. Postembryonic whorls finely radially striated and often ornamented with widely spaced periostracal riblets. Body whorl nearly straight or a little ascending toward aperture. Lower ends of columellar and parietal lamellae are seen at standard position of shell.

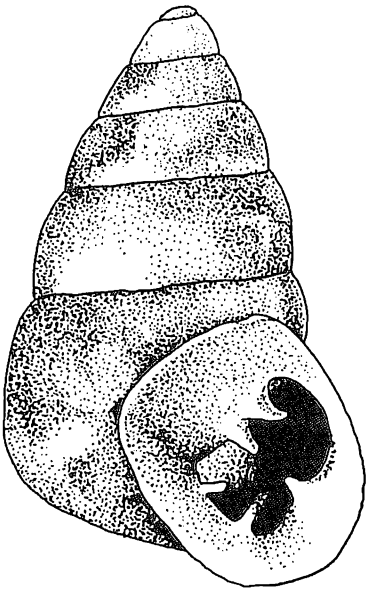


Fig. 69. *Afriboysidia buchmanni* Zilch, 1939. Okuntinto near Kaliombo, SW Africa. Holotype. **Senck.** No. 46 140.

Penial caecum, even if rudimentary, always clearly visible. Penial appendix developed to various degree. Spermathecal duct without morphologically expressed glands, with or without diverticle.

DISTRIBUTION. Europe, Caucasus, Central Asia, Asia Minor, N Africa.

Pilorcula Germain, 1912
Fig. 70

Germain, 1912: 448 (*Orcula* sect.).

Schileyko, 1984: 118. Hausdorf, 1996: 13, 56.

TYPE SPECIES — *Pupa raymondi* Bourguignat, 1863; monotypy.

Shell cylindrical, rather thin, of 5-7 convex to very convex whorls; last whorl more or less ascending. Apex much blunt, often nearly flat, with somewhat prominent embryonic whorls. Embryonic sculpture of spiral threads. Rest surface bears well developed radial membraneous riblets; sometimes peripheral portion of these riblets protruded as cilia-like processes. Aperture ova-

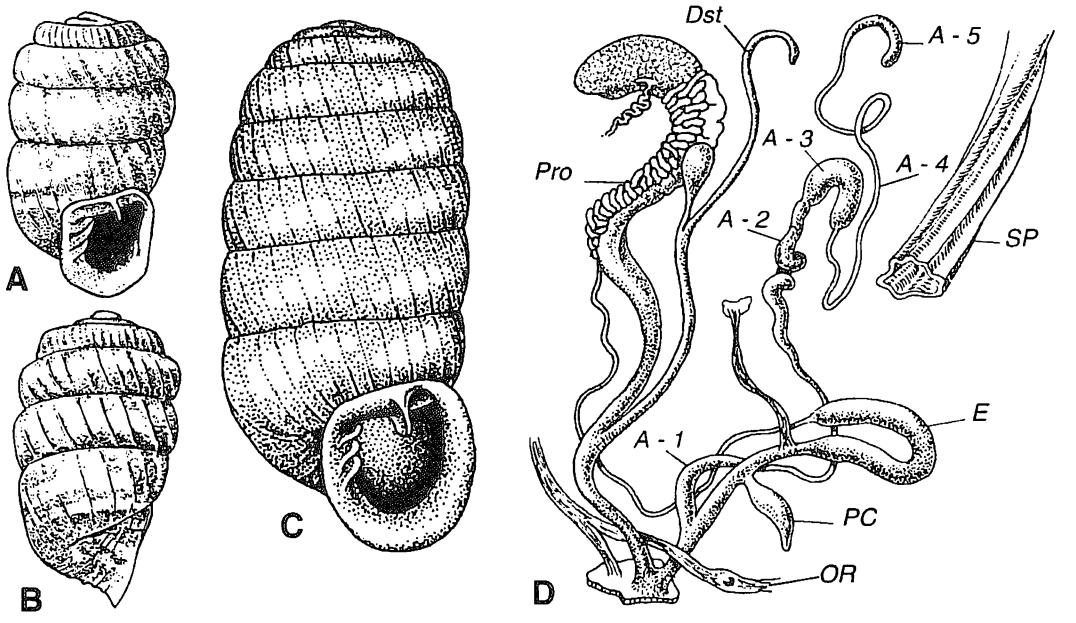


Fig. 70. A, B — ***Pilorcula raymondi*** (Bourguignat, 1863).
Lectotype: "Libanon, Nahr Beirut 6 km von der Ausmündung" — drawing by Dr. Lothar Forcart. C, D, — ! ***Pilorcula trifilaris*** (Mousson, 1856). W Caucasus, Tekhury River Valley, April 30, 1971. **Moscow** No. Lc-23219

te to subcircular, free, with expanded margins. Parietal lamella strong, deeply entering. Columellar margin of aperture equipped with 2-4 fine cord-like lamellae. Very slender and long palatal plica situated deep inside body whorl, that is not visible through aperture. Height 2.5-7.0, diam. 1.4-3.1 mm (4.2 × 2.0 mm).

Vas deferens entering epiphallus terminally. Penial appendix well developed; A-1 unusually long, A-2+A-3 nearly fused, somewhat swollen; A-4 long, A-5 poorly expressed. Penial caecum fusiform. Vagina and free oviduct of about equal length or vagina shorter. Spermathecal stalk with long diverticle. Surface of spermatophore with longitudinal-spiral ridgelets.

DISTRIBUTION. Asia Anterior and Caucasus. 9-10 spp. & subspp.

Schileykula Gittenberger, 1983
Fig. 71

Gittenberger, 1983: 327. Hausdorf, 1996: 13, 36.

TYPE SPECIES — *Orcula batumensis* sensu Hesse, 1924; OD; Gittenberger, Menkhorst, 1993: 341: *"Schileykula" scyphus* (L. Pfeiffer, 1848) [=*Orcula batumensis* sensu Hesse, 1924]; Hausdorf, 1996: 13: *Schileykula batumensis* Gittenberger, 1983 [non Retowski, 1889] = *Schileykula scyphus erecta* Hausdorf, 1996.

Shell cylindrical to ovate-cylindrical, solid, opaque to subtransparent, of 6-10 whorls. Apex not blunt, more or less dome-shaped. Radial periostracal riblets developed to various degree — from weak to sharp, in latter case each of them furnished with cilia-like process (as in *Acanthinula*). Columellar margin of aperture without thread-like folds, but on columella there are 1-3 deeply entering lamellae. Aperture nearly adnate or interrupted on parietal wall. Within body whorl there is long palatal fold, visible through shell wall. Height 5.4-9.6, diam. 2.0-3.9 mm (6.0 × 2.4 mm).

Vas deferens entering swollen end of epiphallus apically or subapically. Penis with well-developed conic or ovate caecum. Penial appendix rudimentary, short, slender, without distinctly separated divisions. Penial retractor attached to epiphallus

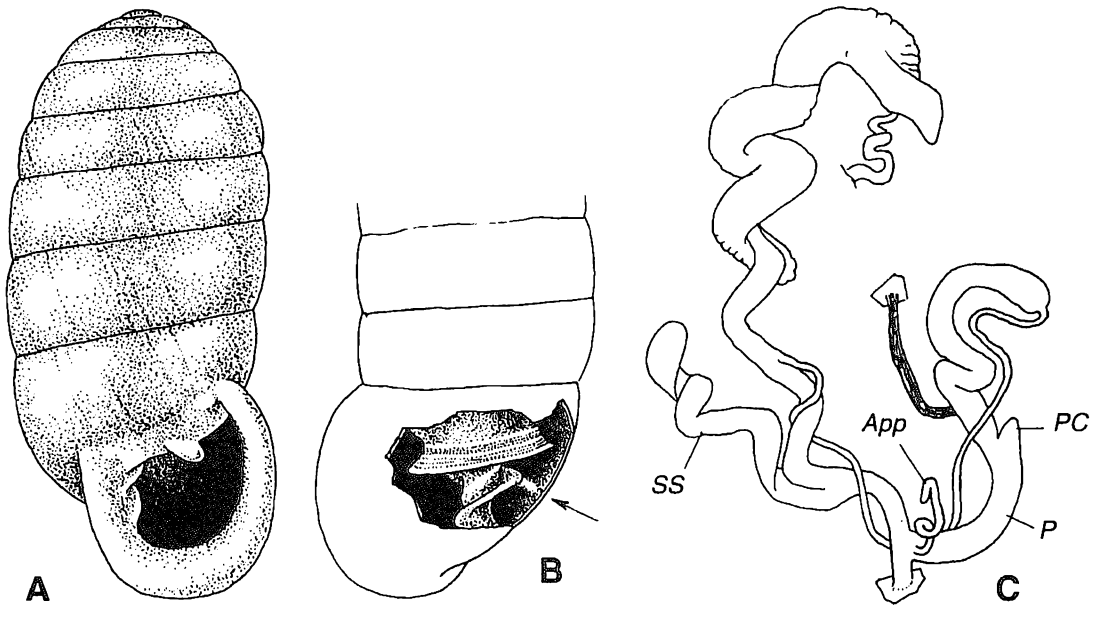


Fig. 71. ! ***Schileykula scyphus scyphus*** (L.Pfeiffer, 1848).
Shell — N Turkey, between Karabük and Kastamonu. Arrow indicates palatal plica. **Moscow** No. Lc-23200. Anatomy — ***Schileykula scyphus erecta*** Hausdorf, 1996. After Hausdorf, 1996.

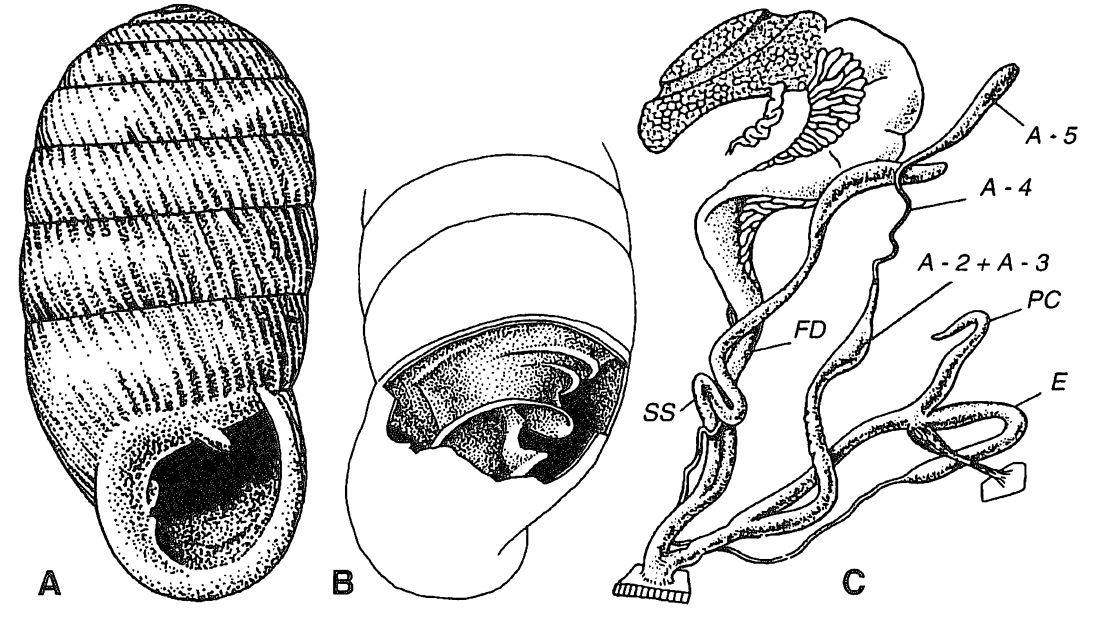


Fig. 72. ***Orculella libanotica*** (Tristram, 1865).
Shell — Antioch, Syria (syntype of ***O. orientalis antiochensis*** Pilsbry, 1931). **Phil.** No. 152880a. Anatomy — ! ***Orculella ruderalis*** Akramowski, 1947. After Schileyko, 1976.

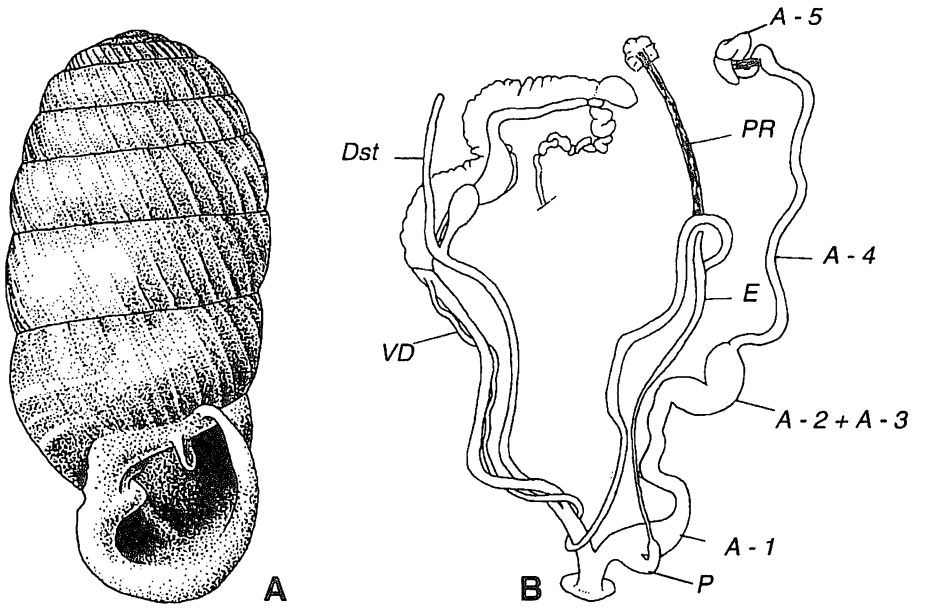


Fig. 73. ***Alvariella multiplicata*** Hausdorf, 1996.
Shell — Kapisu, vilayet Zonguldak, NW Turkey. Paratype. **Moscow** No. Lc-23196 (ex private coll. of Dr. Hausdorf). Anatomy — after Hausdorf, 1996.

above caecum or at its base. Length of free oviduct about equal to length of vagina. Reservoir of spermatheca variously expressed. Diverticle absent.

DISTRIBUTION. Asia Minor. 16-18 spp. & subspp.

Orculella Steenberg, 1925
Fig. 72

Steenberg, 1925: 176.

— *Mesorculella* Schileyko, 1976: 53 (*Orculella* subg.; t.-sp. *Orculella ruderalis* Akramowski, 1947; OD). Schileyko, 1984: 120. Hausdorf, 1996: 11, 14.

TYPE SPECIES — *Pupa orientalis* sensu auct. (non L. Pfeiffer, 1861) (=*Pupa libanotica* Tristram, 1865); OD.

Shell dextral or (rarely) sinistral, much similar to *Schileykula*, but without palatal lamellar plica. Periostracal riblets absent. Aperture generally subcircular, with reflexed and thickened margins. Except parietal lamella, 1-3 additional deeply lying (not visible through aperture) small lamellae on parietal wall may present. Aperture interrupted on parietal wall. Height 4.7-15.5, diam. 2.0-5.2 mm. (9.9 × 4.7 mm).

Vas deferens entering epiphallus apically. Penial caecum long, vermiform or conic, tapering. Penial appendix variously developed. Penial retractor attached to base of caecum. Free oviduct and vagina of same length or vagina somewhat shorter. Spermathecal stalk without diverticle, reservoir fusiform.

DISTRIBUTION. Eastern Mediterranea and Transcaucasia. 17-27 spp. & subspp. (perhaps, some of taxa conventionally assigned to this genus by Hausdorf, 1996, belong to other genera).

Alvariella Hausdorf, 1996
Fig. 73

Hausdorf, 1996: 13, 53.

TYPE SPECIES — *Alvariella multiplicata* Hausdorf, 1996; OD.

Shell cylindrical, solid but more or less

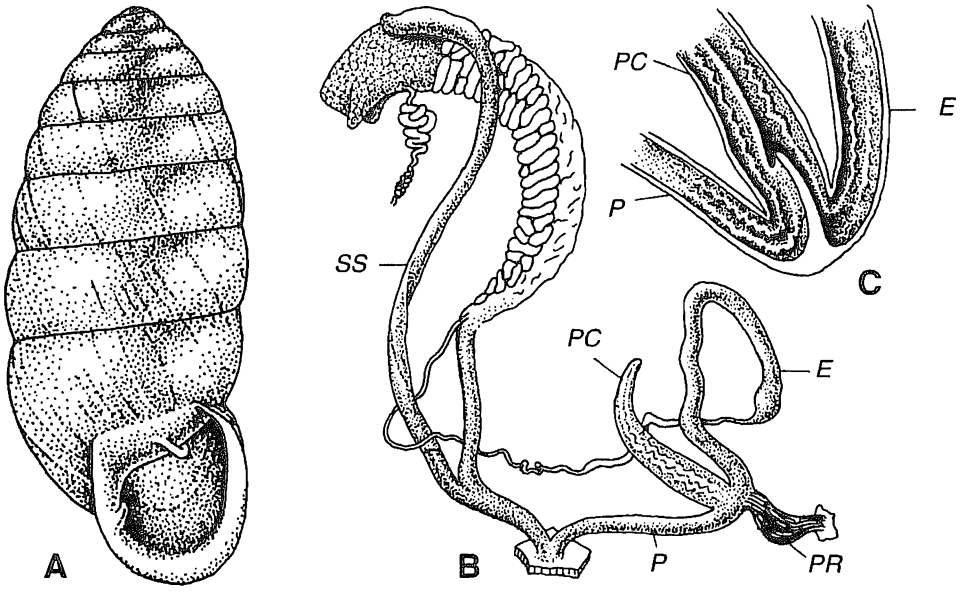


Fig. 74. *Orcula dolium* (Draparnaud, 1801).
A — shell: Poland, Tatra Mts., August 12, 1952. **Moscow** No. Lc-23222. B — reproductive tract; C — interior of male division. B, C — after Schileyko, 1984.

translucent, of 7.5-8.5 flattened whorls. Upper part of shell conic or dome-shaped. Color corneous to dark brown. Embryonic whorls with distinct spiral cordlets. Upper postnuclear whorls finely ribbed, riblets become weaker and more spaced on later whorls. Aperture ovate, places of peristome insertion a little approached. Margins broadly reflexed and expanded. Parietal lamella subvertical, angular tubercle absent or weak; columella with 2 lamellae, lower being stronger. 3-4 palatal deeply entering plicae located deep inside aperture; they can be seen from outside as light-colored spiral lines; one of them usually seen through aperture. Height 6.4-7.7, diam. 2.9-3.2 mm (7.1 × 3.1 mm).

Vas deferens markedly enlarged in distal section. Boundary between vas deferens and epiphallus marked by short caecum. Epiphallus gradually narrowing into thread-like duct and entering penis apically. Penis rudimentary, entering A-1 laterally. Penial appendix well developed; A-1 long, vaguely separated from obesely fusiform or bean-shaped A-2 + A-3; A-4 long, slender; A-5 tightly twisted as a ball; loops of A-5 bound by muscular band. Penial retractor attached to distal enlarged portion of vas deferens at some distance above caecum. Vagina short, free oviduct much longer. Spermathecal shaft long, reservoir seated on its own short duct; diverticle long, slender.

DISTRIBUTION. Asia Minor (NW Anatolia). 1 sp.

Orcula Held, 1837
Fig. 74

Held, 1837: 919.

— *Pupula* Mörch, 1852: 34 (nom. praeocc., non Charpentier, 1837; t.-sp. *Pupa dolium* Draparnaud, 1801; SD Pilsbry, 1922).

Schileyko, 1984: 124.

TYPE SPECIES — *Pupa dolium* Draparnaud, 1801; SD Herrmannsen, 1847.

Shell cylindrical to conoid-cylindrical

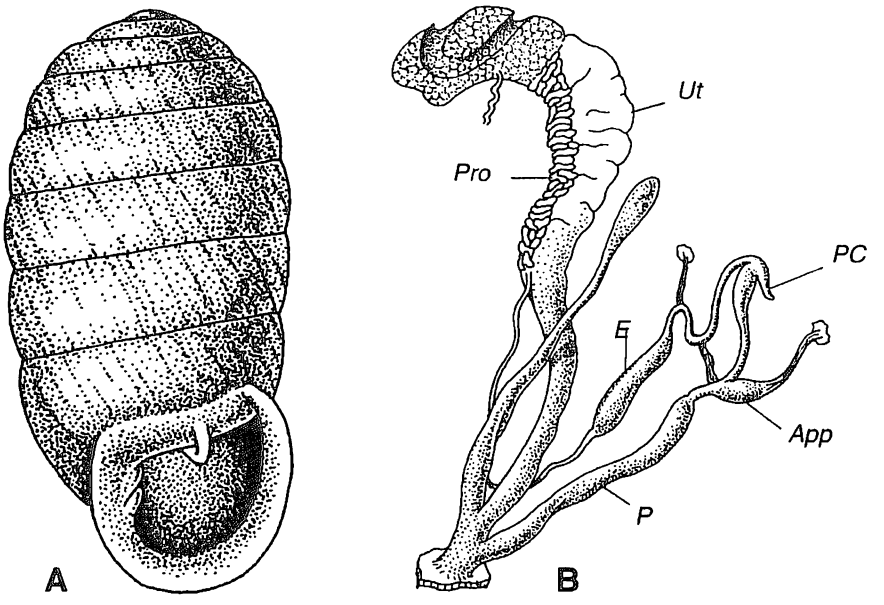


Fig. 75. ***Sphyradium doliolum*** (Bruguière, 1792).
Valley of Fiagdon River, N Caucasus, May 10, 1970. **Moscow** No. Lc-23210. A — shell; B — reproductive tract.

and elongated-ovate, of 8-10 weakly convex whorls, apex mostly somewhat acuminate. Body whorl gradually ascending toward aperture. Color yellowish to dark brown. Embryonic whorls practically smooth (sometimes with exceptionally fine traces of spiral striae). Rest surface covered with fine silky radial striation or plication. Aperture with 1 parietal and 1-2 columellar lamellae. Palatal wall smooth or with one strong plica or tooth within. Height 6-9, diam. 2.5-3.7 mm (8.2 × 3.2 mm).

Vas deferens sometimes slightly swollen in distal portion, entering enlarged end of epiphallus terminally. Penis cylindrical. Penial caecum long, conic. Penial appendix absent. Internally penis, epiphallus and caecum with longitudinal corrugated folds. Penial retractor attached to penis/epiphallus junction opposite to base of caecum. Spermatheca long, sleeve-shaped, reservoir poorly defined; diverticle lacking.

DISTRIBUTION. Mountain regions of Middle and partly South Europe. About 10 spp. with many subspp. & forms.

Sphyradium Charpentier, 1837
Fig. 75

Charpentier, 1837: 15 (*Pupa* subg.).

— *Scyphus* Cecconi, 1908: 7 (t.-sp. *Pupa doliolum* Bruguière, 1792; SD Gittenberger, 1983).

Schileyko, 1984: 126. Hausdorf, 1996: 13, 54.

TYPE SPECIES — *Bulimus doliolum* Bruguière, 1792; SD Martens in Albers, 1860.

Shell cylindrical to clavate, rather thin, slightly translucent, of 8-9.5 weakly convex whorls. Apex more or less dome-shaped. Color light corneous to chestnut. Embryonic whorls ornamented with distinct spiral threads. Postembryonic whorls with well expressed widely spaced radial periostracal riblets. Aperture ovate to subcircular, with well reflexed and expanded margins. Parietal wall with one plate and, sometimes, with angular tubercle. 1-2 entering columellar lamellae visible through aperture at standard position of shell. No palatal folds. Height 3.8-6.0, diam. 2.0-2.5 mm (5.1 × 2.3 mm).

Vas deferens entering swollen section of

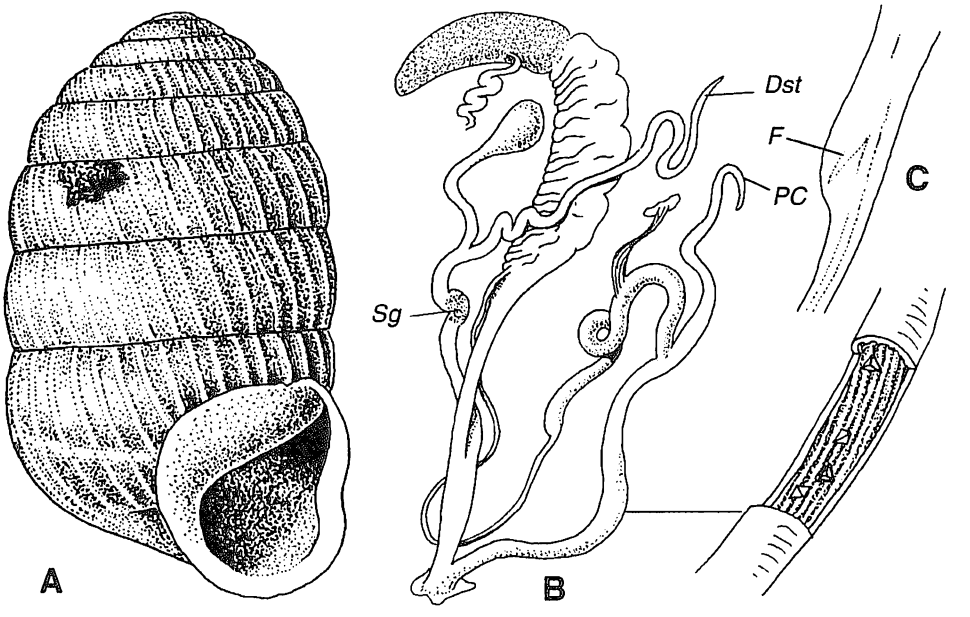


Fig. 76. ***Pagodulina (Pagodulina) pagodula*** (Des Moulins, 1830).
A — shell: Tarvisio, Udine, Italy. Private coll. of A. Kuznetsov. B — reproductive tract and interior of penis; C — diagrmmatic longitudinal section of proximal end of epiphallus. B, C — Bus-del-Que near Iseo, Italy, March 19, 1977 **Moscow** No. Lc-23217.

epiphallus. Penial appendix rudimentary, represented only by weakly developed remnant of A-1, to which a penial retractor attached. Penial caecum also rudimentary, but always clearly expressed, and situated on boundary between epiphallus and penis. Epiphallus with its own very slender retractor; besides, distal portion of epiphallus connected with penis at base of appendix by additional muscular band. Vagina very short, free oviduct much longer. Spermathecal stalk without diverticle.

DISTRIBUTION. Mediterranean countries; south, west and middle Europe; N Africa; Asia Anterior; Crimea, Caucasus, northern Iran; Central Asia. 1 or 2 spp. with numerous forms.

Shell dextral, ovate to ovate-cylindrical. Embryonic whorls smooth. Postembryonic whorls with distinct, fine, regular ribs. Body whorl strongly ascending in front and its upper edge nearly touching suture. Aperture with palatal depression. Teeth situated deep inside body whorl and scarcely or not visible through aperture.

Flagellum rudimentary, may be seen in longitudinal section of proximal part of epiphallus. Penial caecum present or absent. Penial appendix absent. Spermathecal stalk equipped with peculiar bean-shaped gland. Diverticle of spermathecal stalk long.

DISTRIBUTION. South and partly Middle Europe, mountain systems of Asia Anterior and SE Transcaucasia.

PAGODULININAE Pilsbry, 1924

Pilsbry, 1924 (1922-1926): 166.

— Pagodininae Pilsbry, 1918 (1916-1918): X (based on praeocc. name *Pagodina* Stabile, 1864 — see below).

Schileyko, 1984: 128.

Pagodulina Clessin, 1876

Clessin, 1876: 198.

— *Pagodina* Stabile, 1864: 100 [nom. praeocc., non Van Beneden, 1852 (Crustacea); t.-sp. *Pupa pagodula* Des Moulins, 1830; monotypy].

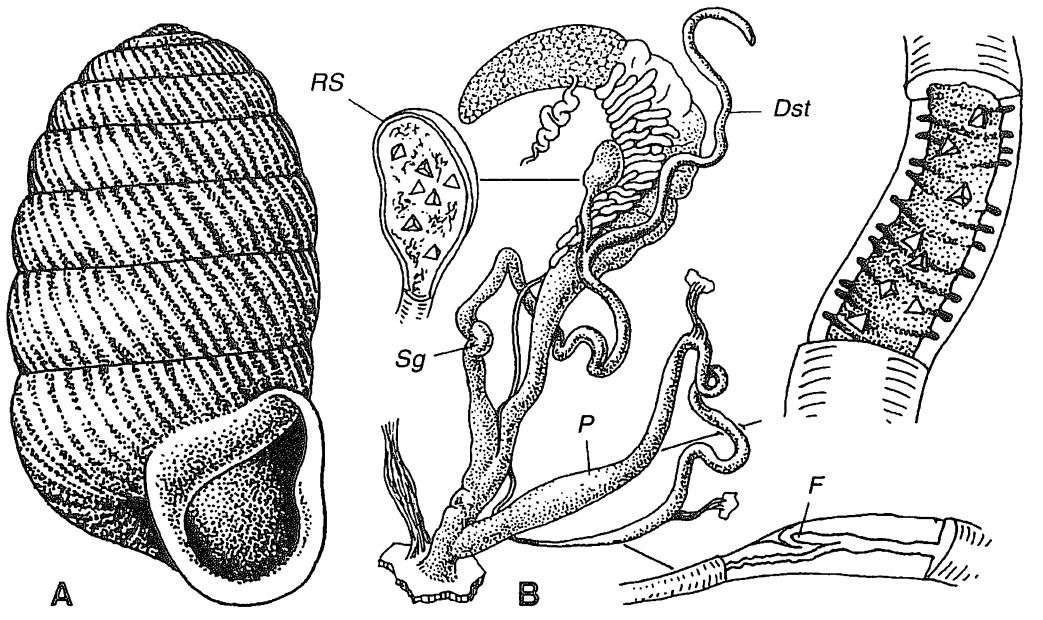


Fig. 77 ***Pagodulina (Crystallifera) lederi*** (O.Boettger, 1886).
Bibiony village, Talysh Mts., SE Transcaucasia, April 8, 1965. **Moscow** No. Lc-23221. A — shell; B — reproductive tract, interior of penis and longitudinal section of proximal end of epiphallus.

— *Pagodula* Hesse, 1916: 124 (nom. praeocc., non Monterosato, 1884; nom. emend. pro *Pagodina* Stabile, 1864).

— *Pagodinella* Thiele, 1917: 24 (nom. nov. pro *Pagodula* Hesse, 1916).

Schileyko, 1984: 129. Hausdorf, 1996: 14, 64.

TYPE SPECIES — *Pupa pagodula* Des Moulins, 1830; monotypy.

Shell ovate to ovate-cylindrical, glossy, rather solid but somewhat translucent, of 7-8.5 rather convex whorls. Color brown to amber-yellow. Aperture ovate, free or nearly so, with thickened and reflexed margins. Parietal wall with weak deeply lying lamella, lower end of which sometimes visible at view from below. Columellar lamella also weak, occupies back surface of columella. Palatal plica long, variously developed. Umbilicus absent, but umbilical depression present.

Vas deferens entering epiphallus apically or somewhat excentrically. Rudimentary flagellum seen in longitudinal section of proximal end of epiphallus. Penial caecum present or absent. Penis internally with longitudinal or circular folds; in all dissected specimens of two species (21 in total) I found minute tetragonal crystals in lumen of penis. Free oviduct and vagina about equal in length or vagina somewhat shorter. Spermathecal duct below bifurcation with conspicuous gland of characteristic bean-shaped appearance. Reservoir of spermatheca well defined, with same crystals as in lumen of penis.

DISTRIBUTION. As of subfamily.

Pagodulina (*Pagodulina* s.str.)
Fig. 76

Conchological characters as in genus. Height 2.8-4.0, diam. 1.8-2.5 mm (3.3 × 2.2 mm).

Penis internally with longitudinal folds. Penial caecum well developed or reduced. Penial retractor one, inserting onto epiphallus well above caecum. Portion of spermathecal stalk between bean-shaped gland and bifurcation very short.

DISTRIBUTION. South and partly Middle Europe. About 15 spp., subspp. & forms.

Pagodulina (*Crystallifera* Schileyko, 1976) Fig. 77

Schileyko, 1976: 57.

TYPE SPECIES — *Pagodina pagodula* var. *lederi* O. Boettger, 1886; OD.

Conchological characters as in genus. Height 3.0-4.5, diam. 1.6-2.5 mm (3.3 × 2.2 mm).

Penis internally with circular folds. Penial caecum absent. Penial retractors two, one of them inserting onto penis/epiphallus junction, the other — onto proximal section of epiphallus. Portion of spermathecal stalk between bean-shaped gland and bifurcation quite long.

DISTRIBUTION. Mountain systems of Asia Anterior and SE Transcaucasia. 5 spp. and subspp.

LAURIINAE Steenberg, 1925

Steenberg, 1925: 201 (Pupillidae subf.). Schileyko, 1984: 133.

Shell ovate to cylindrical. Sculpture of postembryonic whorls of spaced weak radial plication to regular ribbing. Body whorl more or less ascending in front, but angular region of aperture distinctly shifted from suture. Aperture with 2-7 teeth (very rarely toothless), which are quite visible at standard position of shell. Parietal lamella, if present, well developed.

Penial caecum of various external apearance and internal structure. Shaft of spermatheca without morphologically expressed glands. Diverticle of spermathecal stalk usually absent.

DISTRIBUTION. Mediterranean countries, Madeira, Canary Islands and Azores; Europe, Crimea, Caucasus, Turkey.

Euxinolauria Lindholm, 1924

Lindholm, 1924: 80. Schileyko, 1984: 133.

TYPE SPECIES — *Pupa (Charadrobia) pulchra* Retowski, 1883; OD.

Shell ovate-cylindrical to widely ovate-conic, summit slightly pointed or moderately blunt. Surface almost smooth to ribbed. Whorls 6.5-8, last one somewhat ascending in front. Most full set of aperture armature of adult shell represented by 2 parietal and 2 columellar lamellae, 1 basal tooth, 2 palatal plicae and a thickening of palatal margin, lying in plane of aperture. Besides, a series of knobs may present on aperture margin. In case of reduction of armature, columellar lamella (at intensive development of subcolumellar lamella), basal tooth, one of palatal folds, thickening of palatal margin, and knobs may disappear.

Penial caecum typically conic or vermiform, internally mostly with series of small conic tubercles; if tubercles absent, caecum twisted as ball and coated by thin membrane. Penis internally with fine irregular longitudinal folds, without tubercles.

Oviparous animals.

DISTRIBUTION. Caucasus and northern Turkey.

Euxinolauria (*Matschachelia* Schileyko, 1975) Fig. 78

Schileyko, 1975: 1769.

TYPE SPECIES — *Euxinolauria (Matschachelia) rectidentata* Schileyko, 1975; OD.

Shell elongate-ovate, finely sculptured, fragile. Aperture with 2 parietal and 2 columellar lamellae, 1 basal tubercle, 1 palatal plica. Parietal and subparietal lamellae remote from each other and descend nearly vertically. Height 2.7-2.8, diam. 1.3-1.5 mm (2.8 × 1.5 mm).

Epiphallus near penis forms a crook with two longitudinal and one transverse folds inside, thus form of lumen of this portion very complex. Proximal swollen portion of epiphallus with narrow circular slit. Spermathecal stalk with short diverticle.

DISTRIBUTION. Adzharia. 1 sp.

Euxinolauria (*Caucasipupa* Pilsbry, 1926) Fig. 79

Pilsbry, 1926 (1922-1926): 260 (nom. nov. pro *Caucasica* Caziot et Mergier, 1909).

— *Caucasica* Caziot & Mergier, 1909: 141 (nom. praeocc., non O. Boetter, 1877; pro gen.; t.-sp. *Pupa caucasica* L. Pfeiffer, 1857; tautonymy).

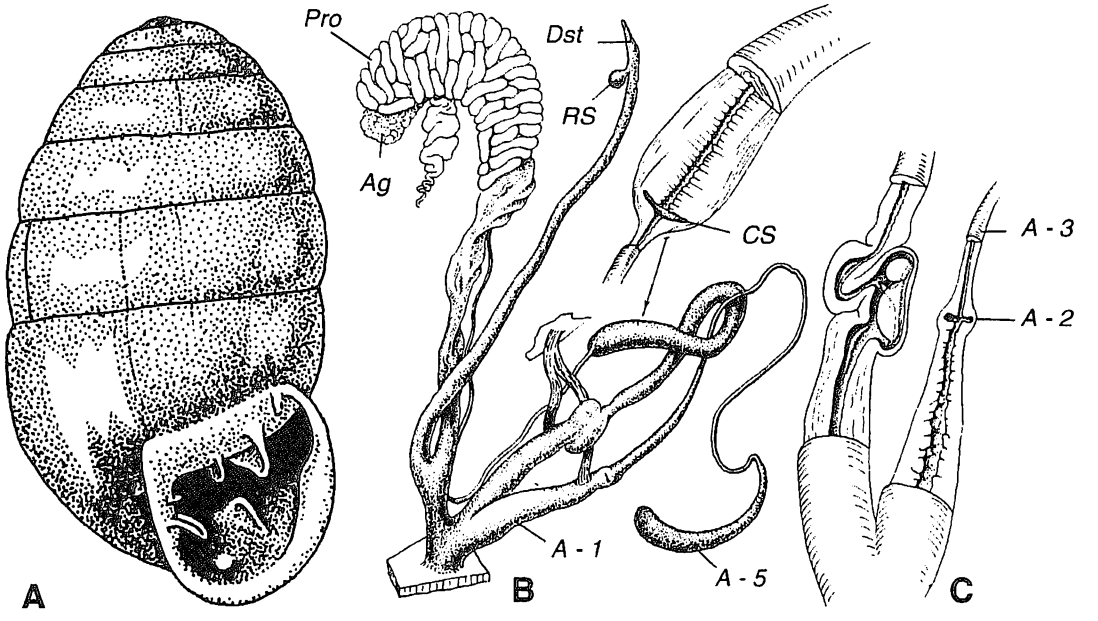


Fig. 78. ***Euxinolauria (Matschachelia) rectidentata*** Schileyko, 1975.
A — shell: Machaheli-tskali Valley, SW Transcaucasia. Holotype, **Spb**. B — reproductive tract; C — interior of penis and appendix. Paratype. Anatomy — after Schileyko, 1975.

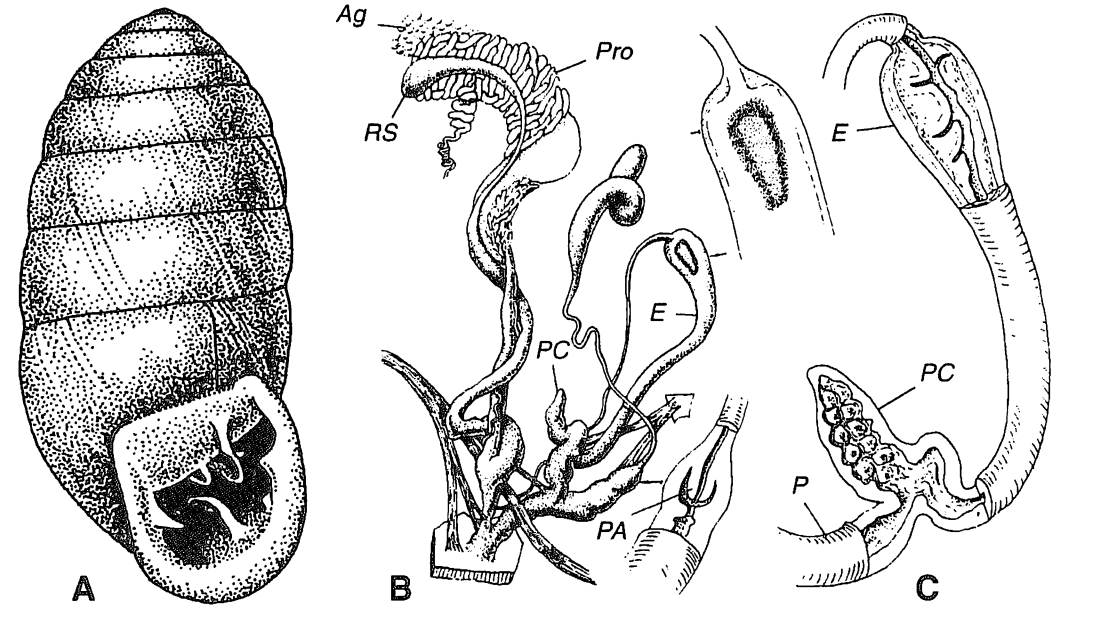


Fig. 79. ***Euxinolauria (Caucasipupa) caucasica*** (L.Pfeiffer, 1857).
A — shell: Pechegel Ridge, Zakataly Natural Reserve, E Transcaucasia, May 20, 1953. **SPb.** B — reproductive tract; C — interior of penis. Anatomy — after Schileyko, 1975.

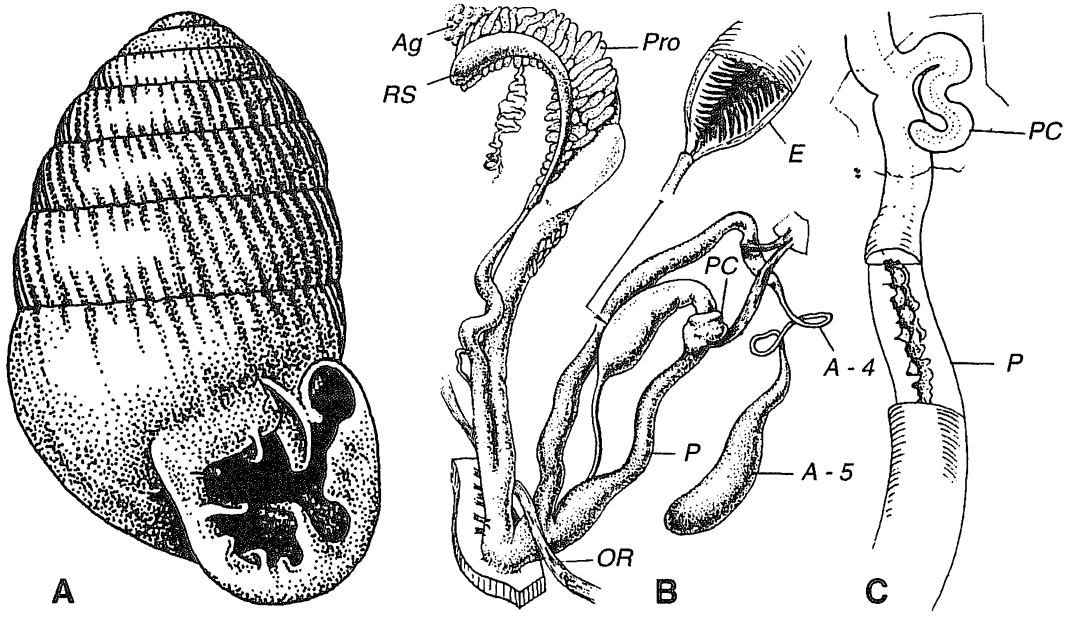


Fig. 80. ***Euxinolauria (Euxinolauria) pulchra*** (Retowski, 1883).
Valley of Ubin River, NW Caucasus, September 17, 1970. **Moscow** No. Lc-23207. A — shell; B — reproductive tract; C — interior of penis.

Schileyko, 1984: 136.

TYPE SPECIES — *Pupa caucasica* L. Pfeiffer, 1857; tautonymy.

Shell elongated-ovate to widely ovate-conic, either thin, fragile or thick, solid; shining or lusterless. Sculpture nearly absent or represented by weak radial wrinklets. Aperture armed with 2 parietal and 1-2 columellar lamellae, 1 palatal plica; basal tubercle may absent. Besides, sometimes there is a basal thickening. Parietal lamellae descend vertically, just their ridges may bent toward palatal wall. Height 2.8-6.5, diam. 1.7-3.0 mm (6.2 × 2.9 mm).

Proximal portion of epiphallus internally with a few semicircular slits. Penial caecum containing a system of distinct tubercles and/or longitudinal fold. Spermathecal stalk without diverticle, its lower portion sometimes coiled or twisted.

DISTRIBUTION. Western areas of Great Caucasus and Transcaucasia. One species penetrates eastward as far as Azerbaijan (Zakataly Natural Reserve). 8-9 spp.

Euxinolauria (*Euxinolauria* s.str.)
Fig. 80

Shell ovate or elongated-ovate, ribbed. Aperture with angular tubercle, 2 parietal and 2 columellar lamellae, 1 basal tubercle (sometimes absent), and 1 or 2 palatal plicae. Besides, there is a strong thickening of palatal edge lying in plane of aperture. Parietal lamellae not approached and descend nearly vertically or slightly deviated toward palatal wall. Height 3.4-4.5, diam. 2.0-2.2 mm (4.3 × 2.2 mm).

Proximal enlarged section of epiphallus internally with numerous circular slits. At boundary between penis and epiphallus there is a slender cylindrical caecum, twisted as a ball and covered by delicate semitransparent membrane. Spermathecal stalk lacking diverticle.

DISTRIBUTION. Western Caucasus and West Pontian Mts. 3-4 spp.

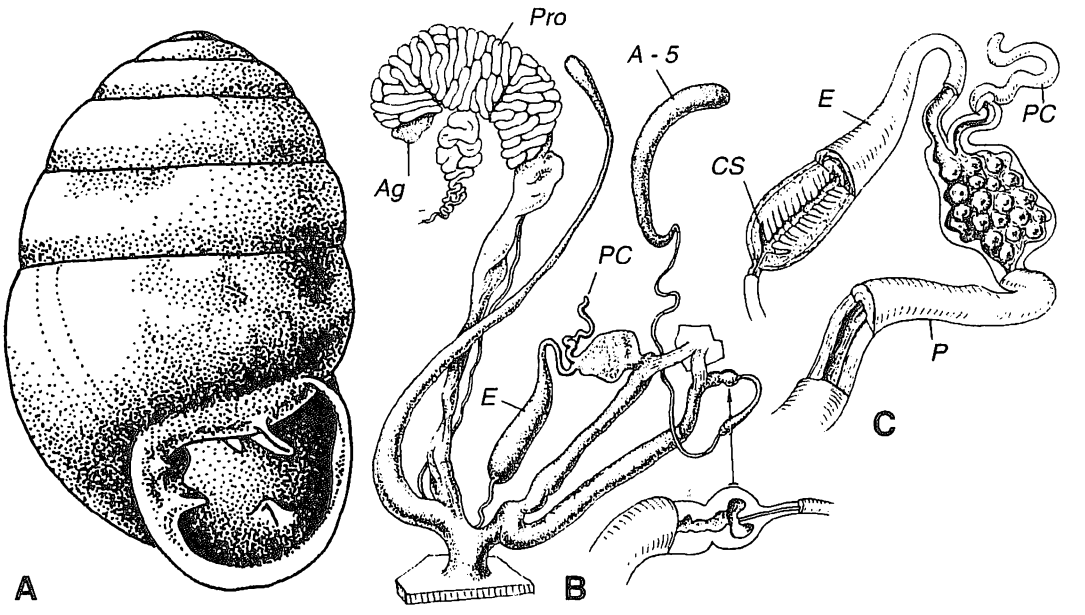


Fig. 81. ***Euxinolauria (Neolauria) mica*** Schileyko, nom. nov.
Ghuseriple, Caucasian Natural Reserve, W Caucasus, August 6, 1956. A — holotype. SPb; B, C — paratype. **SPb.** B — reproductive tract; C — interior of pale part. After Schileyko, 1975).

Euxinolauria (*Neolauria* Schileyko, 1975)
Fig. 81

Schileyko, 1975: 1778.

TYPE SPECIES — *Lauria zonifera* Pilsbry, 1934 (sensu Schileyko, non Pilsbry, 1934 = *Euxinolauria mica* nom. nov. pro *Euxinolauria zonifera* Schileyko, 1975, non Pilsbry, 1934); OD.

Shell ovate, fragile, finely sculptured. Aperture margins thin, with weak palatal thickening. Parietal and subparietal lamellae distant from each other and deviated toward palatal margin. Columellar lamella subhorizontal; basal tubercle sometimes absent; palatal plica short, lying at some distance from aperture edge. Height 3.0-4.0, diam. 1.8-2.0 mm (3.0 × 1.9 mm).

At penis/epiphallus junction there is a complex structure consisting of voluminous thin-walled sac bearing tubercles on its inner surface, and slender cylindrical caecum. Spermathecal shaft nearly straight, without diverticle.

DISTRIBUTION. Western part of Great Caucasus. 1 sp.

Speleodentorcula Gittenberger, 1985
Fig. 82

Gittenberger, 1985: 222.

TYPE SPECIES — *Speleodentorcula beroni* Gittenberger, 1985; OD.

Shell ovate-cylindrical, rather thin, translucent, glass-like, of 6.75-7.75 convex whorls. Last whorl markedly elevated toward aperture. Apex rounded. Colorless. Embryonic whorls smooth, remaining whorls finely regularly ribbed. Aperture ovate, with reflexed margins. Parietal lamella strong, entering, with thickened ridge; columellar lamellae 2, deeply lying. Palatal plicae 2, with thickened ridges; palatal margin with depression, bears a local thickening. Height 4.1-5.2, diam. 2.3-2.7 mm.

Vas deferens distended, entering epiphallus without distinct boundary. Penial caecum well developed. Superficially penial appendix looks like consisting of 3 divisions, because three basal divisions (A-1, A-2, and A-3) fused. Vagina short, inflated.

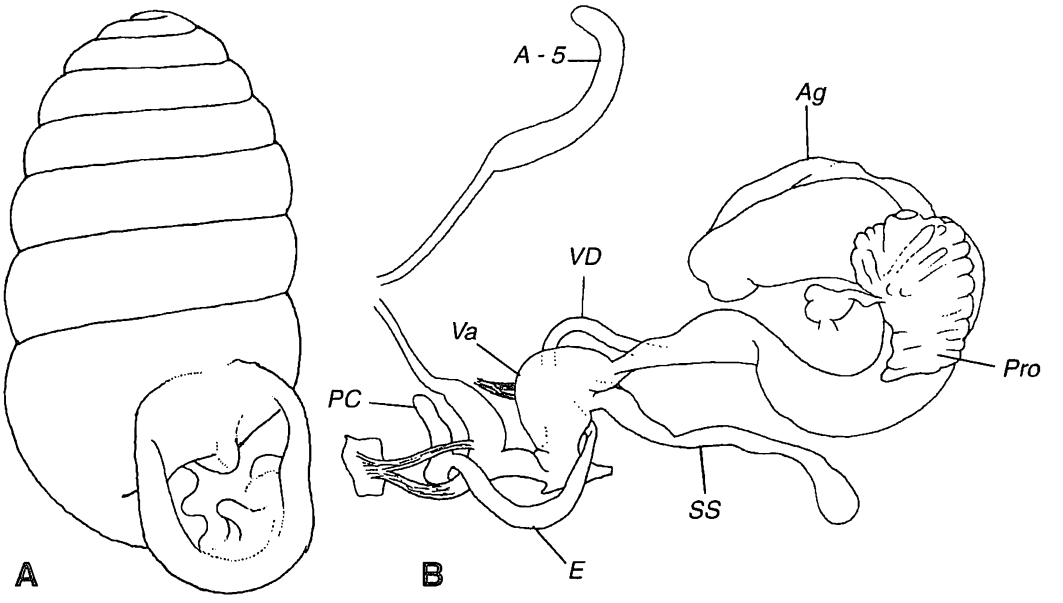


Fig. 82. ***Speleodentorcula beroni*** Gittenberger, 1985.
A — shell; B — reproductive tract. After Gittenberger, 1985.

Spermathecal stalk without diverticle, reservoir elongate.

Oviparous animals.

DISTRIBUTION. Eubea Island (Aegeian Sea). Mollusks live in caves. 1 sp.

REMARK. Schileyko (1988a) described *Speleodentorcula vitrea* based on a single empty shell from a cave in western Caucasus. Recently I have got more specimens, including preserved snails. Study of this additional material showed that the species belongs to *Euxinolauria (Euxinolauria)*.

Leiostyla Lowe, 1852
Fig. 83

Lowe, 1852: 276 (*Pupa* subg).

— *Alvearella* Lowe, 1852: 277 (*Pupa* "group"; t.-sp. *Pupa cassidula* Lowe, 1852; SD Lowe, 1954).

— *Charadrobia* Albers, 1854: 63 (t.-sp. *Helix cheilogona* Lowe, 1831; SD Martens in Albers, 1860).

— *Liostyla* Martens in Albers, 1860: 293 (nom. err. pro *Leiostyla* Lowe).

TYPE SPECIES — *Pupa vincta* Lowe, 1852; SD Pilsbry, 1922.

Shell ovate, thin, translucent, with widely rounded apex. Whorls 5-6, weakly convex, body whorl slightly elevated immediately behind aperture. Color light corneous. Embryonic whorls smooth, rest surface covered with radial wrinkles, which are stronger on early whorls. Aperture subvertical, upper part of palatal margin shifted backwards; parietal callus thin, light. Aperture armature composed of 2 parietal and 1 nearly horizontal columellar lamellae; short lamellar basal tooth may present at some distance from margin. 1 palatal plica lies deeply, but its posterior end nevertheless usually visible at standard position of shell. Also there is palatal callousity, bordering, together with parietal lamella, a sinulus. Umbilicus cylindrical, comparatively wide. Height 2.4-5.0, diam. 1.8-2.5 mm. (4.0 × 2.3 mm).

Proximal section of epiphallus markedly enlarged and distinctly muscular; distal section slender, partially muscular. Distalmost

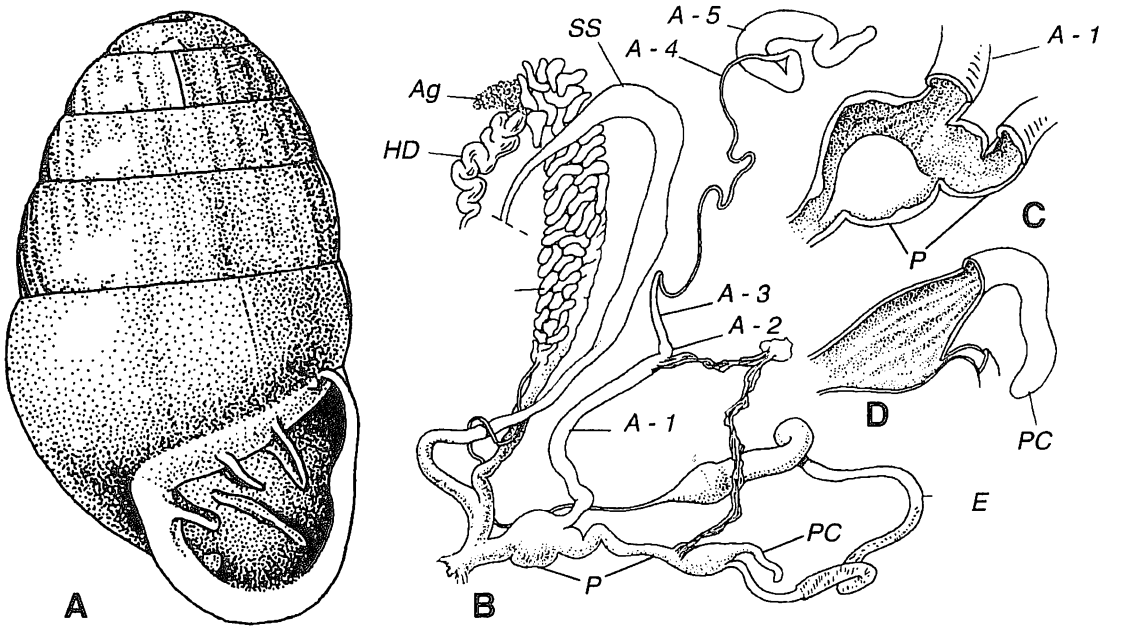


Fig. 83. ***Leiostyla vincta*** (Lowe, 1852).
A — shell: Madeira. **SPb.** B — reproductive tract; C-D — interior of penis, Santana, Madeira, September 15, 1991. **Cardiff** No. 2.1991.092.

part of penis considerably swollen, contains strong tubercle occupying most of penial chamber volume. Proximal part of penis slender, internally with vague longitudinal folds. Penial caecum simple, vermiform, internally with same folds as in proximal part of penis. Spermathecal stalk long, enlarged in middle part.

DISTRIBUTION. West Europe, North Africa, Canary Islands, Madeira, Azores. About 30 spp.

REMARK. Because of wide conchological diversity I tentatively consider the taxa of Madeiran Lauriinae as genera until the anatomy of respective species is known.

Scarabella Lowe, 1852
Fig. 84

Lowe, 1852: 277 (*Pupa* sect.).

TYPE SPECIES — *Helix cassida* Lowe, 1831; monotypy.

Shell pointed-ovate, solid, spire bluntly conic. Whorls 7-7.5, last slightly ascending

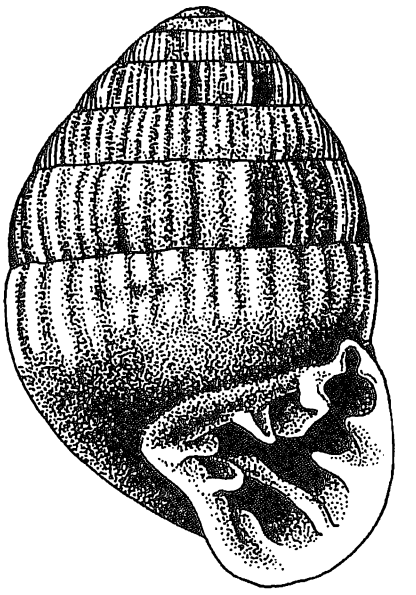


Fig. 84. ***Scarabella cassida*** (Lowe, 1831). Madeira. **SPb.**

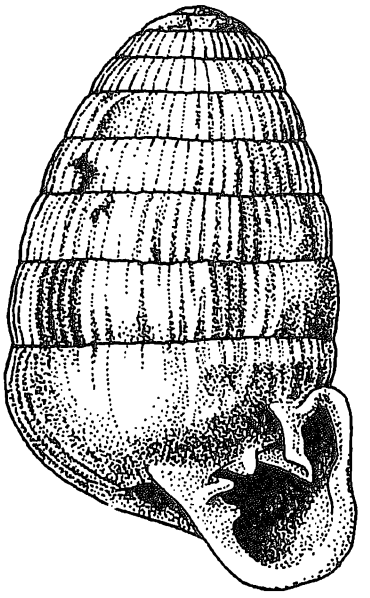


Fig. 85. *Azoripupa tessellata* (Morelet, 1860). Santa Maria, Azores. **Phil.** No. 5075.

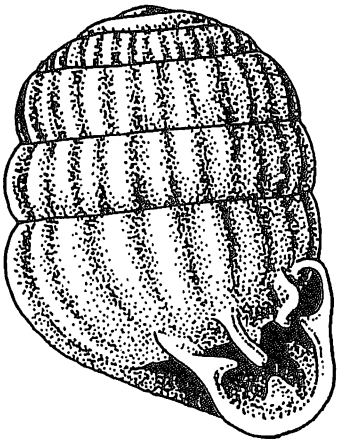


Fig. 86. *Wollastonula gibba* (Lowe, 1952). Madeira. **SPb.**

in front. Coloration consists of rich brown background and diffuse white streaks, expressed predominantely on ribs; body whorl dark below periphery. Embryonic whorls vaguely finely granulate, postnuclear whorls with strong rounded ribs, which become much weaker below periphery of body whorl. Aperture rounded, places of peristome isertion widely remoted. Angular tubercle fused with anterior end of strong, curved parietal plate; subparietal lamella lower and shorter than parietal. Columellar lamellae 2, lower somewhat higher than upper. Basal plica occupies baso-columellar angle. Strong palatal plica with thickened ridge, approaching aperture edge. Above it two smaller folds seat. Small swelling located at the very top of palatal margin, opposite to angular tubercle. Umbilicus dot-like. Height 4.0-5.0, diam. 2.8-3.0 mm (4.9 × 3.0 mm).

DISTRIBUTION. Madeira. 1 sp.

Azoripupa Pilsbry, 1923
Fig. 85

Pilsbry, 1923 (1922-1926): 127 (*Leiostyla* sect.).

TYPE SPECIES — *Pupa tesselata* Morelet, 1860; OD.

Shell elongated-ovate, moderately thin, of 8-9 nearly flat whorls. Apex not pointed. Color corneous, usually with light radial streaks. Embryonic whorls smooth, later whorls with well developed radial wrinkles to fine ribbing. Aperture ovate, palatal wall slightly concave. Angular tubercle small, parietal lamellae strong, deeply entering (for about 2 whorls); subparietal shorter and lower. Columellar lamellae 2, upper stronger. Palatal wall smooth. Height 3.2-4.6, diam. 1.9-2.4 mm (3.2 × 2.1 mm).

DISTRIBUTION. Azores. 1 sp.

Wollastonula Pilsbry, 1922
Fig. 86

Pilsbry, 1922 (1922-1926): 45, 69 (*Leiostyla* sect.).

TYPE SPECIES — *Pupa gibba* Lowe, 1852; OD.

Shell shortly cylindrical, comparatively thin, with widely rounded apex. Whorls 6, convex, body whorl gradually ascending toward aperture. Color uniformly horny. Em-

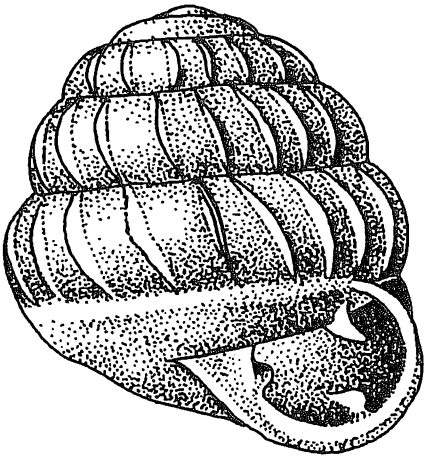


Fig. 87. *Mastula lamellosa* (Lowe, 1852). Madeira. **Phil.** No. 268232.

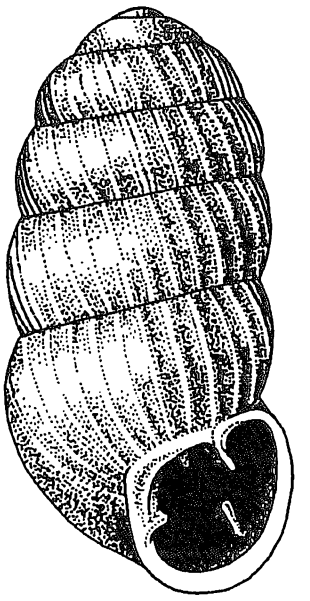


Fig. 88. *Craticula ferraria* (Lowe, 1852). Porto Santo, Madeira. Syntype. **SPb.**

bryonic whorls smooth, rest whorls with widely spaced, strong, wide, rounded, ribs, more crowded on upper spire. Aperture rounded, places of peristome insertion widely remoted from each other. Angular lamella high, fused with supraparietal. Parietal lamella higher than supraparietal. Columellar margin a little concave in middle; columellar lamella strong, nearly horizontal. Basal tubercle deeply lying, directed toward ridge of parietal lamella. Middle portion of palatal margin protrudes anteriorly. Palatal plicae 2, lower lying much deeper than upper; latter represented by lip widening. Umbilicus small, drop-like. Height 2.0-2.2, diam. 1.7-1.8 mm (2.2 × 1.8 mm).

DISTRIBUTION. Madeira. 1 sp.

Mastula Lowe, 1852
Fig. 87

Lowe, 1852: 278 (*Pupa* subg.).

TYPE SPECIES — *Pupa lamellosa* Lowe, 1852; monotypy.

Shell short-ovate (nearly globose), comparatively thick and solid, of about 5 rather convex whorls, last whorl directed. Color light horny. Embryonic whorls distinctly spirally striated, rest surface decorated with strong irregular ribs that are partially periostracal. Aperture wide, subvertical, with a little reflexed margins. Parietal wall with single lamella. Columellar lamella well developed. Palatal wall with tubercle, which sometimes absent. Provisory basal teeth in juveniles very weak or absent. Height 2.0, diam. 1.7-1.8 mm (2.0 × 1.8 mm).

DISTRIBUTION. Madeira. 1 sp.

Craticula Lowe, 1852
Fig. 88

Lowe, 1852: 277 (*Pupa* subg.).

— *Eryma* Albers, 1854: 67 (*Pupa* sect.; t.-sp. *Pupa ferraria* Lowe, 1852; SD Pilsbry, 1923).

TYPE SPECIES — *Pupa ferraria* Lowe, 1852; SD Pilsbry, 1923.

Shell cylindrical, with rounded upper

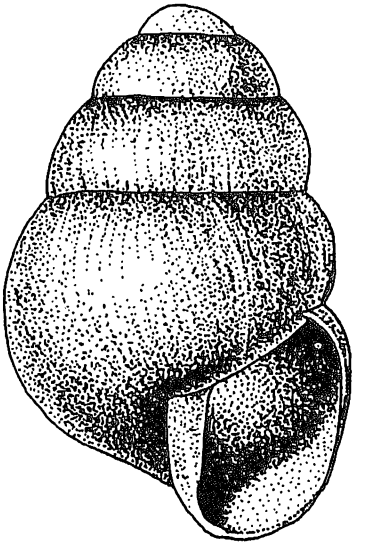


Fig. 89. *Hemilauria limnaeana* (Lowe, 1852). Madeira. **Phil.** No. 117134.

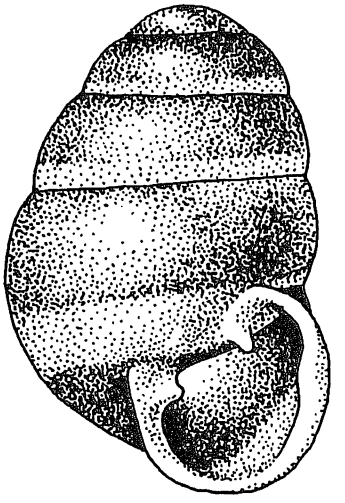


Fig. 90. *Senilauria fasciolata* (Morelet, 1860). Azores. **Phil.** No. 3931.

part, rather thin, not lustrous. Whorls 6, moderately convex, body whorl not elevated. Color corneous, middle portion of whorls sometimes occupied by feeble lighter band of various width. Embryonic whorls with extremely fine periostracal spiral threads. Postembryonic whorls with regular, moderately spaced ribs; elements of spiral sculpture distinguishable locally between ribs. Aperture rounded, places of its attachment connected by thin callus; right side of callus often thickened (angular tubercle) and fused with anterior end of deeply entering parietal plate. Subparietal lamella lower than parietal and lies deeper. Columellar lamella short, subhorizontal. Palatal plica also short, triangular, with thickened ridge. Umbilicus, a minute perforation. Height 2.0-3.3, diam. 1.1-1.5 mm (3.2 × 1.5 mm).

DISTRIBUTION. Madeira. 1 sp.

Hemilauria Waldén, 1983
Fig. 89

Waldén, 1983: 266, 268.

TYPE SPECIES — *Columella limnaeana* Lowe, 1852; OD.

Shell ovate, thin, of about 5 moderately convex whorls. Last whorl direct. Color uniformly corneous. Embryonic whorls smooth, later finely, irregularly, radially striate. Aperture ovate, toothless, with thin and sharp margins; columellar margin reflexed and expanded. Height 3.5-5.0, diam. 2.0-2.6 mm (4.0 × 2.2 mm).

DISTRIBUTION. Madeira. 1 sp.

Senilauria Pilsbry, 1928
Fig. 90

Pilsbry, 1928: 108 (nom. nov. pro *Petrarca* Pilsbry, 1922).

— *Petrarca* Pilsbry, 1922 (1922-1926): 45 [nom. praeocc., non Fowler, 1899 (Cirripedia); t.-sp. *Pupa fasciolata* Morelet, 1860; OD].

TYPE SPECIES — *Pupa fasciolata* Morelet, 1860; OD.

Shell cylindrical-conical to ovate, thin, translucent, of 4.5-5 moderately convex whorls. Color either uniformly light yellowish-brown to chestnut, or with light band on darker background, or bicolor: upper part chestnut, lower part light yellowish-

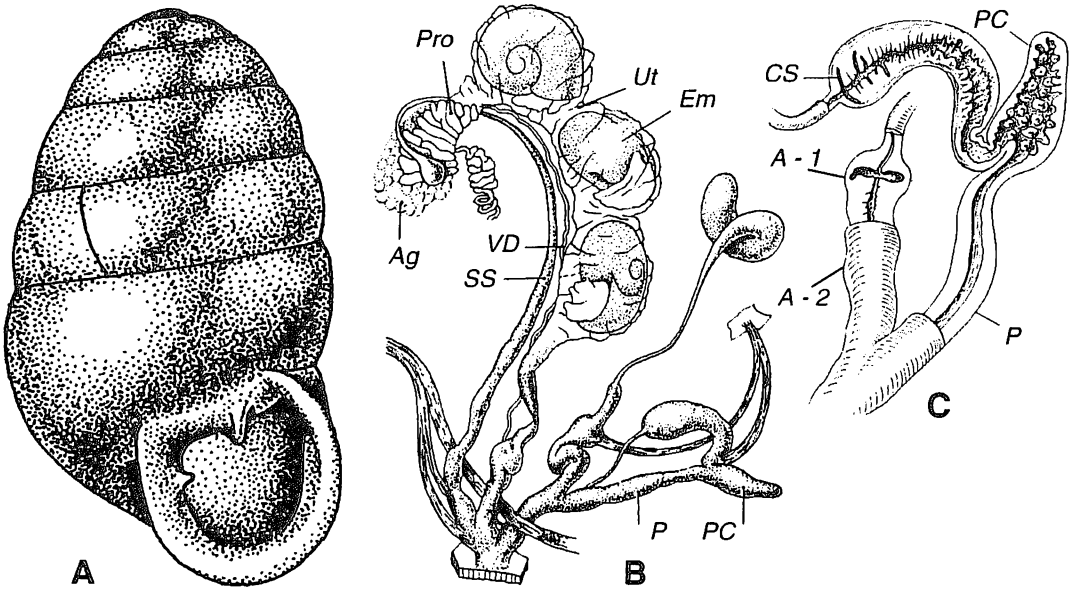


Fig. 91. ***Lauria cylindracea*** (Da Costa, 1778).
Cheghem Valley, N Caucasus, September 23, 1970. A — shell; **Moscow** No. Lc-23198; B — reproductive tract; C — interior ofmale part. B, C — after Schileyko, 1975.

brown. Embryonic whorls smooth, subsequent delicately radially striated. Aperture ovate, with reflexed and slightly thickened margins. Parietal wall with minutely serrated lamella entering at least 0.5 whorl; sometimes deeply lying minute tubercle situated to left of parietal lamella. Columellar lamella moderately developed. In juvenile specimens a number of provisional radial basal folds seen through shell wall. Height 2.3-3.7, diam. 1.7-2.0 mm (2.8 × 1.8 mm).

DISTRIBUTION. Azores. 1 sp.

REMARK. Perhaps *Senilauria* is a subgenus of *Lauria*.

Lauria Gray, 1840
Fig. 91

Gray in Turton, 1840: 193.

— *Eruca* Swainson, 1840: 334 (t.-sp. *Pupa umbilicata* Draparnaud, 1801; SD Herrmannsen, 1847, 1).

— *Gastrodon* Lowe, 1852: 275 (*Pupa* subg.; nom. praeocc., non Rafinesque, 1815; t.-sp. *Pupa fanalensis* Lowe 1852; monotypy).

— *Reinhardtia* O.Boettger, 1879: 29, 403 (t.-sp. *Turbo cylindracea* Da Costa, 1778, SD Pilsbry, 1922).

TYPE SPECIES — *Pupa umbilicata* Draparnaud, 1801 (=*Turbo cylindracea* Da Costa, 1778); SD Herrmannsen, 1847.

Shell ovate-cylindrical or elongated-ovate, thin, translucent, of 5-7 slightly to moderately convex whorls. Last whorl straight or scarcely ascending. Apex rounded. Color yellowish to chestnut. Embryonic whorls smooth. Postnuclear whorls weakly sculptured with fine, irregular, radial wrinklets. Aperture rounded, with thin, broadly reflexed margins. Armature of adult shells represented by only two teeth: parietal and columellar lamellae; besides, angular tubercle may present as well. In juvenils there are series of provisional radial folds, visible through shell wall. Height 2.3-4.5, diam. 1.5-2.0 mm (4.1 × 1.8 mm).

A conic caecum situated at penis/epiphallus junction. Inner surface of this caecum covered with distinct tubercles, as in many species of *Euxinolauria*. Penial appendix of usual structure. Arms of penial retractor splitting at short distance from dia-

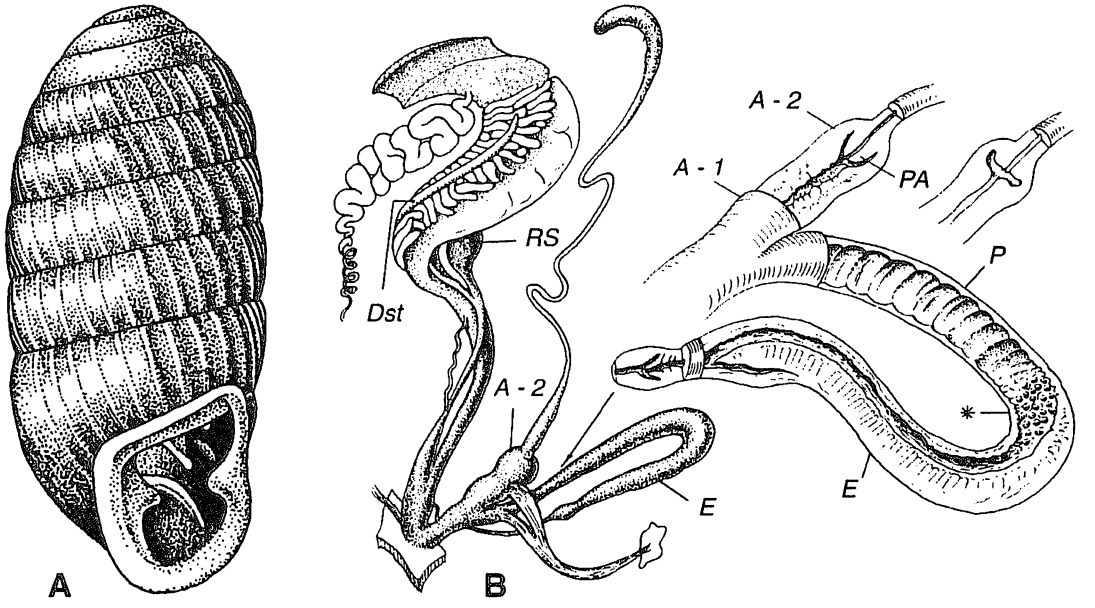


Fig. 92. *Argna ferrari* (Porro, 1838).
A — shell: Esino, Italy. **SPb.**
B — ! *Argna bielzi* (Rossmaessler, 1859), reproductive tract and interior of distal male part. Asterisk — zone covered with tubercles. After Schileyko, 1984.

phragm; appendical arm attached to A-2, the other — to epiphallus at base of caecum. Uterus containing a few embryos. Vagina nearly absent since spermathecal shaft entering adatrial portion of distal female duct. Diverticle absent.

Ovoviviparous animals.

DISTRIBUTION. Mediterranean countries, Europe (except northern and eastern regions), Crimea, Caucasus, NE and E Africa. 2-3 spp. with many subspp.

ARGNINAE Hudec, 1965

Hudec, 1965: 162.

Shell high, cylindrical to ovate-cylindrical. Postembryonic whorls mostly ribbed or rib-striated, ribs without periostracal fringes. Body whorl somewhat elevated toward aperture.

Epiphallic or penial caecum absent. Inside penis, at its border with epiphallus, there is a series of small tubercles. Penial appendix normally developed. Spermathecal stalk without morphologically pronounced glands. Diverticle of spermathecal stalk present or lacking.

DISTRIBUTION. Southern and Eastern Alps, Carpathians.

Argna Cossmann, 1899
Fig. 92

Cossmann, 1899: 1104.

— *Sphyradium* Hartmann, 1840: 53 (nom. praeocc., non Charpentier, 1837; t.-sp. *Pupa ferrari* Porro, 1838; monotypy).

— *Coryna* Westerlund, 1887 (1884-1890): 78, 87 (nom. praeocc., non Billberg, 1833; nom. nov. pro *Sphyradium* Hartmann, 1840).

— *Agardhia* Gude, 1911: 361 (nom. nov. pro *Coryna* Westerlund, 1887).

— *Rhytidochasma* A. Wagner in Sturany & Wagner, 1914: 48 (*Agardhia* subg.; t.-sp. *Pupa ferrari* Porro, 1838; SD Pilsbry, 1924).

TYPE SPECIES — *Pupa ferrari* Porro, 1838; OD.

Shell cylindrical to ovate-cylindrical, translucent, weakly shining, of 8-10 moder-

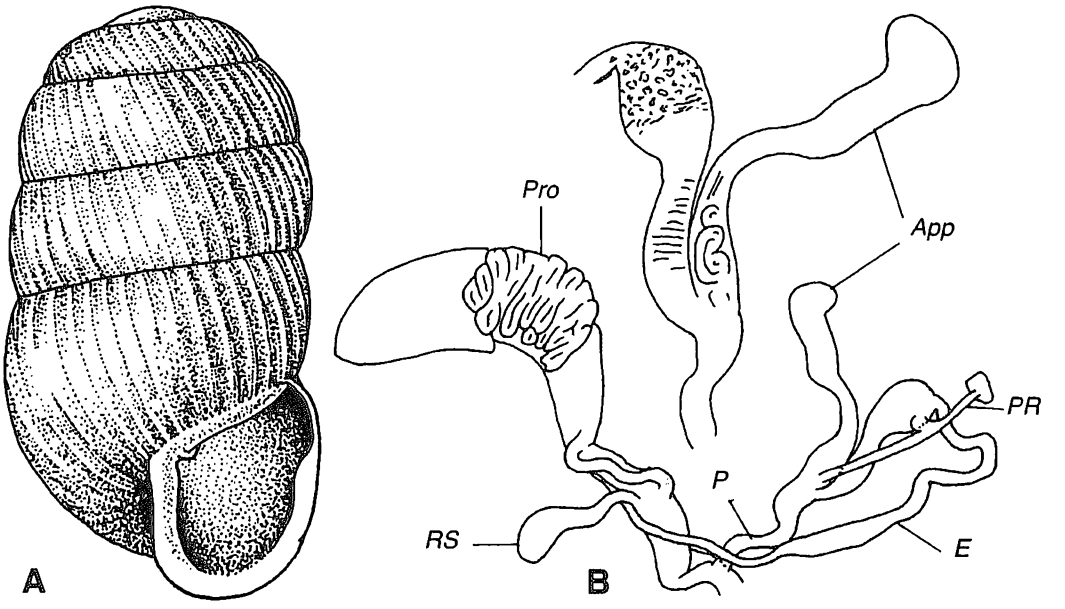


Fig. 93. *Agardhiella truncatella* (L.Pfeiffer, 1846).
A — shell: Malborgath, Carinthia, Austria. SPb. B — reproductive tract. After Gittenberger, 1974.

ately convex to flattened whorls. Apex narrowly rounded. Color uniformly corneous. Embryonic whorls smooth, rest with distinct rounded regular ribs. Aperture adnate or interrupted, subvertical, middle of palatal margin sometimes slightly protruding. Middle of parietal margin occupied by strong deeplying high lamella; minute tubercle-like supraparietal lamella lies deeper (sometimes absent). Columellar lamella well developed. Basal tooth lies so deep that not visible at standard position of shell, but seen from outside through shell wall. There are 2 palatal plicae (they also lie deeply), lower longer than upper. Middle of palatal margin occupied by strong tooth-like palatal thickening. Umbilicus minute, cylindrical, encircled by high rounded crest. Height 4.0-5.0, diam. 1.8-2.0 mm (4.8 × 2.0 mm).

Epiphallus at place of vas deferens entering forms a small swelling, with narrow, slit-like circular cavity inside. Lumen of epiphallus excentrical: wall of duct, facing to penis, thinner and simple, while the other side much thicker and incorporates glandular tissue. At penis/epiphallus junction there is a small zone covered with tiny but distinct conic tubercles. Penis long, cylindrical, internally with irregular circular folds. A-1 short, A-2 of about same length, globular, with minute papilla inside. A-4 long. Appendical arm of penial retractor attached to border between A-1 and A-2, the other arm — to lower section of penis at short distance from base of appendix. Spermathecal stalk long, slightly expanded basally, with well developed diverticle.

DISTRIBUTION. Southern and Eastern Alps, Carpathians, Spain. 7-8 spp. & subspp.

Agardhiella Hesse, 1923
Fig. 93

Hesse, 1923: 195.

TYPE SPECIES — *Pupa truncatella* L. Pfeiffer, 1846; OD.

Shell cylindrical, shining, translucent, of 5-6 moderately convex whorls. Apex widely rounded. Color very light, nearly white. Embryonic whorls vaguely finely granulate,

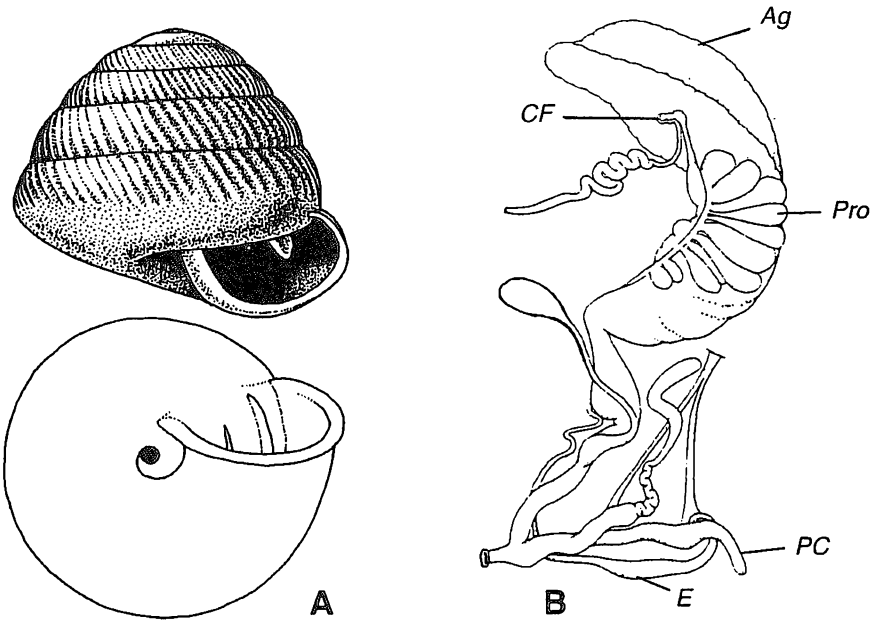


Fig. 94. ***Strobilops labyrinthica*** (Say, 1817).
A — shell: Lincoln, Michigan. SPb.
! ***Strobilops texasiana*** Pilsbry et Ferriss, 1906. B — reproductive tract. After Baker in Pilsbry, 1948.

rest with distinct, thin, sharp riblets. Aperture interrupted, rounded, subvertical, its margins somewhat thickened, slightly reflexed. Small lamella on parietal wall, next to columellar; palatal margin with light swelling. Umbilicus, a minute perforation. Height 3.0-5.3, diam. 1.3-2.4 mm (3.3 × 1.5 mm).

Penis relatively short, swollen at upper end; this section internally with tubercles. Penial appendix rather small, A-4 unusually short. Penial arm of retractor attached to swollen part of penis. Spermatheca very short, without diverticle.

DISTRIBUTION. Southern and Eastern Alps. 5-6 species.

STROBILOPSIDAE Pilsbry, 1918

Pilsbry, 1918 (1916-1918): X (pro subf.).

— Strobilidae Jooss, 1911: 61 (without diagnosis; based on nom. praeocc. "*Strobilus* Morse", 1864 — see below).

Shell microhelicoid, trochiform to subdiscoidal, with diameter always exceeding height. Whorls 4.5-6, periphery of last whorl rounded to carinate. Aperture armed with lamellar teeth, entering deeply inside shell. Margins of aperture mostly reflexed and expanded. Umbilicus narrowly open to broad, funnel-shaped.

Head with two pairs of tentacles.

Prostate short. Vas deferens markedly enlarged at distal section. Penial verge, if present, short. Penial appendix primarily present, sometimes absent. Penial caecum short. Spermathecal diverticle present or wanting.

DISTRIBUTION. SE Asia, Philippines; in America from SE Canada to Venezuela and NE Brazil; Galapagos Islands.

Strobilops Pilsbry, 1892
Fig. 94

Pilsbry, 1892 (1892-1893): 403 (nom. emend. pro *Strobila* Morse, 1864).

— *Strobila* Morse, 1864: 26 [nom. praeocc., non Sars, 1835 (Platyhelminthes); t.-sp. *Helix labyrinthica* Say, 1817; monotypy].

— *Strobilus* Sandberger, 1872 (1870-1875): 258

[nom. praeocc., non Anton, 1839 (Achatinellidae); t.-sp. *Helix labyrinthica* Say, 1817; OD].

TYPE SPECIES — *Helix labyrinthica* Say, 1817; monotypy.

Shell trochiform to dome-shaped, thin, of 4.5-6 closely coiled slightly convex whorls. Last whorl with blunt peripheral angle. Color light corneous to chestnut. Embryonic whorls smooth, postapical whorls with regular radial ribs, basal surface sometimes smooth or nearly so. Aperture semilunar, with more or less expanded and thickened margins. Parietal callus weak. Cavity of last whorl obstructed by two or three long parietal lamellae, upper emerging to edge of parietal callus, lower weaker, emerging or immersed; intermediate one, when present, smallest and remoted from aperture; a series of two or more short plicae on basal wall of cavity lies deep inside last whorl. These lamellae and plicae appear very early in postembryogenesis, growing forward and reducing behind. Umbilicus narrow, excentric. Height 1.5-2.5, diam. 2.2-2.8 mm (1.8 × 2.3 mm).

Hermaphroditic gland consists of two lobes, each divided into few, short-clavate lobules. Carrefour clavate, with ovoid base; talon as such not developed. Prostate short, composed of large clavate acini. Epiphallus fusiform, developed in vas deferens some distance above entrance into penis through a very short verge. Penis relatively short. Penial caecum looks like a continuation of penis above entrance of epiphallus. Sections of penial appendix variously expressed; three basal sections (A-1, A-2, A-3) fused; A-4 sinuous. Penial retractor arising from diaphragm; appendicular arm attached to upper portion of A-1, penial arm inserts alongside entrance of epiphallus. Vagina longer than free oviduct. Spermathecal stalk rather short, without diverticle.

DISTRIBUTION. North, Central and South America to eastern Brazil. About 10 recent spp. & subspp. The genus is known from Miocene and Pleistocene of Europe and Miocene of North Caucasus.

REMARK. Many authors consider some taxa or all of them as subgenera of the genus *Strobilus*.

Coelostrobilops Pilsbry, 1931
Fig. 95

Pilsbry, 1931 (1927-1931): 60 (*Strobilops* sect.).

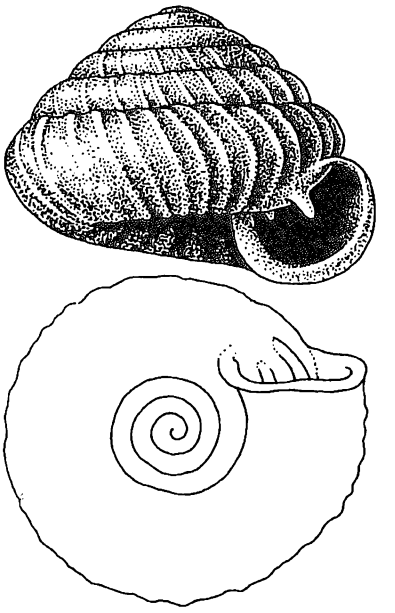


Fig. 95. ***Coelostrobilops wenziana*** (Pilsbry, 1931). Grand Cayman Island. **Phil.** No. 150940.

TYPE SPECIES — *Strobilops wenziana* Pilsbry, 1931; OD.

Shell turbinate, depressed-conic, thin, of 6 rather convex whorls. Last whorl scarcely angled at periphery. Color corneous. Embryonic whorls smooth, later with widely spaced, regular, rounded ribs, equally expressed on upper and lower surfaces of shell. Aperture subcircular, with thin or slightly thickened and a little reflexed margins. Parietal callus weak. Parietal wall with two entering lamellae, subparietal lying deeper than parietal. Umbilicus broad, quite perspective. Height 1.7-2.0, diam. 2.4-3.0 mm (1.9 × 2.5 mm).

DISTRIBUTION. Central America, West Indies. 2-3 spp.

Discostrobilops Pilsbry, 1927
Fig. 96

Pilsbry, 1927 (1927-1935): 46.

TYPE SPECIES — *Helix hubbardi* A. Brown, 1861; OD.

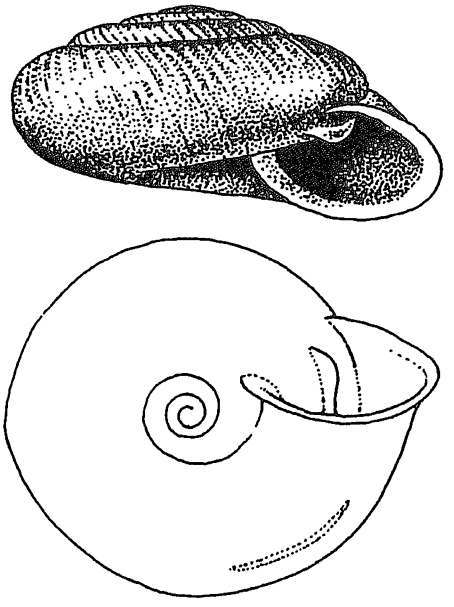


Fig. 96. ***Discostrobilops hubbardi*** (A. Brown, 1861). Woodville, Madison Co., Alabama. **Chicago** No. 103876.

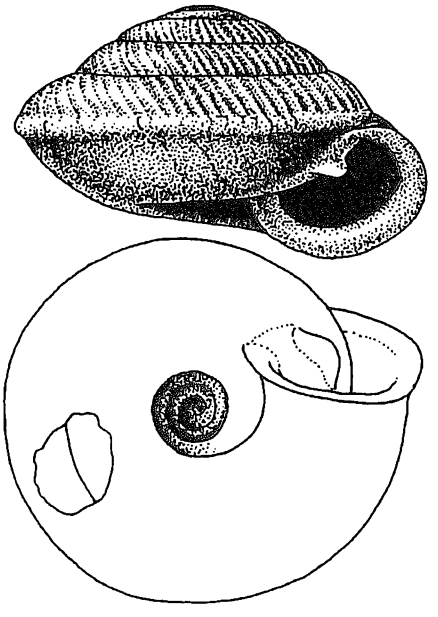


Fig. 97. ***Nesostrobilops helleri*** (Dall, 1900). James Island, Galapagos. **Phil.** No. 327297.

Shell small, low-conic, thin, translucent, of 4-4.5 moderately convex whorls. Body whorl in profile with a very light angulation above mid-line, descending in front with a weak bending. Spire depressedly dome-shaped. Color corneous, monochromate or with lighter radial streaks. Embryonic whorls vaguely granulate, postnuclear finely radially ribbed; on basal surface riblets much weaker. Aperture ovate, well oblique, margins a little thickened and shortly reflexed. Parietal callus practically absent. Parietal lamella with smooth ridge, its posterior end not seen through aperture. Through shell wall two deeply lying plicae visible — basal and longer palatal ones. Umbilicus wide, perspective. Height 1.0-1.4, diam. 2.0-3.1 mm (1.0 × 2.2 mm).

DISTRIBUTION. Texas, Mississippi, Florida, Georgia; NE Mexico; Jamaica; Cuba; Bimini Islands on western edge of Bahamas; Bermuda. 3 Recent spp. The genus is known from Lower Miocene of Europe.

Nesostrobilops Pilsbry, 1931
Fig. 97

Pilsbry, 1931 (1927-1935): 62 (*Strobilops* sect.).

TYPE SPECIES — *Endodonta helleri* Dall, 1900; OD.

Shell lenticular, thin, of 4.5 moderately convex whorls. Last whorl scarcely descending, with distinct cord-like keel at periphery. Color brown. Embryonic whorls smooth, postapical ribbed above and nearly smooth below, however slopes of umbilicus retain delicate ribbing. Aperture broadly lunate, with reflexed margins. Parietal callus weak. Parietal wall with 2 lamellae, subparietal very weak and lies much deeper than parietal. Baso-palatal wall with 1-2 deeply situated plicae. Umbilicus moderately broad, quite perspective. Height 1.6-1.7, diam. 2.8-3.0 mm (1.7 × 2.8 mm).

DISTRIBUTION. Galapagos Islands, ?Lower California. 1 or 2 spp.

REMARK. Miller & Christensen (1980) have described *Strobilops californica* from Sierra de la Victoria of Baja California Sur, Mexico. They discussed the subgeneric position of the species in comparison with *Strobilops* s. str., *Discostrobilops*, and *Enteroplax*.However they did not mention *Nesostrobilops*, to which *Strobilops californica* is more similar than to any other Strobilopsidae.

Enteroplax Gude, 1899
Fig. 98

Gude, 1899: 149 (*Plectopylis* sect.). Solem, 1968: 25.

TYPE SPECIES — *Plectopylis quadrasi* Moellendorff, 1893; OD.

Shell low-conic to nearly flat, thin, of 5.25-6.5 convex whorls. Last whorl not descending, with distinct thread-like keel. Color light-corneous to chestnut. Embryonic whorls smooth, postapical with radial ribs above periphery and in umbilicus; basal surface smooth below keel. Aperture generally lunate, with reflexed and expanded margins. Parietal callus strongly developed. Parietal wall with 2 lamellae, extending posteriorly about 0.5 whorl; upper high and blade-like, smooth or serrated on expanded edge, the other much lower and usually slightly recessed, rarely with a short and deeply recessed interparietal lamella. Columellar lamellae absent. Baso-palatal wall with 3-10 short to long lamellar plicae recessed about 0.25-0.3 whorl behind aperture, connected posteriorly by a transverse callus. Umbilicus broadly open. Height 1.4-2.8, diam. 3.4-4.4 mm (2.3 × 4.0 mm).

DISTRIBUTION. Philippine Islands and New Guinea. 4 spp.

Eostrobilops Pilsbry, 1927
Fig. 99

Pilsbry, 1927 (1927-1935): 42.

TYPE SPECIES — *Strobilops hirasei* Pilsbry, 1927; OD.

Shell turbinate, depressed, thin, of 5-5.5 moderately convex whorls. Last whorl not descending, rounded at periphery. Color corneous. Embryonic whorls smooth; subsequent whorls finely radially striated, this sculpture better expressed on upper surface. Aperture ovate, with widely reflexed and expanded margins. Parietal callus very weak or absent. Parietal wall with 2 lamellae, having minute nodules apart from aperture plane; columellar lamella weak, deeply entering. There are 1 short basal and 3-4 palatal plicae, lowest being longest. Umbilicus narrow, excentric (as in *Strobilops*). Height 1.8-2.2, diam. 3.0-4.0 mm (1.9 × 3.0 mm).

Vas deferens entering epiphallus apically. Penis composed of minute basal (distal) section and rather long proximal. Penial caecum short, blunt. Penial appendix absent. Penial retractor attached to proximal section of penis at some distance below caecum. Free oviduct and vagina long, latter longer. Spermathecal stalk with well-developed diverticle.

DISTRIBUTION. China, Korea, Japan. 4 Recent spp. The genus is known from the end of Oligocene to Upper Miocene of Europe and North Caucasus.

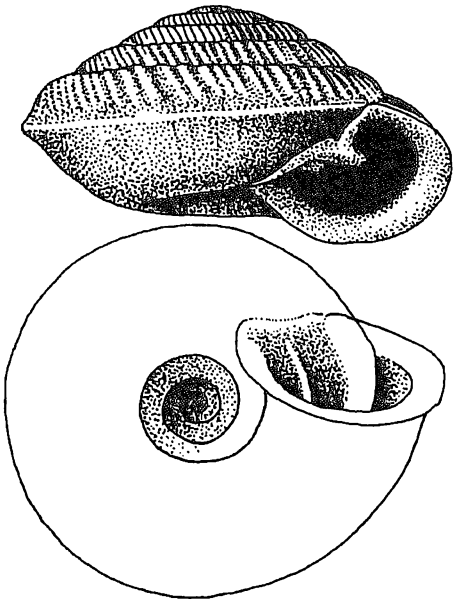


Fig. 98. ! ***Enteroplax misoolensis*** (Adam et Benthem-Jutting, 1939).
5.5 km ENE of Klamona, Cendrawasih Peninsula, prov. Irian Jaya, Indonesia. **Leiden.**

SPELAEODISCIDAE Steenberg, 1925

Steenberg, 1925: 202 (Valloniidae subf.).

— Aspasitinae Steenberg, 1925: 202 (Valloniidae subf.; as a synonym of Spelaeodiscinae).

Shell dextral, rarely sinistral, depressed, microhelicoid. Embryonic whorls with microscopic granulation. Postembryonic whorls distinctly and regularly ribbed. Aperture with or without teeth, but entering lamellae or plicae always absent. Aperture margins moderately reflexed, rarely simple. Umbilicus open, of various width.

Hermaphroditic duct without separate

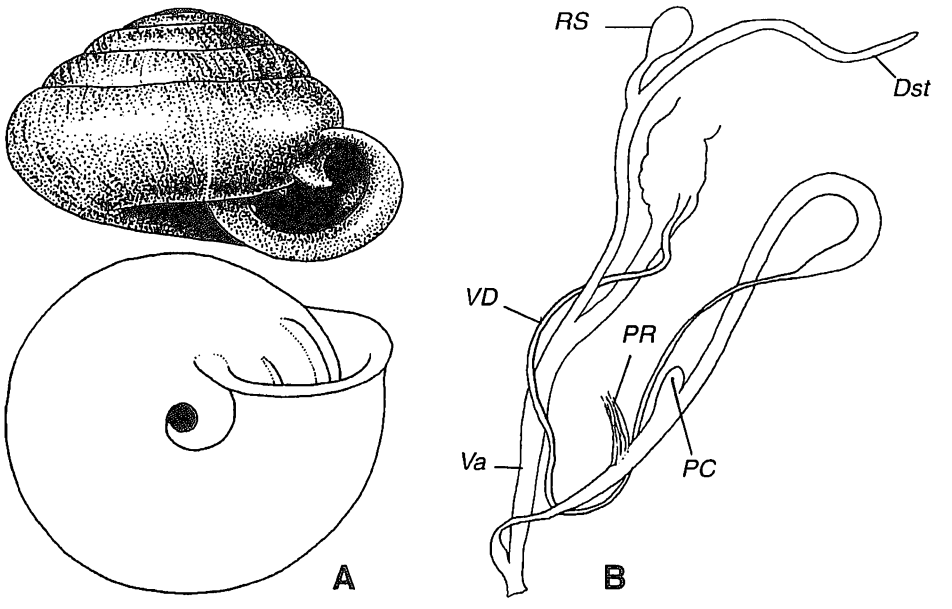


Fig. 99. ***Eostrobilops hirasei*** (Pilsbry, 1927).
A — shell: Quelpart (Cheiju) Island, Korea. Holotype. **Phil.** No. 95251a.
!.***Eostrobilops nipponica*** (Pilsbry, 1927). B — reproductive tract. After Minato, 1975.

seminal vesicles. Prostate short to medium, of many acini. Penial verge lacking. Both penial caecum and penial appendix always present. Spermathecal stalk without diverticle, markedly swollen, reservoir not reaching albumen gland.

DISTRIBUTION. SE Europe.

Spelaeodiscus Brusina, 1886
Fig. 100

Brusina, 1886: 37. Bole, 1965: 349.

TYPE SPECIES — *Helix hauffeni* F. Schmidt, 1855; monotypy.

Shell dextral, flattened, turbinate, rather thin, of 3.5-6.5 moderately convex whorls. Last whorl not descending in front. Color yellowish to brown. Radial ribs on postembryonic whorls without periostracal fringes. Aperture rounded, with thin, simple margins. Umbilicus wide. Height 1.1-2.2, diam. 1.9-3.5 mm (2.0 × 3.4 mm).

Prostate consisting of several large, well-defined acini. Vas deferens long and slender, entering epiphallus terminally. Latter rather long, subcylindrical, with a short caecum. Penis more or less cylindrical, with two appendages: the first (proximal) vermiform, short, located at penis/epiphallus junction; the other is normal pupilloid appendix: A-1 rather long, A-2+A-3 shortly spindle-shaped, A-4 relatively short, A-5 of usual structure. One of arms of penial appendix attached to A-1, the other — at base of proximal appendix. Vagina very short. Spermathecal stalk broad, reservoir voluminous.

DISTRIBUTION. N Albania, Jugoslavia, NE Serbia, Bulgaria, Romania, Austria, Hungary, Slovakia. 5-6 spp.

Aspasita Westerlund, 1889
Fig. 101

Westerlund, 1889 (1884-1890): 18, 26 (*Spelaeodiscus* subg.).

TYPE SPECIES — *Helix triaria* Rossmaessler, 1839; monotypy.

Shell dextral, more or less flattened, turbinate, relatively solid, of 5-6 moderately convex whorls. Last whorl usually somewhat descending in front. Color corneous to

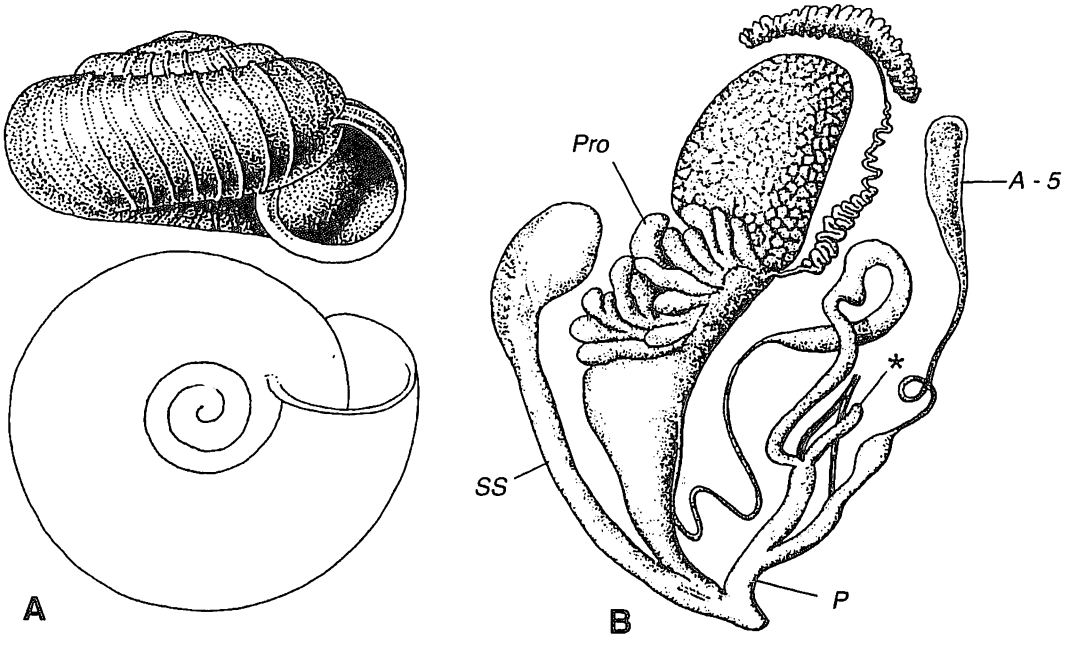


Fig. 100. *Spelaeodiscus hauffeni* (F. Schmidt, 1855).
A — shell: cave "Spodnja Skednevnica" near Velike Lasce, Serbia. **Paris.** B — reproductive tract; asterisk indicates proximal penial appendix. After Bole, 1965;

reddish-brown. Radial ribs on postembryonic whorls without periostracal fringes. Aperture with more or less thickened margins and usually with 1-3 tooth-like tubercles; rarely teeth absent. Umbilicus wide. Height 2.4-3.0, diam. 3.4-6.3 (2.8 × 6.0 mm).

Talon, a short swelling of carrefour apex. Vas deferens long, entering swollen part of epiphallus terminally. Epiphallus rather short, clavate; at entrance of vas deferens, within enlarged section of epiphallus, there is additional narrow slit-like cavity (remnant of epiphallic caecum?). Penis irregularly cylindrical, internally with irregular folds of longitudinal orientation. Penial caecum conic, internally with longitudinal partition. A-1+A-2+A-3 cylindrical, A-4 short. Penial retractor branched at short distance from diaphragm, appendical arm inserted to basal section of appendix (result of fusion of A-1, A-2, and A-3), the other — to upper section of penis just below penial caecum. Spermathecal stalk branched off very low, therefore vagina extremely short.

DISTRIBUTION. Carpathians, High Tatra Mts., Bulgaria, Albania. Probably 1 sp. with a few subspp.

Virpazaria Gittenberger, 1969

Gittenberger, 1969: 297.

TYPE SPECIES — *Virpazaria adrianae* Gittenberger, 1969; OD.

Shell dextral, depressed to nearly flat, thin, glass-like, of 4-5.5 rather convex whorls. Last whorl direct or a little descending in front. Colorless. Postembryonic whorls with thin, regular, partially periostracal ribs. Aperture subvertical, narrow, lunate, almost free, obstructed by elements of aperture armature. Parietal wall with callus hanging downward as a high lamella, which sometimes rd shell position). Basal

and palatal teeth also present.

DISTRIBUTION. Jugoslavia.

Virpazaria (*Virpazaria* s. str.) Fig. 102

Parietal callus thickened. Aperture margins with internal white lip, upon which there are 2-3 tooth-like thickenings. Palatal

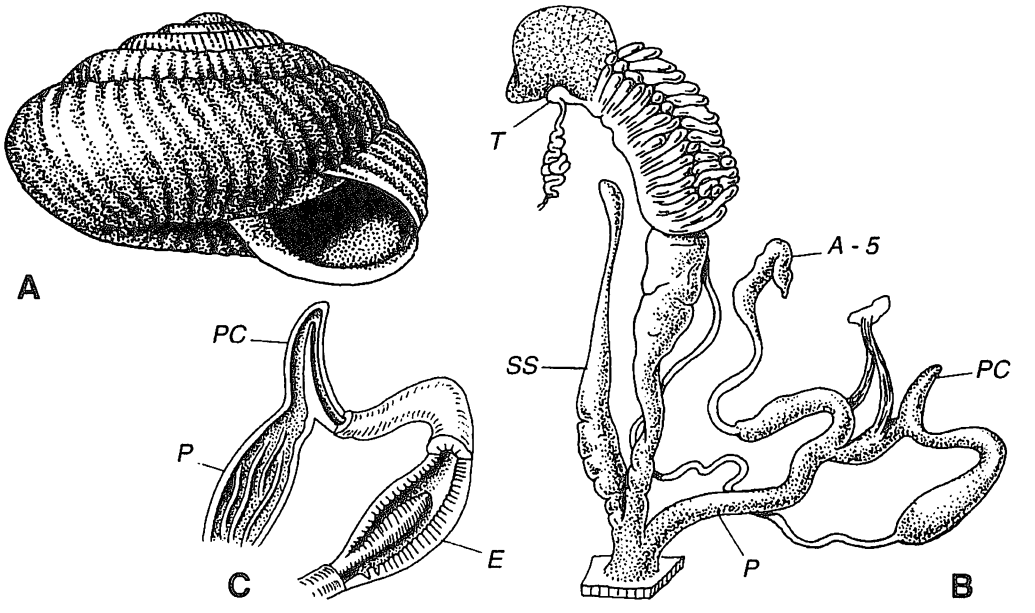


Fig. 101. ***Aspasita triaria*** (Rossmaessler, 1839) f. ***triadis*** Kimakowicz, 1884.
Ledenika Cave, env. of Vrac, Stara Planina, Bulgaria, July 4, 1969. **SPb.** A — shell; B — reproductive tract; C — interior of distal male part.

elongated plica absent. Height 1.5-2.3, diam. 3.0-4.2 mm (1.8 × 3.2 mm).

Talon hidden in albumen gland. Vas deferens short, entering epiphallus apically. Epiphallus of moderate length, without traces of ceacum. Penis of irregular shape, with short, blunt caecum. Penial appendix of common structure. Both arms of penial retractor very short. Appendical branch attached to A-1, the other — to the very upper section of penis at entrance of epiphallus and caecum. Free oviduct and vagina very short, of about equal length.

DISTRIBUTION. Jugoslavia, Montenegro. 4 spp.

Virpazaria (*Aemiliella* Gittenberger, 1969) Fig. 103

Gittenberger, 1969: 302.

Type species — *Virpazaria* (*Aemiliella*) *ripkeni* Gittenberger, 1969; OD.

Parietal callus thin. Aperture margins without lip. There are two basal tubercles and a little elongated palatal plica. Height 1.7-2.5, diam. 3.0-4.3 mm (2.3 × 4.1 mm).

DISTRIBUTION. Cave Soko, Soko Mt., southern Montenegro. 1 sp.

Klemmia Gittenberger, 1969 Fig. 104

Gittenberger, 1969: 304.

TYPE SPECIES — *Klemmia sinistrorsa* Gittenberger, 1969; OD.

Shell sinistral, much flattened, thin, glass-like, of 5-5.5 convex, somewhat shouldered whorls. Last whorl not descending, with slightly flattened, compressed periphery. Colorless. Riblets on postembryonic whorls very thin, periostracal, widely spaced. Aperture narrow, semilunar, nearly vertical, with thin margins, toothless except for more or less developed thickening of palatal margin. Umbilicus comparatively narrow but perspective. Height 1.7-2.5, diam. 3.0-4.3 mm (2.0 × 4.2 mm).

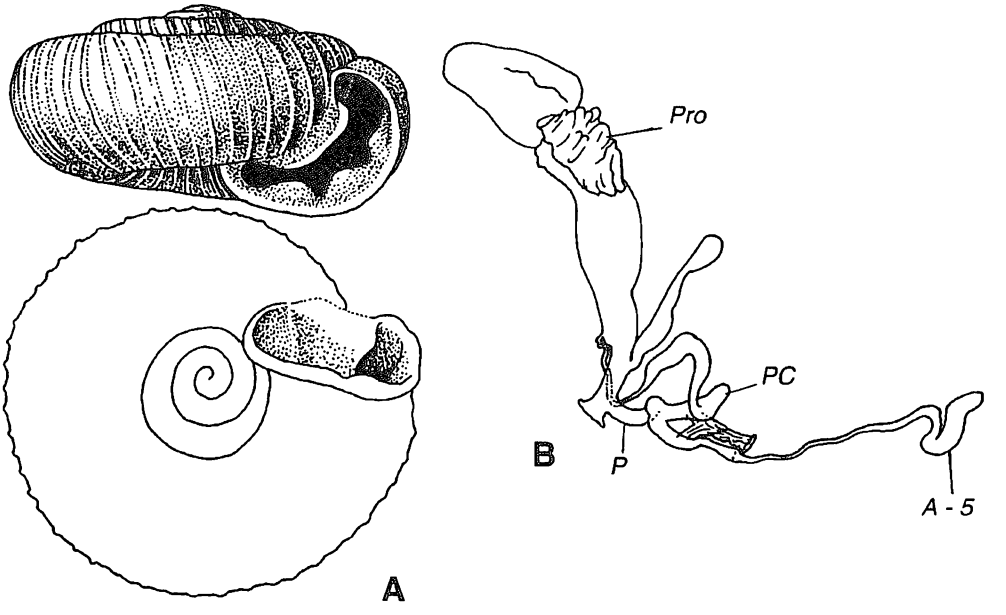


Fig. 102. *Virpazaria (Virpazaria) adrianae* Gittenberger, 1969.
A — shell: Vranjina near Virpazar, Montenegro, Jugoslavia. **Moscow** No. Lc-19573 (**Leiden**). ! *Virpazaria Virpazaria) deelemanorum* Gittenberger, 1975. B — reproductive tract. After Gittenberger, 1975.

Talon not visible superficially. Vas deferens short, entering epiphallus subapically. Epiphallus also short, with a minute side swelling (perhaps, a vestigial epiphallic caecum). Penis bulky, with short, blunt caecum. Penial apendix normally developed. Penial retractor splitted very low, appendical arm attached to A-1, the other arm — to middle section of penis. Free oviduct and vagina of about equal length.

DISTRIBUTION. Jugoslavia, Montenegro. 2 spp.

VALLONIIDAE Morse, 1864

Morse, 1864: 5, 21 (as Valloninae).

Shell small to minute, microhelicoid or depressed, thin-walled, sometimes with periostracal riblets. Aperture generally toothless.

Prostate composed of few lobes at base of albumen gland. Penis internally with or without verge. Penial appendix and caecum primarily present. Spermatheca with short stalk and small reservoir; diverticle of sper-

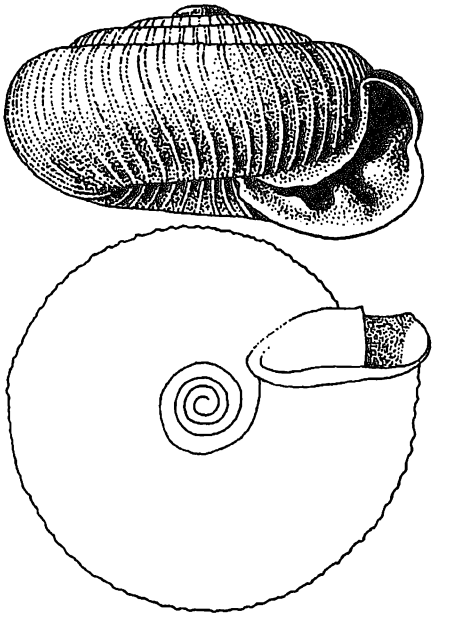


Fig. 103. *Virpazaria (Aemiliella) ripkeni* Gittenberger, 1969.
Cave Soko (Gross Grotte), Soko Mt., at Dupilo W of Virpazar, Montenegro. Paratype. **Leiden**.

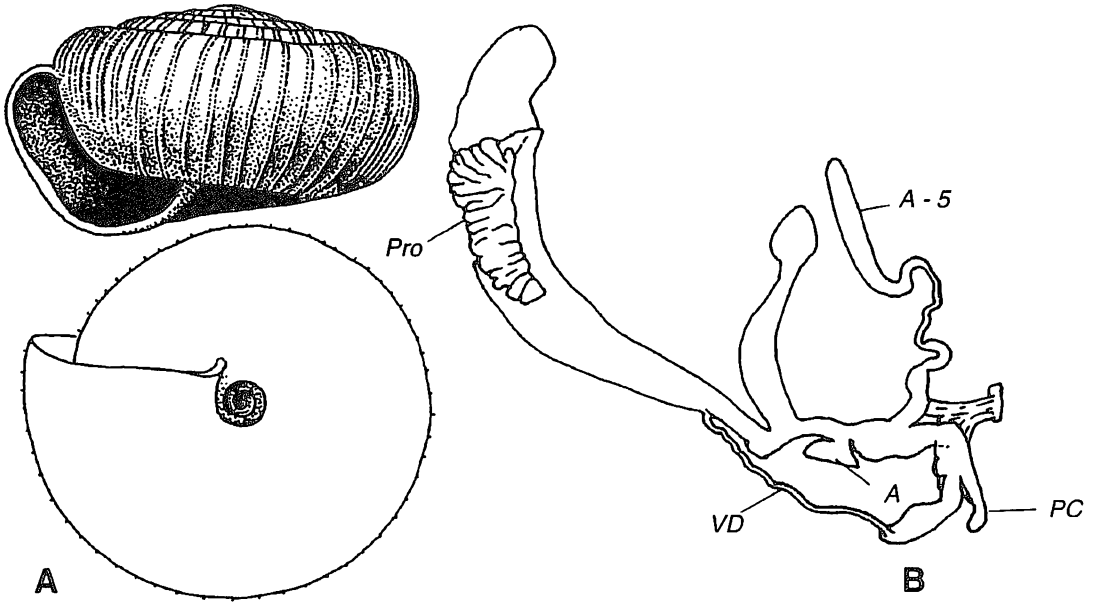


Fig. 104. ***Klemmia sinistrorsa*** Gittenberger, 1969.
A — shell: Vilina Pecina, Montenegro. **Moscow** No. Lc-19637 (**Leiden**). B — reproductive tract. After Gittenberger, 1975.

mathecal stalk sometimes present. Well expressed proterandria is characteristic, which often leads to aphallia.

DISTRIBUTION. World-wide.

REMARK. Generally accepted classification of the family, presented here, seems to be artificial and needs a fundamental revision based on anatomical research; this especially concerns Acanthinulinae.

ACANTHINULINAE Steenberg, 1917

Steenberg, 1917: 14.

— Pupisomidae Iredale, 1930: 236.

Shell high conic, ovate or turbinate, fragile, thin, brownish, olive, or chestnut. Aperture margins thin, not reflexed, without lip (only exception — *Salpingoma*, having a strong lip). Both embryonic and postnuclear whorls sometimes with fine, crowded, spiral, incised lines. Besides, on postapical whorls well developed radial periostracal riblets may be present. Umbilicus narrow.

Anatomical diagnosis at the present time cannot be formulated because of too fragmentary data.

DISTRIBUTION. Almost circumglobally.

Pupisoma Stoliczka, 1873
Fig. 105

Stoliczka, 1873: 32 (*Pupa* subg.).

— *Imputegla* Iredale, 1937a: 305 (t.-sp. *Pupisoma circumlitum* Hedley, 1897; OD).

— *Parazoogenetes* Habe, 1956b: 111 (t.-sp. *Helix orcula* Benson, 1850; monotypy).

TYPE SPECIES — *Pupa lignicola* Stoliczka, 1871; OD.

Shell subconic or ovate, fragile, of 4-5.5 rather convex whorls. Last whorl not deflected. Color light corneous. Embryonic whorls smooth, later whorls with very delicate irregular radial striation and distinct granulation. Aperture ample, irregularly rounded, with thin simple margins. Parietal wall smooth or with small tubercle-like lamella; columellar margin usually with a smoothed

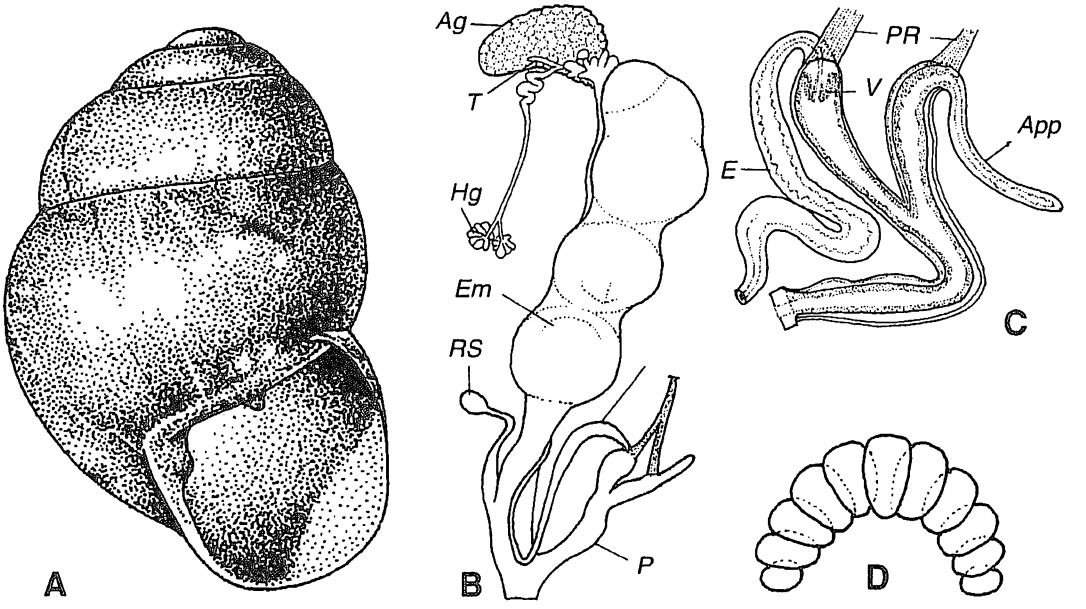


Fig. 105. ***Pupisoma lignicola*** (Stoliczka, 1871).
A — shell: Moulmein, Burma. **Phil.** No. 62168.
! ***Pupisoma mediamericanum*** Pilsbry, 1920. B — reproductive apparatus. After Baker, 1927.
! ***Pupisoma comicolense*** Baker, 1927. C — distal male division; D — jaw. After Baker, 1927

non-entering lamella occupying upper portion of margin. Umbilicus dot-like. Height 1.3-3.0, diam. 1.2-1.8 mm (2.5 × 1.6 mm).

Jaw polyplacognathous, i.e. consisting of plates, that may be either overlapping or each plate separated by very narrow clear space.

Talon short, cylindrical. Epiphallus entering penis through a small completed (closed) verge. Penial appendix somewhat rudimentary, scarcely subdivided into sections. Penial retractor biramous, penial arm attaching to penis/epiphallus junction, the other — to mid part of appendix. Uterus contains a few embryos. Both free oviduct and vagina short. Spermathecal stalk short, reservoir small.

DISTRIBUTION. Humid tropical and subtropical regions of both hemispheres. About 18 spp. & subspp.

REMARK. It is quite possible that Asian-African and American species belong to different genera. Type species occurs in Asia (Burma), while all known anatomical data are based only on American (Mexican) species.

Ptychopatula Pilsbry, 1889
Fig. 106

Pilsbry, 1889: 191.

TYPE SPECIES — *Helix caeca* Guppy, 1868 (=*Helix dioscoricola* C. Adams, 1845); OD.

Shell turbinate, very fragile, silky glossy, of 3.5-4 moderately convex whorls. Last whorl direct, evenly rounded at periphery. Apex widely rounded. Color corneous to dark brown. Embryonic whorls practically smooth, postnuclear whorls silky radially striatulate. Aperture subcircular, with thin and simple margins; columellar margin reflexed. Umbilicus dot-like. Height 1.5-2.2, diam. 1.5-2.3 mm (1.8 × 1.7 mm).

DISTRIBUTION. Tropical and subtropical regions of Africa, Asia, America and Australia. About 10 spp. & subspp.

Salpingoma Haas, 1937
Fig. 107

Haas, 1937: 10 (*Pupisoma* subg.).

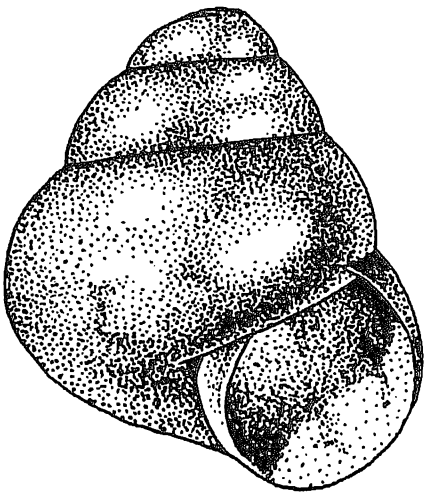


Fig. 106. ! ***Ptychopatula bailyi*** (Pilsbry, 1934). Cuernavaca, State of Moreles, Mexico. Holotype. **Phil.** No. 156099.

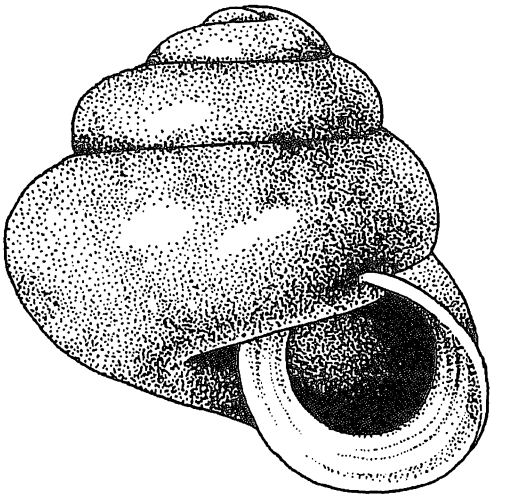


Fig. 107. ***Salpingoma harpula*** (Reinhardt, 1886). Tokyo, Kanda, Japan. Paratype. **Senck.** No. 3 444.

TYPE SPECIES — *Helix (Acanthinula) harpula* Reinhardt, 1886; OD.

Shell turbinate, thin, silky glossy, of 4-5 very convex whorls. Last whorl scarcely descending at very end. Color corneous. Embryonic whorls practically smooth, subsequent whorls with delicate radial striae and distinct spiral grooves (especially on body whorl). Aperture subcircular, toothless, well oblique, with a strong white lip inside; edges of aperture thin. Umbilicus narrow, cylindrical. Height 1.3-1.5 (?2.2), diam. 1.3-1.5 mm (1.4 × 1.3 mm).

DISTRIBUTION. Japan, Java, ?Andaman Islands. 3-4 spp.

Zoogenetes Morse, 1864
Fig. 108

Morse, 1864: 32.

— *Zoogenites* Morse, 1864: 32 [nom. err. pro *Zoogenetes* (line priority)].

TYPE SPECIES — *Helix harpa* Say, 1824; monotypy.

Shell high-conic, fragile, somewhat elastic, translucent, of about 4 convex whorls. Last whorl not descending. Color corneous-greenish or olive. Embryonic whorls with exceptionally fine uneven spiral striae; postnuclear whorls with rather low radial periostracal riblets, and very fine radial striation between them. Aperture ovate, somewhat oblique, with thin, non-reflexed, margins. Umbilicus very narrow, cylindrical. Height 3.0-5.2, diam. 2.5-3.5 mm (4.7 × 3.3 mm).

All 12 specimens dissected, were aphallic; same data were obtained by Steenberg (1925, pl. 29). Pilsbry (1948: 1042, fig. 557) gave a description and drawing of euphallic specimen.

Talon short, non-hidden. Vas deferens short, entering epiphallus apically. Epiphallus elongate-fusiform. A-1, A-2 and A-3 fused, A-4 unusually short, A-5 of moderate length. Uterus containing 2-3 eggs and 2-3 embryos. Spermatheca rather short, slender, without distinct subdivision into stalk and reservoir.

DISTRIBUTION. Circumboreal-Alpine area in Northern hemisphere. 1 sp.

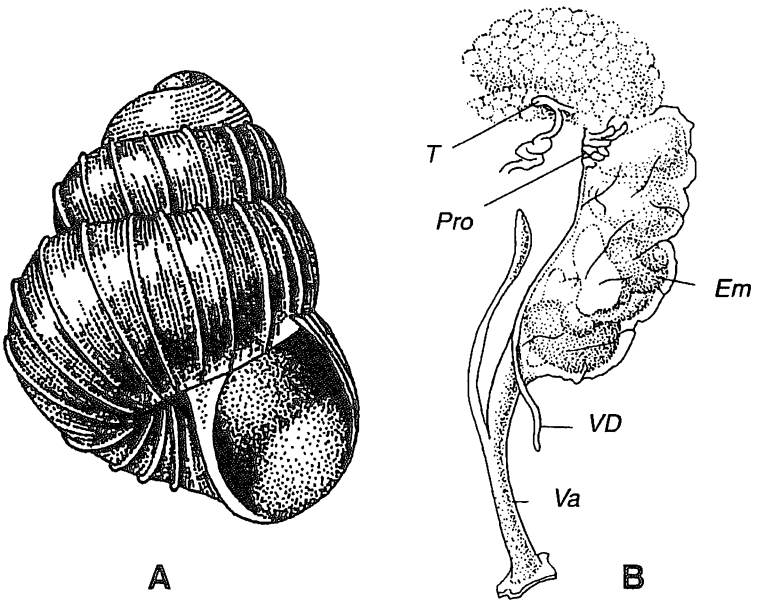


Fig. 108. ***Zoogenetes harpa*** (Say, 1824).
SE shore of Imandra Lake, Kola Peninsula, N Russia, August 20, 1960. Aphallic specimen. **Moscow** No. Lc-23224. A — shell; B — reproductive tract.

Acanthinula Beck, 1847
Fig. 109

Beck, 1847: 109.

— *Achantinula* Betta, 1870: 30 (nom. err. pro *Acanthinula* Beck, 1847).

— *Euacanthinula* Westerlund, 1889 (1884-1890): 16 (t.-sp. *Helix aculeata* Müller, 1774; SD Pilsbry, 1922).

— *Aulaca* Westerlund, 1902: 89 (t.-sp. *Helix aculeata* Müller, 1774; SD Pilsbry, 1922).

TYPE SPECIES — *Helix aculeata* Müller, 1774; SD Martens in Albers, 1860.

Shell turbinate, thin, fragile, of 4 convex whorls. Last whorl not descending. Color corneous to dark brown. Embryonic whorls with distinct spiral threads. Postembryonic sculpture of periostracal lamellate riblets, elongated into triangular processes on periphery of whorls; besides, weak spiral lines sometimes visible. Aperture rounded, oblique, with thin margins; columellar and basal margins more or less reflexed. Umbilicus narrow, cylindrical. Height 1.7-2.1, diam. 2.0-2.3 mm (2.0 × 2.0 mm).

All 9 specimens dissected were found to be aphallic.

Vas deferens unusually short, enlarged distally, entering a short fusiform epiphallus between two small caeca. Penis cylindrical, of moderate length. Penial appendix attached to lower portion of penis. A-1 + A-2 short; A-3 variously developed; A-4 short to rather long, A-5 shortly clavate. Appendical arm of penial retractor attached to A-1 + A-2, the other arm — to one of penial caeca subterminally. Spermatheca composed of slender stalk and small reservoir not approaching albumen gland.

DISTRIBUTION. Europe, Caucasus, N and E Africa, Canary Islands, Azores, Asia Minor. 2 spp.

Spermodea Westerlund, 1902
Fig. 110

Westerlund, 1902: 90.

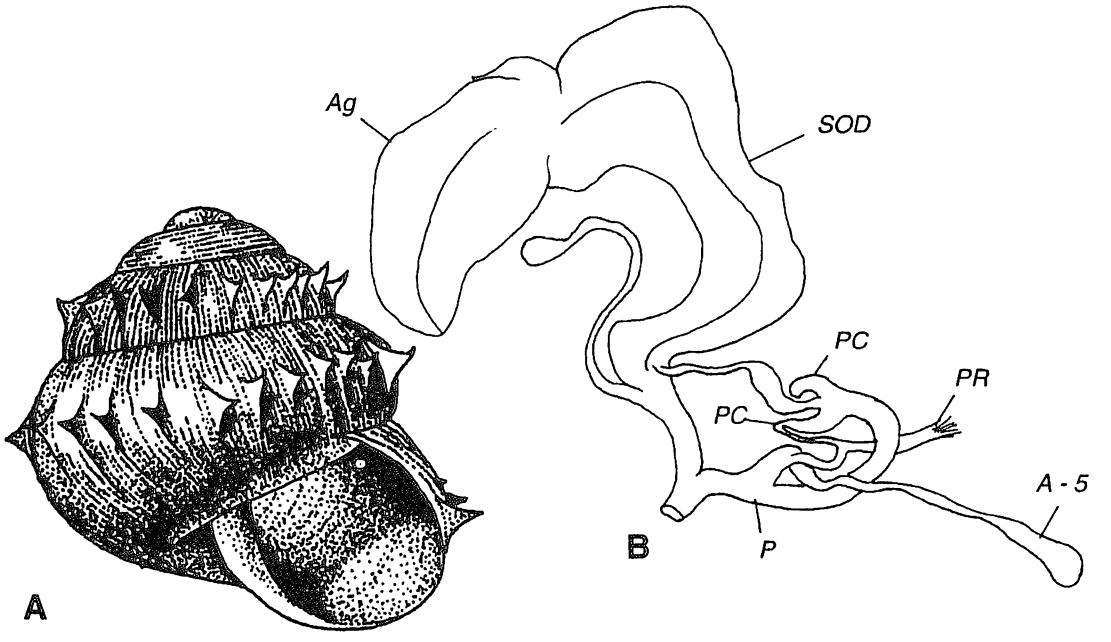


Fig. 109. *Acanthinula aculeata* (Müller, 1774).
A — shell: Zhavoronki village near Moscow. **Moscow** No. Lc-23216. B — reproductive tract. After Giusti, 1968.

TYPE SPECIES — *Helix lamellata* Jeffreys, 1830; monotypy.

Shell dome-shaped, thin, silky glossy, of 5.5-6 convex whorls. Color horn to reddish. Embryonic whorls with microscopical granulae, later whorls with thin, lamellate, periostracal riblets; between riblets there is a very delicate radial striation. Aperture widely lunate, with thin margins. Umbilicus narrowly open, cylindrical. Height 1.5-2.3, diam. 1.9-2.3 mm (2.1 × 2.0 mm).

Two specimens dissected were aphallic.

DISTRIBUTION. West Europe (Germany, Denmark, Norway, Sweden, British islands, Portugal. 2 sp.

VALLONIINAE Morse, 1864

Shell much depressed, light colored, often glass-like, translucent to transparent. Margins of aperture thin, much reflexed and expanded, more or less thickened inside. Spiral sculpture mostly (but not always) absent or expressed weakly and only on embryonic whorls. Later whorls smooth or furnished with spaced periostracal radial ribs; rarely radial sculpture represented by folds of calcareous layer rather than by periostracal elements. Umbilicus wide, perspective.

It is hard to formulate anatomical diagnosis, because aphallia is very characteristic for members of the subfamily, and specimens having well developed male division are very rare. It should be noted that penial appendix present, penial retractor forked, penial caecum and diverticle of spermathecal stalk absent.

DISTRIBUTION. Holarctic.

Plagyrona Gittenberger, 1977
Fig. 111

Gittenberger, 1977: 297.

TYPE SPECIES — *Helix debeauxiana* Bourguignat, 1863 (=*Helix placida* Shuttleworth, 1852: Waldén, 1983); OD.

Shell turbinate, thin, translucent, of about 3.5 convex whorls. Last whorl scarcely descending. Color yellowish-corneous. Embryonic whorls with microscopic spiral threads. Postnuclear sculpture consists of

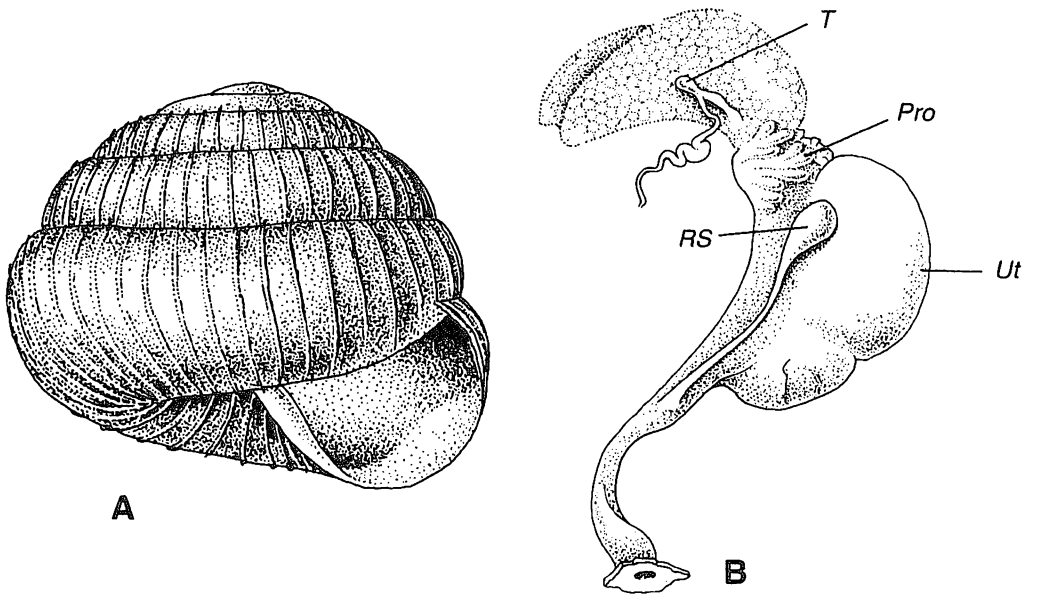


Fig. 110. *Spermodea lamellata* (Jeffreys, 1830).
NW of Witerslack Hall, Westmorland, U.K., May 22, 1982. **Moscow** No. Lc-23223 (**Cardiff** No. 2.1993.052.017).

delicate radial riblets and finer spiral wavy lines. Aperture widely ovate, with simple margins; columellar margin expanded. Umbilicus rather broad. Height up to 1.5, diam. up to 2.2 mm (1.5 × 2.1 mm).

DISTRIBUTION. Canary Islands, Madeira, Algeria, Portugal, Greece (Ionian Islands Kerkyra, Ithaki, Kephallinia). Probably 1 sp.

Gittenbergia Giusti et Manganelli, 1986
Fig. 112

Giusti & Manganelli, 1986: 178.

TYPE SPECIES — *Helix sororcula* Benoit, 1859; OD.

Shell depressed, thin, fragile, of about 4 moderately convex whorls. Last whorl slightly descending in front. Color milky-white or ivory. Embryonic sculpture of microscopic malleation, delicate spiral striae and widely spaced shallow spiral grooves. Postnuclear whorls with low, delicate, periostracal riblets, interimposed with finer radial striae; spiral lines retained. Aperture

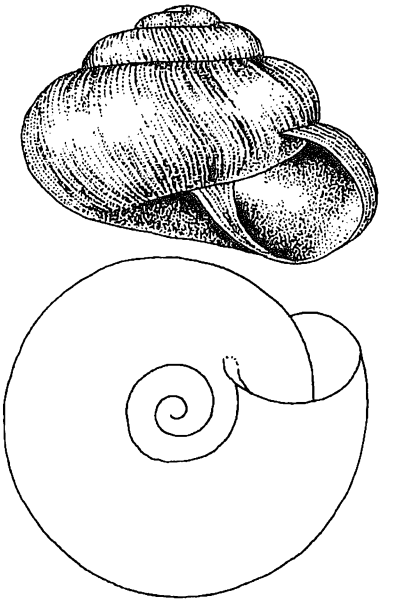


Fig. 111. *Plagyrona placida* (Shuttleworth, 1852).
Madeira. **Moscow** No. Lc-23192 (**Paris**)

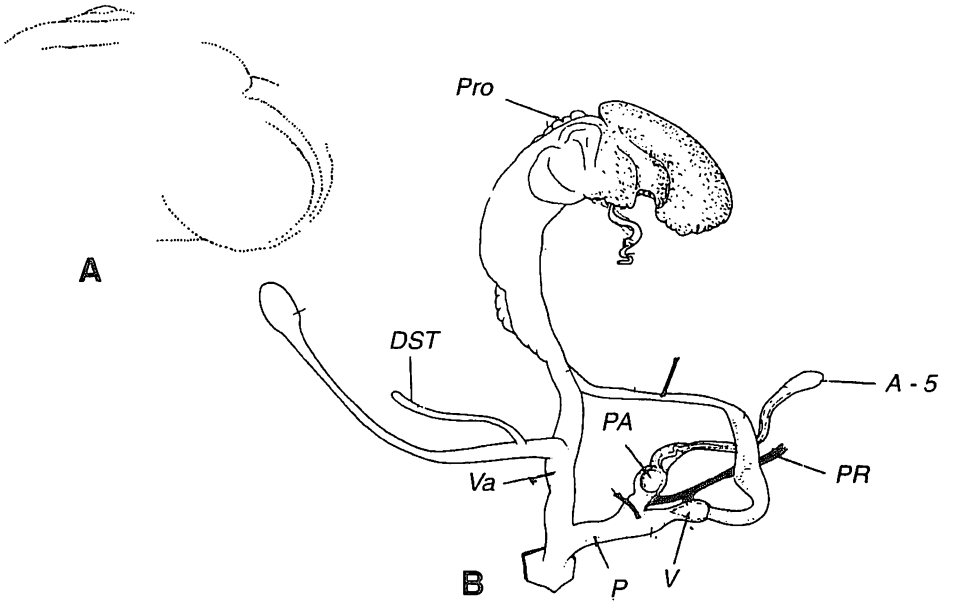


Fig. 112. ***Gittenbergia sororcula*** (Benoit, 1859).
A — shell. After Gittenberger, 1977. B — reproductive tract. After Giusti & Manganelli, 1986.

with thin, simple margins; columellar margin somewhat reflexed. Umbilicus broadly open. Height 1.5, diam. 2.7 mm.

Vas deferens rather short, entering epiphallus apically. Penis internally with long, pointed verge. A-1 very short, A-2 enlarged, containing subglobular papilla. A-3 well developed, A-4 and A-5 relatively short. Spermathecal stalk with slender, short diverticle.

DISTRIBUTION. Italy, western coast of Adriatic Sea and eastern coast of Greece. 1 sp.

Planogyra Morse, 1864
Fig. 113

Morse, 1864: 24.

TYPE SPECIES — *Helix asteriscus* Morse, 1857; by monotypy.

Shell flattened, very thin, silky glossy, subtransparent, of about 3.5 convex whorls. Last whorl a little deflected, evenly rounded at periphery. Color pale brown. Embryonic sculpture of indistinct microscopic granulation; postnuclear whorls with widely spaced membranous periostracal ribs; intervals sharply, minutely radially striated and faintly marked with very crowded spiral lines. Aperture subcircular, with thin peristome. Umbilicus broadly open, quite perspective. Height 0.9-1.2, diam. 1.8-2.0 mm (1.0 × 2.0 mm).

Hermaphroditic gland of two lobes, each composed of few globular acini. Hermaphroditic duct strongly swollen, convolute. Carrefour hidden by prostate, talon scarcely represented as a curvature of hermaphroditic duct. Prostate short, of few digitate acini. Epiphallus swollen, thick-walled, entering slender penis through exceptionally short verge. A-1 and A-2 externally fused, cavity of this section almost filled by a large papilla; A-3 clearly expressed; A-4 and A-5 short. Penial retractor attached around base of epiphallus. Vagina long. Spermathecal stalk of medium length, slightly expanded basally, reservoir more or less swollen.

DISTRIBUTION. Northern parts of North America (territories bordering on the St. Lawrence and Great Lakes drainage; New

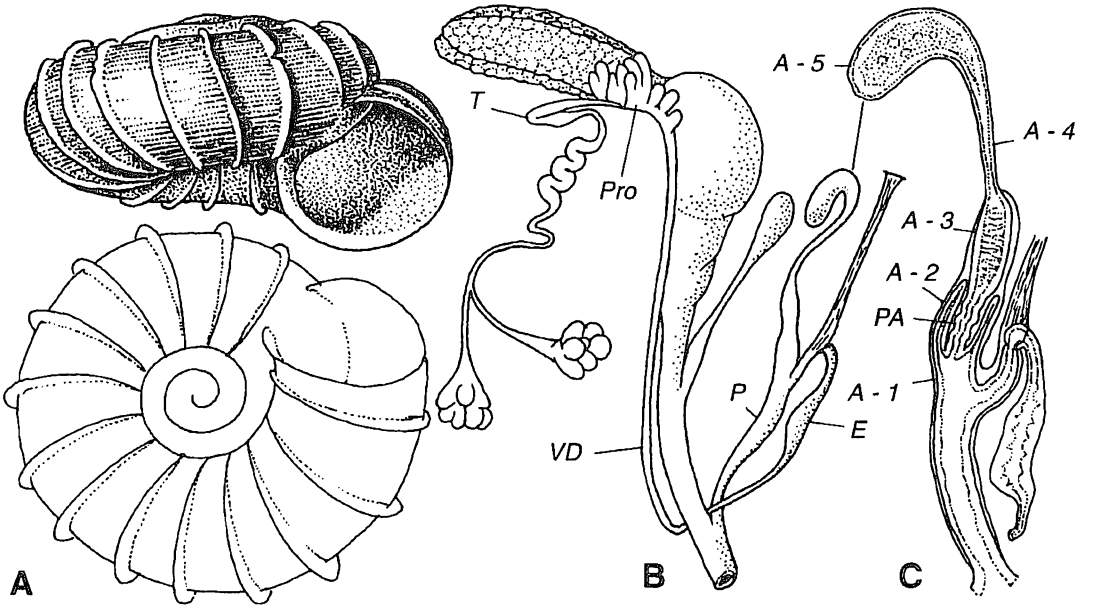


Fig. 113. ***Planogyra asteriscus*** (Morse, 1857).
A — shell: Maine, U.S.A. **Moscow** No. Lc-23225. B — reproductive tract; C — interior of penis and appendix. After Pilsbry, 1948.

England; British Columbia to Oregon, west to the Cascade Range). 2 spp.

Vallonia Risso, 1826

Risso, 1826: 101 (*Helix* subg.).

— *Amplexis* T. Brown, 1827: pl. 12, fig. 76, 77 [t.-sp. *Amplexis paludosus* Brown, 1827 (=*Helix pulchella* Müller, 1774); SD Pilsbry, 1935].

— *Zurama* Leach in Turton, 1831: 64 (in synonymy of *Helix pulchella* Müller, 1774).

— *Circinaria* Beck, 1837: 16 (*Helix* subg.; t.-sp. *Helix pulchella* Müller, 1774; SD Herrmannsen, 1847).

— *Lucena* Gray in Turton, 1840: 142 (nom. praeocc., non Hartmann, 1821; t.-sp. *Helix pulchella* Müller, 1774; monotypy).

— *Amplexus* T. Brown, 1844: 45 (nom. praeocc., non Sowerby, 1814; probably misspelling for *Amplexis* Brown, 1827).

— *Glaphyra* Albers, 1850: 87 (*Helix* subg., t.-sp. *Helix pulchella* Müller, 1774, SD Pilsbry, 1935). Gerber, 1996: 48.

TYPE SPECIES — *Helix* (*Vallonia*) *rosalia* Risso, 1826 (=*Helix pulchella* Müller, 1774); monotypy.

Shell depressed to nearly flat, moderately to quite thin. Aperture subcircular, oblique, with reflexed and expanded margins. Places of peristome insertion approached, sometimes aperture free or nearly so. Umbilicus broad, perspective.

DISTRIBUTION. Holarctic.

Vallonia (*Vallonia* s. str.) Fig. 114

Postembryonic whorls nearly smooth or with calcareous and/or periostracal radial riblets. Aperture interrupted on parietal wall. Height 0.9-2.3, diam. 1.9-4.0 mm (1.3 × 2.4 mm).

I dissected more than 100 specimens of three species from many points of Russia, all of them were aphallic. Recently Giusti & Manganelli (1986) gave description and drawings of reproductive anatomy of euphallic specimens of two *Vallonia* species.

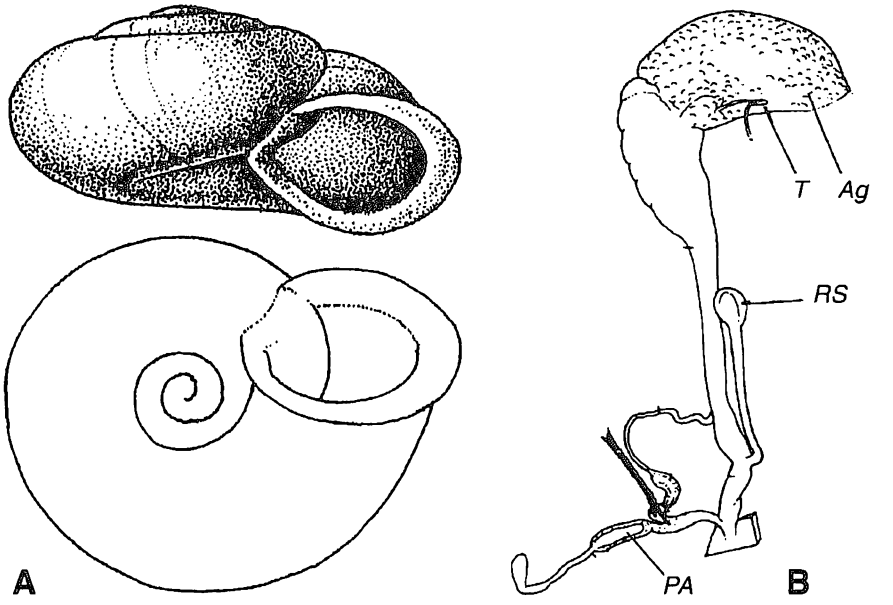


Fig. 114. ***Vallonia (Vallonia) pulchella*** (Müller, 1974).
A — shell: Moscow, Kuntzevo, July 25, 1977. **Moscow** No. Lc-23208.
! ***Vallonia (Vallonia) costata*** (Müller, 1774). B — reproductive tract. After Giusti & Manganelli, 1986.

Talon, a simple bending of distal part of hermaphroditic duct. Vas deferens rather short, entering enlarged epiphallus terminally. Penis short, internally with a verge. Penial appendix composed of 3 sections: basal section (A-1 + A-2 + A-3) containing a long, slender papilla; rather short A-4 and more or less expanded A-5. Penial arm of penial retractor markedly shorter than appendical one. Diverticle of spermathecal stalk absent.

DISTRIBUTION. Holarctic; introduced in a number of countries of South Hemisphere. 22 Recent spp. & subspp.

Vallonia (*Planivallonia* Schileyko, 1984) Fig. 115

Schileyko, 1984: 170. Gerber, 1996: 86 (syn. of *Vallonia* s.str.).

TYPE SPECIES — *Vallonia zaru* Almulıambetova, 1979; OD.

Periostracal riblets on postembryonic whorls absent. Aperture free or nearly so, i.e. slightly detached from penultimate whorl. Height 1.0-1.4, diam. 2.8-3.4 mm (1.0 × 2.8 mm).

DISTRIBUTION. Central Asia, Zailijsky Range. 1 sp.

COCHLICOPOIDEA Pilsbry, 1900

Pilsbry, 1900: 564 (pro fam.).

Shell small, cylindrical-ovate or elongated-ovate, smooth, shining. Embryonic whorls smooth, polished. Aperture ovate, toothless or with complex armature. Aperture margins more or less thickened, not reflexed, without lip. Umbilicus absent.

Head with two pairs of tentacles.

Seminal vesicles not separated from hermaphroditic duct. Prostate ribbon-like. Epiphallus without accessory organs. Penis without characteristic inner structures; sometimes there is a small verge. Penial appendix present or absent, in former case

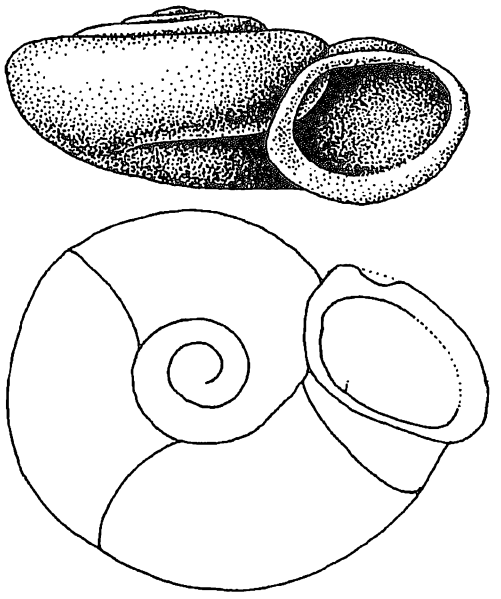


Fig. 115. *Vallonia (Planivallonia) zaru* Almuhambetova, 1979.
Tau-Turgen, Zailijsky Ridge, Kazachstan. Holotype. **SPb.**

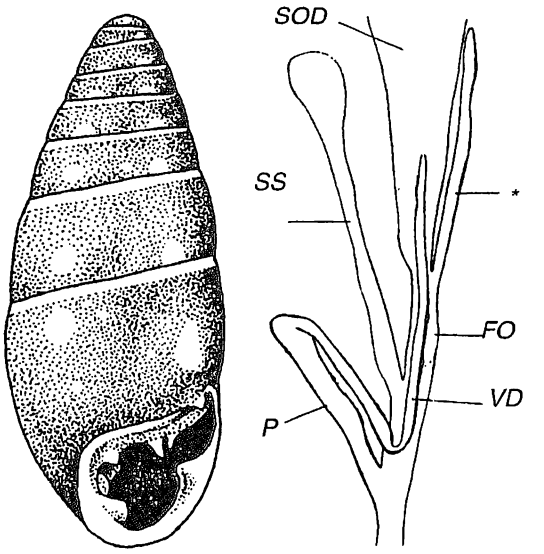


Fig. 116. *Azeca goodalli* (Férussac, 1821).
A — shell: "London" **SPb.** Anatomy — after Boycott, 1919. Asterisk — "diverticle of oviduct"

without its own arm of penial retractor. Spermathecal stalk slender, not long; diverticle, when present, short.

DISTRIBUTION. Holarctic.

COCHLICOPIDAE Pilsbry, 1900

Pilsbry, 1900: 564.

— Zuidae Fagot, 1892: 15, 17 (nom. nud.).

— Cionellidae Kobelt, 1880 (1876-1881): 276 (nom. nud.).

— Azecinae Watson, 1920: 24.

Characters and distribution as in superfamily.

Azeca Fleming, 1828
Fig. 116

Leach in Fleming, 1828: 269.

— ?*Odontalus* Parreyss, 1849: 99 (has been cited as a synonym, but was established for *Pupa tridens* Draparnaud, 1801 = *Helix tridens* Müller, 1774, which belongs to Enidae).

— *Azecastrum* Bourguignat, 1858 (1856-1860): 87 (*Azeca* subg., t.-sp. *Azecastrum tridens*; monotypy).

TYPE SPECIES — *Turbo tridens* Pulteney, 1799 (non Müller, 1774; = *Helix menkeana goodalli* Férussac, 1821); monotypy.

Shell elongated-ovate or fusiform, very shining, rather solid, of 7-8 flattened whorls. Color light corneous to cherry. Suture whitish, margined. Surface polished, with very weak radial wrinklets. Aperture small, triangular pearl-shaped, upper portion of palatal margin shifted backward. Parietal callus usually not thickened, with a small angular tubercle upon it. Aperture margins white. Aperture armature variable, usually well developed. Parietal lamella rather high, thin; supraparietal shorter and lower; subparietal small, curved. Columellar lamella running up vertically along columella. Strong elongated tubercle at baso-columellar angle of aperture. Palatal folds usually two: lower variously developed, remoted

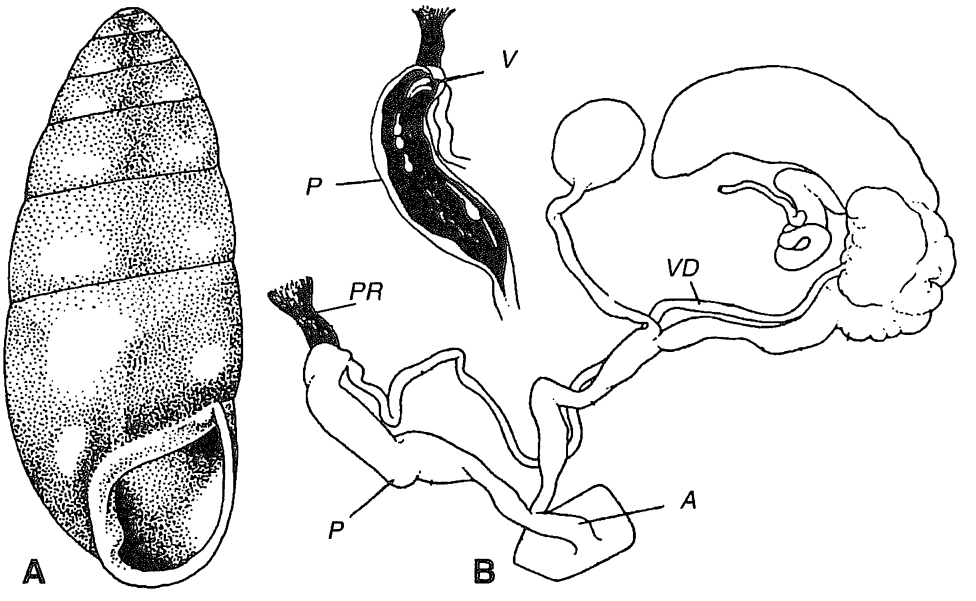


Fig. 117 ***Hypnophila pupaeformis*** (Cantraine, 1836).
A — shell: Zara (Zodar), Croatia. Lectotype. **Leiden.**
! ***Hypnophila dohrni*** (Paulucci, 1882). B — reproductive tract and interior of penis. After Giusti, 1976.

from margin, upper looking like tubercular swelling. Height 5.0-9.0, diam. 2.3-3.0 mm (7.0 × 3.0 mm).

"The vas deferens is remarkably bulky throughout its course, and the walls muscular even in the descending limb, which runs in relation with the oviduct. The ascending limb is really penile in character, and it is hard to fix any point, unless it be at the bend below, where the vas becomes the penis. Arising from the free oviduct, immediately below the beginning of the glandular portion, is a long diverticulum with thin walls, which runs up closely adherent to the spermoviduct, ending blindly above." (Boycott, 1919: 53-54).

DISTRIBUTION. Middle Europe, British Islands. Probably 1 variable sp.

REMARK. Systematic position of *Azeca* is uncertain. First, it is unclear what is "diverticle of oviduct" Gomez & Angulo (1990: 110) report that "unlike the figure published by Boycott, the "diverticulum" is not externally separated from the spermoviduct"and suggest that the diverticle of *Azeca* can be considered homologous to the allospermiduct of other Stylommatophora. Second, we know nothing about inner structure of penis. Third, the structure of kidney is unknown. It can not be excluded that this genus may belong to Ferussaciidae.

Hypnophila Bourguignat, 1858
Fig. 117

Bourguignat, 1858(1856-1860): 88 (*Azeca* subg.).

TYPE SPECIES — *Bulimus pupaeformis* Cantraine, 1836; SD Pilsbry, 1908.

Shell elongate ovate, comparatively solid, of 6-7 flattened whorls. Color amber to chestnut. Suture not or slightly margined. Sculpture practically absent. Aperture rounded to ovate, with well thickened margins. Parietal callus well developed. Aperture armature reduced to a small angular tubercle and short columellar lamella. Height 5-9, diam. 2-3 mm (6.9 × 2.8 mm).

Talon superficially not visible. Vas deferens entering penis subterminally. Penis internally with minute grooved verge and few

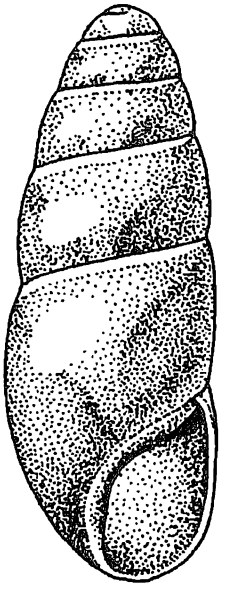


Fig. 118. *Gomphroa boissii* (Dupuy, 1850).
ESE of Le Boulou, Dept. Pyrenees Orient., France. **SPb.**

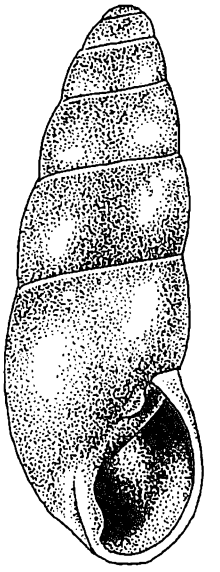


Fig. 119. *Cochlicopa (Sinizua) davidis* (Ancey, 1882).
San-Chuan, China. **SPb.**

minute tubercles. Penial appendix absent. Penial retractor attached to penis apically. Vagina long. Spermathecal stalk without diverticle, reservoir globose, large.

DISTRIBUTION. Southern Europe (Greece, Dalmatia, Italy, Sicily), NW Africa (Algeria, Morocco). 7-9 spp.

Gomphroa Westerlund, 1902
Fig. 118

Westerlund, 1902: 114 (*Zua* subg.).

TYPE SPECIES — *Zua boissyi* Dupuy, 1850; OD.

Shell elongated-ovate to subcylindrical, slender, thin, of about 6 slightly convex whorls. Color yellowish-corneous. Suture markedly margined. Both embryonic and later whorls smooth. Aperture elongate-ovate, toothless, with only slightly thickened margins. Parietal callus weak. Columella indistinctly truncated. Height 3.0-6.0, diam. 1.2-1.8 mm (4.8 × 1.7 mm).

DISTRIBUTION. Pyrenees and Basque country. 1 or 2 spp.

Cochlicopa Férussac, 1821

Férussac, 1821: 28, 50.

— *Cionella* Jeffreys, 1830: 347 (t.-sp. *Helix lubrica* Müller, 1774; subs. monotypy).

— *Zua* Turton, 1831: 82 (t.-sp. *Zua lubrica*; monotypy).

— *Styloides* Fitzinger, 1833: 105 (t.-sp. *Styloides lubricus*; subs. monotypy).

— *Folliculus* Charpentier, 1837: 14 (*Bulimus* subg.; t.-sp. *Bulimus lubricus*; monotypy).

— *Hydastes* Parreyss, 1849: 98 (t.-sp. *Hydastes lubricus*; monotypy).

TYPE SPECIES — *Helix lubrica* Müller, 1774; SD Pilsbry, 1908.

Shell ovate-conic. Aperture relatively narrow, ovate, subvertical, toothless or with angular tubercle. Columella more or less distinctly truncated below.

DISTRIBUTION. Holarctic.

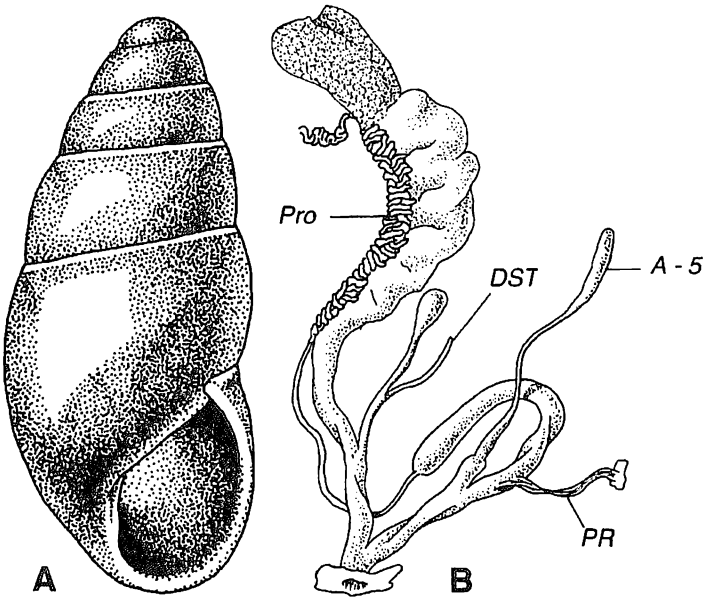


Fig. 120. *Cochlicopa (Cochlicopa) lubrica* (Müller, 1774).
Moscow, Kuntzevo, September 5, 1976. **Moscow** No. Lc-23270: A — shell; B — reproductive tract.

Cochlicopa (*Sinizua* Starobogatov, 1996) Fig. 119

Starobogatov, 1996: 125.

TYPE SPECIES — *Zua davidis* Ancey, 1882; OD.

Shell ovate-turrited to ovate-fusiform, of 5.5-6.3 whorls, with narrowed blunt upper part of spire. Parietal callus thickened at angular region and forms a more or less developed knob or a small tooth. Columellar margin wide above and very slightly narrowing downward; then it abruptly narrowed near basal margin of aperture. Height 5.5-7.5, diam. 2.1-2.8 mm (6.2 × 2.2 mm).

DISTRIBUTION. China, eastern Mongolia. 3 spp.

Cochlicopa (*Cochlicopa* s.str.) Fig. 120

Shell ovate-conic, ovate, or ovate-fusiform, sometimes almost cylindrical, with smoothly blunted apex. Parietal callus thin, without angular thickening or tooth. Width of columellar margin reaching its maximal value at parieto-columellar junction and then smoothly diminishing toward basal margin of aperture. Height 3.6-8.5, diam. 1.8-3.5 mm (5.7 × 2.5 mm).

Vas deferens entering epiphallus apically. Epiphallus subcylindrical to clavate. Penis rather short, cylindrical, interior with indistinct longitudinal folds; no verge. A-1 + A-2 fused, short, remaining sections normally developed; A-4 short. Free oviduct and vagina of moderate length. Spermathecal stalk rather short, diverticle slender, vermiform.

DISTRIBUTION. Holarctic. 6-8 spp. with many forms.

REMARK. Starobogatov (1996) estimated the number of Palearctic species as 24. I prefer to refrain from theoretical discussion on the applicability of comparatory method elaborated and used by Dr. Starobogatov. Just I would like to notice that my experience indicates that this method is not applicable to terrestrial pulmonates.

PUPILLOIDEA Turton, 1831

Turton, 1831: 8 (pro fam.).

Shell small, perforated, ovoid to cylindrical, radially sculptured to nearly smooth. Embryonic whorls smooth or with microscopic vague granulation; rarely pitted. Aperture toothed or toothless, however, entering parietal and columellar lamellae absent; if elongated lamellae present, they occupy only apertural area and developed at subadult stage. Aperture margins more or less reflexed and expanded, often with a lip and neck thickening.

Penis with epiphallus, internally smooth or with weak longitudinal folds. On proximal portion of epiphallus near boundary with penis usually there is a small cylindrical caecum. Penial appendix present. Penial retractor biramous, penial arm inserting more distal than caecum.

DISTRIBUTION. Circumglobally.

PUPILLIDAE Turton, 1831

Turton, 1831: 8, 97.

— Pupidae Fleming, 1828: 255 (as Pupadae).

Aperture with 1-7 teeth, sometimes toothless. Aperture margins mostly reflexed and expanded, rarely nearly straight. Umbilicus narrow — slit-like or dot-like.

Prostata represented by a few acini located under lower edge of albumen gland. Penis internally without verge. Diverticle of spermatheca primarily present, with tendency to reduction.

DISTRIBUTION. All continents.

REMARK. Classification of the family requires a thorough revision based on anatomical investigation. This especially concerns African and Australian taxa. The present system should be considered as only tentative.

PUPILLINAE Turton, 1831

Shell ovate to cylindrical. Whorls tightly coiled, 5-8 in number. Aperture often with neck thickening, mostly with teeth.

Penial caecum present.

DISTRIBUTION. All continents, northward to tundra zone.

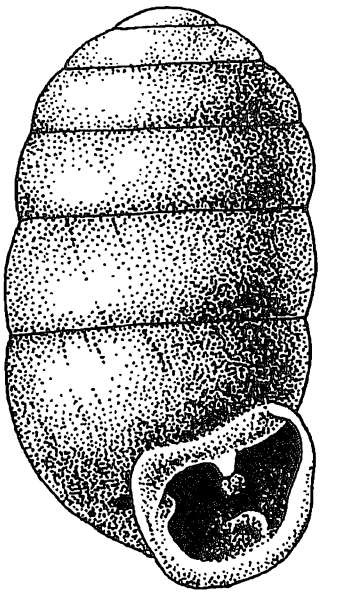


Fig. 121. ***Gibbulinopsis (Gibbulinopsis) pupula*** (Deshayes, 1863).
Reunion Island. **Phil.** No. 64103.

Gibbulinopsis Germain, 1919

Germain, 1919: 265 (*Pupilla* subg.).

TYPE SPECIES — *Orthogibbus pupula* Deshayes, 1863; OD.

Shell ovate to cylindrical-ovate, relatively solid, of 5-7 rather narrow whorls. Color light corneous to chestnut. Aperture usually with 5-6 teeth: angular, parietal, columellar and 2 or 3 palatal; upper palatal often absent. Angular tubercle, when present, lies in plane of aperture; parietal directed perpendicular to plane of aperture.

DISTRIBUTION. Caucasus, Central Asia, Far East, Japan; E Africa; Reunion Island; Australia.

Gibbulinopsis (*Gibbulinopsis* s.str.) Fig. 121

Shell ovate-cylindrical to short-cylindrical, only slightly sculptured. Peristome in-

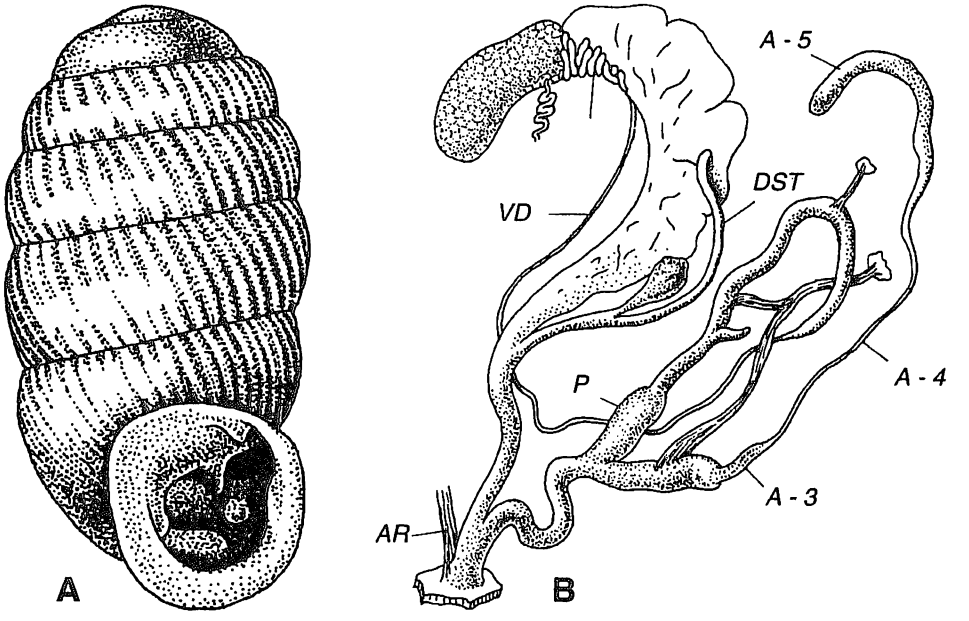


Fig. 122. ***Gibbulinopsis (Primipupilla) signata*** (Mousson, 1873).
Valley of Naryn River above Toktoghul, Tien-Shan Mts. June 1, 1972. **A — shell; B — reproductive tract. Moscow** No.Lc-23194.

terrupted on parietal wall. Height 2.3-3.0, diam. 1.6-1.8 mm (2.8 × 1.8 mm).

DISTRIBUTION. As of genus. About 10 spp.

Gibbulinopsis (*Primipupilla* Pilsbry, 1921)
Fig. 122

Pilsbry, 1921 (1920-1921): 153 (*Pupilla* sect.).
Schileyko, 1984: 174.

TYPE SPECIES — *Pupa signata* Mousson, 1873; OD.

Shell elongated cylindrical, with strong radial ribbing. Aperture entire (uninterrupted) or nearly so. Height 2.3-5.4, diam. 1.2-2.0 mm (4.8 × 1.8 mm).

Vas deferens entering long epiphallus apically. Epiphallus with short conic caecum. Penis long, subcylindrical. Appendical arm of penial retractor much longer than penial; latter attached to epiphallus above caecum. Spermathecal diverticle long.

DISTRIBUTION. Transcaucasia, Iran, Afghanistan, Central Asia, NW China. 5-7 spp.

Pupilla Leach, 1828

Leach in Fleming, 1828: 268.

— *Pupa* Draparnaud, 1801: 32, 56 (part.; nom. praeocc., non Röding, 1798).

— *Torquatella* Held, 1837: 919 (t.-sp. *Turbo muscorum* Linnaeus, 1758; designated here).

TYPE SPECIES — *Pupa marginata* Draparnaud, 1801 (=*Turbo muscorum* Linnaeus, 1758); monotypy (see Gray, 1847: 176).

Shell dextral or (rarely) sinistral, elongated-ovate to cylindrical. Color light corneous to reddish-brown. In aperture no more than 4 teeth: parietal, columellar and 2 palatal; however elements of apertural armature highly variable, teeth relatively weakly developed and tend to reduce down to complete disappearance. Angular tubercle, if present, weakly developed.

DISTRIBUTION. Eurasia, North America, Africa, Australia.

Pupilla (*Afripupilla* Pilsbry, 1921)
Fig. 123

Pilsbry, 1921 (1920-1921): 153 (*Pupilla* sect.).

TYPE SPECIES — *Pupa tetrodus* O. Boettger, 1870; OD.

Shell sinistral, elongated-ovate, tapering upwards, thin, somewhat translucent (like *Gastrocopta*), of about 5 whorls. Color corneous. Embryonic whorls smooth, later whorls with smoothed, not very regular radial wrinklets. Aperture rounded, with reflexed thin margins; columellar margin widely expanded. There are four teeth: parietal lamella vertical; columellar slightly thickened, subhorizontal; palatal tubercle seats at short distance from edge; above it, on the very edge, there is a small swelling of lip. Umbilicus dot-like. Height 3.0-3.5, diam. 1.4-1.7 mm (3.4 × 1.6 mm).

DISTRIBUTION. S Africa. 1 sp.

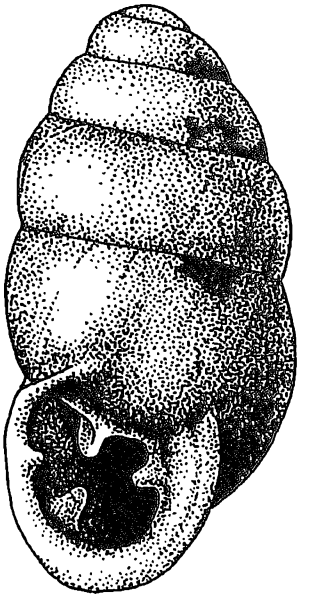


Fig. 123. ***Pupilla (Afripupilla) tetrodus*** (O.Boettger, 1870).
Cradock, S Africa. **Phil.** No. 117280.

Pupilla (*Striopupilla* Pilsbry, 1921)
Fig. 124

Pilsbry, 1921 (1920-1921): 156.

TYPE SPECIES — *Pupa sterkiana* Pilsbry, 1889; OD.

Shell dextral, cylindrical, thin, of 6-7 very convex whorls. Last whorl direct. Apex widely rounded. Embryonic whorls with distinct microsculpture of dots, more or less arranged into spiral rows. Later whorls with regular very thin periostracal riblets. Aperture subcircular, with reflexed and slightly thickened margins. There is a minute tubercle-like columellar lamella at parieto-columellar angle; palatal margin a little concave. Umbilicus dot-like, encircled by weak basal crest. Height 3.8-4.5, diam. 1.3-1.7 mm (4.0 × 1.6 mm).

DISTRIBUTION. Lower California and Guadalupe Island. 3 spp.

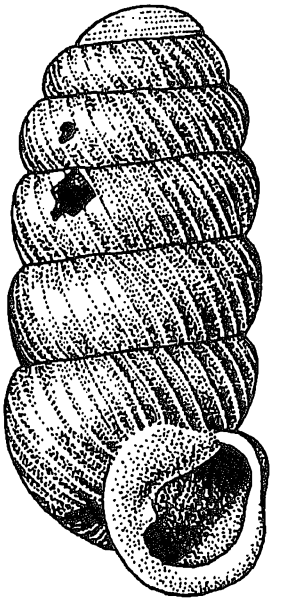


Fig. 124. ***Pupilla (Striopupilla) sterkiana*** (Pilsbry, 1889).
Lower California. Lectotype. **Phil.** No. 60466a.

Pupilla (*Fragipupilla* Schileyko, 1984)
Fig. 125

Schileyko, 1984: 191.

TYPE SPECIES — *Pupilla (Fragipupilla) alabiella* Schileyko, 1984; OD.

Shell dextral, elongated-ovate to nearly cylindrical, thin, fragile, translucent, of 5-6 convex whorls. Last whorl scarcely ascen-

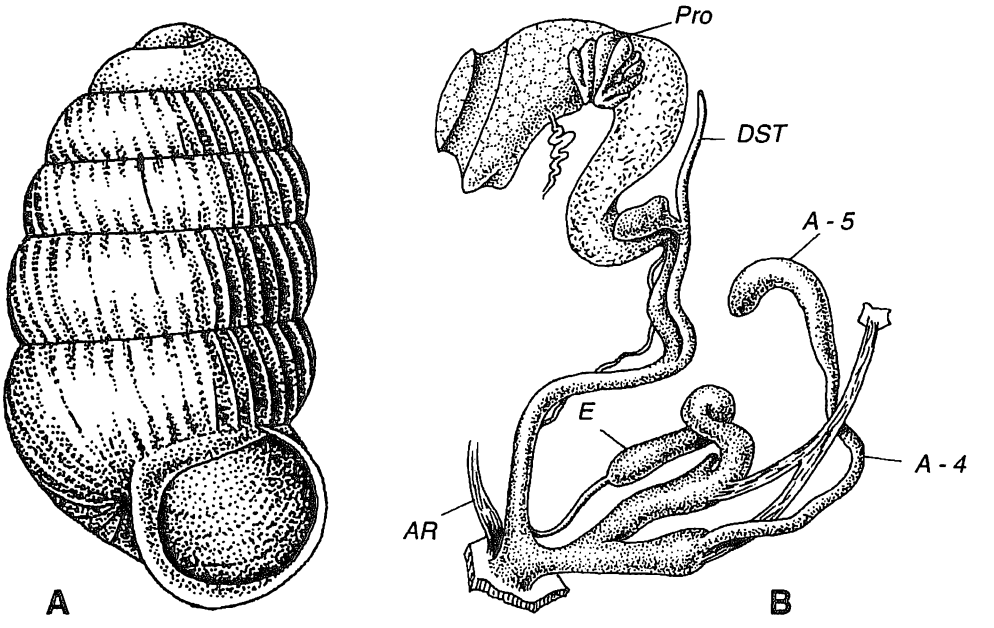


Fig. 125. ***Pupilla (Fragipupilla) alabiella*** Schileyko, 1984.
Verhovsky Islet in Peter The Great Bay, Far East, July 26, 1971. Shell (A) — holotype. **SPb.** Anatomy (B) — paratype. **Moscow** No. Lc-23205.

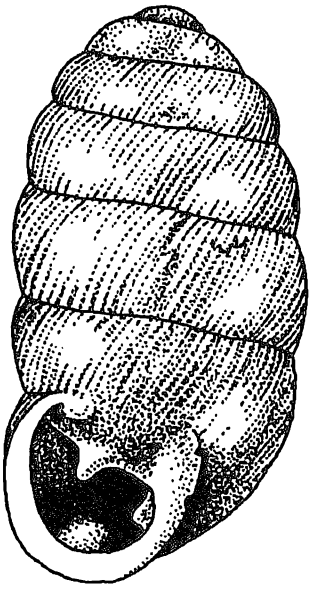


Fig. 126. ***Pupilla (Omegapilla) australis*** (Angas, 1863). Sirins Cove near Sydney, N.S.W. **Phil.** No. 115533.

ding. Color light corneous to brown. Aperture toothless, with thin margins, without neck thickening. Height 2.2-3.3, diam. 1.4-1.7 mm (3.2 × 1.6 mm).

Vas deferens entering epiphallus apically. Epiphallus narrowed near entrance to penis. Penial caecum conic, well developed. A-1 and A-2 fused; A-3 superficially not seen. Appendical arm of penial retractor attached to upper section of A-1 + A-2, the other arm — to penis opposite to base of caecum. Free oviduct markedly shorter than quite long vagina. Spermathecal stalk cylindrical, with well developed diverticle.

DISTRIBUTION. Russian Far East: islands of Peter The Great Bay and Chukchi Peninsula. 2 spp.

Pupilla (*Omegapilla* Iredale, 1937)
Fig. 126

Iredale, 1937b: 304.

TYPE SPECIES — *Pupa nelsoni* Cox, 1864 (=*Vertigo australis* Angas, 1863); OD.

Shell sinistral, ovate-cylindrical, rather

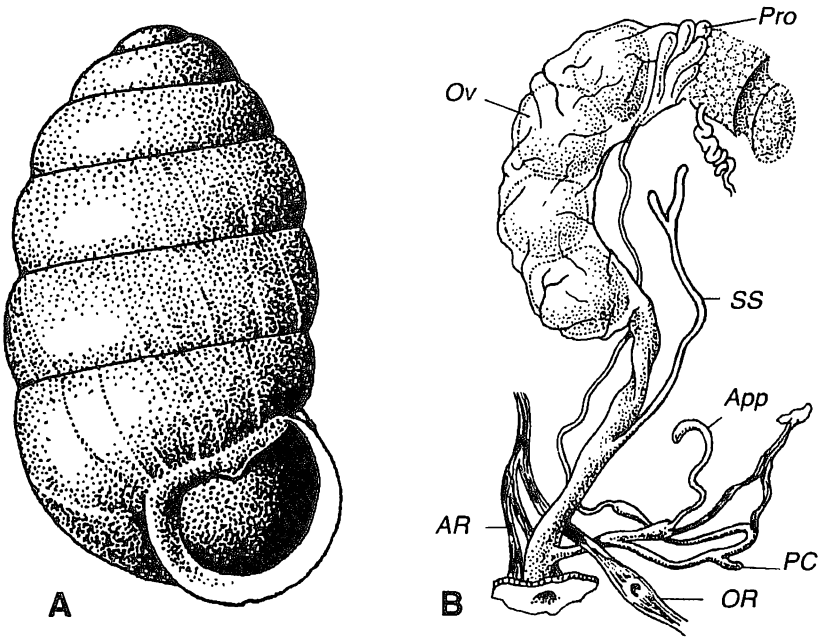


Fig. 127 ***Pupilla (Pupilla) muscorum*** (Linnaeus, 1758).
Beliye Kolodezi, right bank of Oka River, Moscow district, July 7, 1974. **A — shell; B — reproductive tract. Moscow** No. Lc-23206.

thin, of 5-7 moderately convex whorls. Last whorl slightly and gradually ascending in front. Color light-corneous. Embryonic whorls smooth, postnuclear sculpture of oblique silky radial striae. Aperture subcircular, with reflexed, a little thickened margins and with neck thickening. Full set of aperture armature consists of 4 teeth: small but distinct angular tubercle; short parietal lamella; deeply lying columellar lamella; palatal swelling located at some distance from aperture edge; palatal wall outside with shallow depression corresponding to palatal swelling. In many populations aperture teeth more or less reduced. Umbilicus, a tiny perforation. Height 3-5, diam. 1.9-2.2 mm (3.7 × 2.0 mm).

DISTRIBUTION. Australia, Tasmania. 3-4 spp.

Pupilla (*Pupilla* s.str.)
Fig. 127

Shell dextral, rarely sinistral, thin to rather solid, of 5-8 moderately to very convex whorls. Last whorl direct to scarcely ascending. Color light-yellowish to brown. Aperture rounded, with neck thickening; aperture with 1-4 teeth or toothless. Height 2.0-4.0, diam. 1.1-1.8 mm (3.8 × 1.8 mm).

Vas deferens entering epiphallus terminally. Appendical arm of penial retractor inserting to upper part of basal section of appendix, resulted from fusion of A-1, A-2, and A-3. Penial arm of retractor attached to epiphallus above caecum. Spermathecal stalk with short diverticle. Degree of development of distal part of male division strongly depends upon physiological condition of animal: when uterus contains eggs (as in fig. 127), penis with its accessories markedly reduced; when uterus empty, male division well developed.

DISTRIBUTION. Eurasia and North America. About 30 spp.

Microstele O. Boettger, 1886
Fig. 128

Boettger O., 1886: 26 (*Pupa* sect.).

TYPE SPECIES — *Pupa (Microstele) noltei* O. Boettger, 1886; OD.

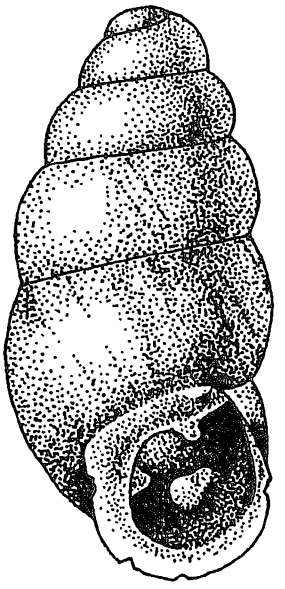


Fig. 128. ! *Microstele muscerda* (Benson, 1853). Ceylon. **Leiden.**

Shell dextral, turrited or subcylindrical to elongated-ovate, thin, of 5-6 moderately to quite convex whorls. Apex narrowly rounded. Color yellowish to brown. Postembryonic sculpture of weak, irregular, radial wrinklets. Aperture rounded to subcircular, with thin reflexed margins and lip inside; columellar margin dilate. Parietal callus well developed. Angular tubercle always present; one parietal and one columellar lamellae short, deeply placed. Palatal wall with 1 or 2 tubercles at some distance from aperture margin. Height 3.2-4.5, diam. 1.4-2.0 mm (4.0 × 1.6 mm).

DISTRIBUTION. E and SW Africa, Hindustan Peninsula, Ceylon. 4-6 spp.

PUPOIDINAE Iredale, 1940

Iredale, 1940: 235 (pro fam.).

Shell generally high conic. Whorls loosely coiled, 4-6 in number. Aperture without neck thickening, toothless, only angular tubercle may present.

Penial caecum absent.

DISTRIBUTION. Tropical and subtropical regions of all the continents.

Pupoides L. Pfeiffer, 1854

Pfeiffer L., 1854 (1854-1860): 192.

TYPE SPECIES — *Bulimus nitidulus* L. Pfeiffer, 1839; SD Kobelt, 1880.

Shell dextral, turrited to subcylindrical or elongated-ovate, thin, of 4-6 more or less convex whorls. Last whorl not elevated toward aperture. Color yellowish to dark brown. Embryonic whorls smooth, postapical whorls weakly wrinkled to delicately ribbed. Aperture rounded to ovate, only slightly oblique, with thin, variably reflexed margins. Teeth absent or angular tubercle present. Columella within shell slender, narrow. Umbilicus, a minute perforation.

DISTRIBUTION. All continents except Europe.

Pupoides (*Pupoides* s.str.)
Fig. 129

Pfeiffer L., 1854 (1854-1860): 192.

— *Leucochila* Martens in Albers, 1860: 296 (*Pupa* subg., t.-sp. *Pupa fallax* Say in Gould, 1842; OD).

— *Leucochiloides* L. Pfeiffer, 1878: 292 (*Bulimina* sect.; t.-sp. *Bulimus lardeus* L. Pfeiffer, 1851; SD Connolly, 1912).

Shell distinctly tapering, of about 6 convex whorls. Color cinnamon to brown, suture sometimes whitish. Postembryonic whorls lightly marked with radial striae. Aperture ovate, peristome reflexed and expanded, strongly thickened inside. Angular tubercle sometimes present. Height 3.0-6.5, diam. 1.4-2.2 mm (4.5 × 1.9 mm).

Hermaphroditic duct entering summit of carrefour which visible on surface of albumen gland; thus talon as such practically absent. Vas deferens long, entering epiphallus terminally. Epiphallus clavate. Penis rather short. Penial appendix not long, all its divisions normally developed. Appendical arm of penial retractor attached to A-1 just below A-2; the other branch inserted onto epiphallus at short distance above penis. Free oviduct and vagina long. Spermathecal stalk rather short, without diverticle.

DISTRIBUTION. N America, Bermuda Islands, Africa, S Asia. About 30 spp.

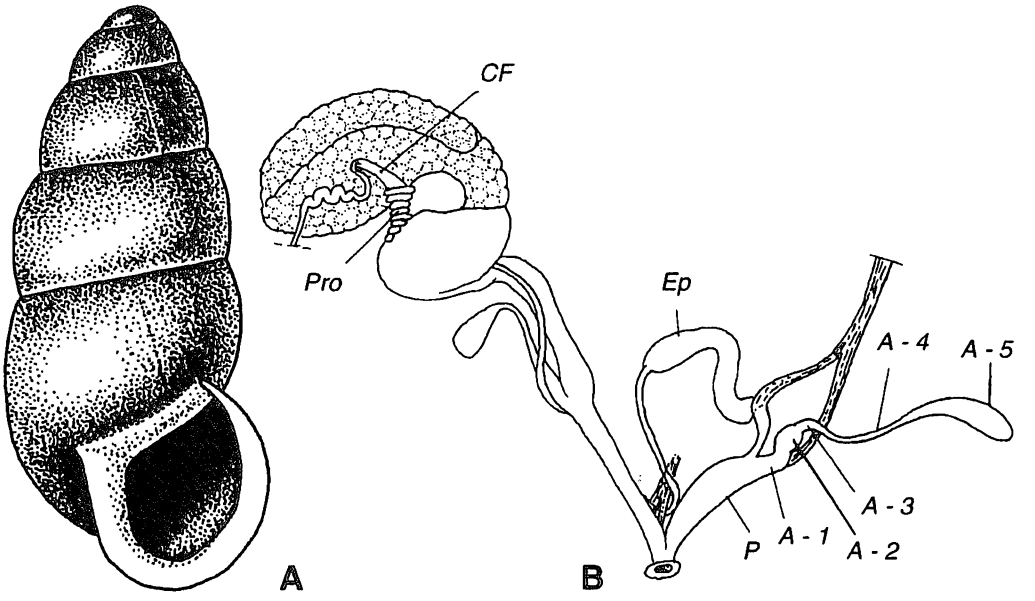


Fig. 129. ***Pupoides (Pupoides) nitidulus*** (L. Pfeiffer, 1839).
A — shell: Drift Rio Purificacion near Carmen, 24 mi of Padilla, Tamaulipas, Mexico. **StB** No. 1558. B — reproductive tract. After Baker, 1935, in Man. Conch. (hermaphroditic gland omitted).

Pupoides (*Ischnopupoides* Pilsbry, 1926) Fig. 130

Pilsbry, 1926 (1922-1926): 250.

TYPE SPECIES — *Pupa hordacea* Gabb, 1866; OD.

Shell (sub)cylindrical, thin, translucent, of 4.5-6 whorls. Color mostly corneous. Postapical whorl surface silky striated. Aperture rounded, slightly oblique. Parietal tubercle small or absent. Height 3.0-4.5, diam. 1.4-1.7 mm (3.8 × 1.4 mm).

DISTRIBUTION. South of N America, Mexico, Bolivia, Peru. 4 spp.

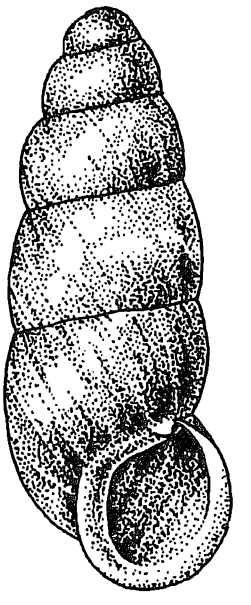


Fig. 130. ***Pupoides (Ischnopupoides) chordaceus*** (Gabb, 1866).
Mazatlan, Mexico. **Phil.** No. 22958.

Pupoides (*Glyptopupoides* Pilsbry, 1926) Fig. 131

Pilsbry, 1926 (1922-1926): 252.

— *Famarinia* Iredale, 1933: 56 (t.-sp. *Diplommatina egregia* Hedley et Mousson, 1891; OD).

TYPE SPECIES — *Pupoides hedleyi* Pilsbry,

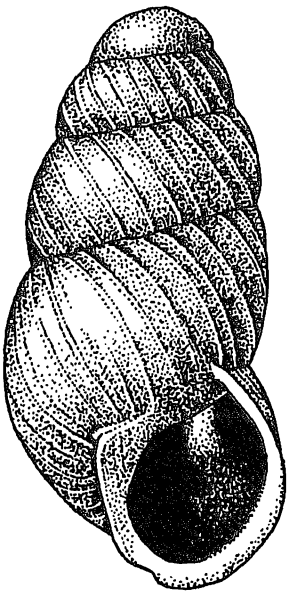


Fig. 131. ***Pupoides (Glyptopupoides) egregius*** (Hedley et Mousson, 1891). Bundaberg, Queensland (paratype of *Pupoides hedleyi* Pilsbry, 1926). **Phil.** No. 134150.

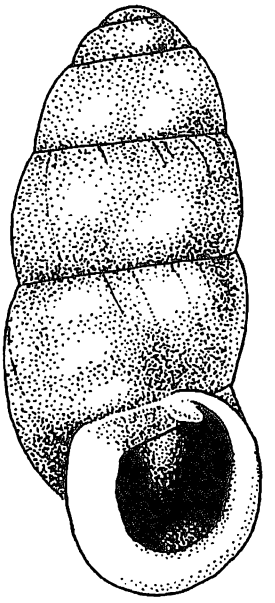


Fig. 132. ***Pupoides (Themapupa) beltianus*** (Tate, 1894).

Australia. **Cardiff.**

1926 (=*Diplommatina egregia* Hedley et Mousson, 1891); OD.

Shell elongated-ovate, thin, translucent, of 4.5-5 whorls. Apex widely rounded. Color light-corneous. Sculpture of postembryonic whorls of widely spaced, distinct, rather regular riblets. Aperture rounded, with thin reflexed margins; columellar margin dilate above. Angular tubercle absent. Height 3.0-3.7, diam. 1.4-1.6 mm (3.0 × 1.4 mm).

DISTRIBUTION. NE Australia (Queensland). 1 sp.

Pupoides (*Themapupa* Iredale, 1930) Fig. 132

Iredale, 1930: 120. Solem, 1988: 511 (syn. of *Pupoides* s. str.).

TYPE SPECIES — *Pupa beltiana* Tate, 1894; OD.

Shell elongated-ovate, thin, of about 5 moderately convex whorls. Apex narrowly rounded. Color yellowish to corneous. Postembryonic sculpture of very fine irregular radial wrinklets. Aperture rounded to subcircular, with widely reflexed and expanded margins. Angular tubercle usually well developed. Height 4.0-6.5, diam. 1.9-2.2 mm (4.2 × 2.0 mm).

DISTRIBUTION. Australia. 6 spp.

Pupoidopsis Pilsbry et Cooke, 1921 Fig. 133

Pilsbry & Cooke in Pilsbry, 1921 (1920-1921): 106.

TYPE SPECIES — *Pupoidopsis hawaiensis* Pilsbry et Cooke, 1921; OD.

Shell dextral, turbinate-conic, thin, of 4-4.5 very convex, slightly shouldered whorls. Color light corneous. Embryonic whorls smooth, later with weak sculpture of irregular radial wrinklets. Aperture ovate, oblique, toothless; peristome insertions somewhat approached and connected by parietal callus. Angular tubercle absent. Columella markedly expanded inside shell. Umbilicus tiny, slit-like. Height 3.4-3.8, diam. 2.0-2.2 mm (3.6 × 2.1 mm).

DISTRIBUTION. Hawaii. 1 sp.

CHONDRINOIDEA Steenberg, 1925

Steenberg, 1925: 201 (pro fam.).

Shell small to medium-sized, turrited, fusiform, depressed, or microhelicoid. Embryonic whorls smooth or microgranulate, later whorls mostly with radial striation or ribbing. Aperture of adult shell primarily heavily armed with lamellate teeth, but armature may be simplified, down to total disappearance of all teeth. Aperture margins not thickened, mostly reflexed, generally without a lip. Umbilicus dot-like, in rare cases cylindrical, nearly closed, or broadly open.

Penis with epiphallus, internally with system of pilasters or folds of various complexity. Boundary between penis and epiphallus marked by conic caecum, which is often absent. Epiphallus gradually passes into vas deferens and place of contact of these ducts usually more or less integrated with tissue of adatrial section of penis. Penial retractor attached near the middle of penis, but often there is additional muscle band to epiphallus. Penial appendix absent.

DISTRIBUTION. Southern Palearctic, eastward to Japan.

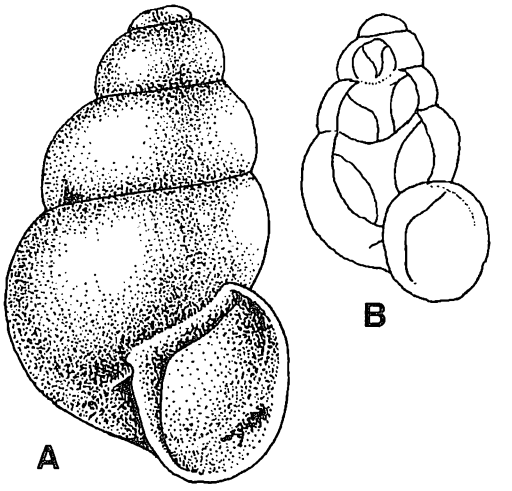


Fig. 133. ***Pupoidopsis hawaiensis*** Pilsbry et Cooke, 1921.
A — Kaelepulu, Kailua, Oahu. Paratype. **Senck.** No. 3 370. B — after Pilsbry, 1921.

CHONDRINIDAE Steenberg, 1925

Steenberg, 1925: 201. Gittenberger, 1973.

Shell conic to turrited, corneous to dark-brown. Aperture toothless to very complex, with numerous lamellae, folds, tubercles, and knobs. Aperture margins reflexed. Umbilicus very narrow or nearly closed.

Vas deferens is in very tight contact with tissue of adatrial section of penis. Penial caecum conic or absent. Penial retractor attached to penis below its middle.

DISTRIBUTION. Western Palearctic.

Granaria Held, 1837
Fig. 134

Held, 1837: 918.

— *Pupella* Swainson, 1840: 334 (t.-sp. *Pupa variabilis* Draparnaud, 1801; SD Pilsbry, 1918: 262).

Gittenberger, 1973: 41.

TYPE SPECIES — *Pupa frumentum* Draparnaud, 1801; SD Herrmannsen, 1847.

Shell conic-cylindrical to fusiform, moderately thin, slightly translucent, of 8-9 rather convex whorls. Apex narrowly rounded. Color yellowish to light-corneous. Embryonic whorls with quite distinct microgranulation. Postnuclear whorls with fine regular ribbing; on lower whorls this ribbing sometimes becomes obsolete. Aperture rounded, with delicate parietal callus; margins of aperture reflexed and well expanded. Parietal wall with 2 lamella: angular and parietal. Columellar lamellae 1 or 2. Palatal wall bears 2-5 long plicae. Height 7-10, diam. 2.7-3.7 mm (9.2 × 3.6 mm).

Epiphallus entering penis through minute pore situated between two short but strong folds. Opposite to pore there is a small zone covered with minute papillae. Folds running up to caecum. Penial caecum well developed, its length no less than 1/3 of penis length. Penial retractor in form of wide splitted band attaching to middle section of penis and middle section of epiphallus. Reservoir of spermatheca reaches albumen gland, its duct mostly adherent to prostate.

DISTRIBUTION. Europe and Asia Minor. 7 spp.

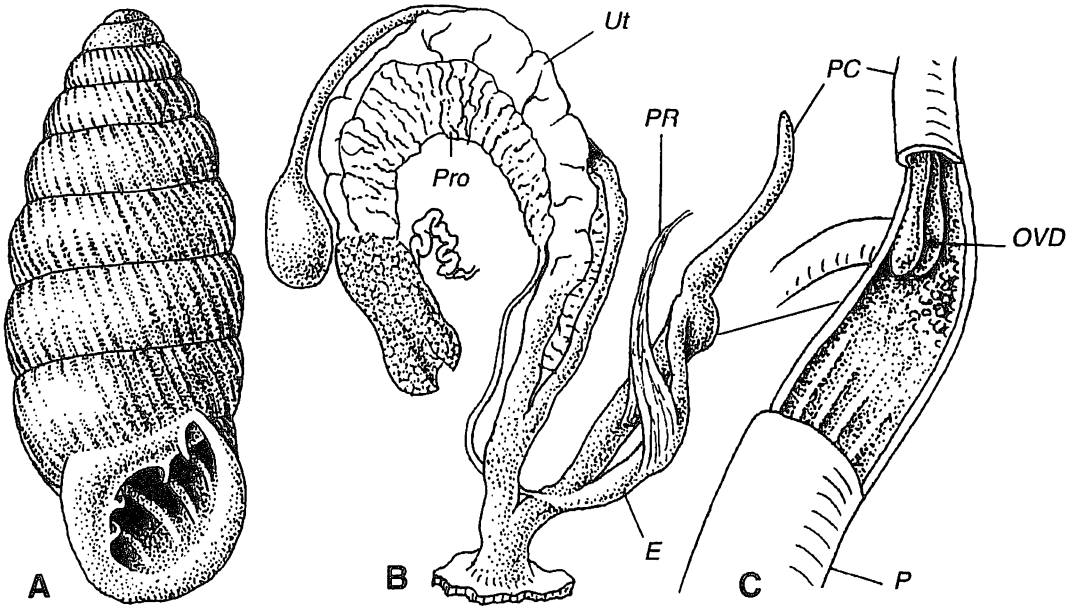


Fig. 134. ***Granaria frumentum*** (Draparnaud, 1801).
Verona, Italy, September 6, 1974. **SPb.**

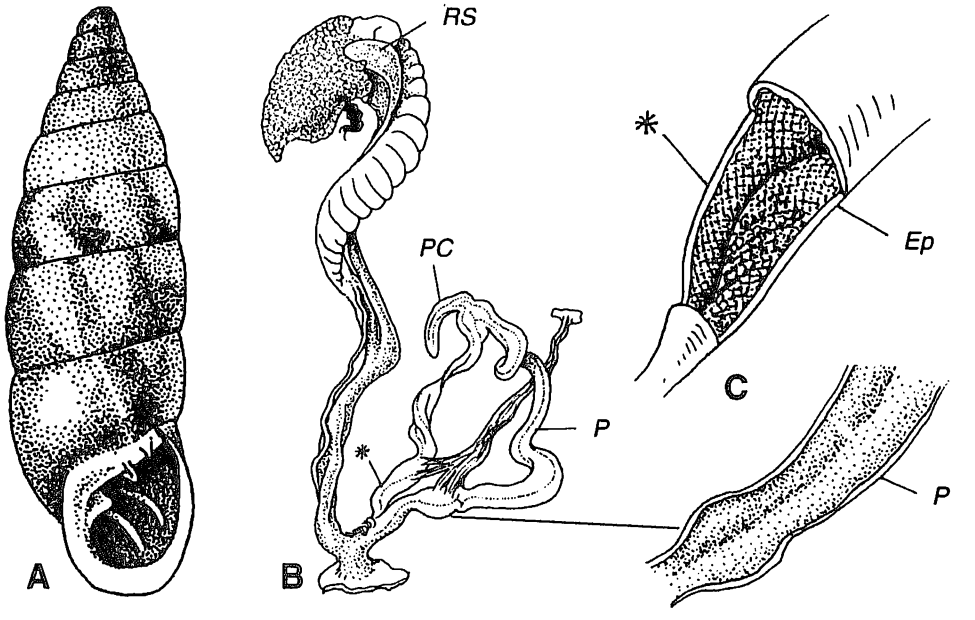


Fig. 135. ***Solatopupa similis*** (Bruguière, 1792).
Volterra ca. 50 km S of Pisa, Italy, April 26, 1996. **Moscow** No. Lc-23211. Asterisks — proximal portion of epiphallus. A — shell; B — reproductive tract; C — interior of epiphallus.

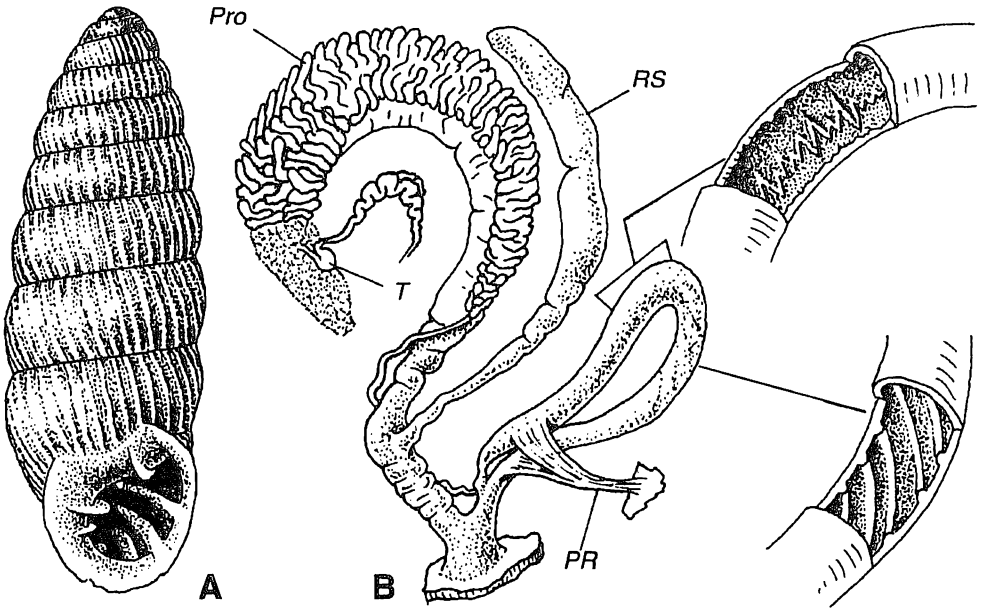


Fig. 136. ***Abida secale*** (Draparnaud, 1801).
Dijon, France, August 23, 1969. **SPb.** A — shell; B — reproductive tract.

Solatopupa Pilsbry, 1917
Fig. 135

Pilsbry, 1917 (1916-1918): 234 (pro sect.). Gittenberger, 1973: 62.

TYPE SPECIES — *Bulimus similis* Bruguière, 1792; monotypy.

Shell fusiform-cylindrical, moderately solid, of 7-10 weakly convex whorls. Last whorl direct. Color usually yellowish or ivory with variously developed irregular brownish radial streaks. Embryonic whorls smooth, later with accurate radial rib-striation. Aperture ovate, with reflexed thin margins; maximal set of armature consists of 7 teeth: short angular tubercle, low entering parietal lamella, subhorizontal also entering columellar lamella, much smaller subcolumellar lamella, and three palatal plicae, lowest of them is smallest. However elements of armature sometimes more or less reduced down to total disappearance. Umbilicus absent. Height 6.5-14.2, diam. 2.8-4.2 mm (11.2 × 3.1 mm).

Vas deferens descending alongside vagina down to atrium and incorporated to tissue of basal section of penis. Epiphallus thin-walled, enlarged, with blunt caecum at penis/epiphallus junction. Proximal portion of epiphallus internally containing longitudinal fold and bears numerous tiny papillae. Penis internally with two broad and low pilasters. Penial retractor biramous: one arm attached to proximal portion of epiphallus, the other — to distal portion of penis. Vagina about 2-3 times longer than free oviduct. Spermathecal stalk nearly cylindrical, reservoir partially burrowed in tissue of upper part of spermoviduct and/or of basal part of albumen gland.

DISTRIBUTION. France, Italy. 7 spp. & subspp.

Abida Turton, 1831
Fig. 136

Turton, 1831: 101.

— *Torquilla* Studer, 1820: 86 (nom. praeocc., non Bruennich, 1771 — see Opinion 326; t.-sp. *Pupa secale* Draparnaud, 1801; SD Gray, 1847).

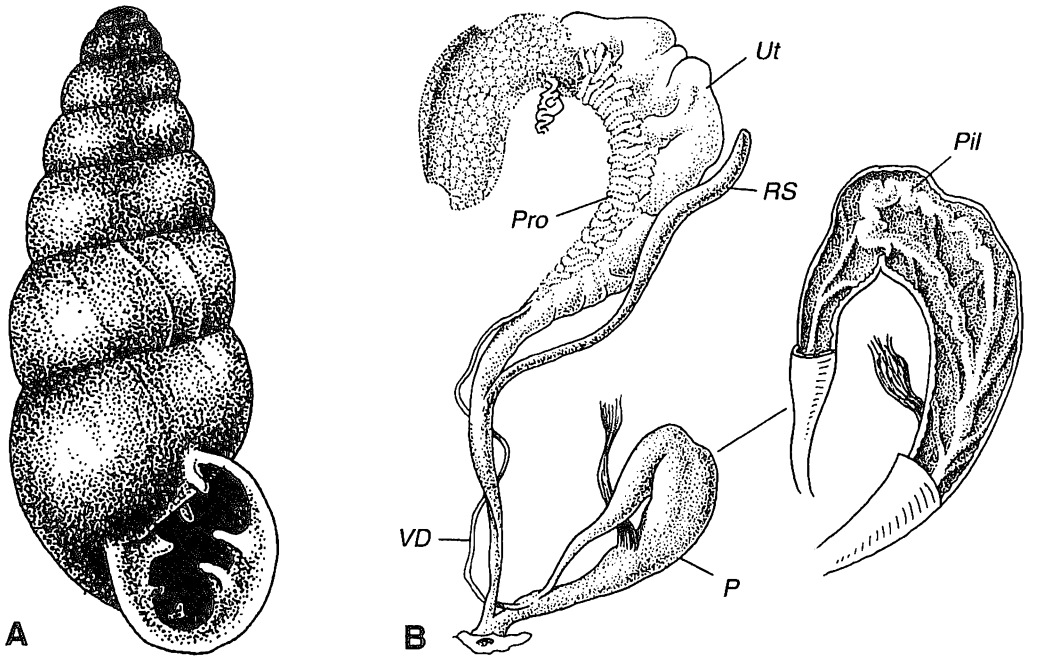


Fig. 137. ***Chondrina (Chondrina) avenacea*** (Bruguière, 1792).
Seewis-Pardisla near Schiers, Switzerland, August 15, 1997. A — shell; B – reproductive tract and interior of penis. **Moscow** No. Lc-23218.

— *Stomodonta* Mermet, 1843: 45 (t.-sp. *Pupa secale* Draparnaud, 1801; SD Pilsbry, 1918).

— *Sandahlia* Westerlund, 1887 (1884-1890): 78, 92 (*Pupa* subg.; t.-sp. *Pupa cylindrica* Michaud, 1829; SD Pilsbry, 1917).

Gittenberger, 1973: 82. Schileyko, 1984: 226.

TYPE SPECIES — *Pupa secale* Draparnaud, 1801; monotypy.

Shell mostly conic-cylindrical, moderately thin, of 8-9.5 slightly convex whorls. Last whorl a little ascending at very aperture. Color isabella to brown, sometimes with dove-colored taint. Embryonic whorls clearly microgranulated, later whorls with fine regular radial wrinkles or riblets. Aperture rounded or ovate, peristome insertions slightly approached and connected by thin transparent callus. Aperture margins reflexed and slightly thickened. Angular tubercle variously developed; parietal lamella long, entering; anterior end of subparietal lamella lies deeply. Columellar lamellae usually two, upper longer than lower. Basal tooth weak or absent. Palatal wall with 3-4 long plicae. In addition, a number of marginal knobs may present. Height 5.0-15.3, diam. 2.0-4.5 mm (8.4 × 2.6 mm).

Talon very short, globular. Epiphallus with deep and narrow zigzagged groove on inner surface. Penis internally with spirally directed folds. Penial caecum absent or rudimentary; in latter case its length not longer than 1/7 of penis length. Penial retractor inserted to distal portion of penis and proximal section of epiphallus. Spermatheca sleeve-like, practically not embedded to prostate, without distinct boundary between duct and reservoir, reaching or nearly so lower edge of albumen gland.

DISTRIBUTION. Mountain regions of Southern and Middle Europe. 22 spp. & subspp.

Chondrina Reichenbach, 1828

Reichenbach, 1828: 93. Gittenberger, 1973: 158. Schileyko, 1984: 228.

TYPE SPECIES — *Bulimus avenaceus* Bruguière, 1792; SD Reichenbach, 1836.

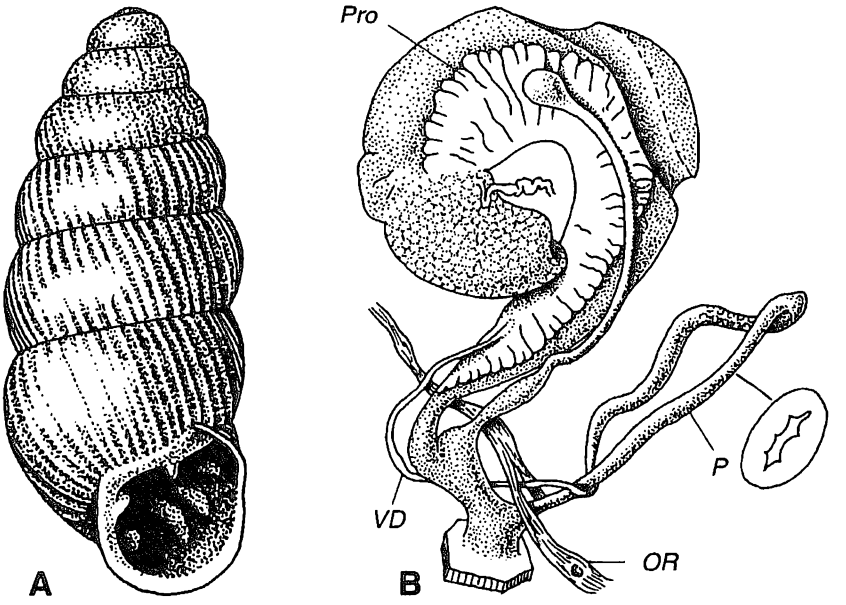


Fig. 138. ***Chondrina (Granopupa) granum*** (Draparnaud, 1801).
Kopetdagh Mts., Turkmenistan, April 28, 1953. **SPb.** A — shell; B — reproductive tract. After Schileyko, 1984 (modified).

Shell typically cylindrical-fusiform or turrited, rather thin, of 6.25-8.5 convex whorls. Aperture primarily with not deeply entering lamellar teeth, which tend to reduce down to complete disappearance.

Penial appendix absent. Enlargement, containing a horse-shoe-shaped pilaster, may present near middle of penial tube. Penial retractor attached to middle or slightly more distally than middle of the organ or absent. Spermathecal reservoir not reach albumen gland, shaft of spermatheca not impressed to prostate or impressed partially.

DISTRIBUTION. Western Palearctic.

Chondrina (*Chondrina* s.str.)
Fig. 137

— *Modicella* H. Adams & A. Adams, 1855: 169 (t.-sp. *Pupa farinesii* Des Moulins, 1835; SD Pilsbry, 1918).

— *Alloglossa* Lindstrom, 1868: 18 (t.-sp. *Bulimus avenaceus* Bruguière, 1792; monotypy).

TYPE SPECIES — *Bulimus avenaceus* Bruguière, 1792; SD Reichenbach, 1836.

Angular lamella elongated, starting from upper edge of palatal margin and running deeply into body whorl. Aperture margins reflexed. Height 3.5-14.0, diam. 1.8-4.1 mm (6.0 × 2.4 mm).

Penis internally with a horse-shoe-like pilaster; in this place penis more or less enlarged. Penial retractor attached to middle portion of penis.

DISTRIBUTION. Southern and partially Middle Europe, Canary Islands, NW Africa, Crimea, Caucasus, Asia Anterior, Iran, Kopetdagh Range. More than 60 spp. & subspp.

Chondrina (*Granopupa* O. Boettger, 1889)
Fig. 138

Boettger O., 1889: 249 (pro gen.).

— *Rupestrella* Monterosato, 1894: 170 (*Pupa* subg.; t.-sp. *Pupa rupestris* Philippi, 1838; virtual tautonymy).

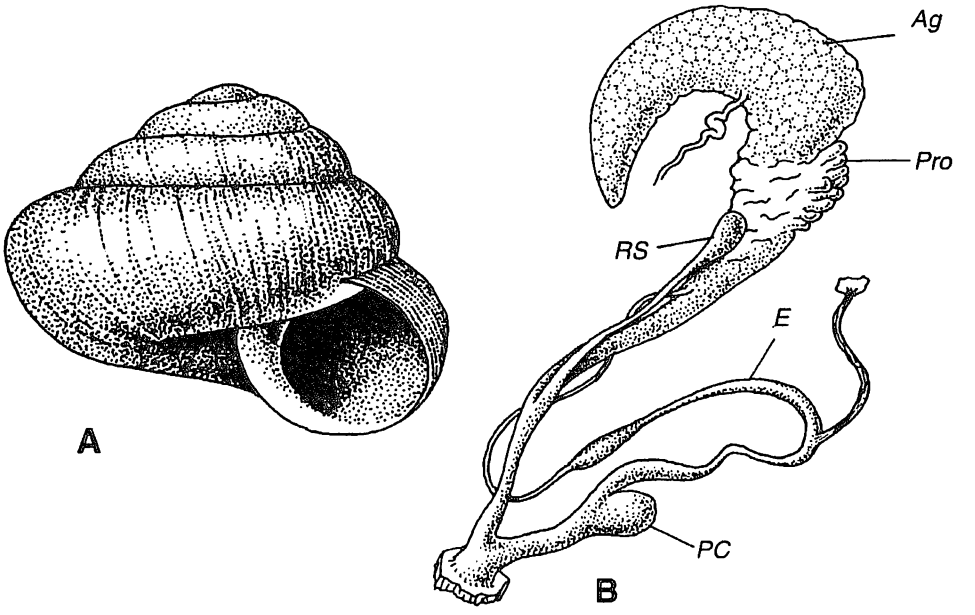


Fig. 139. *Pyramidula rupestris* (Draparnaud, 1801).
A — shell: E Caucasus, Daghestan, Akusha. **Moscow** No. Lc-4851. B — reproductive tract: Agran, Idzhevan District, Armenia, May 6, 1953. **Spb**.

Gittenberger, 1973: 36 (pro gen.).

TYPE SPECIES — *Pupa granum* Draparnaud, 1801; monotypy.

Angular lamella absent or represented by weakly developed rounded tubercle. Aperture margins nearly non-reflexed. Height 3.1-6.0, diam. 1.4-1.8 mm (5.2 × 1.2 mm).

There is no horse-shoe-like fold inside penis; inner surface of penial tube with smoothed, broad, longitudinal folds or pilasters; at penis/epiphallus junction a zone of tiny tubercles may present. Penial retractor absent.

DISTRIBUTION. Mediterranean countries, Canary Islands, Asia Minor, Caucasus, Crimea, Iran, Kopetdagh Range, and Afghanistan. Probably 1 sp. with numerous subspp. & forms.

PYRAMIDULIDAE
Kennard et Woodward, 1914

Kennard & Woodward, 1914: 1, 6.

Shell depressed or microhelicoid, corneous to dark cherry- brown. Aperture toothless, with thin, simple margins. Umbilcius moderately to broadly open.

Vas deferens not integrated with tissue of adatrial section of penis. Penis without appendages or with sac-like process (caecum). Penial retractor attached to middle section of epiphallus. Penial appendix absent. Spermathecal stalk without diverticle.

Ovoviviparous animals.

DISTRIBUTION. Ireland, S Europe, south of Middle Europe, NW Africa, Asia Anterior, Crimea, Caucasus, Himalaya, Central Asia, Japan, Java.

PYRAMIDULINAE
Kennard et Woodward, 1914

Kennard & Woodward, 1914: 1, 6 (pro fam.).

Shell small, microhelicoid, radially striate. Umbilicus nearly cylindrical, moderately open.

Penis with a sac-like process.

DISTRIBUTION. As of family.

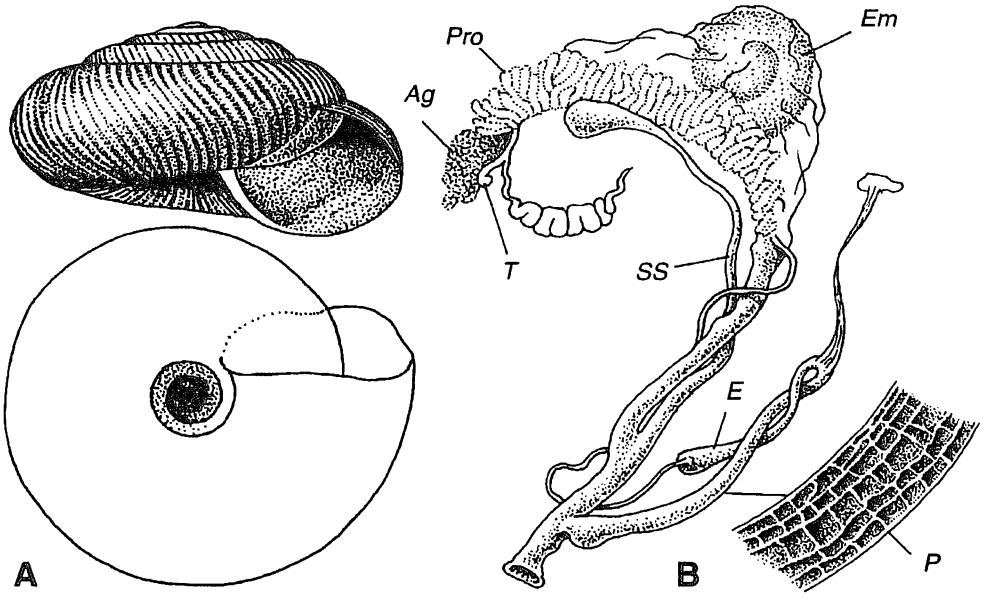


Fig. 140. ***Pleurodiscus balmei*** (Potiez et Michaud, 1838).
Latakia, Syria, August 11, 1994. A — shell; B — reproductive tract and interior of penis. **Moscow** No. Lc-23212.

Pyramidula Fitzinger, 1833
Fig. 139

Fitzinger, 1833: 95.

— *Pyramidulops* Habe, 1956: 117 (*Pyramidula* subg.; t.-sp. *Pyramidula conica* Pilsbry et Hirase, 1902; OD).

TYPE SPECIES — *Helix rupestris* Draparnaud, 1801; monotypy.

Shell microhelicoid, turbinate, thin, dull, of 4-4.5 convex to very convex, somewhat shouldered whorls. Last whorl not or only slightly descending, evenly rounded or slightly angulated at periphery. Apex rounded. Color reddish- or cherry-brown to chestnut or dark brown, often with dove-colored taint. Embryonic whorls smooth, polished, later whorls finely but deeply and densely radially striate. Aperture subcircular, moderately oblique, with thin and sharp margins; upper part of columellar margin more or less reflexed. Umbilicus moderately broad, subcylindrical. Height 1.7-2.1, diam. 2.2-2.7 (1.9 × 2.5 mm).

Talon hidden among acini of albumen gland. Vas deferens entering slightly swollen section of epiphallus. After terminal swelling epiphallus initially narrowed, then expanded, and narrowed again before entering penis. Latter internally indistinctly longitudinally plicate, without verge, furnished with short and subglobular or large and clavate caecum. Penial retractor inserting upon distal swelling of epiphallus. Spermathecal stalk moderately long, reservoir small, not attending albumen gland. In illustrated specimen collected in early of May in Caucasus, uterus was empty; in specimens, collected on September 17, 1996 in Eastern Alps (Styria, Austria) uterus contained few embryos; distalmost of them had well-developed shells of nearly 2 whorls.

DISTRIBUTION. As of family. Snails live on cliffs and rocks. 4-6 spp. & subspp.

PLEURODISCINAE Wenz, 1923

Wenz, 1923: 1069.

Shell medium-sized, flattened, finely radially ribbed. Umbilicus broad, cup-like, quite perspective.

Penis without any processes.

DISTRIBUTION. Sardinia, Sicily, S Italy, Malta, Crete, Rhodos, Asia Minor, Palestine, Algeria.

Pleurodiscus Wenz, 1919
Fig. 140

Wenz, 1919: 78.

Shell flattened, rather thin, of 5-6 moderately convex whorls. Color light corneous to brown. Embryonic whorls smooth and glossy, subsequent with fine, more or less regular riblets. Aperture ovate, parietal callus variously developed. Through umbilicus all preceding whorls are seen. Height 5.5-7.5, diam. 9-15mm (5.8 × 10.6 mm).

Talon short, clavate. Vas deferens entering terminally slightly swollen end of epiphallus. Boundary between epiphallus and penis marked with attachment of thin penial retractor. Penis more or less cylindrical, internally with a number of thin but sharp longitudinal folds, interconnected by circular ridgelets. Free oviduct longer than vagina. Uterus may contain one (or more?) large embryo with well developed shell. Reservoir of spermatheca tightly adherent to upper section of spermoviduct.

DISTRIBUTION. As of subfamily. 3-4 spp.

References

Adams H. & A., 1855 (1853-1858). *The genera of recent Mollusca; arranged according to their organisation.* Vol. 1: 1-256.

Albers J.C., 1850. *Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet.* Berlin. 262 S.

Albers J.C., 1854. *Malacographia Maderensis sive Enumeratio Molluscorum quae in insulis Maderae et Portus Sancti aut viva exstant aut fossilia reperiuntur.* Berlin. 94 S.

Albers J.C., 1860. *Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet. Zweite Ausgabe, nach dem hinterlassenen Manuskript besorgt von Eduard von Martens.* Leipzig. 359 S.

Ancey C.F., 1899. Some notes on the non-marine molluscan fauna of the Hawaiian Islands, with diagnoses of new species. *Proc. Malac. Soc. London*, vol. 3: 268-274.

Ancey C.F., 1901. Considérations sur les faunes malacologiques des parties australes du globe. *J. de Conch.*, vol. 49: 12-33.

Anton H.E., 1839. *Verzeichniss der Conchylien, welche sich in der Sammlung von Hermann Eduard Anton befinden.* Halle. 110 S.

Baker H.B., 1927. Minute Mexican land snails. *Proc. Acad. Nat. Sci. Philad.*, vol. 79: 223-246.

Beck H., 1837-1838. *Index molluscorum praesentis aevi musei principis augustissimi Christian Frederici.* Hafniae. 1837: 1-100; 1838: 101-124, 1-8.

Beck H., 1847. Verzeichniss der Naturaliensammlung, welche auf Befehl Sr. Majestät des Königs aus verschiedenen königlichen Musäen in Kopenhagen...zur 24. Versammlung Deutscher Naturforscher und Ärzte nach Kiel gesandt war. *Amtl. Ber. Vers. dtsch. Naturf. Arzte Kiel 1846*: 122-124.

Betta E. de, 1870. I molluschi terrestri i fluviatili della Provincia Veronese a complemento della malacologia di L. L.Menegazzi. *Atti Acad. agric. Verona*, vol. 47: 1-168.

Boettger O., 1879a. Kaukasische Mollusken. *Jahrb. dtsch. malak. Ges.*, Bd. 6: 1-42.

Boettger O., 1879b. Neue kaukasische *Hyalinia*. *Jahrb. dtsch. malak. Ges.*, Bd. 6: 97-98.

Boettger O., 1886. Beiträge zur Herpetologie und Malakozoologie Südwest-Afrikas. *Ber. senckenb. naturf. Ges., 1885/1886*: 1-28.

Boettger O., 1889. Die Entwicklung der *Pupa*-Arten des Mittelrheingebietes in Zeit und Raum. *Jb. nassau. Ver. Naturk. Wiesbaden*, Bd. 42: 225-327.

Bole J., 1965. Die Vertreter der Gattung *Spelaeodiscus* Brusina 1886 (Gastropoda, Pulmonata) in Jugoslawien. *Intern. J. Speleology*, vol. I, pt. 3: 349-356.

Bourguignat J.-R., 1856-1860. *Aménités malacologiques.* Paris. Vol. 1 (1856): 1-255; vol. 2 (1856-1860): 1-216.

Boycott A.E., 1919. The genitalia of *Azeca tridens*

and *Cochlicopa lubrica*. *J. Conch.*, vol. 16, No. 2: 53-54.

Brown T., 1827. *Illustrations of the recent conchology of Great Britain and Ireland.* Edinbourg. 52 plates.

Brown T., 1844. *Illustrations of the recent conchology of Great Britain and Ireland, with the description and localities of all the species, marine, land, and water.* 2nd ed. London. 59 plates.

Bruggen A.C. van, Meredith H.M., 1983. *Fauxulus grayi* n. sp., a biogeografically interesting addition to the land snail fauna of Malawi, South Central Africa. *Proc. K. Ned. Akad. Wet.* (C), vol. 86: 309-323.

Brusina S., 1886. Ueber die Mollusken-Fauna Oesterreich-Ungarns. *Mitt. nat. Ver. Steiermark*, Bd. 22 (1885): 29-56.

Caziot E., Margier E., 1909. Etude historique de la classification des *Pupa* du système européen. *Bull. Soc. zool. France*, vol. 34: 134-147.

Cecconi G., 1908. Contributo alla fauna delle Isole Tremiti. *Boll. Mus. Zool. Anat. comp. Iniv. Torino*, vol. 23 (583): 1-53.

Charpentier J. de, 1837. Catalogue des mollusques terrestres et fluviatiles de la Suisse. *Neue Denkschr. allg. schweiz. Ges. Naturw.*, Bd. 1, Nr. 2: 1-28.

Clessin S., 1876-1877. *Deutsche Excursions-Mollusken-Fauna.* Nürnberg. 1876: 1-288, 1877: 289-581 S.

Cockerell T.D.A., 1913. [Review of Manual of Conchology, vol. 21. Achatinellidae (Amastrinae). 1911.] *Science*, N.S., vol. 37, No. 946: 255-257.

Connolly M., 1922. Notes on African non-marine Mollusca, with descriptions of many new species. *Ann. Mag. Nat. Hist.*, vol. 10, no. 9: 485-517.

Cooke C.M., Kondo Y., 1960. Revision of Tornatellinidae and Achatinellidae. *Bernice P.Bishop Mus. Bull.* 221: 1-303.

Cossmann M., 1889. in *Annuair géologique universel*, vol. 5 (1888): 1104.

Draparnaud J.-P.-R., 1801. *Tableau des mollusques terrestres et fluviatiles de la France. Paris.* 116 pp.

Fagot P., 1892. Histoire malacologique des Pyrénées Francaises et Espagnoles, 2e partie. *Bull. soc. Ramond*, 25(3): 1-41.

Férussac J.B.L.d'A., 1821. *Tableaux Systematiques des Animaux Mollusques, Deuxieme Partie, Tableaux Particuliers des Mollusques Terrestres et Fluviatiles, Classe des Gasteropodes. Ordre des Pulmones sans Opercules. II. Tableau Systematique de la Famille des Limaçons, Cochleae.* Paris. 90 pp.

Fitzinger L. I., 1833. Systematisches Verzeichniss der im Erzherzogthume Oesterreich vorkommenden Weichthiere, als Prodrom einer Fauna desselben. *Beitr. Landesk. Oesterr. Enns (Ver. vaterl. Gesch. Wien)*, Bd. 3: 88-122.

Fleming J., 1828. *A history of British animals,...* Edinburgh.

Gerber J., 1996. Revision der Gattung *Vallonia* Risso 1826 (Mollusca: Gastropoda: Valloniidae). *Schr. Malakozool.*, Heft 8: 1-227.

Germain L., 1912. Mollusques terrestres et fluviatiles de l'Asie anteriéure. 5. Catalogue des gastéropodes de la Syrie et de la Palestine. *Bull. Mus. Hist. nat. Paris*, no. 7: 440-452.

Germain L., 1919. Contributions à la faune malacologique de l'Afrique équatoriale. LVII. Sur quelques genres et espèces de Pulmonés de l'Afrique Orientale. *Bull. Mus. nat. Paris*, vol. 25, no. 4: 258-265.

Gittenberger E., 1969. Beiträge zur Kenntnis der Pupillacea. I. Die Spelaeodiscinae. *Zool. Meded.*, Deel 43, no. 22: 287-306.

Gittenberger E., 1973. Beiträge zur Kenntnis der Pupillacea. III. Chondrinidae. *Zool. Verhandel.*, no. 127:1-267.

Gittenberger E., 1974. Beiträge zur Kenntnis der Pupillacea. IV Ergänzungen zur Kenntnis der Gattung Argna. *Basteria*, vol. 38: 1-12.

Gittenberger E., 1975. Beiträge zur Kenntnis der Pupillacea. V Die Spelaeodiscinae, erster Nachtrag. *Zool. Meded.*, Deel 48, no. 23: 263-277.

Gittenberger E., 1977. Beiträge zur Kenntnis der Pupillacea VII. Über zwei wenig bekannte Valloniidae. *Zool. Meded.*, Deel 50, no. 19: 295-301.

Gittenberger E., 1978. Beiträge zur Kenntnis der Pupillacea. VIII. Einiges über Orculidae. *Zool. Verhandel.*, no. 163: 3-44.

Gittenberger E., 1983. Beiträge zur Kenntnis der Pupillacea. IX. Nochmals über Orculidae. Proc. Konink. *Neder. Akad. Wetensch.*, ser. C., vol. 86, no. 3: 325-342.

Gittenberger E., 1985. Beiträge zur Kenntnis der Pupillacea. XI. *Speleodentorcula beroni* gen. & spec. nov. (Mollusca: Gastropoda: Orculidae) aus einer Hohle in Euboea, Griechenland. *Zool. Meded.*, Deel 59, no. 19: 221-228.

Gittenberger E., Menkhorst H.P.M.G., 1993. *Schileykula aculeata* spec. nov., a conspicuous species from Turkey with spiny ribs on its shell (Mollusca: Gastropoda Pulmonata: Orculidae). *Zool. Meded.*, Deel 67: 341-343.

Giusti F., 1968. Notulae Malacologicae II. Il genere *Oxychilus* nell'Arcipelago Toscano. *Atti Soc. Toscana Sci. Nat. Mem.*, ser. B, vol. 75: 218-235.

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'Arcipelago toscano e descrizione di una nuova specie. *Lavori della societa Italiana di biogeografia.* N. ser., vol. V: 99-355.

Giusti F., Manganelli G., 1986. Notulae Malacologicae, XXXIII. "*Helix*" *sororcula* Benoit 1859 and its relationships to the genera *Vallonia* Risso and *Planogyra* Morse (Pulmonata: Pupilloidea). *Arch. Moll.*, Bd. 116 (4/6): 157-181.

Golikov A.N., Starobogatov Ja.I., 1988. Problem of phylogeny and system of the Prosobranchiate gastropods. *Proc. Zool. Inst. Acad. Sci. USSR*, vol. 176: 4-77 (in Russian).

Gomez B.J., Angulo E., 1990. Anatomical and histological studies on the spermoviduct of *Azeca goodalli* (Pulmonata: Orthurethra). *J. Moll. Stud.*, vol. 56: 109-112.

Gould A.A., 1847. [On the shells collected by the United States Exploring Expedition]. Description of shells of the genera *Achatinella* and *Helicina*. *Proc. Boston Soc. Nat. Hist.*, vol. 2 (1848): 200-203.

Gray J.E., 1847. A list of the genera of recent mollusca, their synonyma and types. *Proc. Zool. Soc. London*, vol. 15: 129-219.

Gude G.K., 1899. Armature of helicoid landshells, with new sections of *Plectopylis*. *Science Gossip*, vol. 4: 147-149.

Gude G.K., 1911. Further note on preoccupied molluscan generic names and a proposed new genus of the family Helicidae. *Proc. Malac. Soc. London*, vol. 9: 361-362.

Gulick J.T., 1873. On diversity of evolution under one set of external conditions. *J. Linn. Soc. London*, vol. 11: 496-505.

Haas F., 1937. Neue und kritische Pupilliden. *Arch. Moll.*, Bd. 69 (1/2): 2-18.

Habe T., 1956. Anatomical studies on the Japanese land snails (7). *Venus*, vol. 19, no. 2: 109-117.

Hartmann J.D.W., 1840-1844. *Erd- und Süsswasser-Gastropoden der Schweiz. Mit Zugabe einiger merkwurdigen exotischen Arten.* St. Gallen. 1840: 1-60; 1841: 61-116; 1842: 117-156; 1843: 157204; 1844: 205-227.

Hausdorf B., 1996. Die Orculidae Asiens (Gastropoda: Stylommatophora). *Arch. Moll.*, Bd 125 (1/2): 1-86.

Held F., 1837. Notizen über die Weichthiere Bayerns. *Isis (Oken)* (4): 303-309; (12): 901-919.

Herrmannsen A.N., 1846-1852. *Indicus generum malacozoorum primordia.* Casselis. Vol. 1: 1-232 (1846), 233-637 (1847); vol. 2: 1-352 (1847); 353-492 (1848); 493-717 (1849); Supplementa et corrigenda: 1-140 (1852).

Hesse P., 1916. Kritische Fragmente. XVI. Zur Nomenklatur. *Nachr.-Bl. dtsch. malak. Ges.*, Bd. 48: 122-124.

Hesse P., 1923. Kritische Fragmente. XXV. *Fruticocampylaea (?) pratensis* Pfr.; XXVI. Nomenklaturfragen; XXVII. Das Genus *Aegopina* Kob. *Arch. Moll.*, Bd. 55: 193-198.

Hudec V., 1965. Neue Erkenntnisse über die Anatomie von *Argna bielzi* (Rossmässler), und Bemerkungen zur systematischen Stellung der Gattung *Argna* Cossmann. *Arch. Moll.*, Bd. 94 (3/4): 157-163.

Hyatt A., 1911. See Pilsbry H.A., 1911c.

Iredale T., 1930. Notes on some desert snails. *Victorian Naturalist*, vol. 47, no. 7: 118-120.

Iredale T., 1933. Systematic notes on Australian land shells. *Rec. Austral. Mus.*, vol. 19, no. 1: 37-59.

Iredale T. 1937a. A basic list of the land mollusca of Australia. *Australian Zoologist*, vol. 8, pt. 4: 287-333.

Iredale T., 1937b. An annotated check list of the land shells of South and Central Australia. *South Austral. Naturalist*, vol. 18, no. 2: 6-56.

Iredale T., 1940. Guide to the land shells of New South Wales. *Australian Naturalist*, vol. 10, pt. 7: 227-236.

Iredale T., 1944. The land mollusca of Lord Howe Island. *Australian Zoologist*, vol. 10, no. 3: 299-334.

Jeffreys J.G., 1830. A synopsis of the testaceous pneumonobranchous mollusca of Great Britain. *Trans. Linn. Soc. London*, vol. 16, no. 2: 323-392.

Jooss C.H., 1911. Die Molluskenfauna der Hydrobienschichten des Hessler bei Mosbach-Biebrich. *Jahrb. Nassau. Ver. Naturk.*, Bd. 64: 50-74.

Kennard A.S., Woodward B.B., 1914. *List of British non-marine Mollusca.* London. 12 pp.

Kobelt W., 1876-1881. *Illustriertes Conchylienbuch.* 2 Bande. Nurnberg. Lief.1 (1876): 1-40; 2 (1877): 41-64; 3 (1878): 65-88; 4 (1878): 89-104; 5 (1878): I-XVI, 105-144; 6 (1879): 145-176; 7/8 (1879): 177-264; 9 (1880): 265-312; 10 (1881): 313-344; 11 (1881): 345-392.

Kondo Y., 1962. Nomenklatorische Bemerkungen. *Auhea* n. nom. pro *Atea* Pilsbry & Cooke, 1933. *Arch. Moll.*, Bd. 91: 125.

Likharev I.M., 1962. Clausiliidae. *Fauna USSR*, vol. III, pt. 4, N.S., no. 83. 317 pp. (in Russian).

Lindholm W.A., 1924. A revised systematic list of the genera of the Clausiliidae, recent and fossil, with their subdivisions, synonymy, and types. *Proc. Malac. Soc. London*, vol. 16: 53-80.

Lindstrom G., 1868. Om Gotlands nutida Mollusker. Wisby. 48 S. Link H.F., 1807. *Beschreibung der Naturalien-Sammlung der Universität zu Rostock.* Rostock. 101 S.

Lowe R.T., 1852. Brief diagnostic notices of new Maderan land shells. *Ann. Mag. Nat. Hist.*, vol. 9, ser. 2: 112-120, 275-279.

Lowe R.T., 1854. Catalogus molluscorum pneumonatorum insularum Maderensium: or a list of all the land and freshwater shells, recent and fossil, of the Madeiran Islands: arranged in groups according to their natural affinities; with diagnoses of the groups, and of the new or hitherto imperfectly defined species. *Proc. Zool. Soc. London*, pt. 22: 161-218.

Mermet C., 1843. Histoire des mollusques terrestres et fluviatiles vivant dans les Pyrénées-Occidentales. *Act. Soc. sci. Pau*, 1843: 1-96.

Miller W.B., Christensen C.C., 1980. A new *Strobilops* (Mollusca: Pulmonata: Strobilopsidae) from Baja California Sur, Mexico. *Proc. Biol. Soc. Wash.*, 93 (3): 593-596.

Minato H., 1975. Genital studies of Japanese Land Snails. V The genitalia of *Eostrobilops nipponica* (Pilsbry, 1927) from Nagano Prefecture, Japan. *Venus*, vol. 33, No. 4: 207-209.

Monterosato T.A. di, 1894. Conchiglie terrestri viventi e fossili di Monte Pellegrino. *Natural. Sicil.*, vol. 13: 165-173.

Mörch O.A.L., 1852. *Catalogus Conchyliorum quae reliquit D.Alphonso d'Aguirra & Gadea, Comes de Yoldi.* Fasc. 1. Cephalophora. 76 pp.

Morse E.S., 1864. Observations on the terrestrial Pulmonifera of Maine, including a catalogue of all species of terrestrial and fluviatile mollusca known to inhabit the State. *J. Portland Soc. nat. Hist.*, vol. 1, no. 1: 1-63.

Nevill G., 1878. *Hand list of mollusca in the Indian Museum, Calcutta.* Part I. Gastropoda. XV+338 pp.

Odhner N.Hj., 1922. Mollusca from Juan Fernandez and Easter Island. In: C.Skottsberg, *The natural history of Juan Fernandez and Easter Island*, vol. 3, no. 22: 219-254.

Odhner N.Hj., 1963. *Ambrosiella kuscheli* n. gen., n. sp., a tornatellinid land shell from San Ambrosio Island. *Proc. Malac. Soc. London*, vol. 35, pt. 5: 207-209.

Paetel F., Schaufuss L.W., 1869. *Molluscorum systema et catalogus. System und Aufzahlung sammtlicher Conchylien der Sammlung von Fr. Paetel.* Dresden. 119 S.

Parreyss L., 1849. Systematisches Verzeichniss der im Erzherzogthume Oesterreich bis im Jahre 1849 aufgefundenen Land- und Fluss-Conchylien. *Ber. Mitth. Freund. Naturw. Wien*, Bd. 6, No. 7: 97-102.

Pease W.H., 1860. Descriptions of six new species of land shells, from the Island of Ebon, Marshall's Group, in the collection of H.Cuming. *Proc. Zool. Soc. London*, pt. 28: 439-440.

Pease W.H., 1870. On the classification of the Helicterinae. *Proc. Zool. Soc. London*, 1869: 644-652.

Petit de la Saussaye M., 1843. [*Elasmatina*]. *Proc. Zool. Soc. London*, pt. 11: 2-3.

Pfeiffer L., 1854. Skizze einer Monographie der Gattung *Achatinella* Swains. *Malak. Bl.*, Bd. 1: 112-145.

Pfeiffer L., 1854-1879. *Novitates Conchologicae. Serie prima. Mollusca extramarina. Beschreibung und Abbildung neuer oder kritischer Land- und Süsswasser-Mollusken (Mit Einschluss der Auriculaceen).* 5 Bde. Cassel. Bd.1 (1854-1860): 1-138; Bd. 2 (1860-1866): 139-303; Bd. 3 (1867-1869): 304-510; Bd. 4 (1870-1876): 1-171; Bd. 5 (1877-1879): 1-197.

Pfeiffer L., 1855. Weitere Beobachtungen über die Gattung *Achatinella*. *Malak. Bl.*, Bd. 2: 1-7.

Pfeiffer L., 1878-1881. *Nomenclator Heliceorum viventium quo continetur nomina omnium hujus familiae generum et specierum hodie cognitarum disposita ex affinitate naturale. Opus postumum Ludovici Pfeiffer Dr. ed. S.Clessin.* Casselis. 606 pp.

Pilsbry H.A., 1889. Nomenclature and check-list of North American land shells. *Proc. Acad. Nat. Sci. Philad.*, vol. 41: 191-210.

Pilsbry H.A., 1892-1893. *Manual of Conchology*, ser. 2, vol. 8. Helicidae, vol.VI. 314 pp.

Pilsbry H.A., 1900. On the zoological position of *Partula* and *Achatinella*. *Proc. Acad. Nat. Sci. Philad.*, vol. 52: 561-567.

Pilsbry H.A., 1907-1908. *Manual of Conchology*, ser. 2, vol. 19. Oleacinidae, Ferussaciidae. 366 pp.

Pilsbry H.A., 1910. Notes on the classification of the Tornatellinidae. *Nautilus*, vol. 23, no. 10: 122-124.

Pilsbry H.A., 1911. *Manual of Conchology*, ser. 3, vol. 21. 240 pp.

Pilsbry H.A., 1914-1916. *Manual of Conchology*, ser. 2, vol. 23. Appendix to Amastridae. Tornatellinidae index, vols. 21-23. 256 pp.

Pilsbry H.A., 1916-1918. *Manual of Conchology*, ser. 2, vol. 24. Pupillidae (Gastrocoptinae). 371 pp.

Pilsbry H.A., 1920-1921. *Manual of Conchology*, ser. 2, vol. 26. Pupillidae (Vertigininae, Pupillinae). 248 pp.

Pilsbry H.A., 1922-1926. *Manual of Conchology*, ser. 2, vol. 27. Pupillidae (Orculinae, Pagodulinae, Acanthinulinae, Etc). 335 pp.

Pilsbry H.A., 1927-1935. *Manual of Conchology*, ser. 2, vol. 28. Geographic distribution of Pupillidae; Strobilopsidae, Valloniidae and Pleurodiscidae. 96 pp.

Pilsbry H.A., 1928. The name *Petrarca* in Pupillidae. *Nautilus*, vol. 41: 108.

Pilsbry H.A., 1948. Land Mollusca of North America (North of Mexico). *Acad. Nat. Sci. Philad., Monogr.* Nr. 3, vol. II, pt. 2: I-XLVII, 521-1113.

Pilsbry H.A., Cooke C.M., 1914-1915. (in Tryon-Pilsbry) *Manual of Conchology*, ser. 2, vol. 23.

Pilsbry H.A., Cooke C.M., 1933. Notes on the land snail family Tornatellinidae. *Nautilus*, vol. 47, No. 2: 59-62.

Pilsbry H.A., Vanatta E.G., 1905. Notes on some Hawaiian Achatinellidae and Endodontidae. *Proc. Acad. Nat. Sci. Philad.*, vol. 57: 570-575.

Reichenbach H.G.L., 1828. *Allgemeine Taschenbibliothek der Naturwissenschaften.* 5. Theil. Zoologie oder Naturgeschichte des Thierreiches. Dresden.

Reichenbach H.G.L., 1836. *Allgemeine Taschenbibliothek der Naturwissenschaften*, 5. Zoologie oder Naturgeschichte des Thierreiches. Zweites Bandchen. Zittau und Leipzig.

Risso A., 1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*, 4. Paris. 439 pp.

Sandberger F., 1870-1875. *Die Land- und Süsswasserconchylien der Vorwelt.* Wiesbaden. (1870): 1-96, (1871): 97-160; (1872): 161-256; (1873): 257-352; (1874): 353-616; (1875): 617-1000.

Schileyko A.A., 1972. Morphology of the radula of the Helicidae and taxonomical significance of radular characters. *Trans. Zool. Mus. Moscow Univ.*, vol. 12: 157-168. (in Russian).

Schileyko A.A., 1975. Molluscs of the subfamily Lauriinae of the USSR fauna (Pulmonata, Pupillidae). *Zool. J.*, vol. 54, no. 12: 1767-1782. (in Russian).

Schileyko A.A., 1976. Peculiarities of organization and system of the Orculidae (Gastropoda). *Sci. Rep. High School. Biol. Sci.*, 1976, N. 4: 47-58. (in Russian).

Schileyko A.A., 1979. System and phylogeny of the order Geophila (=Helicida). *Proc. Zool. Inst. Acad. Sci. USSR*, vol. 80: 44-69. (in Russian). [English translation by K.J.Boss and M.K.Jacobson, 1985: Special Occ. Publication, No 6, published by Dept. of Moll., Harvard Univ., Cambridge, Massachusetts].

Schileyko A.A., 1984. Terrestrial mollusks of the suborder Pupillina of the USSR fauna (Gastropoda, Pulmonata, Geophila). In: *Fauna USSR*, N.S., N.130. Mollusca. Vol. III, no. 3. 399 pp. (in Russian).

Schlüter F., 1838. *Kurzgefasstes systematisches Verzeichniss meiner Conchyliensammlung nebst Andeutung aller bis jetzt von mir bei Halle gefundenen Land- und Flussconchylien.* Halle. I-VII, 1-40 S.

Schmidt A., 1855. Der Geschlechtsapparat der Stylommatophoren in taxonomischer Hinsicht. *Abh. naturw. Ver. Halle*, Bd. 1: 1-52.

Solem A., 1968. *"Ptychodon" misoolensis* Adam & van Benthem Jutting, 1939, a New Guinea Strobilopsid Land Snail and Review of the genus *Enteroplax. Veliger*, vol. 11, No. 1: 24-30.

Solem A., 1972. *Tekoulina*, a new viviparous tornatellinid land snail from Rarotonga, Cook Islands. *Proc. Malac. Soc. London*, vol. 40, no. 93: 93-100.

Solem A., 1973. Convergent evolution in pulmonate radulae. *Malacologia*, vol. 14: 144-146.

Solem A., 1974. Patterns of radular tooth structure in carnivorous land snails. *Veliger*, vol. 17 (2): 81-88.

Solem A., 1976. *Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part I. Family Endodontidae.* Field Mus. Nat. Hist. Chicago. 508 pp.

Solem A., 1982. *Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, Zoogeography.* Field Mus. Nat. Hist. Chicago. 336 pp.

Solem A., 1988. Non-Camaenid land snails of the Kimberley and Northern Territory, Australia. I. Systematics, affinities and ranges. *Invertebr. Taxon., Austral. J. Sci. Res.*, vol. 2, nr. 4: 455-604.

Solem A., Van Goethem J.L., 1974. Scanning electron microscope and optical microscope observations on urocyclid land snail radulae (Mollusca, Pulmonata, Urocyclidae). *Bull. Inst. r. Sci. nat. Belg., Bruxelles. Biol.* Vol. 50(7): 1-9.

Stabile J., 1864. Mollusques terrestres vivants du Piémont. *Atti Soc. ital. Sci. nat. Milano*, vol. 7: 1-142.

Starobogatov Ya.I., 1996. Eurasiatic species of the

genus *Cochlicopa* (Gastropoda, Pulmonata, Cochlicopidae). *Ruthenica*, vol. 5, no. 2: 105-129.

Steenberg C.-M., 1917. Anatomie des *Acanthinula* et des *Vallonia*. *Vidensk. Medd. Dansk. Naturh. Forening*, Bd. 69 (1): 1-15.

Steenberg C.-M., 1925. Etudes sur l'anatomie et la systématique des Maillots (Fam. Pupillidae s.lat.). *Vidensk. Medd. Dansk. naturh. For.*, Bd. 80: 1-211.

Studer S., 1820. Kurzes Verzeichnis der bis jetzt in unserem Vaterlande entdeckten Conchylien. *Naturw. Anz. schweiz. Ges. Naturw.*, Bd. 3, Heft 11: 83-90; Heft 12: 91-94.

Sturany R., Wagner A.J., 1914. Über schalentragende Landmollusken aus Albanien und Nachbargebieten. *Denksch. k. Akad. Wiss. Wien, math.-nat. Klasse*, Bd. 91: 19-138.

Swainson W., 1820-1833. *Zoological illustration, or original figures and descriptions of new, rare, or otherwise interesting animals, selected chiefly principally from the Classes of Ornithology, Entomology, and Conchology.* (1) 1-3 (1820-1823); (2) 1-3 (1829-1933). London.

Swainson W., 1840. *A treatise on Malacology; or the natural classification of shells and shellfish.* VIII+419 pp.

Sykes E.R., 1900. Mollusca. In: D.Sharp, *Fauna Hawaiiensis or the Zoology of the Sandwich (Hawaiian) Isles*, II.: 271-412.

Thiele J., 1917. Bemerkungen über das "Tierreich" und den Nomenclator Generum Animalium. *Nachr.-Bl. dtsch. malak. Ges.*, Bd. 49: 19-24.

Thwing E.W., 1907. Reprint of the original descriptions of the genus *Achatinella* with additional notes. *Occ. Pap. Bernice P. Bishop Mus.*, vol. 3, no. 1: I-XI, 13-196.

Turton W., 1831. *A manual of the land and freshwater shells of British Islands, arranged according to the more modern systems of classification: and described from perfect specimens in the author's cabinet: with coloured plates of every species.* London.

Turton W 1840. *A manual of the land and freshwater shells of the British Islands.* London. Ed. 2 by J.E.Gray. 324 pp.

Waldén H. W. 1983. Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated checklist. *Ann. zool. fenn.*, 20(4): 255-275.

Watson H., 1920. The affinities of *Pyramidula, Patulastra, Acanthinula,* and *Vallonia*. *Proc. malac. Soc. London*, vol. 14, pt. 1: 6-30.

Wenz W., 1919. Zur Systematik tertiärer Land- und Süsswassergastropoden. I. *Nachr.-Bl. dtsch. malak. Ges.*, Bd. 51: 76-79.

Wenz W., 1923-1930. *Gastropoda extramarina tertiaria. Fossilium Catalogus I.* 4 Bde. Berlin. 3387 pp.

Westerlund C.A., 1884-1890. *Fauna der in der Paläarctischen Region (Europa, Kaukasien, Sibirien, Turan, Persien, Kurdistan, Armenien, Mesopotamien, Kleinasien, Syrien, Arabien, Egypten, Tripolis, Tunesien, Algerien und Marocco) lebenden Binnenconchylien. I. Fam. Testacellidae, Glandinidae, Vitrinidae & Leucochroidae.* 1886a. Lund. 88+7 pp. *II. Genus* Helix. Berlin. 1889. 473+31 pp. *III. Gen.* Buliminus, Sesteria, Pupa, Stenogyra & Cionella. 1887. Lund. 183+15 pp. *IV Gen.* Balea *Prid. & Clausilia* Dr. 1884. Karlskrona. VII, 212+18 pp. *V. Fam. Succinidae, Auriculidae, Limnaeidae, Cyclostomidae & Hydrocenidae.* 1885. Lund. 135+14 pp.... I. Supplement. Berlin. 1890. 179 pp.

Westerlund C.A., 1902. Methodus dispositionis conchyliorum extramarinorum in regione palaearctica viventium, familias, genera, subgenera et stirpes sistens. *Rad Jugosl. Akad. znanosti i umjetnosti.* Knjiga 151: 82-139.

Zilch A., 1939. Landschnecken aus Deutsch-Südwest-Afrika. *Arch. Moll.*, Bd. 71: 216-253.

Zilch A., 1959-1960. Gastropoda Teil 2. Euthyneura. *Handbuch der Paläozoologie*, Bd. 6. Lfg. 1: 1-200; Lfg. 2: 201-400 (1959). Lfg. 3: 401-600; Lfg. 4: 601-834 (1960).