

Supplementary Material for:

“Lost vent gastropod species of Lothar A. Beck” in *Zootaxa*, by Chong Chen and Julia D. Sigwart

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Systematics and phylogenetic relationship of new archaeogastropod limpets from hot vents at North-Fiji- and Lau Basins (South West Pacific)

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Abstract

The morphology of both shell and radula and external anatomy of soft parts of 10 new archaeogastropod taxa from hydrothermal vents at North Fiji Basin and the adjacent Lau Basin are examined. The following new taxa are described (localities in parentheses, systematic position in square brackets): *Bathyacmaea nadinae* sp.n. (North Fiji and Lau Basins), *Nipponacmaea* gen.n. (Okinawa Trough), [Pectinodontinae, Acmaeoidea]; *Pyropelta ovalis* sp.n. (North Fiji-Basin), [Pyropeltidae, Lepetelloidea]; *Pseudorimula leisei* sp.n. (North-Fiji and Lau Basins), [Clypeosectidae, Fissurelloide]; *Lepetodrilus schrolli fijiensis* subsp.n. (North Fiji and Lau Basins), [Lepetodriiloidea]; *Shinkailepas conspira* sp.n. (Lau Basin), *Olgasolaris ethmoconcha* sp.n. (North Fiji and Lau-Basins), [Shinkailepadinae, Neritoidea]; *Symmetromphalus macleani* sp.n. (North Fiji and Lau-Basins), *Fumocapulus alayseae* gen.n., sp.n. (Lau Basin), [Neomphalidae, Neomphaloidea]; *Symmetriapelta wareni* gen.n., sp.n. (North Fiji and Lau Basins), [Peltospiridae, Peltospiroidea]. The systematic position of each taxon is discussed and reflections on their respective phylogenetic relationships, are added.

Introduction

Deep-sea hydrothermal activity at North Fiji and Lau Basins (south-west Pacific) has been known since the middle of the last decade (e. g. Cronan et al. 1984; von Stackelberg 1985, 1988, 1990; Hawkins & Helu 1986; Jollivet 1989; Auzende et al. 1988, 1989; Fouquet et al. 1990; Foucher et al. 1990). The intention of most of these expeditions was to investigate geological processes at mid-oceanic spreading zones, but some cruises also included biological investigations. Biological material was first successfully sampled during the BIOLAU and STARMER II cruises to the south-west Pacific in 1989 (Auzende et al. 1989; Auzende & Urabe 1994). Similar to the conditions described for other known vent sites (Tunnicliffe 1991; Lutz & Kennish 1993; Hessler & Kaharl 1995), the investigated hydrothermal communities at North Fiji and Lau Basins were found to be based on high bacterial primary production (Antoine et al. 1991, Elsgaard et al. 1995). Thus, the faunal composition of these communities is comparable to that reported from the Mariana Trough (Hessler & Lonsdale 1991) and the Manus Back-Arc Basin (Tufar 1990). Abundant mesogastropods such as *Alviniconcha*

hessleri and *Ifremeria nautili* (= *Olgaconcha tufari*) dominate the communities at the west and south-west Pacific vents (Desbruyères et al. 1994) whereas vestimentiferans, vesicomyid clams, and alvinellid polychaetes are the most remarkable animals at east Pacific hot vents sites. Besides the striking mesogastropods which have chemoautotrophic symbionts associated with their gills (Beck 1996 in press), many other gastropods were recovered from active hot-vent sites during the BIOLAU and STARMER II cruises. Reports on the coiled gastropodes - including many new taxa - have already been published (Bouchet & Warén 1991; Okutani & Ohta 1993; Warén & Bouchet 1993), however, the limpets still remain undescribed. Thus, the aim of the present study is fill this gap by giving information on the limpet's morphology, anatomy, and systematic position as well as by making some considerations on their ecology and phylogenetic relations.

Material and methods

The specimens on which this study is based on, were collected during joint French-Japanese explorations of the hydrothermal activity in the North Fiji Basin (cf. Fig. 1; Auzende et al. 1989, Jollivet et al. 1989, Fouquet et al. 1991). The material examined mainly originates from the BIOLAU cruise (chief scientist: Anne Marie Alayse, from May 12-May 27 1989, at the Ridge of Valufa, "Hine Hina" and "Vailili", Lau Basin, 22°S - 177°W, 1900 m) and the STARMER II cruise (chief scientists: D. Desbruyères & S. Ohta, from June 30 - July 17, 1989, at "White Lady" and "Mussel Valley", North Fiji Basin 17°-19°S - 173°-174°W, 2000-2750 m). The specimens were sorted at CENTOB and were sent to me between 1993 and 1996 for taxonomical research. Furthermore, many specimens (including BIOLAU-material from JAMSTEC, Yokosuka) were provided by A. Wären, Swedish Museum of Natural History, Stockholm.

Selected type material and further specimens examined are listed under the respective heading that also includes the respective repository. Radulae were usually extracted from preserved specimens after dissolution of tissues in 10% KOH, washed in water, air-dried, and coated with gold (Baker Union Sputter) for examination with a SEM (Hitachi S-530). Since parts of the acmaeid radulae dissolve in alkaline solutions, they were mounted without KOH dissolution. Soft parts of all species examined were critical-point-dried via acetone and CO₂, then sputtered with gold and examined with SEM. A dissecting microscope (Wild, Switzerland) with mounted drawing reflector was used for the drawings.

Abbreviations used in the text

CENTOB	Centre National de Tri d'Océanographic Biologique, Brest
EPR	East Pacific Rise
JAMSTEC	Japan Marine Science and Technology Center
MNHN	Muséum National d'Histoire Naturelle, Paris
NSMT	National Science Museum Tokyo
SMF	Senckenberg Museum Frankfurt

Abbreviations used in the figures

a	anus
bu	buccal mass
ca	calcified part of operculum
co	conchiolin part of operculum

cpv	circum pallial vein
ct	cephalic tentacle
dg	digestive gland
ebv	efferential branchial vein
ep	epipodial appendage
fgo	footgland opening
fs	foot sole
ga	gill axis
gl	gill lamella
gon	gonade
i	intestine
ja	jaw
lk	left kidney
nu	nucleus of operculum
ol	oral lobe
op	operculum
ov	ovary
p	pericard
pe	penis
pm	pallial margin
r	rachidian tooth of radula
ra	radula
re	rectum
rk	right kidney
rva	region of ventricle and auricle
s	shell
sg	seminal groove
sm	shell muscle
sn	snout
te	testis
tf	transverse furrow on oral lobe
trs	transition to radular sac
ugp	uro-genital papilla
vd	vas deferens

Systematic part

Preliminary remarks. Recently, the "archaeogastropod" concept has been discussed by several authors. While Hickman (1988) defines this group very restrictive including only the Pleurotomarioidea, the Fissurelloidea and the Trochoidea (all of which all are probably paraphyletic themselves), Haszprunar (1988 a, b) gives a wider definition that comprises the Docoglossa, the Neritimorpha, the Cocculinimorpha, the Vetigastropoda, the Seguenzina and the Architaenioglossa. As neither proposition represent monophyletic clades, I cannot agree to either concept for the following reasons: the suborder Vetigastropoda sensu Haszprunar must not include the Lepetodrilioidea and the Trochoidea (partim) since these groups do not share the vetigastropod synapomorphies, (ctenidial bursicles and epipodial sense organs (Beck 1993, 1996 in press)). Furthermore, the Cocculiniformia sensu Haszprunar certainly are a paraphyletic "Informal Group" (cf. Warén & Bouchet 1993, Ponder & Lindberg 1996). The synapomorphies used to define the Cocculiniformia (Haszprunar 1988, Fig. 5) are suspected to be homoplastic by most authors. Even a new phylogram presented by Salvini-Plawen & Steiner (1996) failed to solve this problem. Hickman neglects, on the other hand, the recently established superfamilies such as the Neomphaloidea, the Peltospiroidea and the Lepetodrilioidea which are probably all of paleozoic origin (McLean 1993, Beck 1993, 1996 in press) and therefore are "archeogastropods" in the original meaning of the word. Ponder & Lindberg (1996) presented a cladogram which distinguishes Patellogastropoda, Vetigastropoda, Neritopsina, Cocculinidae and "Vent-taxa". Although one cannot agree with all conclusions drawn by these authors, their suggestion of grouping these taxa (Ponder & Lindberg 1996, Fig. 11.3D) is closest to the hypothesis outlined by Beck (1996 in press, Figs. 9, 10). Consistently, the classification which is used in this study refers partly to Lindberg (1988, 1996) and mainly to Beck (1996 in press) using the Patellogastropoda and the Rhipidoglossa as suborders of the order Archaeogastropoda.

Subclass Prosobranchia
Order Archaeogastropoda
Suborder Patellogastropoda
Superfamily Acmaeioidea
Family Acmaeidae

The type species of the genus *Bathyacmaea* Okutani, Tsuchida & Fujikara, 1992, is *B. nipponica* Okutani, Tsuchida & Fujikara, 1992 from off Hatsushima Island (Sagami Bay) usually lives attached to the vesicomid bivalve *Calyptogena soyae*. In addition to the type species, up to now only one further species, *B. jonassoni* Beck, 1996 from Edison Seamount (Lihir Island) has to be ranked to *Bathyacmaea* and another species is ranked in this paper to the new genus *Nipponacmaea* (cf. Remarks).

Subfamily Pectinodontinae

***Bathyacmaea nadinae* sp.n. (Figs. 2-5)**

Type material. Holotype and two paratypes in MNHN, three paratypes in NSMT, two paratypes in SMF.

Type locality. Lau Basin (Hine Hina) 22°32'S - 176°43'W, 1900 m; BIOLAU BL 02.

Material examined. The type material and: BIOLAU BL 02 2 specimen; STARMER II Pl. 18 (Mussel Valley) 1 adult without shell, 3 complete juveniles; STARMER II Pl. 20 (White Lady) 12 empty shells, material Yokosuka, 7 specimens.

Distribution. Lau Basin and Fiji Basin in bathyal areas of diffuse hydrothermal venting.

Etymology. Named after my daughter Nadine who had to suffer from my time-consuming job. Species name refers to the latinized form of the name Nadine.

Description

Shell (Figs. 2A-F, 3A, B). In adults: very solid, with oval outline, profile low to medium, anterior slope somewhat steeper than posterior slope, slopes with fine irregular growth-lines and up to three conspicuous steps of growth, apex on mid-line, strongly eroded, protoconch lost, external shell surface smooth except the effects of growth and hydrothermal black incrustations. Internal surface with transparent outer margin (parallel-lamellar prismatic layer) and barely marked muscle scar (myostracum). In juveniles: shell thin and fragile without an inner, radial, crossed-lamellar layer, external surface with irregular, weak, radial riblets; sporadically, the crescent shaped scar of the protoconch is preserved. Shell structure (Figs. 3A, B) shows three layers: an outer, parallel - lamellar (foliated), a middle, concentric, crossed - lamellar and an inner, compact, prismatic layer with amorphous fillings. In the apical region, the foliated layer usually is eroded. The myostracum is not demonstrated here.

Dimensions. Holotype: length: 23.0 mm, width 18.9 mm, height 8.3 mm; paratype 1: 17.7 x 14.2 x 6.7; paratype 2: 16.0 x 12.5 x 5.9; paratype 3: 11.0 x 8.3 x 3.2; paratype 4: 11.1 x 8.2 x 3.4; paratype 5: 8.1 x 6.0 x 2.3.

Radula (Figs. 4, 5B). Docoglossate, central teeth and marginal teeth completely lacking, formula 0.1.0.1.0, lateral teeth asymmetrically arranged within a transverse row, the distal third of each tooth is impregnated with ferrous oxides causing the dark brown colour that can be seen by using a microscope. Lateral tooth with long basal plate and a trifid distal part which shows a short and slender inner ramus, a broad, middle, non-determined ramus and a well developed, outer ramus, the middle ramus towers somewhat above the inner and outer rami. In juveniles (specimen of 3.0 mm shell length), the basal plate appears to be weaker and the inner and outer rami appear to be stronger.

Soft parts (Figs. 3, C-E, 5A). Operculum lacking. Animal of white colour. Head with small tapering cephalic tentacles, no eyes, snout tapering with a small mouth-opening, oral fringe folded in retracted condition and weakly papillated. Surface of odontophore (Figs. 3D, E) equipped with rows of minute pins. Foot with a large, ciliated footsole without a footgland-opening, no epipodial appendages; pallial edge with numerous, minute papillae, pallial skirt thin and transparent in the posterior two thirds but thicker and non-transparent in the anterior third; the pallial margin is attached to the shell. Shell muscle horseshoe-shaped, anterior ends bent to midline, while the end of the right arm is somewhat larger than the end of the left arm; shell muscle arranged in bundles of unequal size; pallial cavity shallow extending to about one third of animal length from anterior end; gill of moderate size, bipectinated, dorsal and ventral gill lamellae of equal size, gill on left side delimited by efferent branchial vein, on right side by the afferent branchial vein, finger-shaped anus papilla and urogenital-papilla on right dorsal side of the cavity; at nuchal region and pallial floor loops of oesophagus, intestine and oesophageal pouches can hardly be observed.

Visceral mass. The loops of the gut system continue into the visceral mass whereas the large intestine is recognizable by black mineral crystals and grayish flaky material, the stomach is covered by the digestive gland which is situated apically, the rectum crosses the visceral mass diagonally, running parallel to one loop of the intestine. The right kidney and its opening (the uro-genital-papilla) can be recognized in the excretory system, but the left kidney, which is usually situated anterior to the rectum in *Bathyaacmaea*, is not clearly detectable without cross-sectioning. The gonad lies under the digestive gland and reaches to the posterior end of the visceral mass. Of the circulatory system, the region of ventricle and auricle can be seen on left side at the base of the gill; a circumpallial vein as well as efferent and afferent branchial veins

are clearly visible; capillary vessels could not be detected. Apparently, osphradia are not present.

Remarks. In differentiation to these taxa, the new species described here is diagnosed by a medium to low shell profile, a smooth shell surface, a conspicuous anterior pallial rim fixed to the shell, ends of shell muscle arms widened and bent to mid-line, lateral tooth of radula with a slender smooth shaft and a short inner ramus.

B. nadinae is closely related to *B. jonassoni* because of similar radular characters such as long slender shafts and somewhat lamellar rami whereas *B. nipponica* has a shell with radial sculpture and much solidier radular teeth.

In the course of this study it became evident that *B. secunda* is quite different from *B. nipponica*, *B. jonassoni* and *B. nadinae*, mainly with respect to the radular characters. Therefore, a new genus name for that monotypic taxon is proposed here:

***Nipponacmaea* n. gen.**

Type species: *Nipponacmaea secunda* (Okutani, Fujikura & Sasaki, 1993), syn. *Bathyacmaea secunda* Okutani, Fujikura & Sasaki, 1993.

Diagnosis: Shell patelliform, thin and oval in outline, surface with numerous white radial threads, inner surface with a low thick ridge running along the mantle edge, marginal area translucent. Radula docoglossate, rachidian teeth and marginal teeth lacking; lateral teeth trifid, showing a long shaft with a deep longitudinal groove inside, a slender innermost ramus with a sharp tip, a middle ramus which is broadly triangular, and an outermost ramus which is rectangular in outline. Particularly the long shaft with the deep longitudinal groove and the outermost, large, rectangular ramus of the lateral tooth are reasons for establishing a new genus. In the closely related genus *Bathyacmaea*, the radular characters are very different in having a shaft without a groove and a slender outermost ramus.

Suborder Rhipidoglossa
Superfamily Lepetelloidea
Family Pyropeltidae

***Pyropelta ovalis* sp.n. (Figs. 6-8)**

Type material. Holotype and one paratype in MNHN, two paratypes in NSMT, two paratypes in SMF.

Type locality. North Fiji Basin (White Lady), 2000 m. STARMER II Pl. 20, 21.

Material examined. The type material and: STARMER II Pl. 20. 3 adult and 7 juvenile specimens; Material Yokosuka, 1 specimen.

Distribution. North Fiji Basin in bathyal, sulfide-rich areas.

Etymology. Species name refers to the oval form of the shell.

Description.

Shell (Figs. 6 A-E) medium sized for genus, moderately thick, of opaque white colour; outer surface heavily eroded which is caused by acidic hydrothermal solutions. Surface characterized by concentric and irregular steps of thin shell layers; outermost layer, if present, with fine naps of irregular distribution (discernable by SEM only); in most specimens the horse-shoe-shaped scar of shell muscle is visible from outside due to the transparency of the shell; apex slightly posterior to the center, shell profile low; protoconch lost in all specimens. Inner shell surface smooth except the heavily marked muscle scar. Shell structure consists of a multitude thin prismatic layer.

Dimensions. Holotype; length 5.4 mm, width 3.6 mm, height 1.0 mm; paratype 1 length 5.2 mm, width 3.7 mm, height 1.2 mm.

Radula (Fig. 7 B). Rhipidoglossate with about 45 transverse rows of teeth, formula 50-60 x 5 x 1 x 5 x 50-60, transverse rows of teeth roughly M-shaped; rachidian tooth with a broad base, laterally equipped with weak ridges, rachidian cusp reduced, rachidian shaft ends bluntly; rachidian base forms a hump with the bases of the first laterals; first laterals with overhanging cusps bearing 4-5 inner coarse denticles; cusps of second, third and fourth laterals with finely denticulated inner edges; fifth lateral claw-like and with 8-9 coarse denticles at cusps, base with distal flap, short pin-like first marginal teeth probably functions like a lateromarginal plate; marginal teeth with slender shafts and well-denticulated short and stiff cusps, outermost marginal teeth more flabelliform.

Soft parts (Figs. 6 A, 7 A, 8). Cephalic lappets lacking, cephalic tentacles of equal size and equipped with micropapillae, snout with oral disc and small lateral lappets; foot with flat sole and a marginal bulge on which anteriorly the slit of the foot gland is discernable; foot sides bear a broad epipodial lobe which is posteriorly accompanied with two appendages and shows somewhat broadened area anteriorly, posterior appendages arise from areas above the epipodial lobe. Pallial margin thickened and entirely fused to the shell, outermost area densely covered with micropapillae (can be seen by SEM only); on right ventral side of the pallial margin, 25-28 small secondary gill leaflets are located, each leaflet consists of a basal (anterior), thickened, partly ciliated part and a distal (posterior), non-ciliated flap; pallial cavity shallow and short at left neck side (inhalant opening), ciliary bundles function as sensory control of incoming hydrothermal solutions, at right neck side, a densely ciliated area causes the exhalant flow of solutions, mantleskirt above neck extremely thin and translucent. Shell muscle horseshoe-shaped, with left and right arm of about equal size, inner bounds irregular. Half of the visceral mass is occupied by the hermaphrodite gonad whereas the ovary covers the testis in the posterior and left area; at the center, a loop of the intestine shines through; the right area includes the digestive gland and a somewhat granular area interpreted here as the right kidney; the rectum penetrates the pericard and ends at the right side of the pallial cavity; rectum contents include flaky material and some mineral particles; apparently, the ducts of the right kidney and the gonad are fused and end in a common uro-genital papilla towards the end of the right shell muscle arm. More detailed anatomical information requires dissections; therefore, data on the digestive system, left and right kidneys as well as the circulatory and nervous systems cannot be given here.

Remarks. *P. ovalis* is the fifth species of the genus *Pyropelta* (and also of the monotypic family Pyropeltidae). While *P. musaica* (from the Juan de Fuca Ridge off Washington), *P. corymba* (from the Guaymas Basin, Gulf of California), and *P. wakefieldi* (from a whale bone off Point Sur, California) are clearly distinguished by - among others - a more reduced rachidian tooth as well as by weaker lateral tooth bases at the radula, *P. ovalis* sp.n. is similar to *P. bohlei* (from Edison Seamount, West Pacific) with respect to the radular characters. However, *P. ovalis* sp.n. is different to *P. bohlei* in the following characters: the shell is larger and not vitrinous, the radula has a rachidian shaft that ends bluntly instead of tapering and the cusps of the marginal teeth have short and stiff denticles instead of long and flexible ones; with respect to soft parts, the diagnostic characters of *P. ovalis* are: arms of shell muscle of equal size, much higher number of secondary gill leaflets (up to 28), leaflets comparatively small and not reaching to the pallial cavity.

Pseudorimula leisei sp. n. (Figs. 9, 10)

Type material. Holotype and one paratype in MNHN, two paratypes in NSMT, two paratypes in SMF.

Type locality. North Fiji Basin and Lau Basin (White Lady and Hine Hina).

Material examined. The type material and partly damaged specimens from BIOLAU BL 03 and 1 juvenile specimen from BL 04, 5 subadult specimens from STARMER II Pl. 20.

Distribution. North Fiji Basin and Lau Basin in bathyal, sulfide-rich areas.

Etymology. Species is named after Dr. Thorsten Leise, entomologist, in remembrance of the good times we shared at the Dept. of Biology/Zoology at the Philipps-University of Marburg.

Description.

Shell (Figs. 9 A-E). Shell moderately large for genus, maximum length 5.1 mm. External surface coated with blackish and brownish mineral encrustations. Periostracum light brown, projecting slightly past the shell margin. Aperture oval in outline, margin of aperture not protruding. Profile relatively high, height of holotype 0.40 to 0.45 times length. Highest elevation of shell at about one-half its length. Protoconch not preserved. Juvenile shells with open slit, in adult shells slit open about one-third of the length of anterior slope, slit strongly deflected to the right; anteriorly, the slit is in adults sealed by the periostracum, posteriorly, it is sealed by a calcitic callus. Sculpture consists of numerous very fine radial ribs and small, sharp periostracum-lamellae, which occur sporadically in approximately 20 radial lines. Shell interior opaque, muscles scars (2 lateral, 1 posterior) and pallial attachments well marked by darker areas. Apical whorl contains parts of the visceral mass apparently also present in adults; adjacent to shell slit and surrounding the foramen, a thickened callus strengthens the shell. Suture with a zig-zaged outline.

Radula (Figs. 10 A, B). Rhipidoglossate, ribbon symmetrical, consisting of 60-70 rows of teeth in specimens of 4.3 mm shell length. Formula 10-12 x 4 x 1 x 4 x 10-12. Rachidian tooth with a broad base equipped with lateral ridges and with an extremely strong, overhanging cusp; cusp laterally with about 8 large denticles, at top acutely pointed. Lateral teeth similar in morphology to rachidian but somewhat narrower and denticulated at distal margins of cusps only. Marginal teeth relatively low in number, with broad tips, which are finely serrate, and have a long, tongue-like process distally.

Soft parts (Figs. 9 A, 10 C, D). Anterior end of foot much broader in comparison to posterior end; anterior foot gland-opening represented by a very long, transverse slit. Three pairs of posterior epipodial tentacles with extended bases and two finger-like tentacles carrying micropapillae. Cephalic tentacles thickened and relatively long (in preserved condition) carrying micropapillae as well. Oral disc not folded and without clearly separated lappets, head without eyes. Pallial skirt deeply emarginated, which corresponds to the shell slit, oroficium has about 10-15 tentacles on each margin anteriorly, posteriorly the marginal membrane becomes the smooth, posterior end of the oroficium which is marked by a single tentacle directed outwards. Pallial margin slightly swollen, inner rim papillated, pallial skirt anteriorly attached to shell. One pair of lateral, equal-sized muscles and one isolated, posterior shell muscle present. Posterior muscle roughly in mid-line, covered on its left margin by the tip of the visceral mass. Arrangement of pallial cavity and visceral mass somewhat asymmetrical, reflecting a remnant of shell coiling which can be seen more clearly in juveniles. Pallial cavity deep, right ctenidium smaller than left. No sexual dimorphism detectable except granular ovary or somewhat striped testis. No operculum.

Remarks. Up to now, two species with an extremely disjunct distribution have been known, *Pseudorimula marianae* McLean, 1989 from Snail Pits vents, Mariana Back-Arc Basin, and *P.*

midatlantica McLean, 1992, from Snake Pit, Mid-Atlantic Ridge. The new taxon, *P. leisei*, is separated from either of the former by the following diagnostic characters: shell with apex close to posterior margin and with a much steeper posterior slope; shell surface without strong radial ribs; rachidian and lateral teeth with very coarse denticulation and sharply pointed cusps.

Superfamily Lepetodrilioidea
Family Lepetodrilidae

***Lepetodrilus schrolli fijiensis* subsp. n. (Fig. 11)**

Type material. Holotype, five paratypes from Vailili and five paratypes from White Lady in MNHN, five paratypes in NSMT, five paratypes in SMF.

Type locality. Lau Basin, BIOLAU BL 12, Station 2; Vailili, 23°13'S - 176°38'W, 1750 m.

Material examined. The type material and: BIOLAU BL 01 33 specimens, BL 02 ca. 200 specimens, BL 03 139 specimens, BL 04 24 specimens, BL 05 1 specimen, BL 06 6 specimens, BL 07 1 specimen, BL 08 19 specimens, BL 09 1 specimen, BL 10 19 specimens, BL 11 1 specimen, BL 12 110 specimens. STARMER II Pl.10 343 specimens, Pl. 11 300 specimens, Pl. 12 43 specimens, Pl. 13 50 specimens, Pl. 14 121 specimens, Pl. 15 6 specimens, Pl. 16 366 specimens, Pl. 17 1 specimen, Pl. 18 326 specimens, Pl. 19 245 specimens, Pl. 20 923 specimens, Pl. 21 53 specimens.

Distribution. Lau Basin and North Fiji Basin in bathyal hot-vent fields.

Etymology. Name of subspecies refers to the distribution at North Fiji Basin and Lau Basin.

Description: As the new taxon is very similar in conchological, anatomical and radular characters to the type species, *Lepetodrilus schrolli schrolli* Beck, 1993, only diagnostic characters are given here. Shell (Fig. 11). Dimensions much higher, largest specimen: length 12.0 mm, width 8.3 mm, height 4.0 mm; apex in slightly more right-posterior position. *Radula.* Rhachidian with long tapering cusp.

Soft parts. Pallial cavity deeper and shell muscles slightly shorter than in Type. *Dimensions.* Holotype shell length 11.0 mm, width 8.3 mm, height 4.5 mm.

Remarks. No evident morphological-anatomical diagnostic character was found to separate North Fiji specimens from Lau specimens. However, as Denis et al. (1993) reported for the mesogastropod *Alviniconcha hessleri*, *Lepetodrilus* specimens from populations of the North-Fiji Basin might differ from those of the Lau Basin, thus forming cryptic species. It must also be mentioned here that "*L. cf. elevatus*" from Mariana Trough (Hessler & Lonsdale 1991, McLean 1993) as well as "*L. elevatus*" from North Fiji and Lau Basin (Warén & Bouchet 1993) were only tentative identifications mainly based on similar shell characters. As outlined by Sobjinski & Beck (1996), there are three subspecies recognized in the West Pacific: *L. schrolli marianae*, *L. schrolli schrolli*, and *L. schrolli fijiensis*.

Superfamily Neritoidea
Family Phenacolepadidae

***Shinkailepas conspira* sp.n. (Figs. 12, 13)**

Type material. Holotype and two paratypes in MNHN, two paratypes in NSMT, two paratypes in SMF.

Type locality. Lau Basin (Hine Hina).

Material examined. The type material and 1 specimen from BIOLAU BL 02, 6 subadult specimens from BL 03, 2 juvenile specimens from BL 06, 2 subadult specimens from BL 08, 2 subadult and 1 adult from BL 09, 1 subadult from BL 11.

Distribution. Lau Basin at bathyal hydrothermal vents

Etymology. Species name from Latin roots, *con* for with, and *spira* for coiled

Description. Shell (Fig. 12). Shell large for genus, almost limpet-shaped in adults but with conspicuous remnants of shell-coiling in juveniles; aperture oval in outline; shell margin not in plane, anterior margin clearly overhanging causing an arched line of the margin in a lateral view; apex (oldest shell stages) at posterior shell margin, mostly eroded in adults but intact in juveniles up to about 4 mm; diameter of protoconch about 0.8 mm, coiled several times, reflecting the planktotrophic development; shell surface with fine radial and strong concentric riblets, surface (periostracum) usually of whitish colour, some specimens with large irregular black encrustations (mainly at apex), old shells from Lau Basin completely black; shell interior opaque-white, inner margin of aperture slightly denticulated in juvenile and subadult specimens, otherwise smooth; no overhanging periostracum; at posterior part of shell-interior a strongly marked and thickened septum is evident; left and right muscle scars marked by oval, reniform smooth patches at otherwise rough interior of shell, roughness caused by numerous shell-pores which are concentrated particularly at the interior of the apex.

Dimensions. Holotype: length 21.3 mm, width 19.0 mm, height 9.0 mm.

Radula (Fig. 13). Rhipidoglossate, dentition typical for genus, formula 70-80 x 4 x 1 x 4 x 70-80, rachidian teeth rectangular in outline, anterior part equipped with a horseshoe-shaped inner ridge and a much weaker outer ridge; first lateral teeth enlarged and oblique, basal part with U-shaped cross-section, distal part ear-shaped, at transition from basal to distal part, the inner margin forms an overhanging flap. Second lateral small, hook-shaped, overhanging cusp doubled, with 5-7 irregular small denticles. Longish third lateral tooth with deformed cusp, into which the cusp of the second lateral tooth fits in. Fifth lateral tooth with divided base and broadened cusp, showing a broad inner terminal denticle and four more slender outer denticles. At the descending rows of marginal teeth, four types of cusps are recognizable: the innermost type (8 teeth) with long, slender shafts and heavily denticulated cusps, the second type (40-45 teeth) has a terminal slit and denticles of very different size, the third type (approx. 20 teeth) has a fine denticulation and a distal, tongue-like process, the outermost type is simply flabelliform.

Soft parts (Figs. 13, 14). Eyes lacking; cephalic tentacles moderately long, ventrally equipped with 4-5 stripes of micropapillae; mouth-opening comparatively small, circular, and papillated; oral lobe huge, reaching to the foot sides; cephalic lappets usually small (in females), in males right cephalic lappet modified to function as a penis; foot sole large, only central third ciliated; opening of the anterior foot gland small, slit-like; epipodial lobe extremely enlarged, particularly at the posterior end of foot, bearing up to 60 large, paddle-like flaps arranged in several lines. Pallial margin slightly swollen, pallium thin but not translucent, bearing numerous papillae which are concentrated at the apex; furthermore, minute reddish dots speckle the pallium as well as the neck and gill. In adults, males' neck extremely swollen forming a transverse ridge which contains spermatophores; pallial cavity deep at left side and shallow at right side; at right neck side, a small field of folds represents the osphradium; gill of moderate size, bipectinated. operculum present at dorsal side of the foot, even in juveniles completely covered by the visceral mass; operculum with an anterior calcareous part, a posterior corneous part and a small paucispiral, corneous nucleus having a small inner process; overall asymmetric, anterior left corner and posterior right corner are lengthened.

Remarks. Up to now, only two *Shinkailepas*- species have been known, *S. kaikatensis* from Kaikata Seamount, Japan, and *S. tufari* from Manus Back-Arc Basin, Papua New Guinea; the

third species, *S. conspira* sp.n., is well separated from either of the former two by having the following characters: shell dimensions much larger, shell sculpture with conspicuous concentric riblets; operculum clearly asymmetric; oral and epipodial lobes strongly enlarged, epipodial lobe equipped with several rows of large paddle-like flaps (up to 60).

***Olgasolaris ethmoconcha* sp.n. (Figs. 14, 15, 16)**

Type material. Holotype and 10 paratypes in MNHN, 5 paratypes in NSMT, 5 paratypes in SMF.

Type locality. Lau Basin (Vailili).

Material examined. The type material and material from BIOLAU: 2 specimens BL 02, 21 specimens BL 03, 105 specimens BL 04, 1 specimen BL 05, 34 specimens BL 06, 30 specimens BL 07 (Yokosuka), 3 specimens BL 08, 95 specimens BL 09, 13 specimens BL 10, 29 specimens BL 11, 76 specimens BL 12, from STARMER II: 69 specimens Pl. 10, 92 specimens Pl. 13, 7 specimens Pl. 19.

Distribution. Lau Basin and North Fiji Basin, in hot-vent fields.

Etymology. Species name has Greek and Latin roots: *ho ethmós* meaning sieve, *concha* meaning shell; named referring to the numerous shell pores.

Description. Shell (Fig. 15). Limpet-shaped, moderately high; anterior slope slightly longer than posterior slope, apex always eroded at midline, in adults nearly at center, in juveniles at posterior end of shell but not overhanging; protoconch not preserved; periostracum broadly overhanging; shell sculpture with up to 400 fine radial riblets, aperture circular to oval in outline; interior of shell with large scars of the two lateral, longish-oval shell muscles; shell interior otherwise opaque-white, with fine lines at margin reflecting the cross-lamellar shell structure, in the direction of the apex, interior equipped with numerous noticeable shell pores which fit in numerous papillae on the mantle skirt; at posterior margin of calcareous interior, a minute septum represents the only vestige of shell-coiling.

Dimensions. Holotype male: length 11.2 mm, width 9.6 mm, height 3.9 mm.

Radula (Fig. 16). Rhipidoglossate as is typical for genus; formula: about 80-90 x 4 x 1 x 4 x about 80-90; arrangement of teeth essentially as described for *O. tollmanni* except: rachidian nearly plane, with only weak anterior swelling, at third lateral tooth, the inner cusp bears up to 10 blunt denticles, and both the third and the fourth lateral teeth are not joined by an articulation, the number of marginal teeth is higher but they appear slightly weaker in general than in *O. tollmanni*.

Soft parts (Figs. 14, 15). Head with papillated, circular mouth-opening; oral lobe huge and thickened; cephalic tentacles long and tapered; cephalic lappets small and of equal size in females, in males, right lapped enlarged and equipped with a dorsal seminal groove having longitudinal rows of cilia. Foot with small slit of anterior foot gland and a broadened footsole which is ciliated at the middle part, lateral parts without ciliation; epipodial lobe at posterior end only, consisting of a weak ridge from which 7-8 small flaps arise on each side. Pallial skirt with marginal swelling and two marginal grooves reflecting the overhanging periostracum; epithelium with numerous papillae of varying thickness; thin and hairy at palial margin, thickened at the apex; large left and right shell muscles of equal size, reaching from neck nearly to the end of the visceral mass. Pallial cavity extremely deep at left side and shortened at right side, arrangement of inner organs as described before for *O. tollmanni*. Gill bipectinated, dorsal lamellae recognizably smaller than ventral ones, rod densely covered by ciliar bunches, probably used to create a water current in the deep mantle cavity; lamellar interspaces of gill densely colonized by globular bacteria in all specimens examined via SEM (n=5). Operculum (Fig. 14 B) very thin and flat in internal position at dorsal side of foot, completely covered by the visceral mass; anterior part of operculum calcareous, posterior part corneous, paucispiral nucleus at left-anterior margin.

Remarks. The new taxon is closely related to *O. tollmanni* from Manus Basin, the only species described up to now. There are several diagnostic characters to separate *O. ethmoconcha* from this sister species: shell sculpture with finer riblets (up to 400 compared to 350; shell height slightly lower; rachidian tooth at radula nearly plane, cusp of third lateral tooth with 10 blunt denticles (compared to of none), fourth lateral without articulation to third lateral tooth, i.e. there is no special deep notch at distal end of the shaft of the third lateral.

Superfamily Neomphaloidea
Family Neomphalidae

***Symmetromphalus macleani* sp.n. (Figs. 17, 18, 19)**

Type material. Holotype (female) from STARMER II Pl. 20 and two paratypes (male and juvenile) from STARMER II Pl. 20 as well as two paratypes from BIOLAU Bl. 12 in MNHN, two paratypes in NSMT, and two paratypes in SMF.

Type locality. North Fiji Basin, (White Lady) active hot vents, 16° 59. 50' S -173° 55. 47' W, 2000 m.

Material examined. The type material and from North Fiji Basin: STARMER II Pl. 16, 15 female, 2 male, and 15 juvenile specimens; STARMER II Pl. 18, 1 female, 10 juvenile specimens; STARMER II Pl. 19, 1 juvenile specimen; STARMER II Pl. 20, 17 female, 10 male, and 3 juvenile specimens. From Lau Basin: BIOLAU BL 03, 1 male and 6 juvenile specimens, BIOLAU BL 3 male and 1 juvenile specimen.

Distribution. North Fiji Basin and Lau Basin at bathyal hydrothermal vents.

Etymology. Species is named after James H. McLean, Los Angeles County Museum of Natural History.

Description.

Shell (Fig. 17, 18 A, B). Small for genus, almost limpet-shaped with remnants of shell-coiling at apex, even in adults, aperture irregularly oval in outline reflecting up to 12 radial broad ribs which appear not before 4-5 mm shell length; protoconch diameter 180 µm; juvenile teleoconch smooth, at shell length exceeding 1.0 mm with fine radial riblets (in adults more than 200 riblets present), which can only be seen by SEM, riblets finely knobbed; periostracum white to yellowish-brown, slightly overhanging and flexible at shell margin, in adults additionally slightly scaly at shell margin; apex approximately at mid-line, its position changes during shell growth from posterior shell margin to center of the shell; shell margin not in level but describing an irregular line corresponding to the surface of the substratum; interior of shell white, of silky brightness; horseshoe-shaped scars of shell muscles weakly marked; inner surface (except muscles scars) with numerous irregular micropores into which the filamentous papillae of the pallial surface fit, pores penetrate the ostracum but not the periostracum.

Dimensions. Largest specimen (empty shell) length 8.9 mm, width 5.1 mm, height 2.5 mm; holotype female 7.1 mm x 4.2 mm x 2.0 mm, paratype 1 (male) 5.9 mm x 3.8 mm x 2.0 mm.

Radula (Fig. 18D, E, F). Rhipidoglossate, as is typical for genus, formula 10-12 x 4 x 1 x 4 x 10-12; rachidian and four lateral teeth of similar shape, rachidian cusp slightly larger than cusp of first lateral, cusps of laterals increasing in size distally, no serrations except at distal margin of cusp of fourth lateral; there, the lowermost serration is most prominent; only 10-12 marginal pairs of teeth present, bearing finely denticulated cusps with distal, tongue-like processes.

Soft parts (Figs. 17A, D, H, 18C, E, 19A-E). Head with short tentacles directed posterio-ly; in males, the left cephalic tentacle is transformed and enlarged to function as a penis, snout

transformed, having no oral disc with marginal papillae but a large transverse furrow; neck elongated, in males with deeply marked seminal groove leading to the left cephalic tentacle; neck dorso-ventrally compressed with laterally thickened edges; eyes lacking; penis with longitudinal furrows and with a tubule at the tip. Footsole round in outline, anterior third broader than the rest, with minute slit-shaped opening of anterior foot gland; footsides laterally and posteriorly with epipodial ridge bearing up to ten pairs of tentaculiform appendages, posterior appendages of approximately the same size as the cephalic tentacles; pallial margin smooth but pallial epithelium with numerous minute, filamentous papillae fitting into the shell micropores; pallial cavity deep containing the very large bipectinate gill which apparently is used for filter feeding, afferent membrane completely absent, massive efferent axis arises at posterior of pallial cavity on left side and reaches up to or beyond anterior margin of head, gill lamellae thin and elongate (curled in contracted condition) increasing in length from posterior to anterior; visceral mass comparatively small, gonad appears to be its essential part, rectum leads to the anus at anterior right corner of pallial cavity; shell muscle horseshoe-shaped with longish left arm and slightly shorter and broader right arm, both arms posteriorly connected by an extremely thin muscular ligament. Operculum present in all specimens examined, very thin and translucent, last volutions enlarged rapidly.

Remarks. *S. macleani* sp.n. is the third species of the genus *Symmetromphalus* which lives at active hot vents in the western Pacific. The type species, *S. regularis* from Mariana vents, is reported to live in dense aggregations on basalt boulders in the path of hydrothermal effluents (McLean 1990). The same is true for *S. hageni* reported from the surface of active smokers at Manus vents (Beck 1992). All morphological evidence of the new species described here point out that *S. macleani* sp.n. is also sessile and lives as a filter-feeder. The new species' morphology is clearly distinguished from the known species by the following characters: shell with up to 12 broad radial ribs and a slightly scaly periostracum at shell margin; shell dimensions smaller; number of marginal teeth reduced to 10-12 pairs.

All specimens have intact shells with no mineral encrustations or damaged periostraca as is usual for other hot-vent taxa (e.g. species described earlier in this paper). However, as a consequence of a sessile mode of life, soft parts are in some places colonized by bacteria. At the epipodium threads of organisms similar to *Beggiotea* are common. At seminal groove, coccal organisms were found to exist in dense colonies.

***Fumocapulus* gen. n. (Figs. 20, 21, 22, 23)**

Type species. *Fumocapulus alayseae* sp. n.

Diagnosis. Rhipidoglossate archaeogastropods of moderate size. Shell cap-shaped, first teleoconch whorls overhanging posterior shell-margin, sculpture consists of fine radial ribs alternating with radial rows of leafy periostracum scales; protoconch in 240 μ m diameter, with net-like sculpture; aperture almost circular, edged by overhanging flexible periostracum. Radula formula 12-15 x 4 x 1 x 4 x 12-15, cusps of third and fourth lateral teeth with distal serrations. Neck long, perioral surface anteriorly with broad oral lobe and transverse furrow; cephalic tentacles short, directed posteriorly; in males, left tentacle thickened tremendously and transformed to function as a penis, seminal groove arises at deep left side of pallial cavity, leading to the left side of the neck and to penis, penis with thin ventro-proximal lappet covering the seminal groove as well as the small terminal tubule; epipodium restricted to a weak posterior ridge which bears small, tentaculiform appendages, three on left and six on right side of the foot. Gill bipectinate, afferent membrane absent, gill lamellae elongate, efferent gill axes of free tip do not extend beyond neck; shell muscles separate, left one longish-oval, right one of same length but broader. Operculum with multispiral initial whorls followed by whorls that extremely increase paucispirally, extending to the side of foot up to the third epipodial tentacle. Entire extension joined with side of foot.

Remarks. *Fumocapulus* differs from *Symmetromphalus* and *Neomphalus* among others in the following characters of shell and external anatomy: shell with overhanging first whorls, sculpture with thin, leafy periostracum scales, shell muscles separate, left and right one almost equal in size; gill shorter, not reaching to the neck; operculum with lateral extension on right side, which is adhered to the side of the foot; radula with serrations at cusps of third and fourth lateral teeth. These distinctions are regarded as significant at the genus level.

Classification within the Neomphalidae is mainly based on: similarity in radular morphology, protoconch diameter and sculpture, and in the morphology of penis and seminal groove, as well as in the gill modified for filter-feeding.

Etymology. Genus name has Latin roots: *fumo* for chimney, *capulus* for cap.

***Fumocapulus alayseae* sp.n. (Fig. 20, 21, 22)**

Type material. Holotype (female) and paratype 1 (male) in MNHN, two paratypes in NSMT, two paratypes in SMF.

Type locality. Lau Basin (Vailili) at active hot vents.

Material examined. The type material and four males, seven females and ten juvenile or subadult specimens all from BIOLAU BI 12.

Distribution. Lau Basin.

Etymology. Species named after Anne-Marie Alayse, Chef de Mission of the BIOLAU campaign, May 1989.

Description. In addition to the characters used to define the new genus (which also serve as species description, the following characters are considered to be significant at the species level.

Shell (Figs. 20A-G, 21A). Surface in each specimen sculptured with four fine radial riblets that alternate with conspicuous, radial rows of leafy periostracum scales, scales shaped tongue-like.

Dimensions. Holotype. Length 8.0 mm, width 7.0 mm, height 2.5 mm; paratype 7.1 mm x 5.0 mm x 2.0 mm.

Radula (Fig. 21B, C). Serration at third lateral consists of about 15 fine denticles, at fourth lateral it consists of 6-7 fine denticles and one lowermost, slightly larger blunt denticle.

Remarks. Apparently, *F. alayseae* sp.n. is rare as it was only found at one locality. This is probably due to the ecology of the species which is considered to inhabit regions that are well suited for filter feeders, i.e. places of warm to temperate hydrothermal effluents with a high content of bacteria. These places may not be sampled on every dive during the campaign. Thus, *F. alayseae* may be more common than sampling circumstances makes us believe.

Superfamily Peltospiroidea

Family Peltospiridae

***Symmetriapelta* gen.n. (Figs. 24, 25)**

Type species. *Symmetriapelta wareni* sp.n.

Diagnosis. Rhipidoglossate archaeogastropods with limpet-shaped shell of small size. Apex slightly left of mid-line, nearly at center of shell in adults, in juveniles near posterior margin of shell; in juveniles with the first teleoconch whorl present; in adults it is eroded at apex; sculpture of beaded radial ribs of varying thickness and number; aperture oval with lateral parts running almost parallel in adults; periostracum not overhanging; shell interior opaque to white with fine, coalescing, concentric lines corresponding to the shell structure, no nacre; muscle scars barely marked; depth of shell interior with minute remainder of teleoconch whorl even in adults with eroded apex. Radula with formula about 18 x 4 x 1 x about 18; of peltospirid type, first and second lateral toothbases each with additional ridge (or node), cups

of fourth lateral with delicate denticulation on inner side whereas outer side has four conspicuous denticles.

Animals with eyeless head, snout with greatly thickened circumoral roll which is divided ventrally, cephalic tentacles of equal size, very thick, directed anteriorly, extending beyond margin of snout; neck short, passing over to a deep and large concave depression in which the visceral mass is embedded; depression translucent as foot sole is very thin; foot sole oval, with continuous marginal flap that is broadened and elongated anteriorly and that bears a moderate-sized slit of the anterior foot gland; epipodium well developed, it consists of a continuous basal ridge which bears about 25 antero-lateral epipodial tentacles and two slightly solitary posterior tentacles. Pallial cavity is of moderate depth reaching to the left on half of animal length; deeper and larger on left side where it contains the gill with long afferent membrane at ventral-right side; efferent membrane fused to the pallial skirt on 80% of gill length, free tip tapering; dorsal gill lamellae short but ventral lamellae large and triangular. Anterior right part of pallial cavity short, containing anus and openings of kidney and gonad. Pallial margin adhering to the shell throughout its length, pallial skirt with micropapillae that fit into the shell pores. Visceral mass small, not filling the concave depression on dorsal side of the foot. Gonad is mostly covered by the digestive gland. Operculum absent.

Remarks. Recently, Warén & Bouchet (1993) described two new species of coiled minute peltospirids (*Planorbiella depressa*, *Pachydermia sculpta*) from Lau Basin, and recorded one juvenile specimen similar to *Planorbiella* or *Pachydermia* which could not be named.

Hence, *Symmetriapelta* is the first limpet-shaped peltospirid from the western and southwestern Pacific. However, the main area of peltospirid distribution is at EPR, where 11 genera are recognized (with coiled shell: *Depressigyra*, *Lirapex*, *Melanodrymia*, *Pachydermia*, *Planorbidella*; with limpet-shaped shell: *Peltophora*, *Rhynchopelta*, *Hirtopelta*, *Ctenopelta*, *Nodopelta*, *Echinopelta*). *Symmetriapelta* gen. n. differs from all these genera in having an almost central apex, however, there are some characters which point to a close relationship with *Nodopelta* and foremostly, with *Echinopelta*: aperture of shell with lateral margins running parallel, anatomy of the epipodium, and the presence of ridges or nodes at the bases of lateral radular teeth. While *Symmetriapelta* gen. n. is different from *Nodopelta* in having no vestige of an operculum and no glandular pallial margin, the new taxon substantially differs from *Echinopelta* in the following characters: apex of shell is almost positioned centrally (as opposed to being near the shell margin), shell margin smooth, following the line of the radial ribs on the shell surface (compared with an undulating shell margin), number of epipodial tentacles about 50 (in contrast to of more than 100), periostracum with beaded radial ribs of different size (instead of hollow spines).

It is the first record of a peltospirid genus with a limpet-shaped shell from western Pacific hot vents.

Etymology. Genus name has Latin roots, *symmetria* for symmetrical and *pelta* for shield.

***Symmetriapelta wareni* sp. n. (Figs. 24, 25)**

Type material. Holotype, 3 paratypes from type locality and 5 paratypes from Lau Basin (Vailili) in MNHN, two paratypes in NSMT; two paratypes in SMF.

Material examined. The type material and STARMER I 5 specimens, STARMER II (White Lady) PL 10 two specimens, PL 11 6 adult specimens, 3 juvenile specimens, PL 12 5 adult specimens, 14 juvenile specimens, PL 13 4 adult specimens, 3 juvenile specimens, PL 14 1 adult specimen, PL 15 1 empty shell, PL 20 1 adult specimen; BIOLAU BL 03 3 adults, 1 juvenile, BL 04 13 adults, BL 09 1 adult, BL 12 11 adults, 7 juveniles.

Type locality. North Fiji Basin (White Lady)

Distribution. North Fiji Basin and Lau Basin at hot-vent fields.

Etymology. Species is named after Anders Warén, Swedish Museum of Natural History, Stockholm.

Description. The characters defining the genus also serve as the description of the species. In addition, the following characters are worth mentioning:

Shell (Figs. 24, 25B). Shell surface with three to five beaded, fine, radial riblets alternating with thicker, beaded radial ribs; these thicker ribs are extremely variable as comparison of Figs. 24A with Fig. 24E shows. There are both character states present at North Fiji and Lau vents with all possible states of transition.

Dimensions. Largest specimen length 5.7 mm, width 4.1 mm, height 1.8 mm; Holotype 3.9 mm x 2.6 mm x 1.5 mm.

Discussion.

As it is the case in the Pectinodontinae, *Bathymacra nadinae* represents a genus which probably branched off from acmaeid patellogastropods in early geological times. While shell characters and the characters of the soft parts are largely conservative or are suspected to be pedomorphic, radular characters clearly demonstrate a long evolutionary path of separation. Starting out from the plesiomorphic radular condition in patellogastropods (i.e. having rachidian teeth as well as lateral and marginal teeth) in the Pectinodontinae marginal and rachidian teeth are absent and the lateral teeth are much more complicated in being elongated and consisting of three-parts. Black mineral encrustations of the shell, crystalline particles in the intestine and at the footsole of most of the examined specimens prove that *B. nadinae* lives in zones of hydrothermal activity. The conspicuous steps of growth on the shell indicate that it is subjected to rhythmical/periodical changes of ambient. However, it cannot be deduced from the present data whether these steps are caused by long-term fluctuations of hydrothermal activity or by seasonality. Endogenous causes can also be imagined.

Serradonta appears to be the most progressive genus judging from its strongly modified, auriculated and serrated lateral tooth (cf. Okutani, Tsuchida & Fujikura 1992, Figs. 5, 6). Like most other genera of the Pectinodontinae, the *Bathymacra*, the *Nipponacmaea*, and the *Serradonta* are endemic to hydrothermal habitats (only *Pectinodonta* Dall, 1915 inhabits normal deep-sea habitats). Thus, it can be concluded that these genera are as old as other hot-vent taxa, i.e. at least of mesozoic origin. (Beck 1993, McLean 1991, Newman 1985).

Pyropeltid limpets live at sulphide-rich deep-sea areas, i.e. at hydrothermal vents or on whale carcasses (*P. wakefieldi*); therefore, the family is not endemic to sulphide-rich hydrothermal vents but most species take advantage of these habitats (McLean & Haszprunar 1987). As evident in *P. ovalis*, the well-developed gut system along with a well functional radula, and a large odontophore as well as the gut contents hint at a nourishment that is based on grazing bacterial films from hard substrates. The shell with its deeply marked muscle scar reveals, that *P. ovalis* is adapted to high concentrations of aggressive H_2S . Apparently, the shell remains thin and translucent at muscle scar whereas the rest of the shell is thickened by continuous growth, i.e. by the deposition of numerous thin layers all over the inner surface. From an ecological point of view, pyropeltids therefore are one of the numerous groups of primary consumers which benefit from sulphide-producing processes in deep-sea environments.

However, in an evolutionary point of view, the systematic position of the pyropeltids is rather interesting. While the systematic position of *P. ovalis* within the Pyropeltidae is unquestionable, the phylogenetic relationship of the pyropeltids as a group can be discussed. In opposition to the data defining the genus *Pyropelta* (or the Pyropeltidae, respectively) given by McLean (1992), the new species, *P. ovalis*, has small oral lappets and numerous micropapillae at the pallial margin and at the head tentacles. Especially, the presence of micropapillae points at relationship with other Rhipidoglossa (e.g. Trochoidea, Pleurotomarioidea) and that pyropeltids may be descendents of a coiled rhipidoglossan group. Furthermore, this view is supported by radular characters. As outlined earlier (Beck 1996) and in comparison with other families of the Lepetelloidea, the pyropeltid radula is primitive in having all radular teeth fully developed, where only the rachidian develops partial reduction. Other families of the Lepetelloidea (e.g. Lepetellidae, Osteopeltidae, Addisoniidae, Bathyphytophilidae, Pseudococculinidae) or of the Cocculinoidea (Cocculinidae), are characterized by the general trend to reduce and transform the central field of the radula (cf. McLean & Harasewych 1995; Dantart & Luque 1994; Marshall 1985, 1987; McLean 1987, 1988, 1991; Haszprunar & McLean 1996). Especially, Marshall (1987) provides a good example for this tendency.

The present findings in conjunction with some results published by Ponder & Lindberg (1996) are in perceivable contradiction to the hypothesis given by Haszprunar (1988 a, b), who maintains that Lepetelloidea (and Cocculinoidea) have derived from an early, symmetrical limpet ancestor which had already developed the rhipidoglossan radula. However, due to constraints of space, Haszprunar's controversial concept has to be discussed elsewhere in detail.

Rather, the phylogenetic relationship of clypeosectids (*Pseudorimula*, *Clypeosectus*) are discussed. McLean (1989, 1992) and Haszprunar (1989) correctly assigned both genera to a new, separate family (Clypeosectidae) based on conchological, anatomical and radular characters. However, it seems worth to consider the conclusion of integrating these taxa within the Fissurelloidea. Several characters used for backing this view are either plesiomorphic (shell slit, two ctenidia), homoplastic (vestigial left kidney, internal fertilisation, form of salivary glands, epipodial sense organs (ESO), shell muscles without hooks), or of doubtful homology (anal gland). Moreover, there are some arguments which indicate that clypeosectids are not closely related to the fissurellids: internal fertilization is unknown in fissurellids, there are no shell pores, there is a very large anterior opening of the foot gland and, most of all radular characters represent a very distinct type. These radular characters are close to neomphalid/peltospirid ancestors. Particularly, the morphology of marginal teeth having long slender shafts with serrate tips and a large distal tongue-like process (= large denticle of McLean 1989), is identical in clypeosectids, neomphalids and peltospirids. Considering this closeness in such a specialized and intricate character, the classification of the clypeosectids among the fissurellids appears to be rather problematically.

The lepetodrilids, which are not only one of the most abundant hot vent limpet groups but also a group with very wide distribution, range from the EPR, the JdFR, the Galapagos Rift, the Guaymas Basin to the Mariana Trough, the Manus Basin, the North Fiji and the Lau Basins (McLean 1988, 1993; Fretter 1988; Warén & Bouchet 1993) as well as the Mid-Atlantic Ridge (Warén, pers. comm.). The reason for this abundance and ecological success is not quite clear. There is no significant endosymbiosis with chemoautotrophic bacteria as is described for many pogonophorans, bivalve mollusks and the mesogastropods *Alviniconcha hessleri* and *Ifremeria nautilei* (cf. Stein et al. 1988, Beck 1996 in press, Fisher 1990, Nelson & Fisher 1995). Endocytosis on the gill of *L. fucensis*, as reported by de Burgh & Singla (1984), apparently does not create a great, interspecific advantage. Thus, only the smallness and the agility of the

species as well as the high reproductivity remain as possible explanations for the abundance of this gastropod.

The systematics and the phylogeny of this species have recently been revised by Sobjinski & Beck (1996), who recognized a further subspecies at the Mariana Trough, *Lepetodrilus schrolli marianae*, and who formulate a first phylogenetic hypothesis stemming from the assumption that the center of origin of lepetodrilids was at the EPR and the Galapagos Rift. In addition, this comparative study suggests that lepetodrilids are related to neomphalids and peltospirids.

Obviously, neritoids have invaded the sulfide-rich environments only in two marine areas: on the Louisiana Slope (U.S.A.), the coiled *Bathynnerita naticoidea* is reported from "Bush Hill"-vents (Warén & Bouchet 1993) and at west and southwest Pacific vents, the limpet-shaped species of the genera *Shinkailepas* and *Olgasolaris* show several adaptations to the hot vent milieu reflecting a long evolutionary pathway separate from other deep-sea or littoral neritoids (Okutani et al. 1989; Beck 1992 b). Especially, the enlargement of the periostracum in *Olgasolaris* and the development of shell pores complete with fitting mantle papillae can be seen as trends aiming at the protection against aggressive hydrothermal fluids. The same is true for the enlargement of the oral lobe and paddle-like epipodial flaps which produce high quantities of mucus. Unusual for hot vent taxa, both genera have to be classified among the Phenacolepadidae, whose other members mainly comprise species occurring in the marine littoral and in freshwater. However, close relationship to these genera (e.g. *Phenacolepas*) is substantiated by soft parts and radular characters (Beck 1992 b). Therefore, it may be assumed that coiled ancestors of Phenacolepatidae lived in the marine littoral zone and were replaced by modern gastropoda (e.g. Caenogastropoda). In this view, freshwater habitats and hot vent habitats are relict ranges of this group. Since classification should reflect this distribution, a new subfamily, Shinkailepadinae, for the hydrothermal vent taxa is proposed here.

Neomphalid and peltospirid species were classified inconsistently by taxonomists. While McLean (1981, 1989, 1990), Fretter (1989) and Haszprunar (1988a, b) treated both groups as superfamilies, Warén & Bouchet (1989, 1993) classified the peltospirids as a family of the Neomphaloidea. In my opinion, McLean (1990) provides sufficient arguments for separating the two groups as superfamilies (e.g. tapered snout with protrusible subradular organ). Therefore, his classification is maintained in this paper accepting two families for Neomphaloidea, Neomphalidae for the limpet- or cap-shaped members and Cyathermiidae for the coiled members. However, the Peltosperoidea comprising only one family, the Peltospiridae, probably are polyphyletic (cf. Warén & Bouchet 1993) as it contains both coiled members and limpets. In addition, there are species with net-sculpture on the protoconch as well as species with longitudinal ribs on the protoconch. Moreover, there are atypical peltospirids such as *Melanodrymia* (cf. Hickman 1984, Haszprunar 1989b) which may represent a separate branch. Therefore, the phylogeny of peltospirids needs reconsideration, e.g. applying a cladistic analysis.

The neomphalids examined in this study have clearly to be ranked among the Neomphalidae. *Symmetromphalus mcleani* sp. n. is a sister-species to *S. hageni* from the Manus Basin and *S. regularis* from the Mariana vents. In comparison to *Neomphalus fretterae* from EPR, I have argued earlier (Beck 1992a) that *Symmetromphalus* is more derived than *Neomphalus*. New results produced by the examination of *Fumocapulus* gen. n. justify to change this view. The two genera *Neomphalus* (with a special food groove and only one shell muscle) and *Symmetromphalus* (incorporating all typical characters of symmetrical limpets), are highly derived within the Neomphaloidea whereas *Fumocapulus* may be interpreted as a rather primitive form.

Though cap-shaped, *Fumocapulus* has retained remnants of shell coiling, which can even be seen in the anatomy of soft parts. Also, the gill is still comparatively small although it is modified for filter-feeding. The long growing edge of the operculum and the special periostracum scales can be recognized as autapomorphies for this genus. Taking all this in account, it is imaginable that *Neomphalus* was separated from *Symmetromphalus* and *Fumocapulus* during early geological times when the EPR came into existence (cf. Weijermars 1989). McLean (1990) notes that Neomphaloidea and Peltospiroidea can only be united by symplesiomorphies such as the lack of nacre, lack of the ctenidial bursicles, and an unspecialized radula. I will add another plesiomorphic character which, nevertheless, reveals the groups related to both the neomphalids and the peltospirids: these two groups share a special type of marginal tooth (long shaft with finely denticulated cusp and a tongue-like distal process). The same type can be found in the Lepetodriloidea, the Clypeosectidae and, surprisingly, even in Shinkailepadinae (Neritoidea) where this type is present in a few numbers at the outer margin of the radula (cf. Beck 1992b and Fig. 13c of this paper). Consequently, there must have been a common ancestor of all these groups which developed the synapomorphy described above. Though the radula of neomphalids and peltospirids (see also Hickman 1983) is rather unspecialized (no reduction or extreme enlargement of teeth as in other archaeogastropod superfamilies), the basic pattern of the radula is nearly identical in both groups. This suggests that they may be a clade and a mutual branch of an early Palaeozoic archaeogastropod stock that was separated from the ancestors of Lepetodriloidea, Clypeosectidae and Shinkailepadinae in very early geological times. However, in the fossil record there is no trace of either group and neomphalids apparently seem to be not related to the Palaeozoic Euomphaloidea as supposed by McLean (1981). Shell structure (Batten 1984) and the absence of close relatives among the Mesozoic and Caenozoic genera (*Amphitonaria*, *Discohelix*, *Weeksia*, cf. Bandel 1988) furnish evidence for that hypothesis. Up to now, only two minutely coiled peltospirids have been known from western Pacific vents, *Pachydermia sculpta* and *Planorbidella depressa* (cf. Warén & Bouchet 1993). *Symmetria pelta wareni* is the first record of a limpet-shaped peltospirid from that locality. This species bears resemblance to *Nodopelta* and *Echinopelta*, both highly derived genera from the EPR (13°N; 21°N) but further phylogenetic consideration requires more detailed information acquired by cross-sectioning. It is evident that the centre of peltospirid distribution is still at the EPR where 11 genera are recognized. The recently described *Rhynchopelta? nux* (Okutani, Fujikura & Sasaki, 1993) was discovered to be a *Lepetodrilus* species (Sobjinski & Beck 1996).

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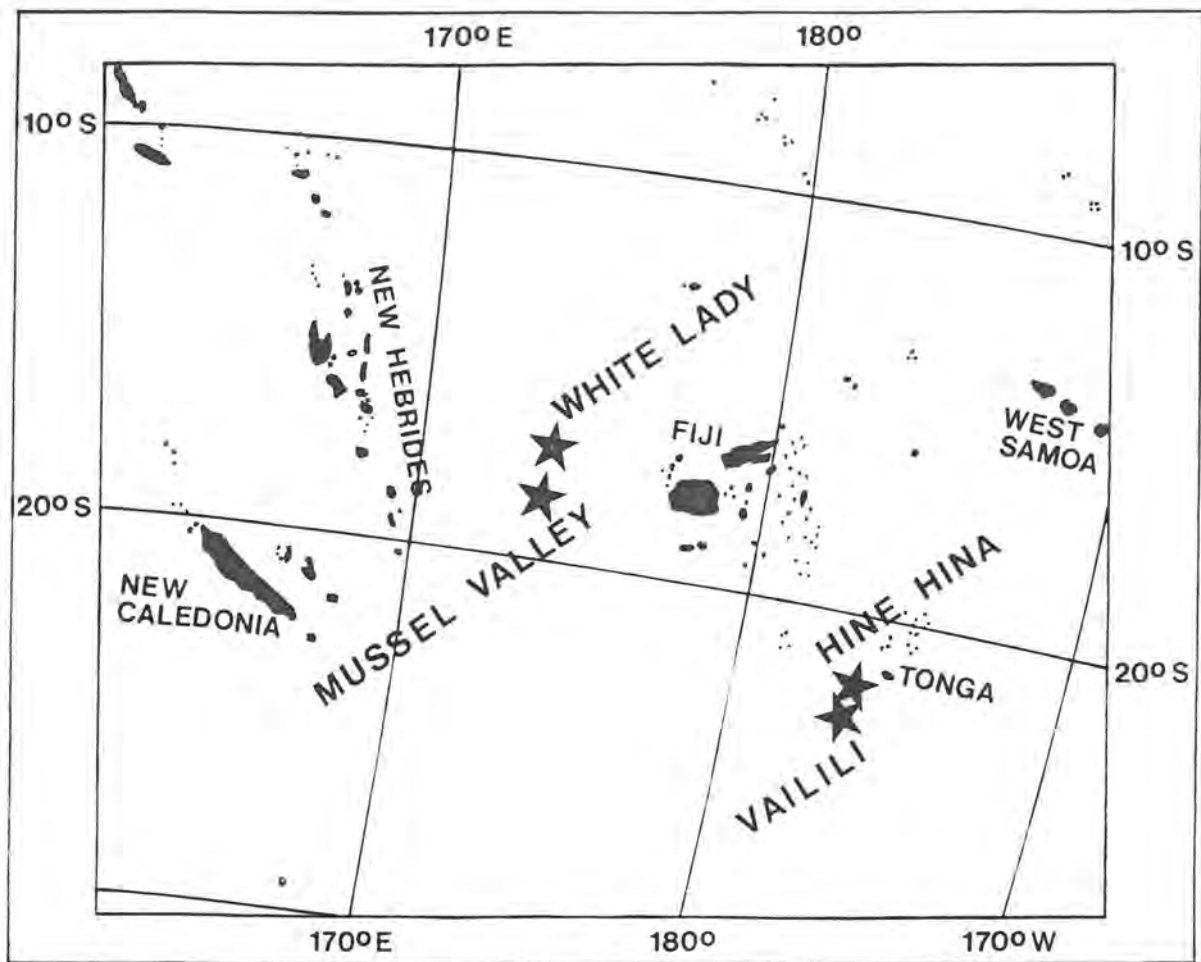


Fig. 1. Map of investigated areas. BIOLAU: Hine Hina ($22^{\circ} 32'S$, $176^{\circ} 43'W$, 1900 m) and Vailili ($23^{\circ} 13'S$, $176^{\circ} 38'W$, 1750 m); STARMER II: White Lady ($16^{\circ} 59.50'S$, $173^{\circ} 55.47'W$, 2000 m) and Mussel Valley ($18^{\circ} 50'S$, $173^{\circ} 29'W$, 2750 m).

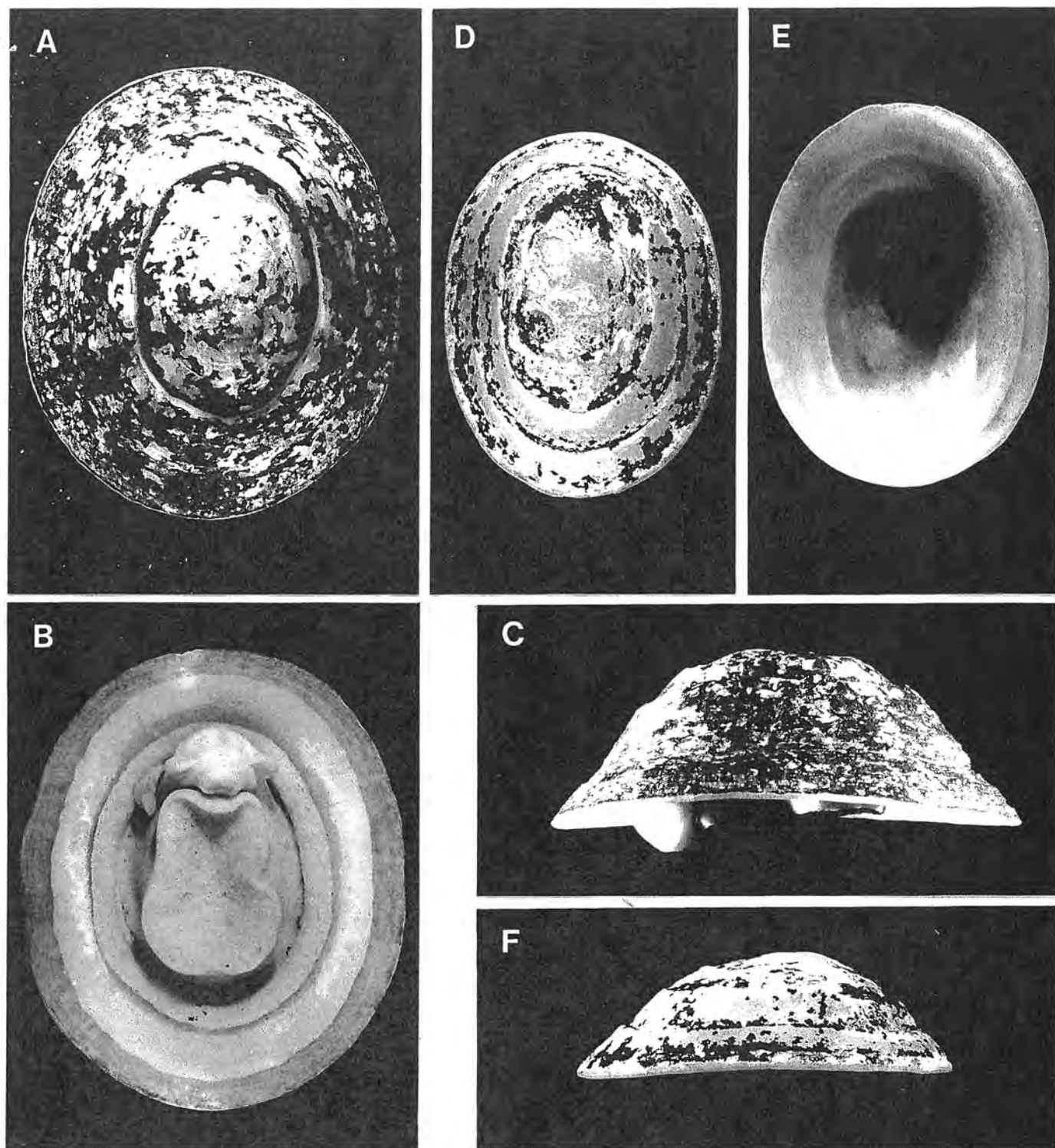


Fig. 2.

A-F. *Bathyacmaea nadinae* sp. n., shell and soft parts. A-C. Holotype (shell length 23.00 mm). A. Apical view. B. Ventral view showing soft parts in retracted condition. C. Lateral view of left side. D-F. Shell of paratype 2 (shell length 12.0 mm). D. Apical view, apex eroded. E. Ventral view. F. Lateral view of right side showing conspicuous steps of growth.

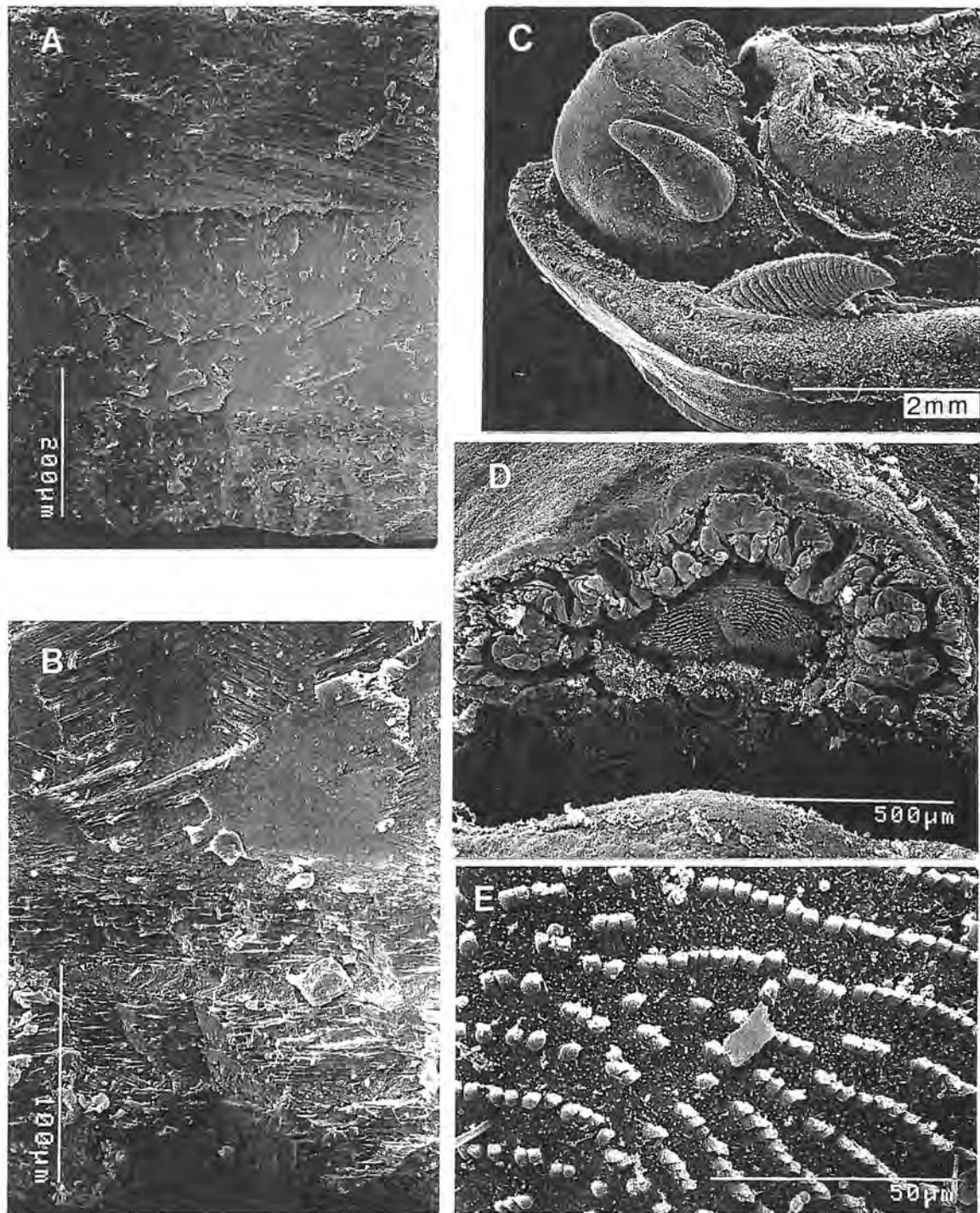


Fig. 3.

A-E. *Bathyacmaea nadinae* sp. n., SEM micrographs of shell and soft parts. A, B. Tangential shell fracture from the mid-point at the middle between apex and shell margin showing three layers: A. Shell layers (from top to bottom) concentric, crossed-lamellar and radial-lamellar prismatic. B. Concentric crossed-lamellar and radial crossed-lamellar layer. C-E. Soft parts. C. Anterior part, oblique view from right. D. Snout with mouth-opening, oral fringe and slightly protruded odontophore. E. Surface of odontophore equipped with rows of minute pins.

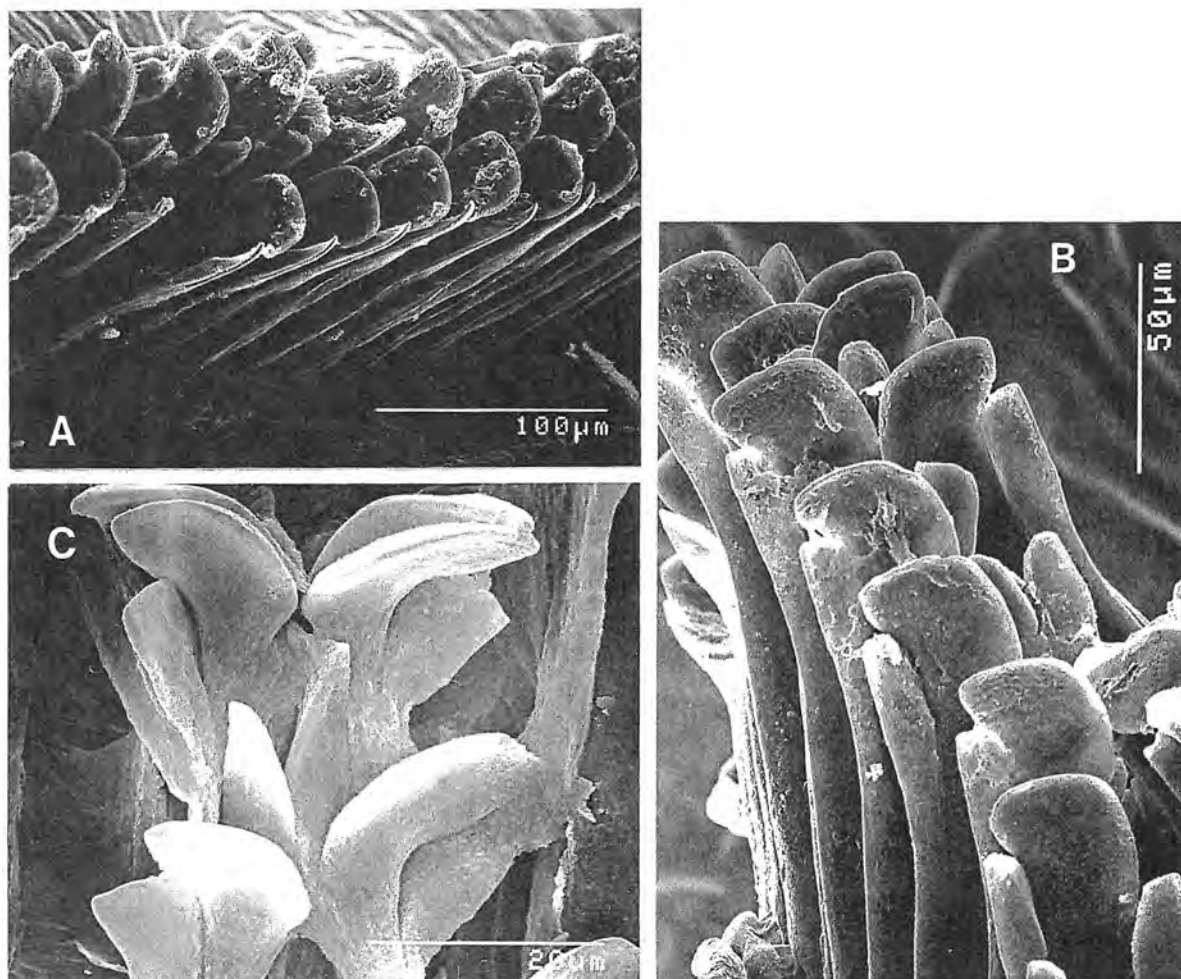


Fig. 4. A-C. *Bathyacmaea nadinae* sp. n., SEM micrographs of radulae. A. Specimen from BIOLAU BL 02. B. Specimen from STARMER II Pl. 18. C. Juvenile specimen from BIOLAU BL 07 (shell length 3. mm).

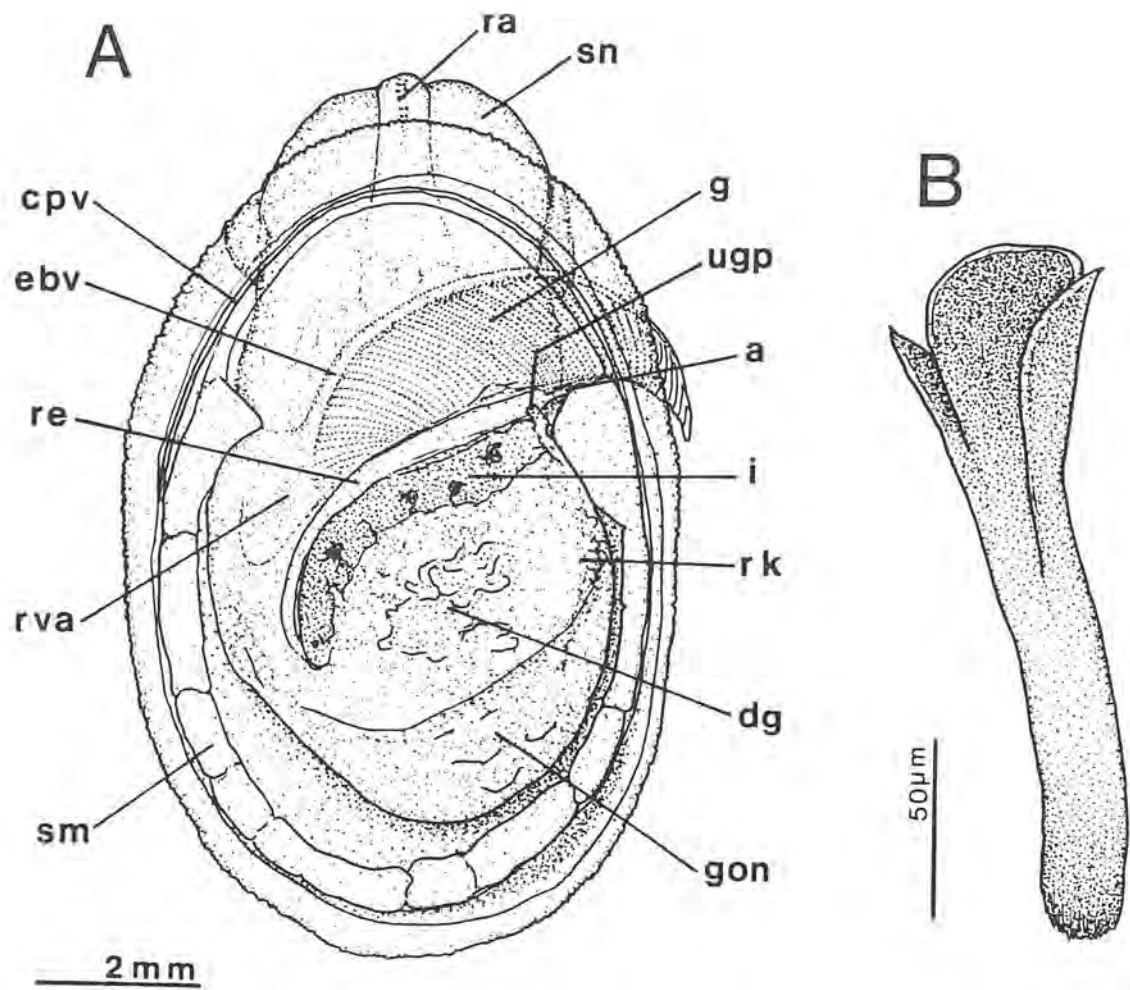


Fig. 5. A-B. *Bathyacmaea nadinae* sp. n.
 A. Dorsal view of soft parts, neck and gill seen by transparency.
 B. Single, right, lateral, trifid tooth of radula.

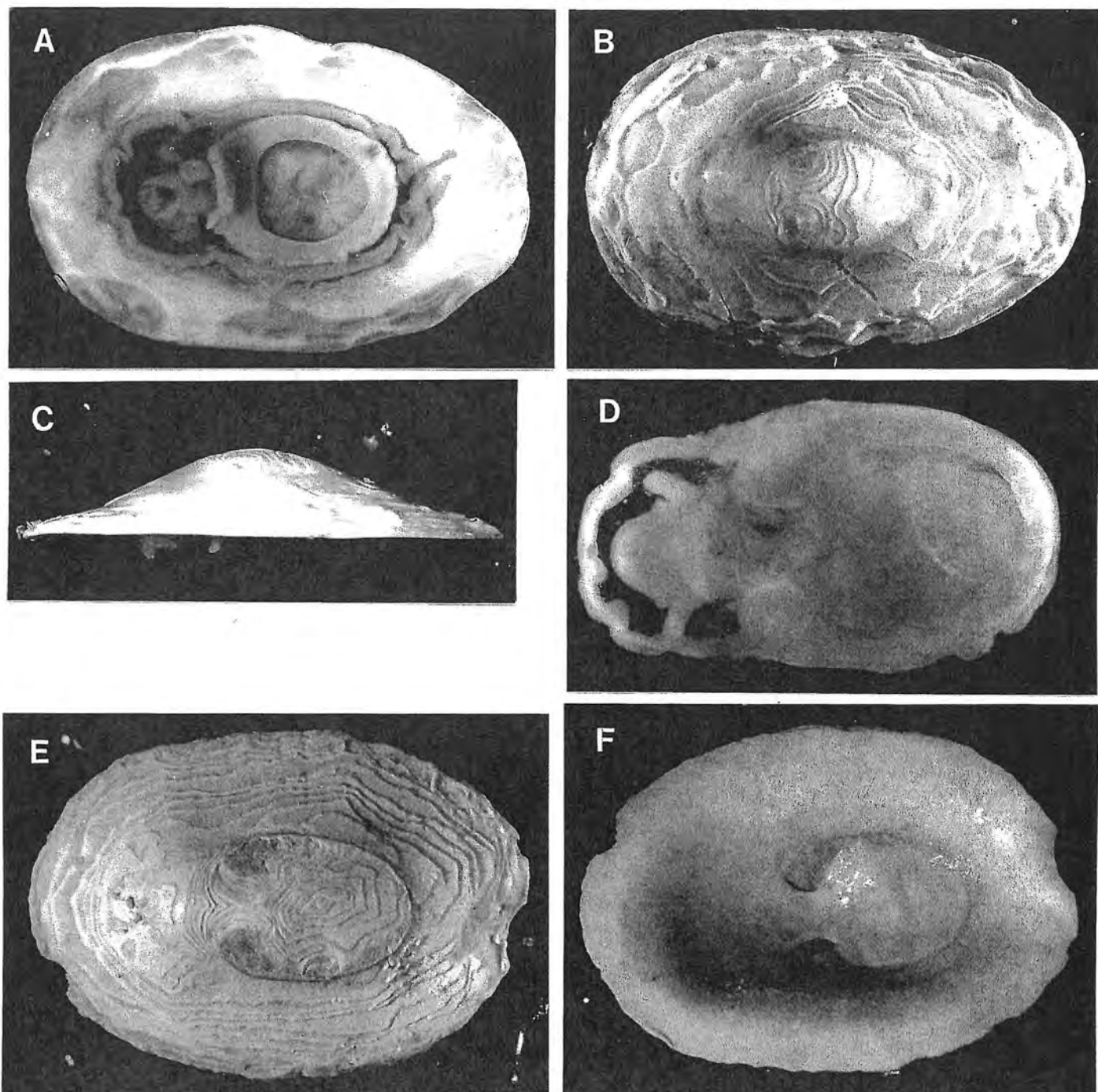


Fig. 6.

A-F. *Pyropelta ovalis* sp. n., shell and soft parts.

A,B,C. Holotype (shell length 5.4 mm; anterior to the left). A. Ventral view.

B. Apical view. C. Lateral view. D,E,F. Paratype 1 (shell length 5.2 mm; anterior to the left). D. Soft parts removed from shell in dorsal view; cf. Fig. 8.

E. Apical view on shell. F. Ventral view on shell; note the heavily marked horseshoe-shaped scar of shell muscle.

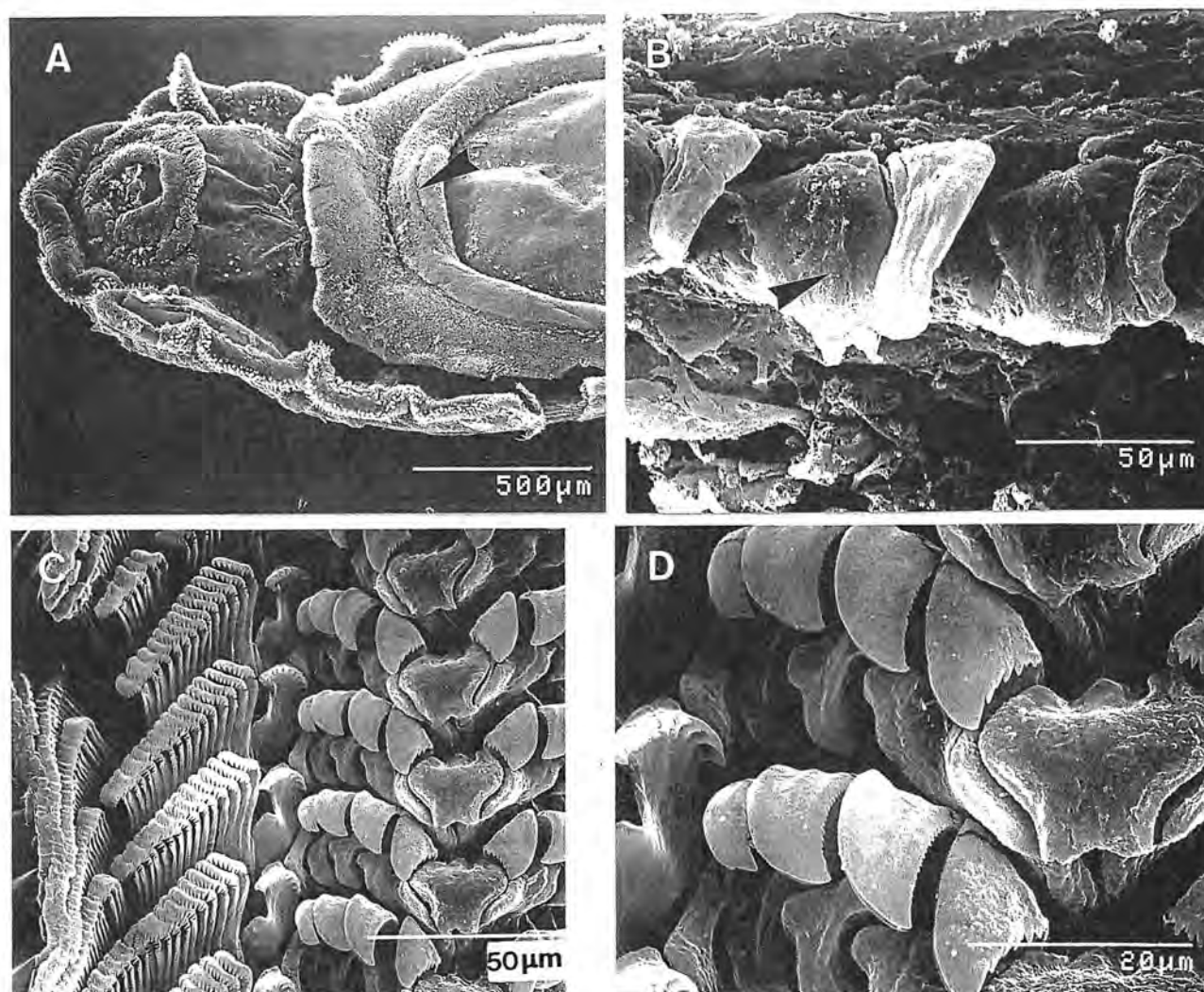


Fig. 7.

A.-D. *Pyropelta ovalis* sp. n., soft parts and radula.

A. Anterior half of soft parts in oblique ventral view; arrow points to the opening of the anterior foot gland. B. Gill lamellae at ventral right side of soft parts (cf. Fig. 8), arrow indicates the ciliated and thickened base of gill lamella anterior to the non-ciliated flap. C. Radula. D. Half of the central field of radula.

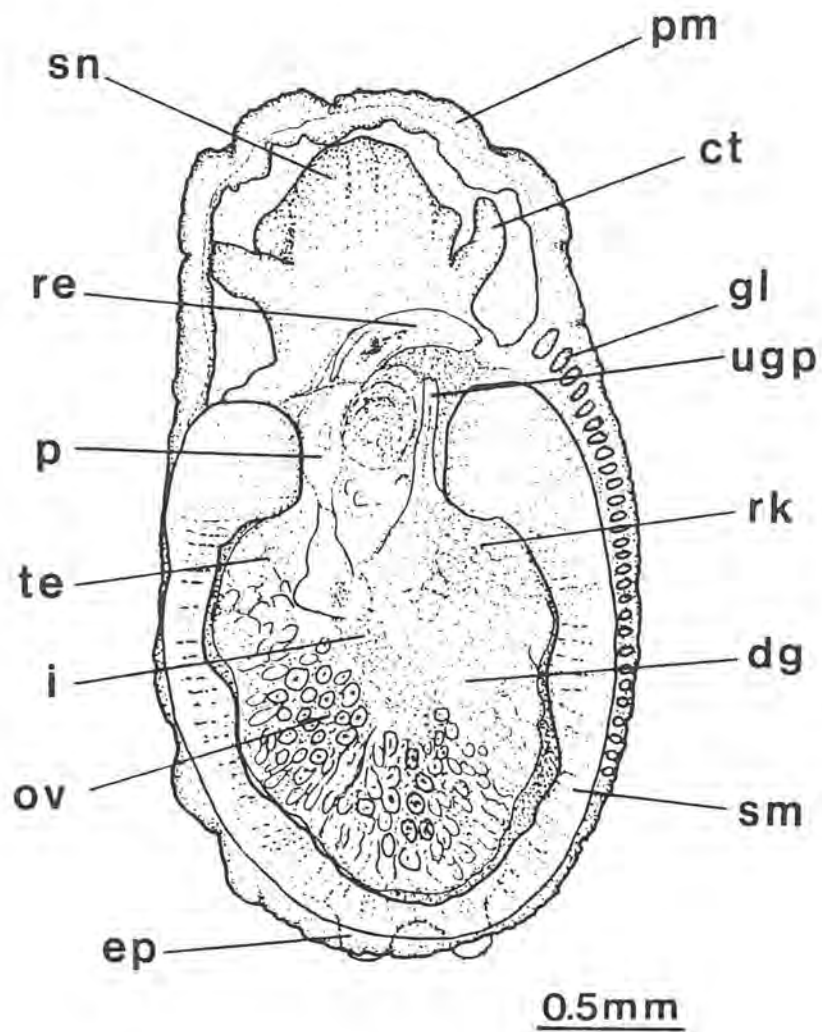


Fig. 8. *Pyropelta ovalis* sp. n., soft parts depicted in dorsal view, gill lamellae shown by transparency. (Abbreviations cf. material and methods).

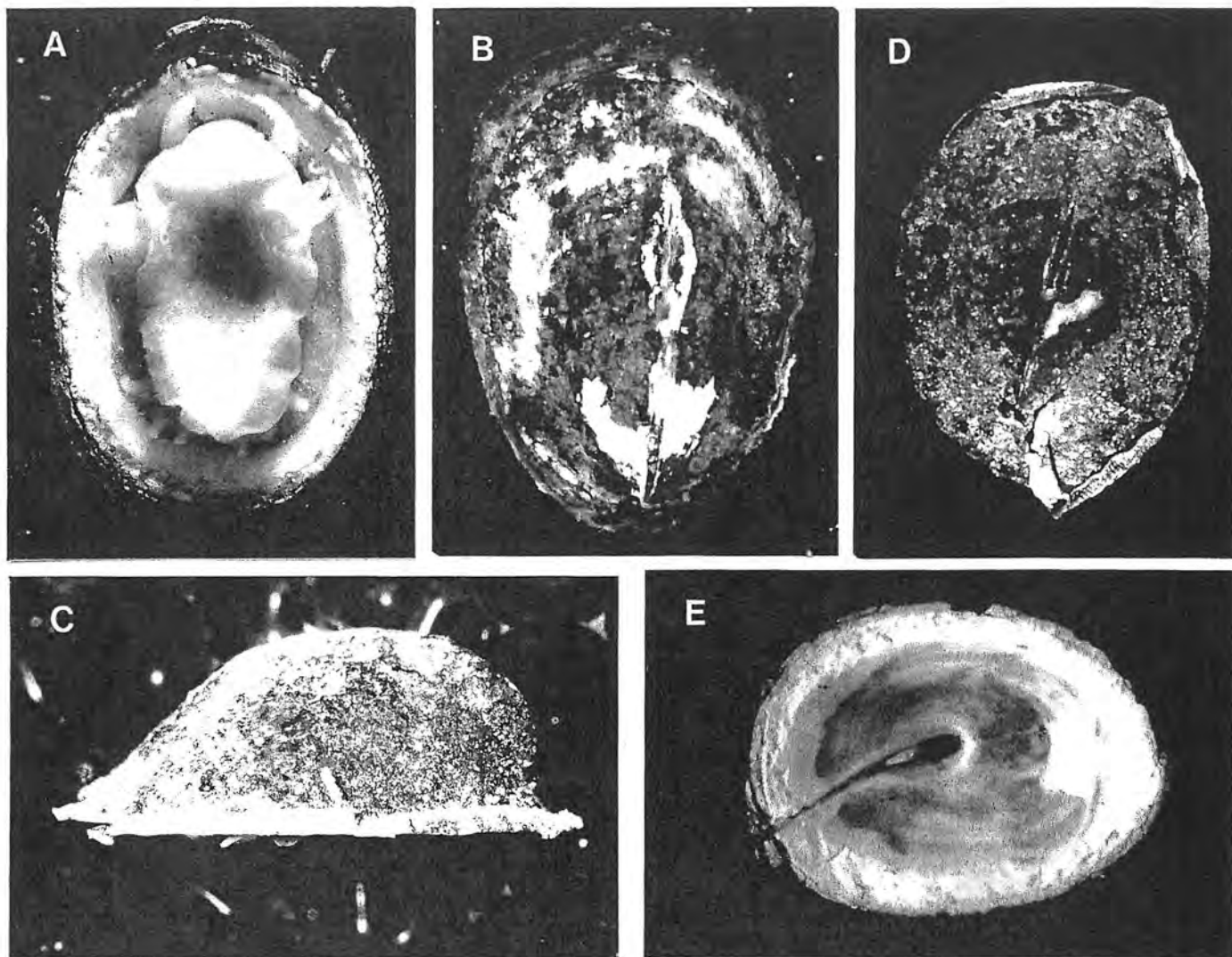


Fig. 9. *Pseudorimula leisei* sp. n., shell and soft parts. A; B, C Holotype (shell length 4.5 mm). A. Ventral view. B. Apical view. C. Lateral view from left. D, E Paratype 1, (shell length 5.1 mm). Apical and ventral view.

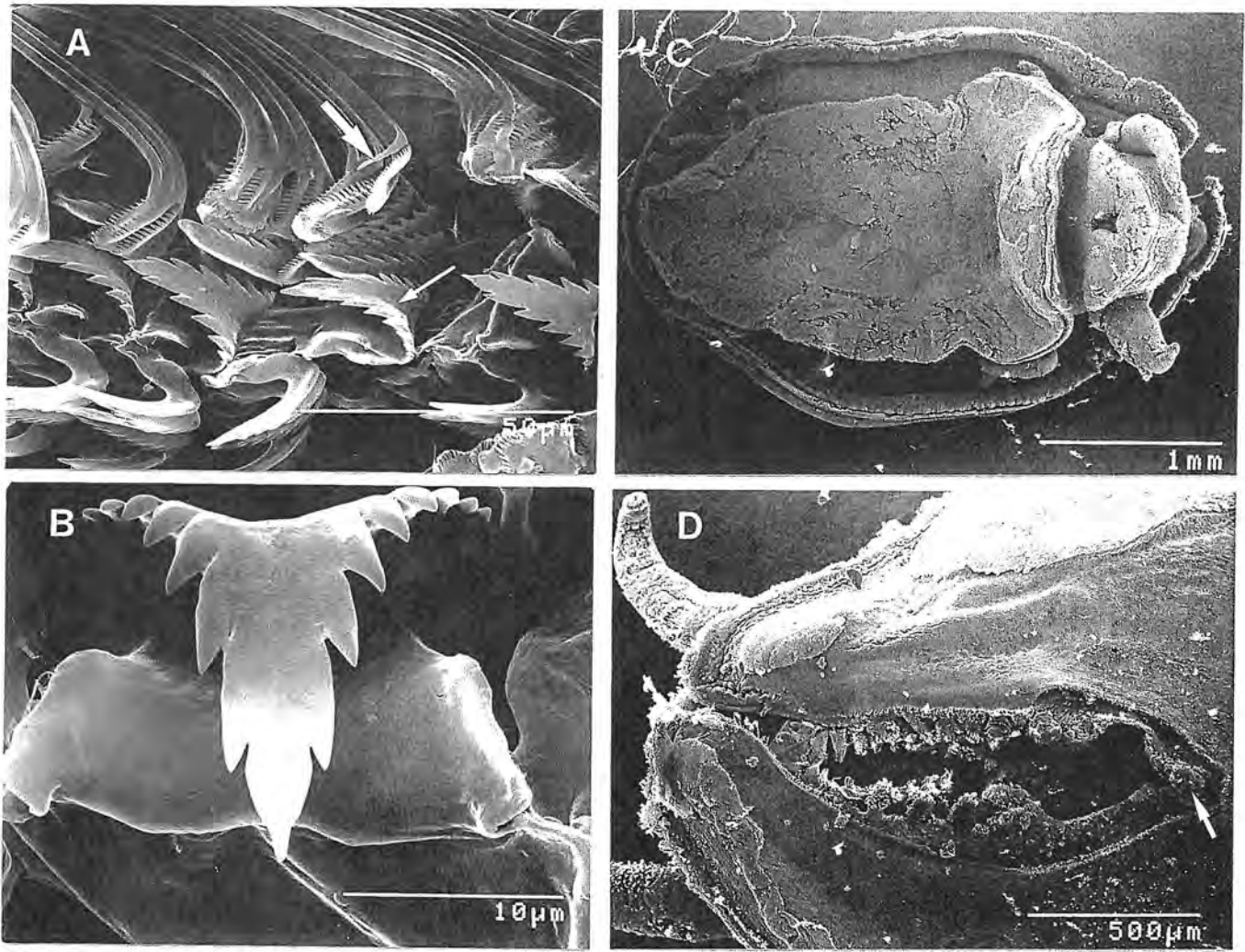


Fig. 10.

Pseudorimula leisei sp. n., radula and soft parts. A, B, C. Radula. A. Overview depicted in lateral view, thin arrow: rachidian tooth, bold arrow: tongue-like process at marginal tooth. B. Rachidian tooth with serrate, extremely overhanging cusp. C. Top of marginal teeth (arrow points to the distal tongue-like process). D. Soft parts (critical-point dried). Orofium with many tentacles at the anterior slit, with thin membranes at opening, and a single tentacle (arrow) at its posterior end.

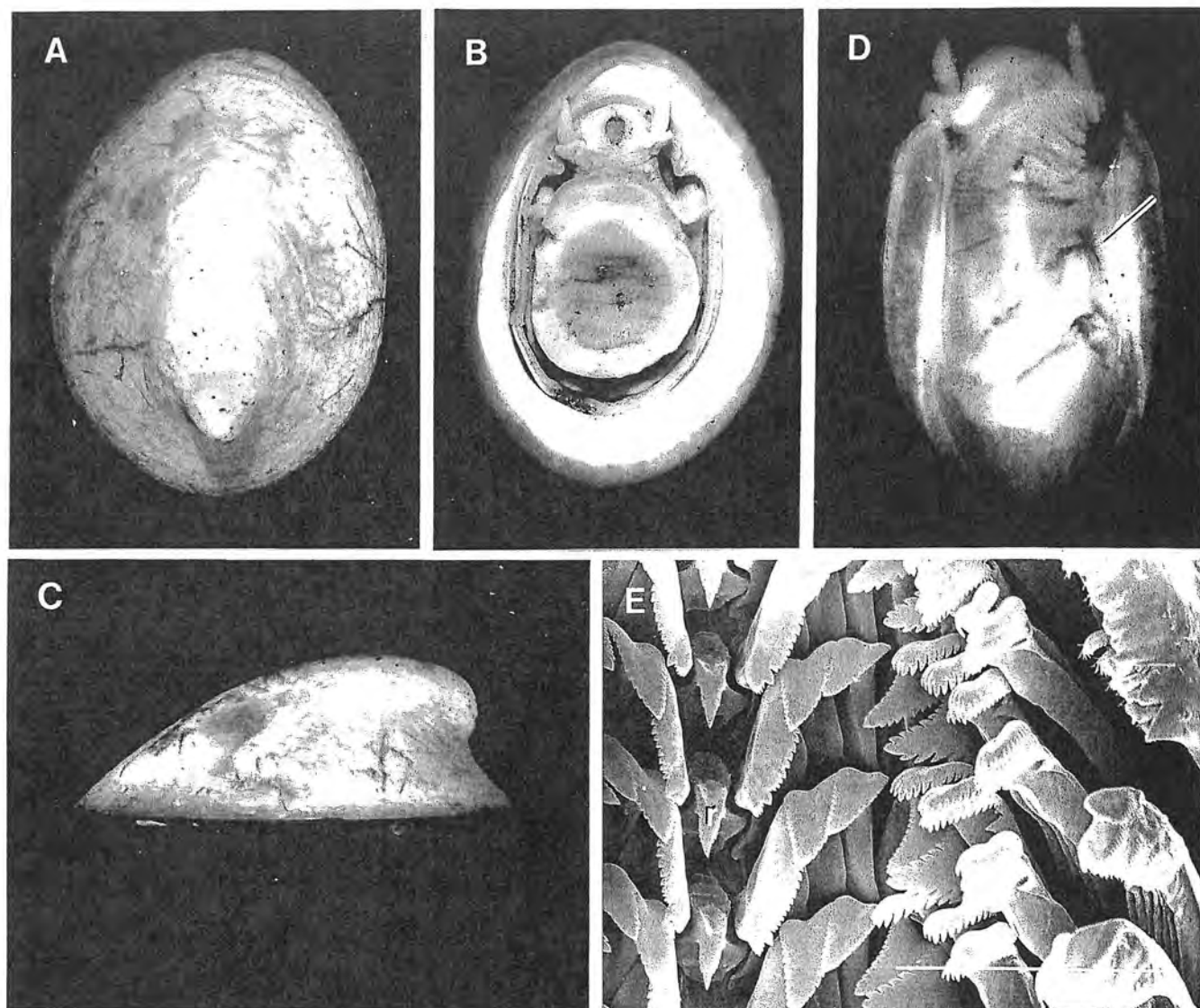


Fig. 11.

Lepetodrilus schrolli fijiensis subsp. n.

Shell, soft parts and radula. A, B, C. Holotype, shell length 11.0 mm. A. Dorsal view. B. Ventral view. C. Lateral view. D. Specimen from BIOLAU BL 12 removed from shell, anterior part of mantle skirt dissected, arrow points to the rudimentary right gill. E. Radula, detail of right half-row.

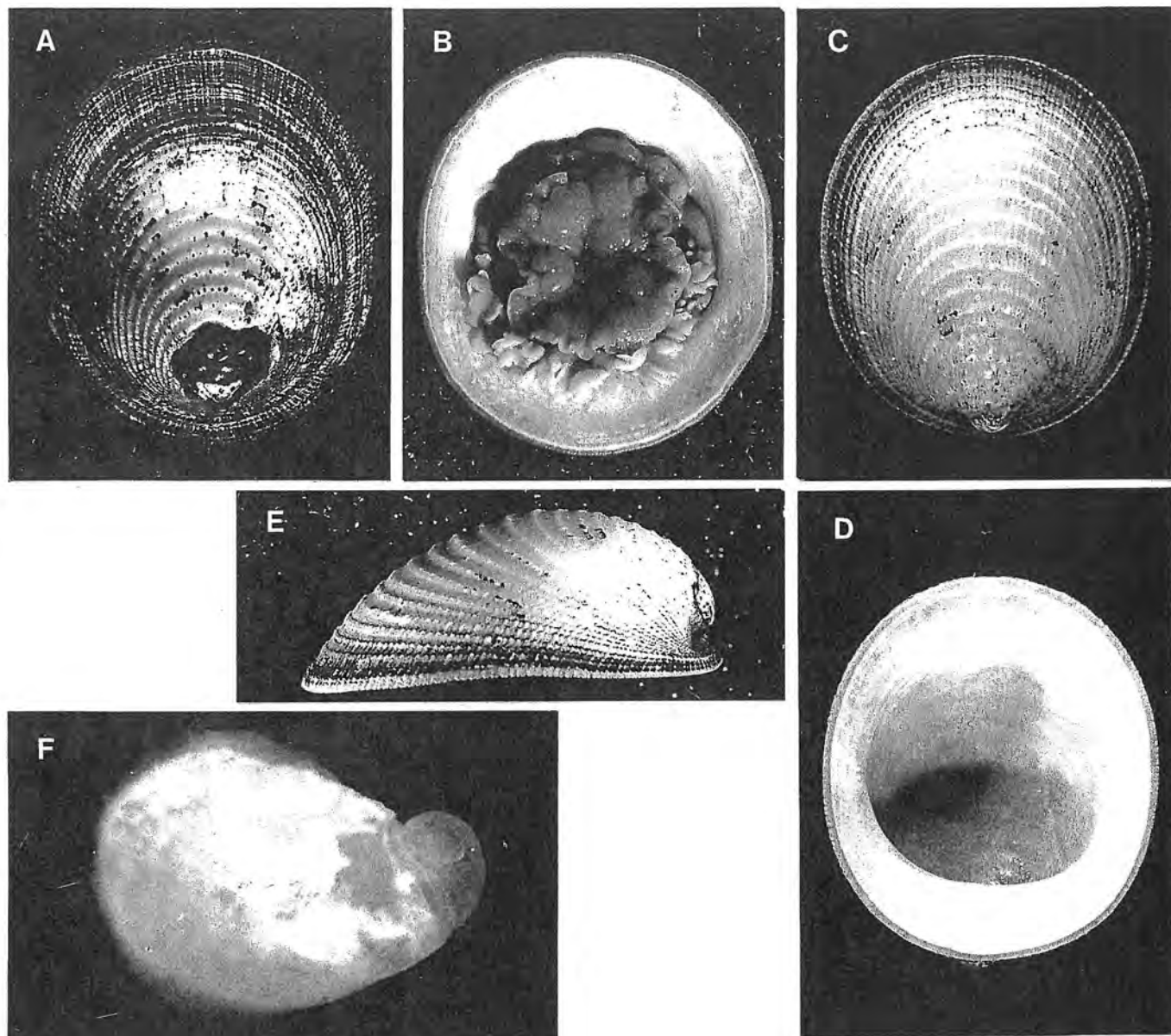


Fig. 12. *Shinkailepas conspira* sp. n.
 A, B. Holotype (shell length 21.3 mm), C, D. E. Paratype (NSMT, shell length 9.7 mm) and F. Juvenile specimen BIOLAU BL 06 (shell length 4.0 mm).
 A. Holotype, dorsal view. B. In ventral view. C. Paratype, dorsal view. D. In ventral view. E. In lateral view. F. Juvenile shell with coiled protoconch.

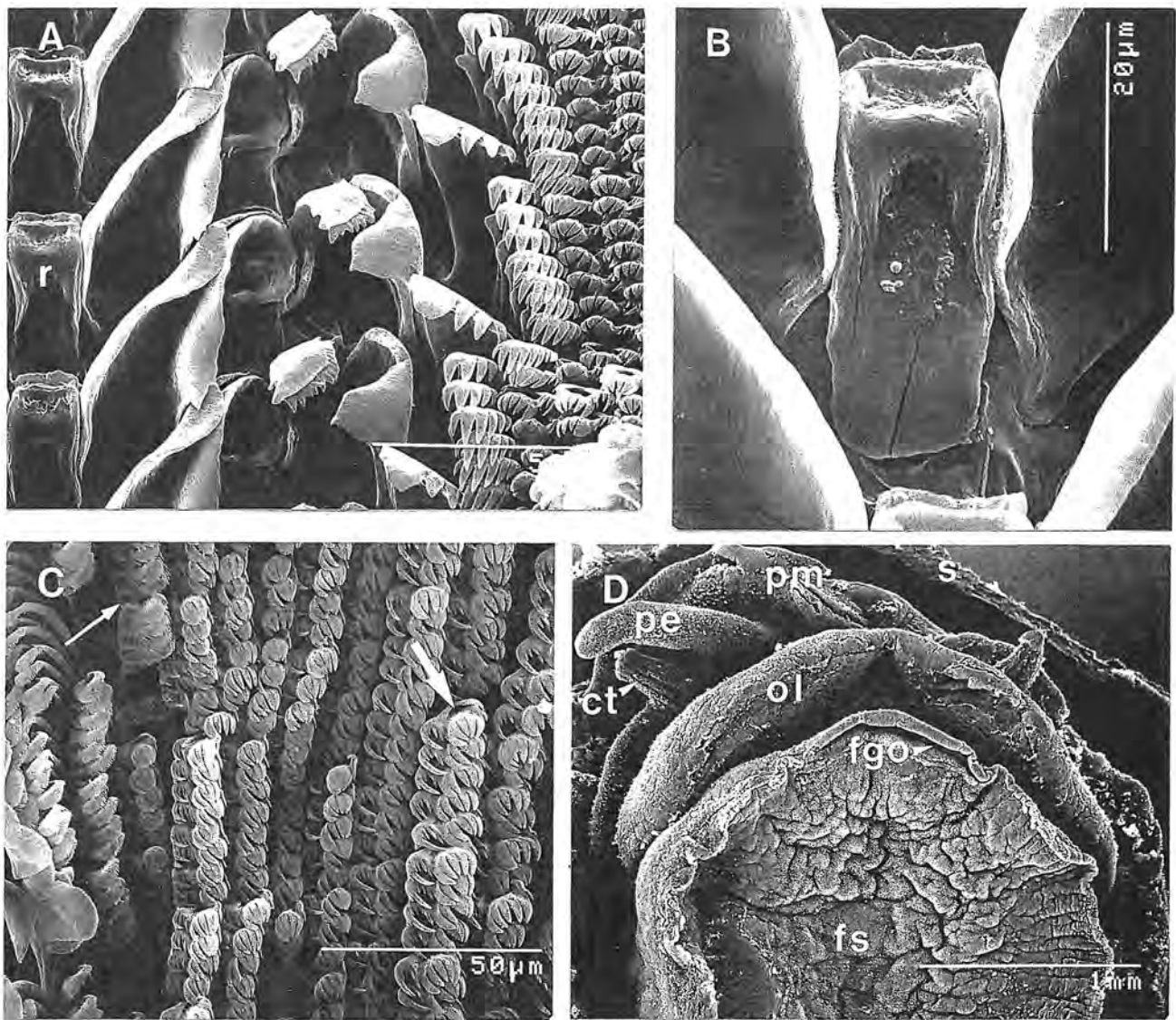


Fig. 13. *Shinkailepas conspira* sp. n.
 A, B, C. Radula. D. Soft parts. A. Detail, right half-row. B. Rachidian tooth with anterior, horseshoe-shaped ridges. C. Detail of marginal teeth, small arrow points to the tooth-type with distal tongue-like process, large arrow points to the tooth-type defining *Shinkailepas* and *Olgasolaris*. D. Male, anterior part, viewed from ventrally.

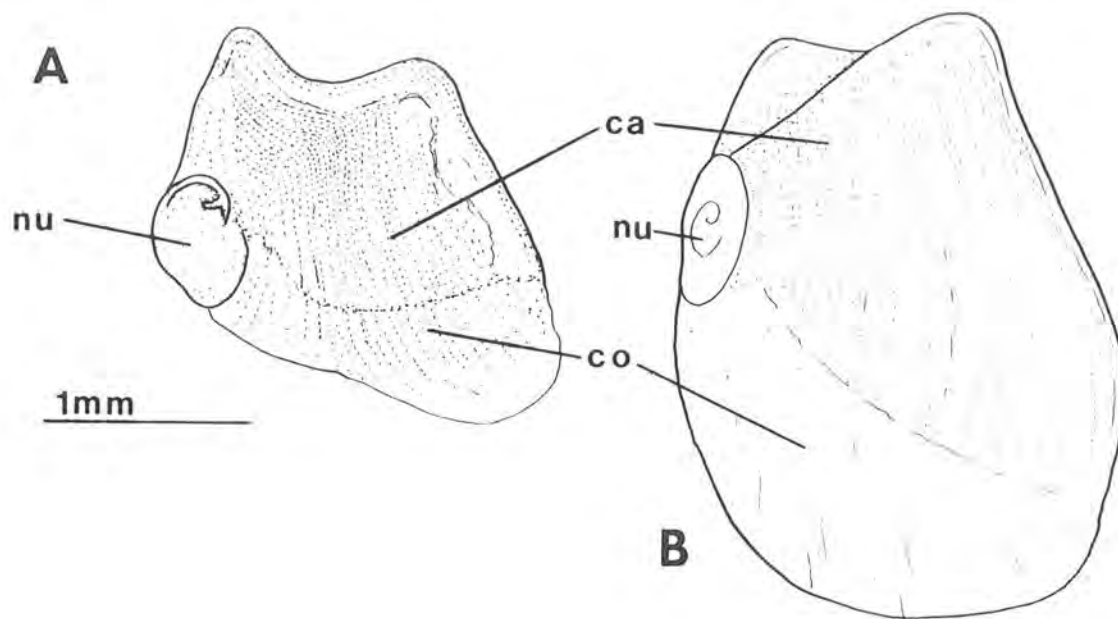


Fig. 14 A. Operculum of *Shinkailepas conspira* sp. n., (shell length 10.1 mm) in dorsal view. B. Operculum of *Olgasolaris ethmoconcha* sp. n. (shell length 9.9 mm) in dorsal view.

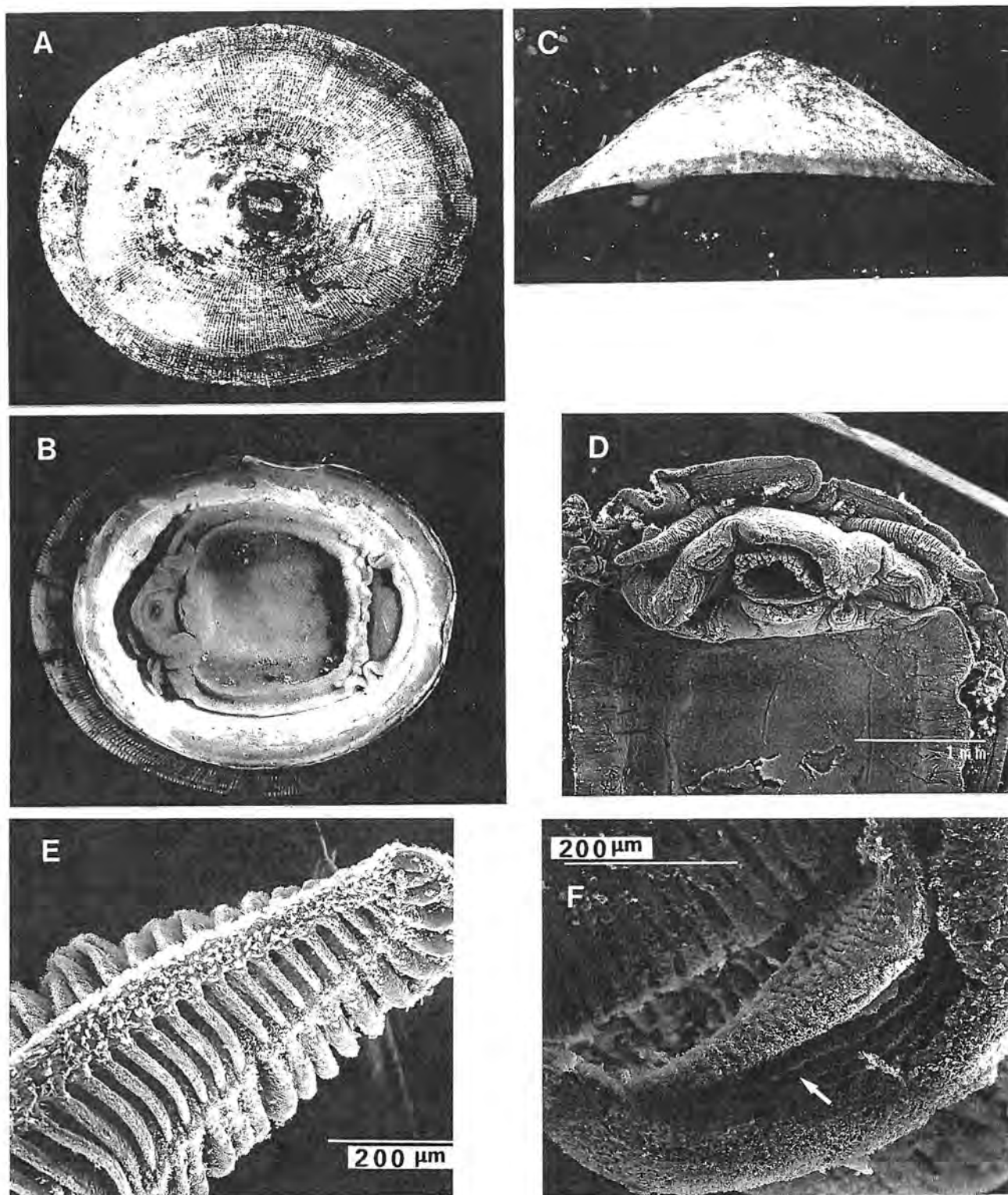
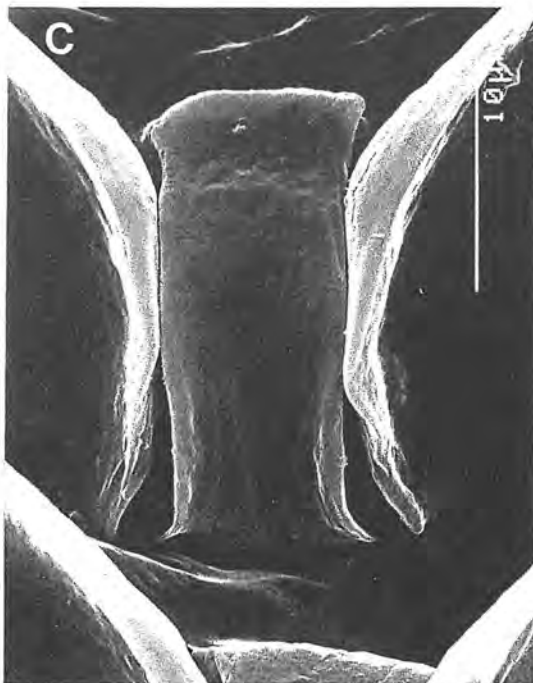


Fig. 15. A-F. *Olgasolaris ethmoconcha* sp. n., shell and soft parts. A, B, C. Paratype BL 12, shell length 10.8 mm; anterior to the left. A. Dorsal view. B. Ventral view, C. Lateral view. D. Critical-point dried specimen (female) in ventral view. E. Tip of bipectinated gill in dorsal view, gill rod densely covered with ciliary bunches. F. Right cephalic lappet of male specimen transformed to a penis with seminal groove, arrow points to longitudinal rows of cilia.



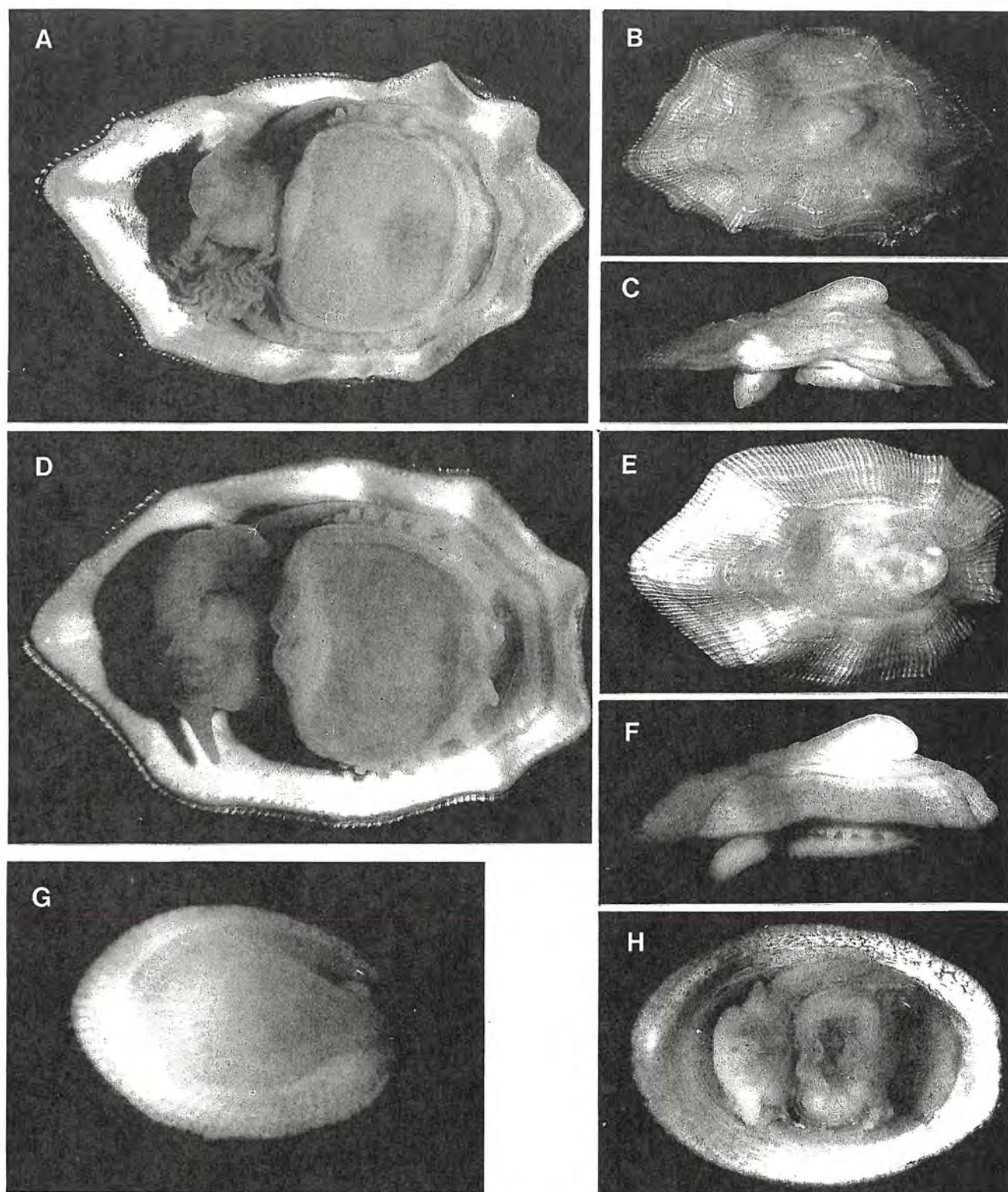


Fig. 17. A.-C. *Symmetromphalus macleani* sp.n., holotype, female, shell length 7.1 mm. A. Ventral view. B. Dorsal view. C. Viewed from left. D.-F. *S. macleani* sp.n., paratype 1, male, shell length 5.9 mm. D. Ventral view. E. Dorsal view. F. Viewed from left. G. H. *S. macleani*, sp. n., juvenile specimen, shell length 2.3 mm. G. Dorsal view. H. Ventral view.

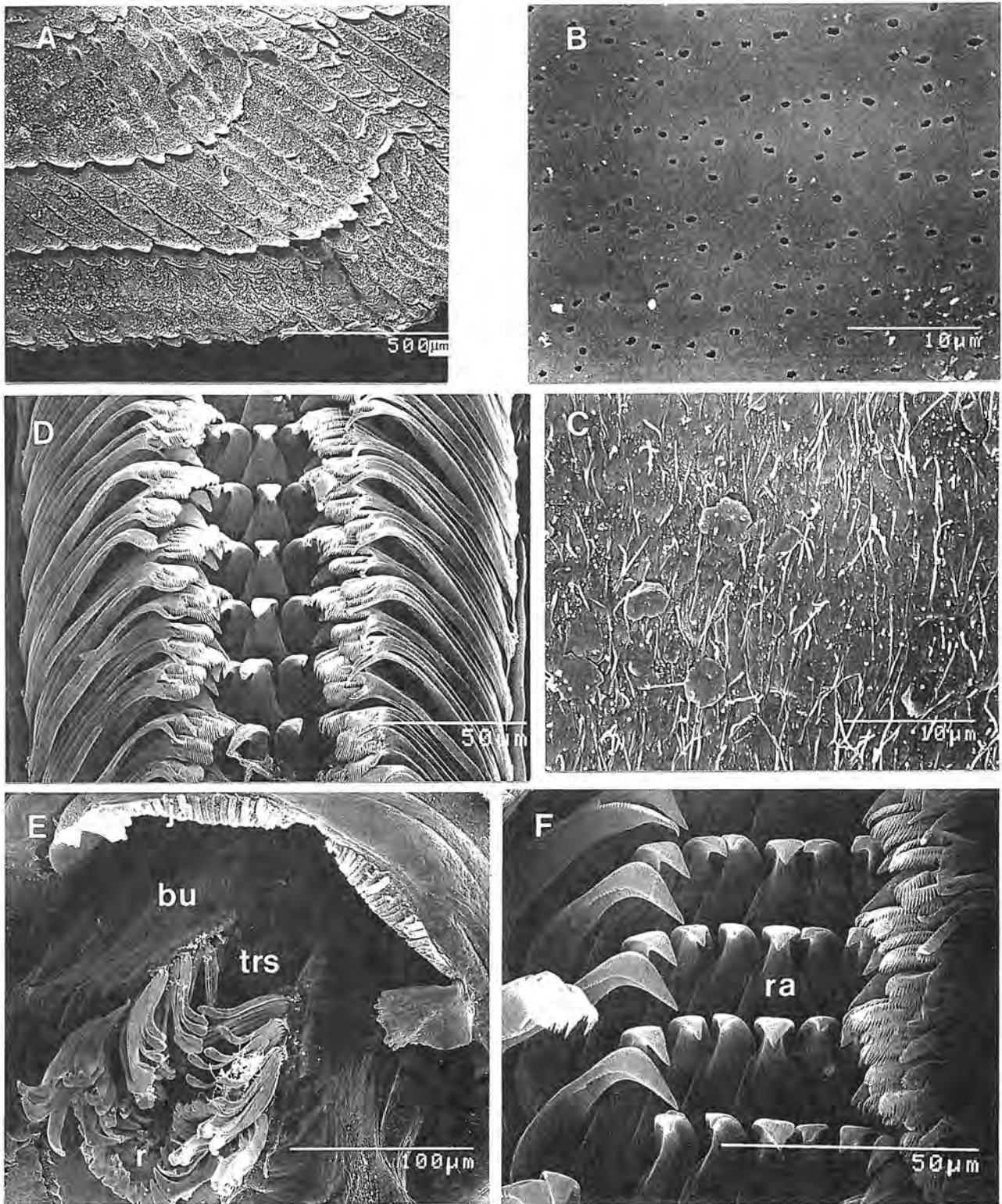


Fig. 18. A.-F. *Symmetromphalus macleani* sp.n. A. Periostracum at shell margin. B. Interior of shell with micropores. C. External surface of pallial skirt with filamentous papillae fitting to the shell micropores. D. Radula, overview. E. Dorsal jaws and protruded buccal mass with radula.

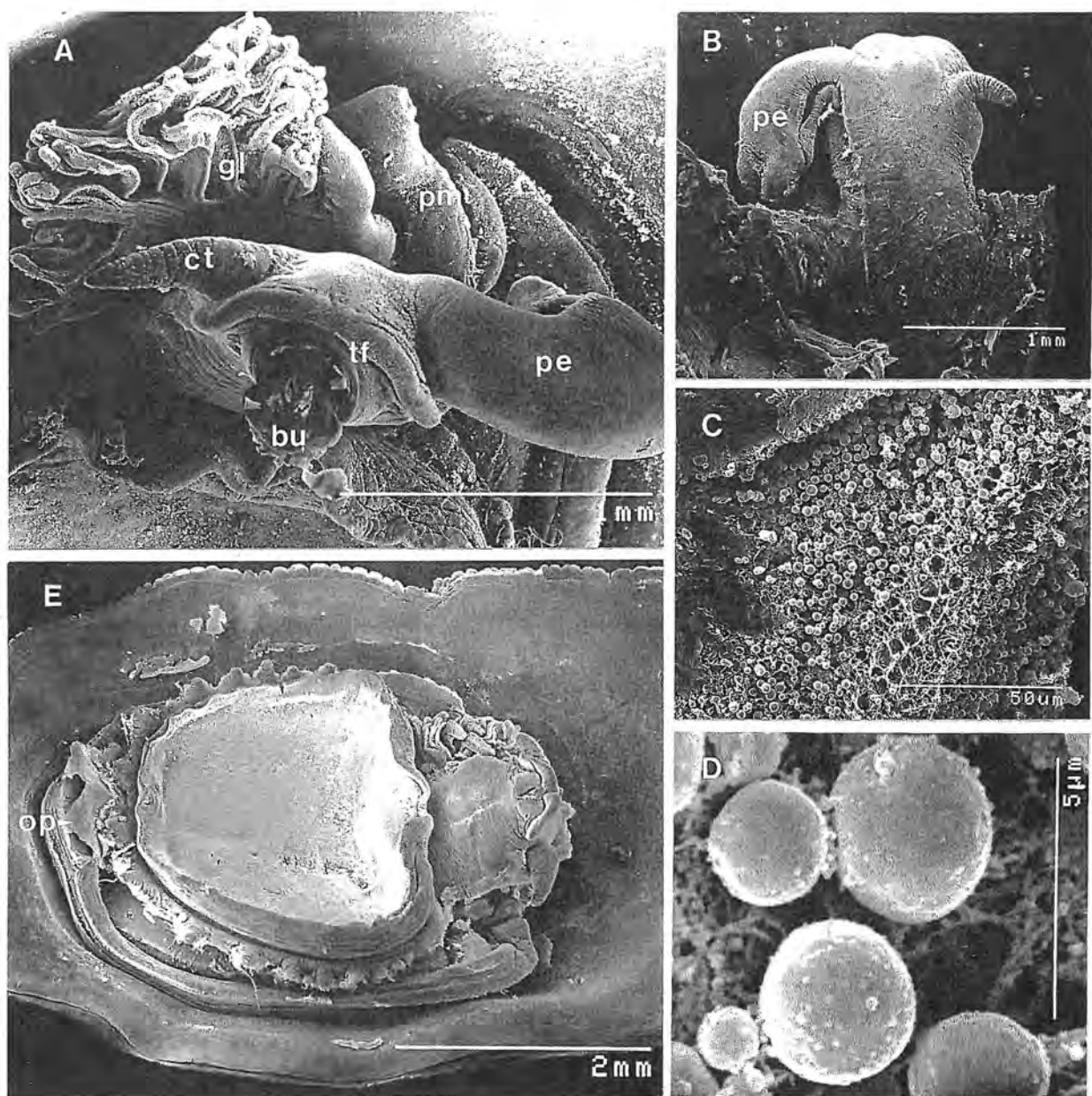


Fig. 19. A.-E. *Symmetromphalus macleani* sp.n.. A.-D. Male. A. Front view of the head. B. Dorsal view of the head. C. Coccal bacteria in seminal groove. D. Coccal bacteria. E. Female, ventral view.

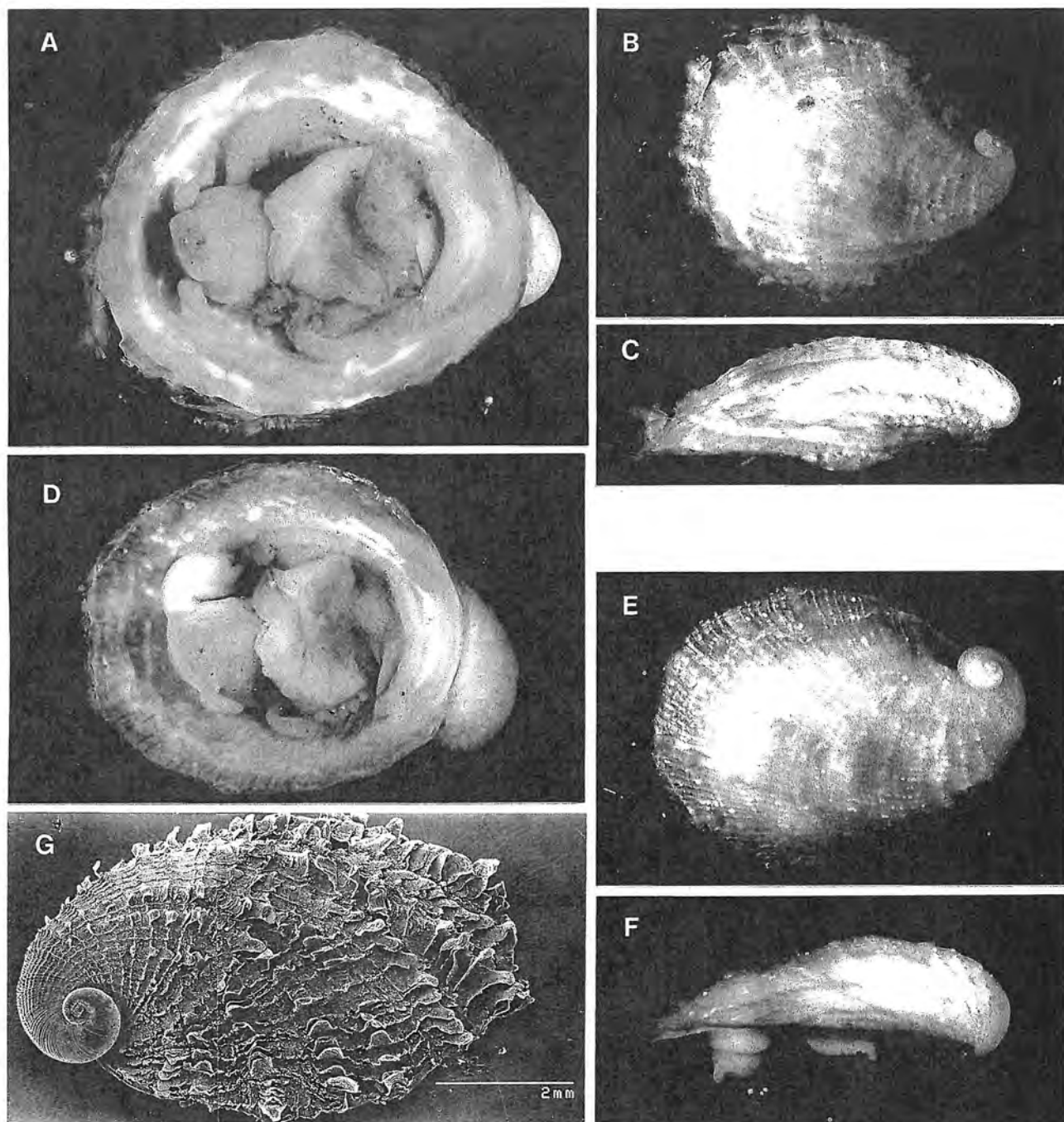


Fig. 20. A.-E. *Fumocapulus alayseae* gen. n. et sp. n.. A, B, C. Holotype, female, shell length 8.0 mm. A. Ventral view. B. Dorsal view. C. Viewed from left. D.-F. Paratype 1, male, shell length 7.0 mm. D. Ventral view. E. Dorsal view. F. Viewed from left. G. Critical point dried shell showing leafy scales of periostracum.

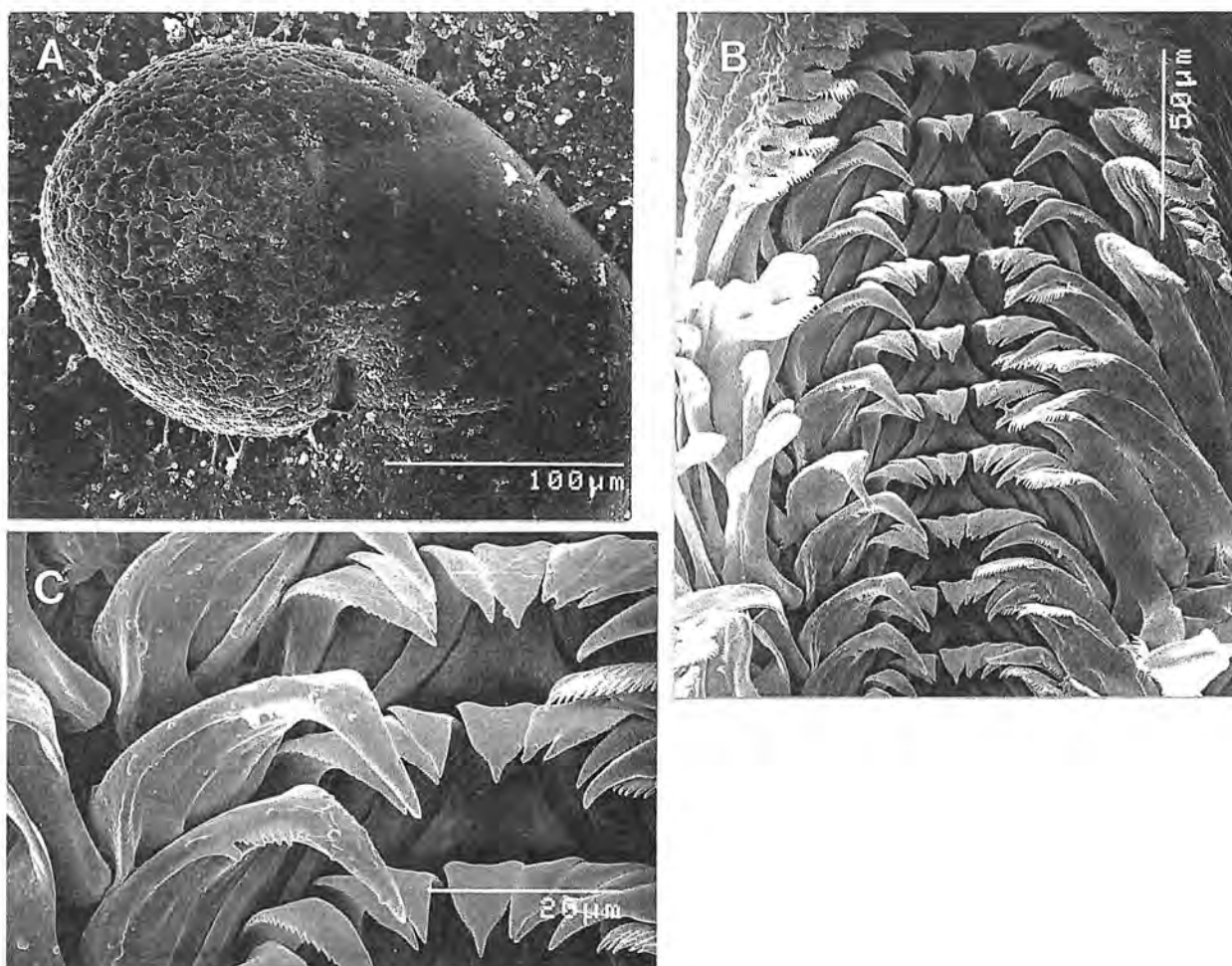


Fig. 21. A.-C. *Fumocapulus alayseae* gen. n. et sp. n.. A. Protoconch. B. Radula. C. Central field of radula.

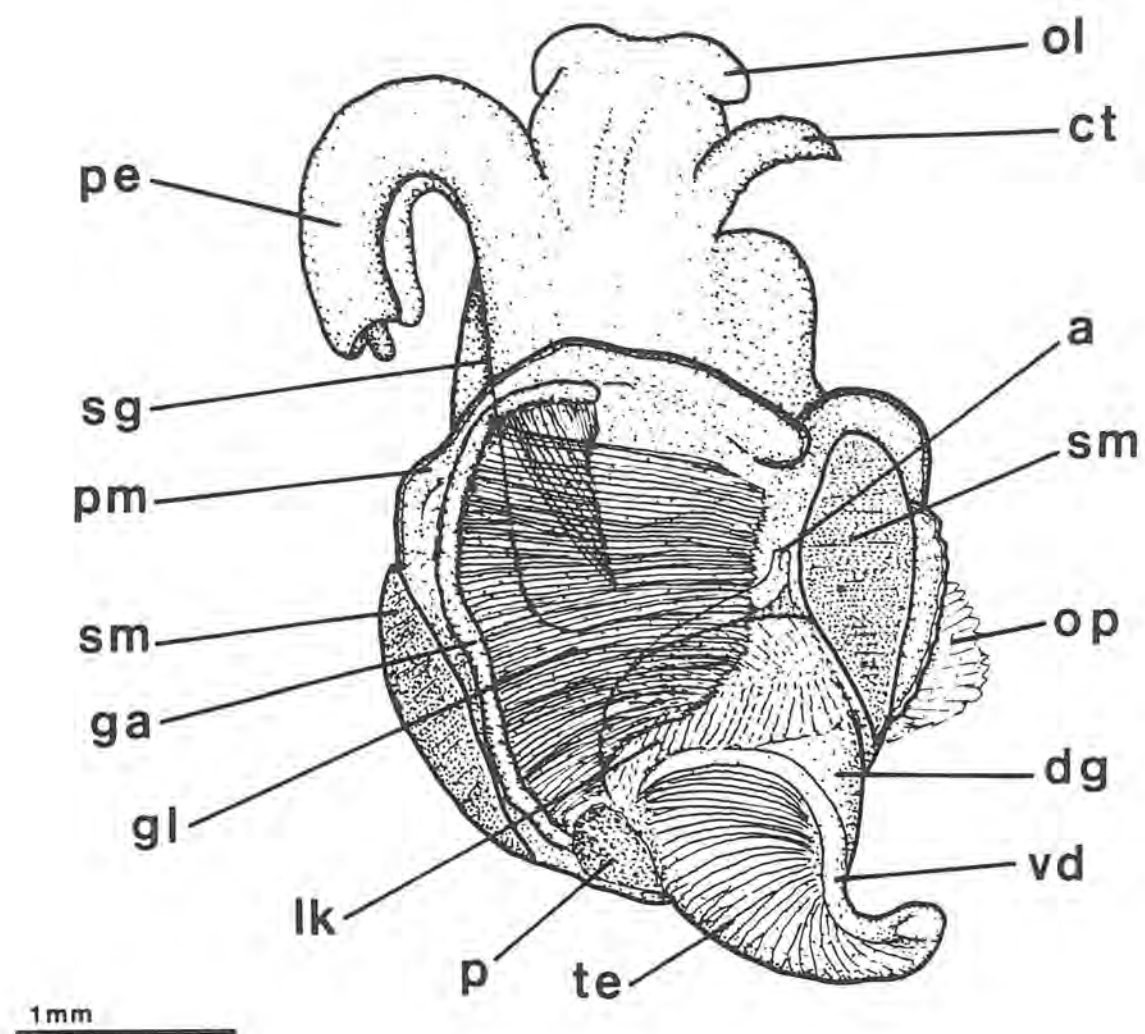


Fig. 22. *Fumocapulus alayseae* gen. n. et sp. n., paratype 1, male, animal removed from shell, in dorsal view, gill and posterior part of seminal groove seen by transparency.

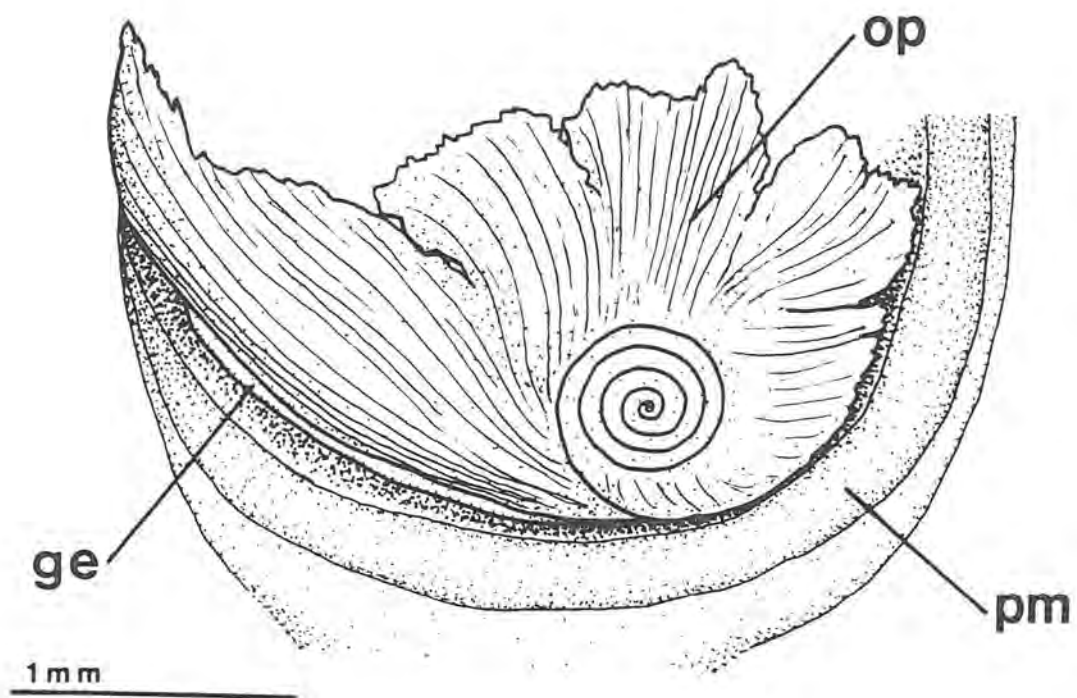


Fig. 23. *Fumucapulus alayseae* gen. n. et sp. n., operculum with enlongate growing edge, on postero-ventral view.

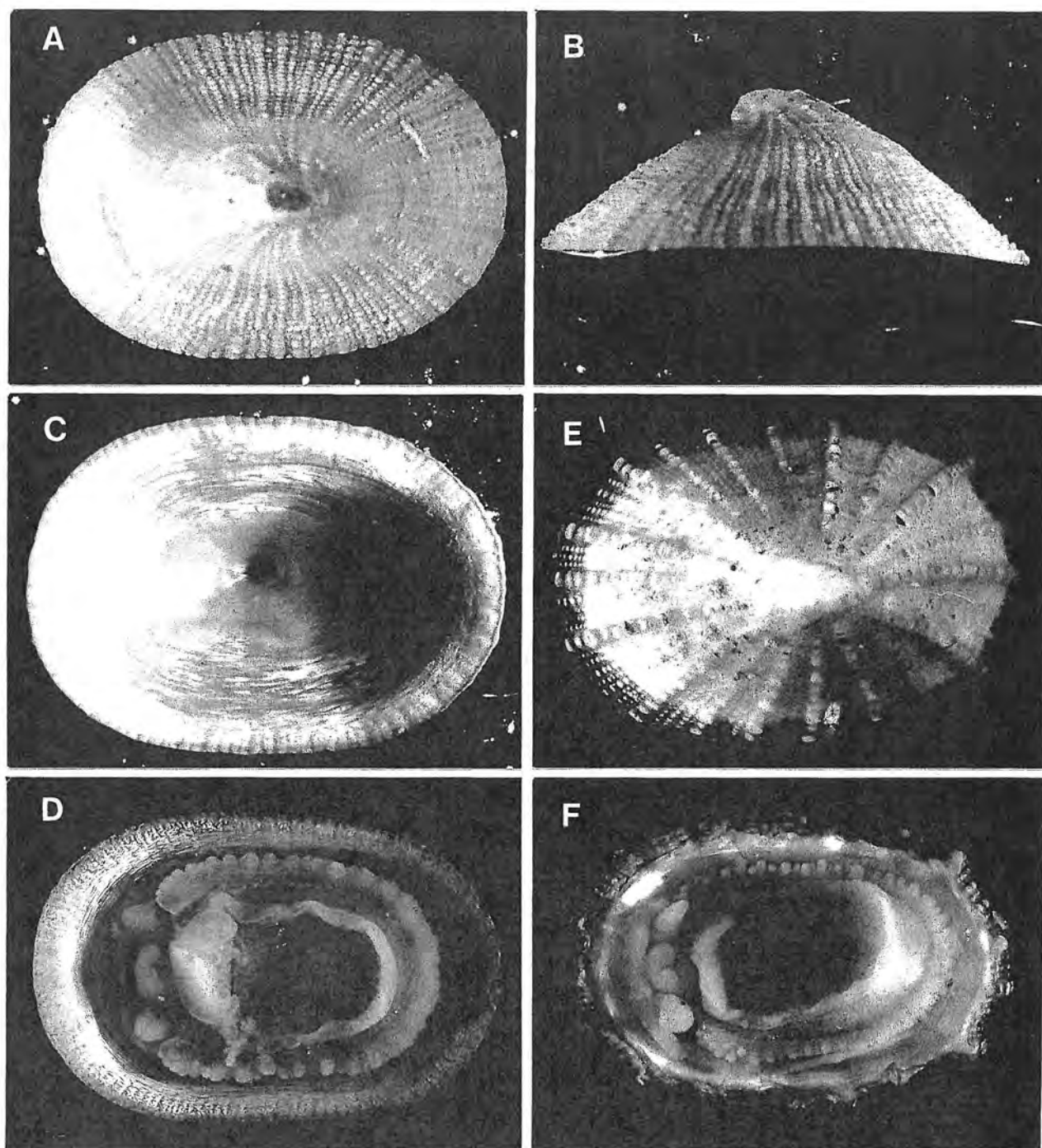


Fig. 24. A.-F. *Symmetriapelta wareni* gen. n. et sp. n.. A.-C. Paratype from type locality, shell length 3.8 mm. A. Dorsal view. B. Viewed from right. C. Shell interior; anterior on left. D. Paratype from Lau Basin in ventral view. Shell length 4.1 mm. E, F. Paratype from type locality with extremely thick radial ribs; calcareous layers partly dissolved, shell length 2.7 mm. E. Dorsal view. F. Ventral view.

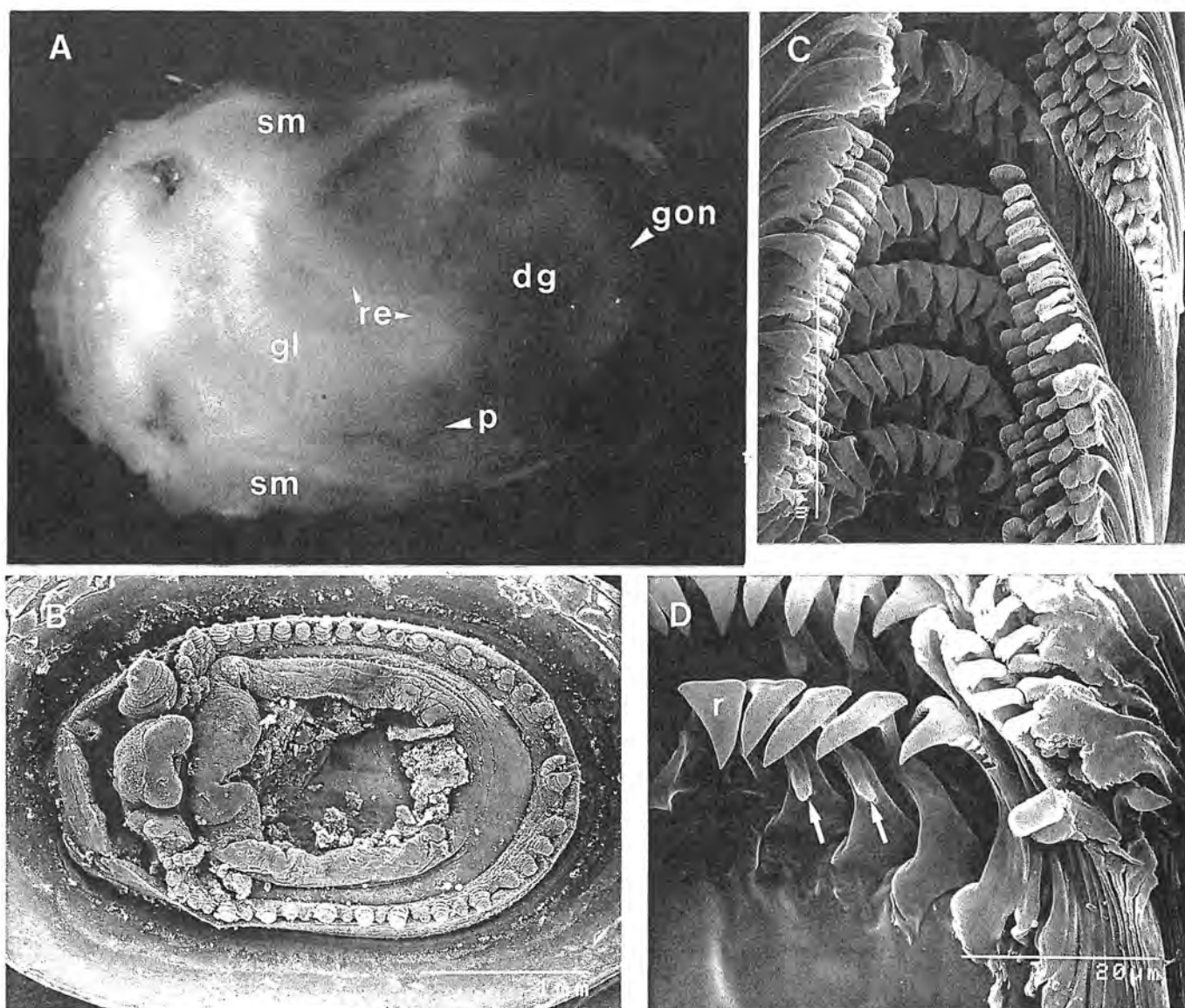


Fig. 25. A.-D. *Symmetriapelta wareni* gen. n. et sp. n.. A. Animal removed from shell, in dorsal view, length 2.1 mm. B. Critical point dried specimen in ventral view. C, D. Radula. C. Overview. D. Half-row of radula teeth, arrows indicate nubs on the bases of first and second lateral teeth.