

REVISION OF THE GENUS *BENTHOBIA* (CAENOGASTROPODA, PSEUDOLIVIDAE)

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ABSTRACT

A revision of the genus *Benthobia* Dall, 1889, which inhabits deep waters worldwide, is provided. In addition to *B. tryonii*, which inhabits the North Atlantic, four new species are described: *B. atafona*, from south-east Brazil; *B. complexirhina* from the Tasman Basin, Australia; *B. tornatilis*, from the Coral Sea, Australia and *B. sima*, from Madagascar. Species separations are based on conchological and anatomical features. An anatomical diagnosis for the genus is provided, leading a discussion of the systematics of the family. Distinguishing anatomical characters for the genus include: eyes lacking; posterior furrow in foot sole; horseshoe-shaped attachment to operculum; single, massive, muscular and hollow accessory salivary gland with narrow duct; salivary gland separated into two parts; closed pallial sperm duct; penis with closed penial duct and broad, sub-terminal, dome-shaped papilla; pallial oviduct generally with a posterior seminal receptacle, and terminal, muscular bursa copulatrix positioned between vestibule and pore, partly attached to pallial floor. Most of the remaining features are typical of muricoideans. A discussion on the possible validity of *Nux alabaster*, from the Atlantic coast of South Africa, is provided; based on conchological, opercular and radular characters, it is concluded that it is closely related to *Benthobia*.

INTRODUCTION

The marine gastropod genus *Benthobia* was introduced by Dall (1889) for the single species *B. tryonii* Dall, 1889, reported from deep water (1300 m) off North Carolina, USA. However, gastropods belonging to this genus have been collected worldwide and have been identified as this single species. After study of shell characters and anatomy of specimens collected from widely separated locations in different oceans, I concluded that the animals from each site were sufficiently distinct to justify separation into species, and their description is the subject of this paper.

Benthobia was first described within the Cancellariidae (Dall, 1889), and was maintained in this family until the 1980s (e.g. Abbott, 1974), although some authors considered the genus a synonym of the cancellariid *Admete* Kröyer, 1842 (Thiele, 1929; Wenz, 1938). However, most authors regarded the genus valid and monotypic (Abbott, 1974: 249; Bouchet & Warén, 1985). The family Pseudolividae was more recently defined by Kantor (1991), based on anatomical characters. He reunited species previously placed in different muricoidean families, such as Olividae and Cancellariidae. Among the examined species was a sample of *Benthobia*, and Kantor (1991) defined the genus by a set of anatomical features, including the single, enlarged accessory salivary gland. More recently, Vermeij (1997, 1998) revised the family Pseudolividae, including reviews of the fossil species. Moreover, Vermeij (1998) also revised the concept of the genus *Benthobia*, redescribing the genus based on shell and anatomical characters, considering it monotypic and closely related to the fossil *Fusopsis* Ravn, 1939, because of its multispiral protoconch and sculpture confined to the upper part of the whorls. The monotypic genus *Nux* Barnard, 1960 also seemed closely related to *Benthobia* and was included in the synonymy of *B. tryonii* by Bouchet & Warén (1985) and Vermeij (1998).

This study is part of a larger project concerning a systematic and phylogenetic revision of the families of the Caenogastropoda. The project is mostly based on detailed investigations of anatomy and provides new anatomical character for phylogenetic analysis of relationships among the taxa.

MATERIAL AND METHODS

Specimens were dissected in 70% ethanol and observed with a stereomicroscope. Scanning electron microscopy (SEM) was used to examine the radulae. All drawings were made with the aid of a camera lucida. Specimens dried inside their shells were extracted and rehydrated in a solution of 70% ethanol (about 15 ml), with three or four drops of 40% KOH and 8–10 drops of detergent, for 3 days prior to dissection. Some specimens were studied by means of photographs, sent by the Smithsonian Institution and by the South African Museum.

Anatomical abbreviations (Figs 7–12)

aa, anterior aorta
ad, accessory salivary gland duct
ae, accessory salivary gland
af, afferent gill vessel
ag, albumen gland
an, anus
ap, aperture of pallial gonoducts
as, anal siphon
au, auricle
bc, bursa copulatrix
br, subradular membrane
ce, cerebro-pleural ganglia
cg, capsule gland
cm, columellar muscle
cm, columellar muscle
cv, ctenidial vein
dd, duct to digestive gland
df, dorsal fold of buccal mass
dg, digestive gland
ea, anterior oesophagus
ep, posterior oesophagus
es, oesophagus
fp, female pore
fs, foot sole
ft, foot
gi, gill
gl, gland of Leiblein

he, head
 hg, hypobranchial gland
 in, intestine
 ki, kidney
 kl, kidney dorsal lobe
 km, membrane between kidney and pallial cavity
 ld, duct of gland of Leiblein
 m1 to m14, extrinsic and intrinsic odontophore muscles
 mb, mantle border
 mj, muscles of jaws, buccal mass and oral tube
 mo, mouth
 ne, nephrostome
 ng, nephridial gland
 nr, nerve ring
 oc, odontophoral cartilage
 od, odontophore
 oo, odontophoral tube connecting to oral tube
 op, operculum
 os, osphradium
 ot, oral tube
 ov, pallial oviduct
 pa, penial aperture
 pb, proboscis
 pc, pericardium
 pd, penial duct
 pe, penis
 pf, posterior pedal furrow
 pg, anterior furrow of pedal glands
 pp, penial papilla
 pt, prostate
 pu, pedal ganglion
 py, pallial cavity
 ra, radula
 rh, rhynchostome
 rm, retractor muscle of proboscis
 rn, radular nucleus
 rs, radular sac
 rt, rectum
 rv, afferent renal vessel
 sc, subradular cartilage
 sd, salivary duct
 se, septum between oesophagus and odontophore in buccal mass
 sg, salivary gland
 si, siphon
 sr, seminal receptacle
 st, stomach
 su, suboesophageal ganglion
 sv, seminal vesicle
 te cephalic tentacle
 tg, integument
 to, tissue over middle region of radula (before its exposure)
 ts, testis
 vd, vas deferens
 ve, ventricle
 vl, valve of Leiblein
 vo, visceral oviduct

Institutional abbreviations

AMS, Australian Museum, Sydney
 MNHN, Musée National d'Histoire Naturelle, Paris
 MZSP, Museu de Zoologia da Universidade de São Paulo
 NZOI, New Zealand Oceanographic Institute
 SAM, South African Museum, Cape Town

SYSTEMATIC DESCRIPTIONS

Genus Benthobia Dall, 1889

Benthobia Dall, 1889: 131–132 (type species *B. tryonii*, original designation). Thiele, 1929: 540 (as possible synonym of *Admete*). Wenz, 1938: 1369 (as synonym of *Admete*). Abbott, 1974: 249. Bouchet & Warén, 1985: 249. Vermeij, 1998: 66. Bouchet & Vermeij, 1998: 47–49, 52.

Diagnosis. See Vermeij (1998: 66).

Supplementary diagnosis. Eyes lacking. Posterior, longitudinal furrow in foot sole. Special horseshoe-like arrangement of operculum attachment. Anal siphon muscular. Osphradium with short monopectinate anterior region. Proboscis short. Accessory salivary gland single, as a large muscular bulb, walls relatively thin; duct long and narrow. Retractor muscle of odontophore (m2) forming a muscular platform inserted in posterior surface of odontophore. Stomach simple, with single duct to digestive gland in region of oesophageal insertion. Pallial vas deferens closed (tubular); mostly with thick walls. Pallial sperm ducts closed. Penis with a broad, dome-shaped, sub-terminal papilla. Pallial oviduct generally with a posterior, small, seminal receptacle and large, anterior, terminal, thick and muscular bursa copulatrix, partly connected to pallial floor.

Benthobia atafona new species

(Figs 1, 2, 7 and 8)

Types: Holotype: MNHN (8.0 × 5.3 mm), preserved (dissected); *type locality:* 24°00' S 42°14' W, off Santos, São Paulo, Brazil, 1020 m depth (MD55, stn 107). *Paratypes:* MNHN, 1 shell (9.0 × 6.3 mm) from type locality; MNHNP, 1 dry (8.6 × 5.3 mm), 1 preserved (dissected), 1 shell (9.4 × 7.3 mm), 19°02' S 37°48' W, off São Mateus, Espírito Santo, Brazil, 1500–1575 m depth (MD55, stn CB79); MZSP 35386, 1 preserved (dissected), 1 shell (11.3 × 7.5 mm), 21°36' S 39°58' W, off São João da Barra, Rio de Janeiro, Brazil, 1190–1205 m depth (MD55, stn CB99).

Etymology: The specific epithet refers to the angel called Atafon, an entity who directs the deep zones of the abyss of human lost souls, in the book *O Abismo* (Ranieri, 1998); an allusion to the deep water habitat of the species.

Diagnosis: Shell obese, spire small, pointed, body whorl large. Sculpture weak, some low subsutural nodes. Spire angle about 60°. Aperture about half of total shell length. Siphonal canal broad, weakly delimited. Operculum with a upper corner. Pallial anal siphon weak. Osphradium narrow, about one-third of pallial cavity width. Osphradial filaments simple. Rachidian tooth with about seven tall, sharply pointed cusps, increasing in size gradually towards central. Off southern Brazil.

Shell (Fig. 1A–D): Up to 12 mm, white, obese, turbiform. Outer surface opaque, irregular, growth lines well marked. Sculptured by subsutural nodes of irregular size, about 12 on body whorl, longer axially; spiral furrow, slightly inconstant and interrupted, situated between middle and lower thirds of body whorl. Protoconch broad, flat, eroded, with about two convex, smooth whorls. Teleoconch of up to four whorls, first whorl with profile almost straight. Spire pointed, small, of about half body whorl length, spire angle about 60°. Body whorl much larger, convex, obese. Aperture broad, elliptic. Peristome white, glossy. Outer lip with sharp edge, weakly projected; anal region with broad, shallow, sub-terminal notch. Siphonal canal poorly defined. Inner lip concave, callus low, somewhat broad. Umbilicus absent.

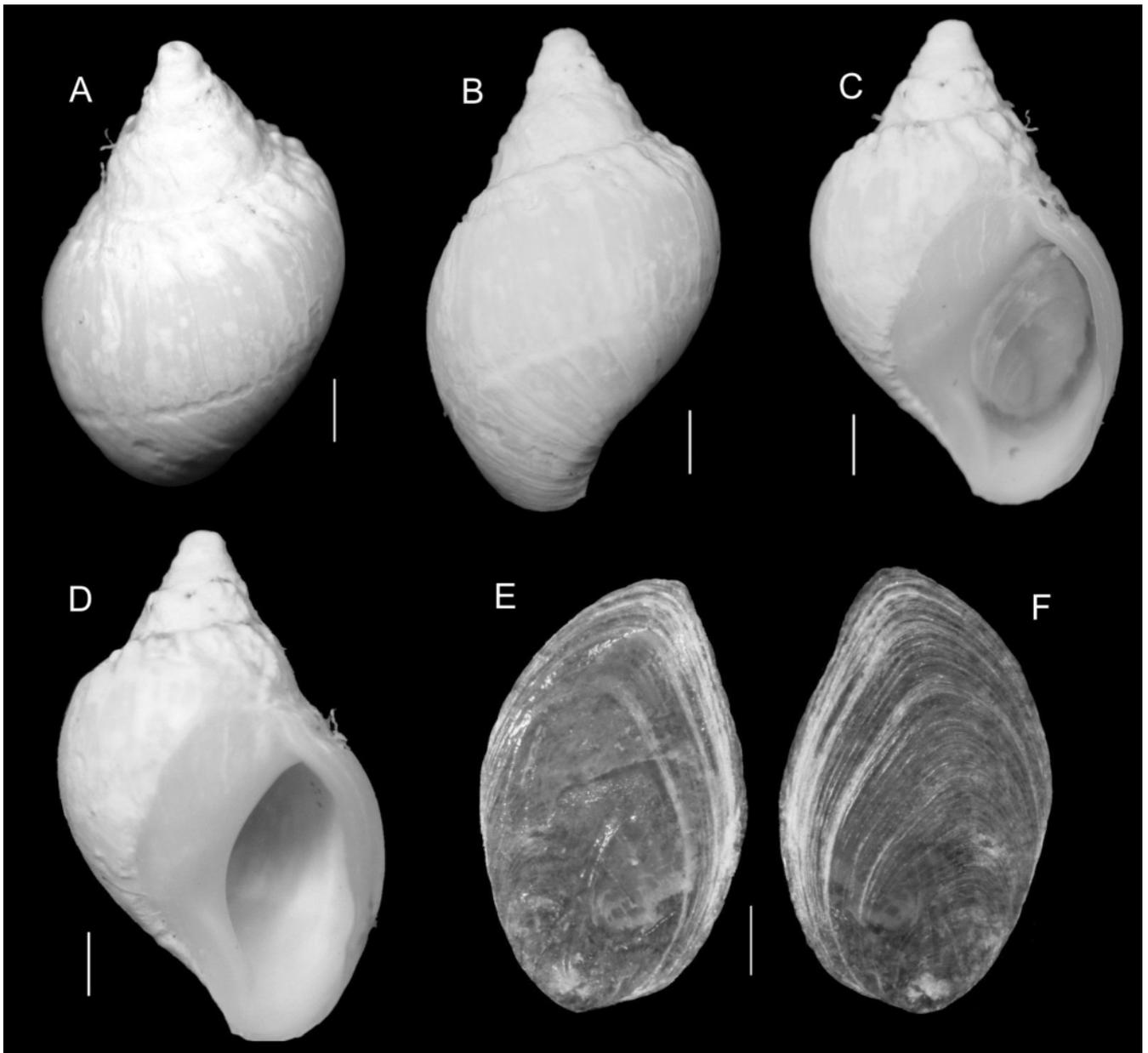


Figure 1. *Benthobia atafona* holotype. **A–D.** Shell. **A.** Dorsal, slightly apical view. **B.** Dorsal view. **C.** Frontal-slightly lateral view. **D.** Frontal view. **E, F.** Operculum, inner and outer views. Scale bars: **A–D** = 1 mm; **E, F** = 0.5 mm.

Head-foot (Fig. 7A, E): Colour whitish. Head not protruded. Tentacles long; width uniform along their length; tip rounded. Eyes absent. Rhynchostome elliptical, situated ventral to a low flap uniting both tentacles. Foot large, occupying about two-thirds of head-foot mass; edges thick. Anterior furrow of pedal gland deep, restricted to anterior edge of foot. Sole of foot with a posterior, short, median, longitudinal, terminal, notched furrow (Fig. 7A: pf). Opercular pad occupying most of dorsal-posterior surface of foot, with a special attachment of operculum (Fig. 7D), in a broad, asymmetrical horseshoe-shaped insertion. Columellar muscle simple, flat, of half a whorl. Penis large, situated to right and posterior to right cephalic tentacle, described below.

Operculum (Fig. 1E, F): Elliptical, thin, corneous, semi-transparent, yellowish, occupying entire aperture. Nucleus terminal, situated in middle region of lower edge. Edges sharp, fragile.

Outline with a broadly pointed upper edge. Outer surface with well marked, concentric undulations. Inner surface glossy; scar occupying most of this surface, in form of a broad and irregular horseshoe.

Mantle organs (Fig. 7B, C): Pallial cavity broad, about three-quarters of a whorl deep. Pallial edge thick, simple, whitish. Siphon short, broad, thick, edges simple, distal end rounded. Anal region thickly muscular, forming weak anal siphon. Osphradium occupying about one-third of pallial cavity area; mostly bipectinate, except for a short monopectinate portion in anterior region (close to siphon base), formed of right filaments only. Osphradial filaments tall; left filaments about half size of right filaments; right filaments with a short, broadly pointed projection covering ctenidial vein. Gill long, narrow, curved, surrounding right and posterior edges of osphradium, width about one-fifth of that of pallial cavity. Gill anterior end pointed, slightly

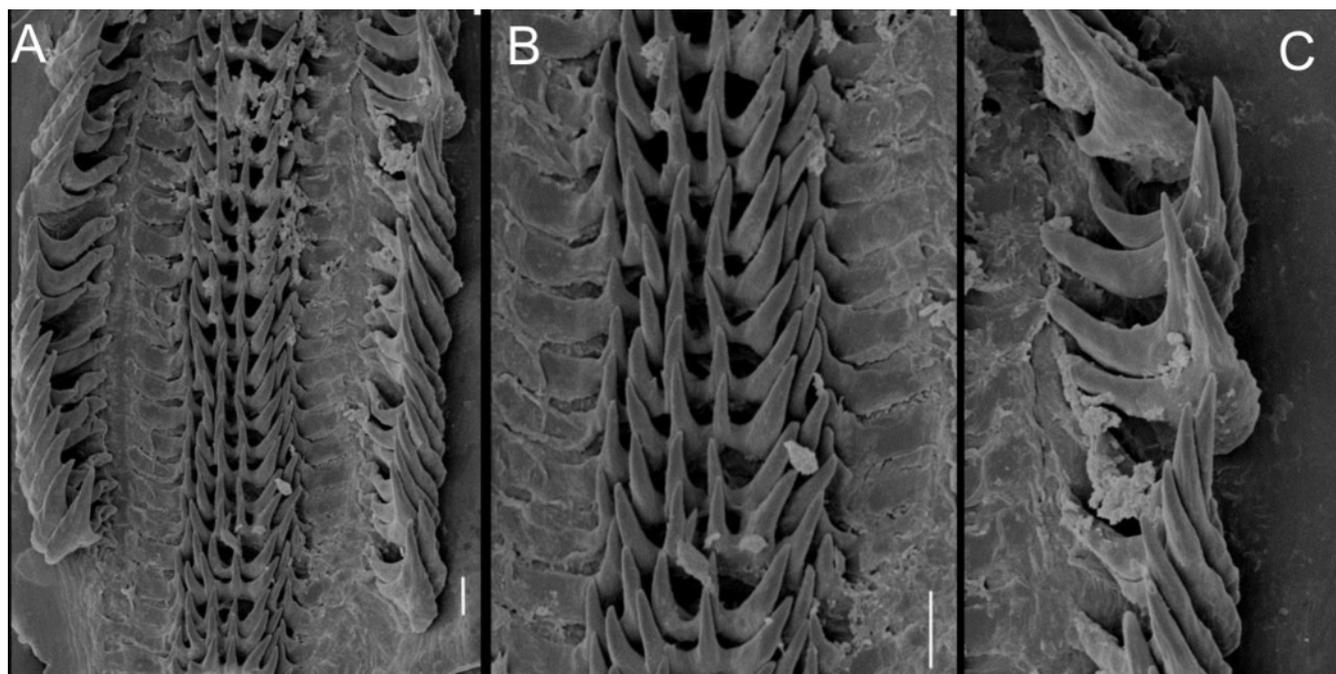


Figure 2. *Benthobia atafona* radula in SEM. **A.** Whole view. **B.** Detail of rachidian region. **C.** Detail of the lateral teeth. Scale bars: **A** = 10 μm ; **B** = 10 μm ; **C** = 6 μm .

curved towards left; posterior end rounded. Gill filaments an almost equilateral triangle, with pointed tip. Ctenidial vein narrow. Area between gill and rectum equivalent to half width of total pallial cavity. Hypobranchial gland tall, thick, white, occupying posterior two-thirds of region between gill and rectum, partially covering this. Rectum narrow, exiting into pallial cavity in middle region of ventral-posterior border of pallial cavity floor, gradually running towards right; its anterior half running in right border of this cavity. Anus simple, situated between middle and anterior thirds of pallial cavity. Prostate described below.

Visceral mass: Length about three whorls posterior to kidney, pale yellow, gonad same colour as digestive gland, occupying superior and peri-columellar regions.

Circulatory and excretory systems (Fig. 7B): Heart relatively small (about one-tenth of renal volume). Ctenidial vein insertion in to auricle forming a strong curve. Ventricle with thick walls. Common aorta very short, situated in ventral ventricle surface. Anterior aorta about three times broader than posterior aorta and running diametrically opposed to that. Kidney incompletely seen (posterior region damaged), colour white, possessing a single lobe U-shaped lobe, with ventral and dorsal branches partially connected along right edge, dorsal branch thinner and flat. Renal afferent vessel broad, with a branch to each lobe. Nephridial gland very thin, situated along dorsal region of membrane between kidney and pericardium.

Digestive system (Figs 7E–H and 8A, B, D–F): Proboscis broad and very short (shorter than buccal mass if extended); walls thin, muscular, colour white. Pair of proboscis retractor muscles situated in ventral surface, left muscle closer to median line and several times broader than right muscle; origin in middle region of ventral surface of haemocoel, inserting gradually along proboscis to a short distance from mouth (Figs 7E, F). Mouth small, rounded. Buccal mass occupying about one-third of haemocoel volume. Oral tube broad, length equivalent to that of odontophore (Fig. 7G); walls thick, muscular. Oral tube entirely covered by a thin chitinous layer, inner surface with a pair of

dorsal folds, becoming very broad at odontophore level (Fig. 7H). Ventral inner surface with three or four narrow, longitudinal folds (Fig. 7H). Odontophore possessing a short tube connected to oral tube (Fig. 7G; oo), with walls of longitudinal muscle fibres. Odontophore large, elliptical. Odontophore muscles (Figs 7G and 8A, B, D–F): m1, several small and thin jugal muscles connecting buccal mass to adjacent inner surface of haemocoel and proboscis, more concentrated around mouth, where they work to open it; m1a, differentiated pair of ventral jugal muscles working as ventral protractors of buccal mass, originating in anterior-ventral inner surface of haemocoel, running close to ventral surface of buccal mass, inserting into posterior-ventral surface of odontophore, one on each side of odontophore; mj, muscle of oral tube, inserts in two bundles on each side of odontophore, along lateral region of cartilages; m2, pair of retractor muscles of odontophore, relatively broad, originating in median-posterior region of ventral surface of haemocoel, running flanking ventral surface of proboscis and buccal mass, inserting in posterior surface of odontophore, covering radular nucleus; m3, auxiliary buccal mass protractor, muscular layer relatively thin, with longitudinal fibres externally covering oral tube, covering mj, inserting between middle and posterior thirds of odontophore both ventrally (m3v) and dorsally (m3d); m4, large pair of dorsal tensor muscles, originating in odontophore cartilages surrounding mj insertion, surround almost entire cartilages (except median region), inserting into lateral edges of subradular membrane and, by means of short ligaments, into tissue on the radula preceding its exposed part (to); m5, pair of ventral-posterior tensor muscles, originating on posterior surface of m4, running towards median and anterior, inserting along ventral surface of radular ribbon on side opposite its exposed portion; m6, horizontal muscle short and thin, connecting both odontophoral cartilages, inserting along their mid-ventral edge, length about half of cartilage length; m11a, pair of ventral-anterior tensor muscles, originating in posterior-ventral region of odontophore, on m2 insertion and on m4, running towards anterior attached to ventral region of subradular membrane, insertion broader, in distal edge of radula and subradular cartilage (Fig. 8E). Other non-muscular odontophore

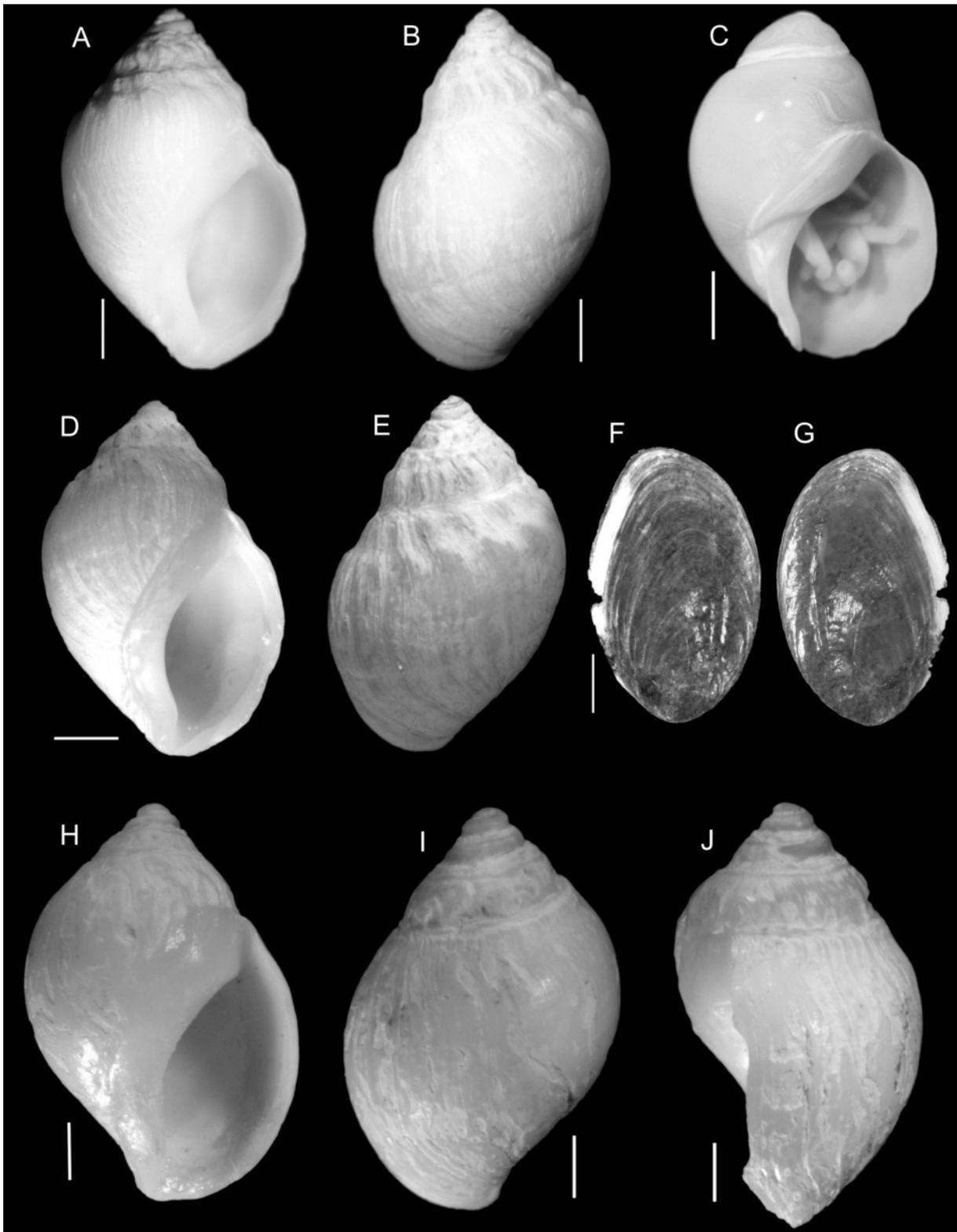


Figure 3. *Benthobia* species. **A-G.** *Benthobia complexirhyna*. **A, B.** Shell of specimen from stn P929, frontal and dorsal views. **C.** Shell of specimen from P934, frontal view, specimen with intensely eroded shell, soft parts partially extracted (foot only). **D, E.** Holotype (NZOI, from stn P929), frontal and dorsal views. **F, G.** Operculum, outer and inner views. **H, J.** *Benthobia tornatilis* shell (AMS157289), frontal, dorsal and side views. Scale bars = 2 mm, except **F, G** = 1 mm.

structures: to, tissue on radula preceding its exposed (in use) portion, firmly attached to radular surface (Fig. 8A, D), on teeth that will immediately replace lost teeth; sc, subradular cartilage, extending along both sides of exposed portion of radula, cover-

ing and protecting subradular membrane in region exposed into buccal cavity; oc, odontophoral cartilages, paired, soft, white, flat, elliptical (Fig. 8F). Radula relatively short, extending little beyond posterior end of odontophore (Fig. 8D); radular

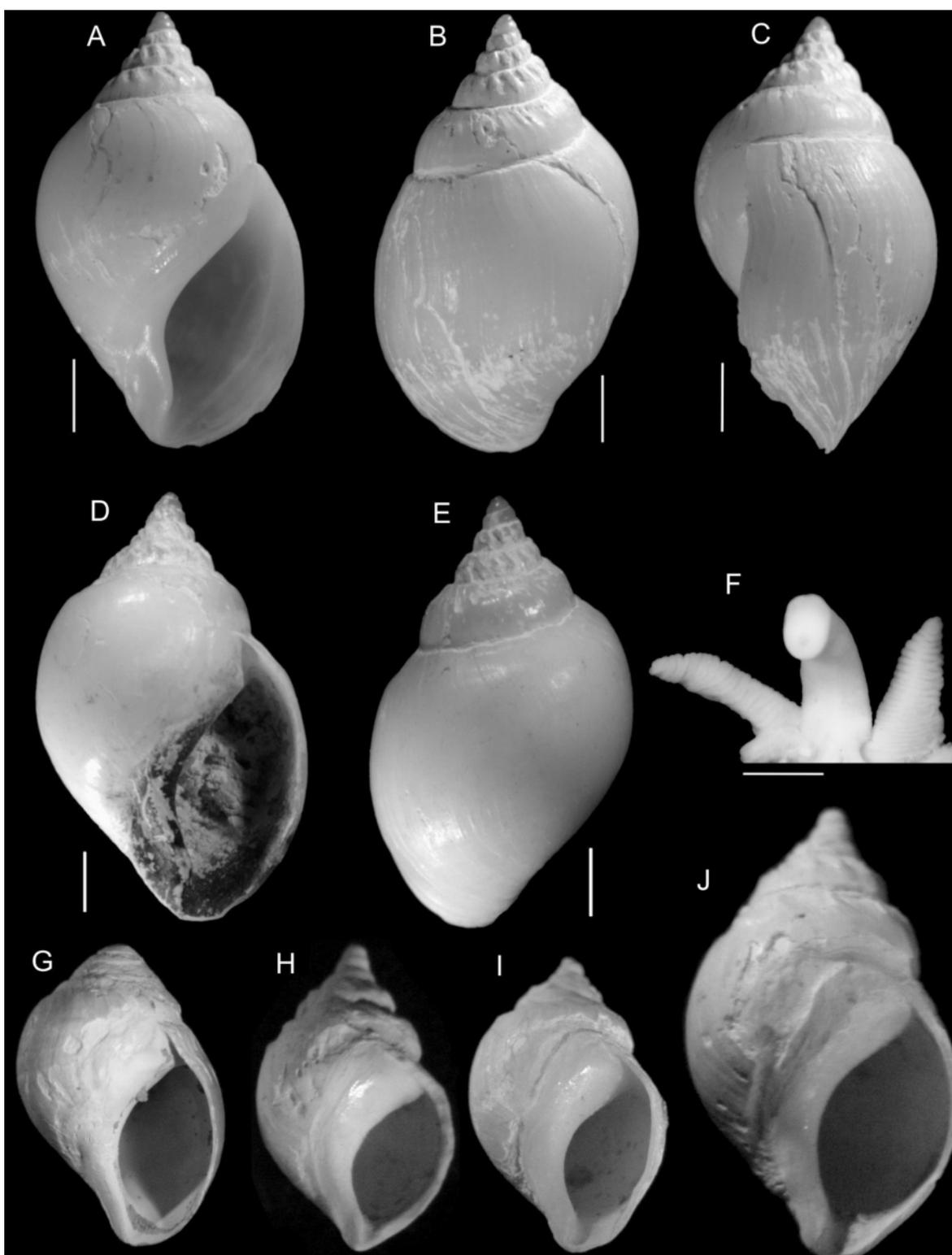


Figure 4. *Benthobia* species. **A–F.** *Benthobia tornatilis*. **A–C.** Shells of holotype, frontal, dorsal and profile views. **D, E.** Paratype (MNHN, from stn DW790) shell, frontal and dorsal views. **F.** head with fully extended proboscis, ventral view. Scale bars = 2 mm, except **F** = 1 mm. **G.** *Benthobia sima* (USNM 717352), shell, frontal view. **H–J.** *Benthobia tryoniisynotype* (USNM 93441; no scale provided, approx. length = 10 mm).

ribbon narrow. Radular teeth (Fig. 2A–C): rachidian very broad (about 70% of radular width), short, with about seven tall, sharply pointed cusps, central cusps larger than lateral cusps, increasing gradually, cusps not uniform in size and shape along

rows (Fig. 2B); rachidian lateral region smooth (about one-quarter of its width of each side), flat; lateral tooth less than half of rachidian width, triangular, curved inwards, base broad and flat, remaining region tall, narrowing gradually up to pointed

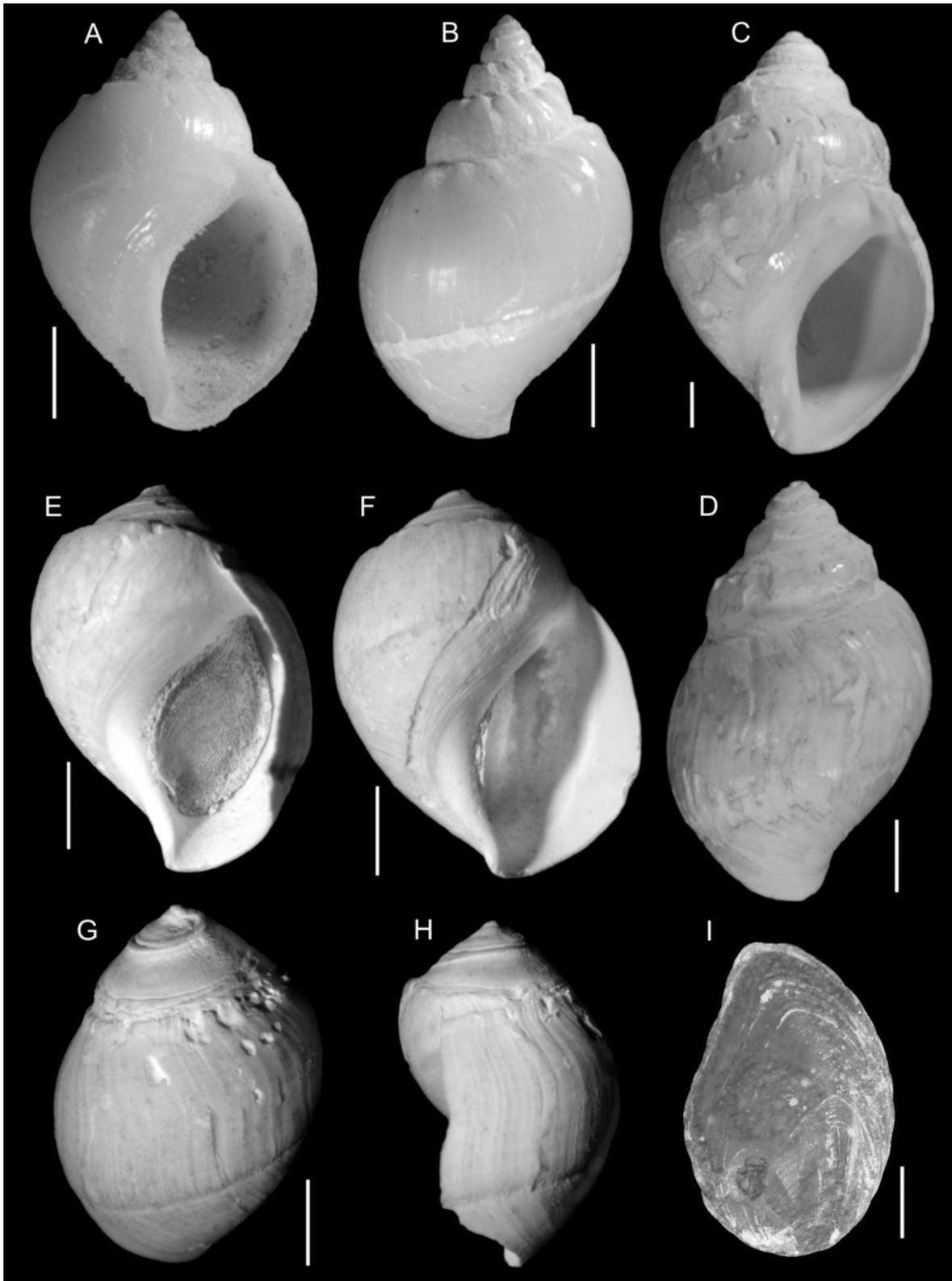


Figure 5. *Benthobia* species: **A–D.** *Benthobia tryonii* shell. **A, B.** MNHN (stn 165), frontal and dorsal views. **C, D.** MNHN (stn 68-A13), frontal and dorsal views. **E–I.** *Benthobia sima*. **E–H.** Holotype (MNHN) shell, oblique, frontal, dorsal and profile views respectively. **I.** Operculum, outer view. Scale bars = 2 mm, except **I** = 1 mm.

tip (Fig. 2A, B). Anterior oesophagus narrow, originating in oral tube just anterior to anterior edge of odontophore, running over dorsal-median surface of odontophore and extending little beyond it (Fig. 7F, G). Inner surface with pair of low, narrow,

longitudinal folds, continuous with dorsal folds of buccal mass (Fig. 7H). Valve of Leiblein relatively large, with normal structure; lacking any oblique inner furrow; ciliated valve iridescent, forming about half of total valve length; glandular portion of

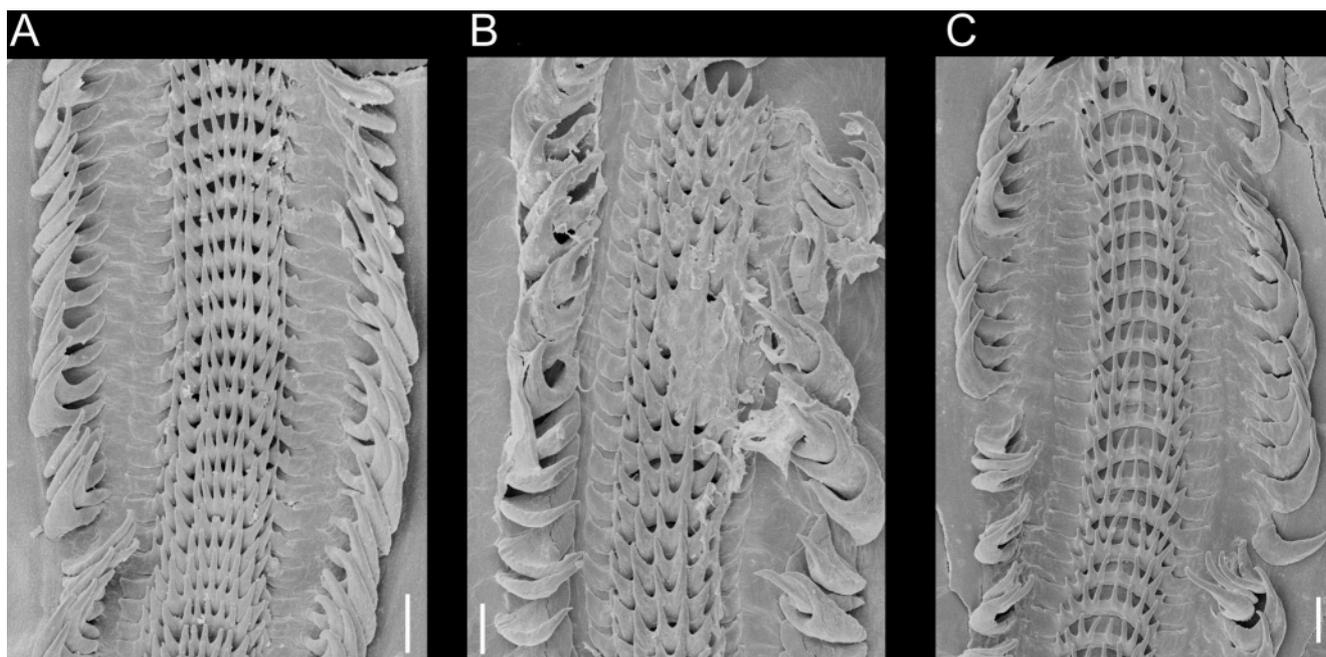


Figure 6. Radulae of *Benthobia* species in SEM. **A.** *B. complexirhyna*. **B.** *B. tornatilis*. **C.** *B. sima*. Scale bars = 20 μm .

valve thick and white (Fig. 7F). Pair of salivary glands separated into two elliptical masses, surrounding valve of Leiblein and nerve ring, and connect directly to anterior oesophagus just anterior to valve, without any apparent ducts (Fig. 7F). Accessory salivary gland single, in form of a large muscular bulb (Figs 7E, F), walls relatively thin, inner space voluminous and filled by mucus (Fig. 7F: ae—detail); its duct very narrow, running towards anterior ventrally around buccal mass; inserting into ventral-anterior region of oral tube. Middle oesophagus short (shorter than valve of Leiblein) (Fig. 7F), inner surface covered by thin gland. Gland of Leiblein broad, large, flat, somewhat triangular (Figs 7E, F); a deep furrow almost dividing it into two lobes where anterior aorta crosses from dorsal to ventral region. Duct of gland of Leiblein broad, close to its anterior end (Fig. 7F), inner surface simple and smooth. Posterior oesophagus long, narrow. Stomach not seen in detail.

Male genital system: Testis and visceral vas deferens not seen in detail. Seminal vesicle forming a zigzag in mid-ventral region of last visceral whorl (Fig. 7B), very broad, iridescent. In region preceding pallial cavity, seminal vesicle gradually narrows and runs obliquely to right. Vas deferens connects very narrowly to prostate gland in middle-ventral region of posterior edge of pallial cavity (Fig. 7B). Prostate gland long, open, running obliquely towards anterior and right, ventrally flanking rectum on floor of pallial cavity (Fig. 7B: pt). Prostate with two thin glandular laminae gradually narrowing; in middle level of pallial cavity both laminae become thin, running along right edge of pallial cavity, fusing within a short distance, becoming a duct. This duct runs along floor of pallial cavity (Fig. 8G), forming a broad zigzag up to penial base. Penis broad, long, flat, thick, perpendicularly twisted at its base (Figs 7A and 8G, H). Penis uniformly wide along its length, penial tip broad and rounded. Penial aperture sub-terminal, ventral, at tip of broad, low, dome shaped, elliptic papilla (Fig. 8I). Papilla sub-terminal, turned ventrally, edges protected by a low fold, with a deep furrow surrounding it (Fig. 8I). Penial duct narrow, running along middle region of penis, weakly coiled (Fig. 8H).

Female genital system: No females examined.

Central nervous system (Fig. 8C): Ganglia concentrated into large mass situated in anterior-ventral region of haemocoel at proboscis base. Cerebral and pleural ganglia fused, both cerebral ganglia connected by a broad and short connective. Each pedal ganglion of same size as cerebral plus pleural ganglia. Sub-oesophageal ganglion situated close to nerve ring, joined to it by narrow, short connectives.

Distribution and habitat: South-eastern Brazilian coast, from Esp rito Santo to S o Paulo. Abyssal, from 1000 to 1600 m depth.

***Benthobia complexirhyna* new species**
(Figs 3A–G, 6A, 9 and 10)

Types: Holotype: NZOI (11.6 \times 7.7 mm), type locality: 40°42.8' S 167°56.0' E, Tasman Basin, Australia, 1029 m depth (R.V. *Tangaroa*, stn P929). Paratypes: NZOI, 1 shell from type locality (12.8 \times 8.0 mm); NZOI, 1 shell (7.3 \times 5.4 mm), 41°00.6' S 169°06.0' E, 914 m depth (stn P942); NZOI, 1 shell (9.6 \times 6.3 mm), 1 shell (10.0 \times 7.6 mm), 4 shells 41°15.2' S 167°07.2' E, 1436–1457 m depth (stn P941); NZOI, 1 shell, 41°39.1' S 165°13.6' E, 4405–4411 m depth (stn P934).

Etymology: The specific epithet refers to the complexity of the osphradium, which possess a notch at distal edge, from Latin *complexus* and Greek *rhinos* meaning nose or olfactory organ.

Diagnosis: Shell fusiform, spire broad. Sculptured by two series of broad, subsutural nodes. Spire angle about 80°. Aperture little longer than half of total shell length. Siphonal canal somewhat narrow. Operculum with elliptical outline. Osphradium elliptical, filaments with a notch in distal region. Radular rachidian broad, short, about 10 equi-sized cusps. Seminal receptacle located posterior to rest of pallial oviduct. Bursa copulatrix broadly attached to pallial floor.

Shell (Fig. 3A–E): Up to 13 mm, white, obese, fusiform. Outer surface opaque, irregular, growth lines marked. Sculptured by two series of subsutural nodes of rather regular size, about 12 on body whorl, longer axially, lower series of nodes slightly opisthocline in

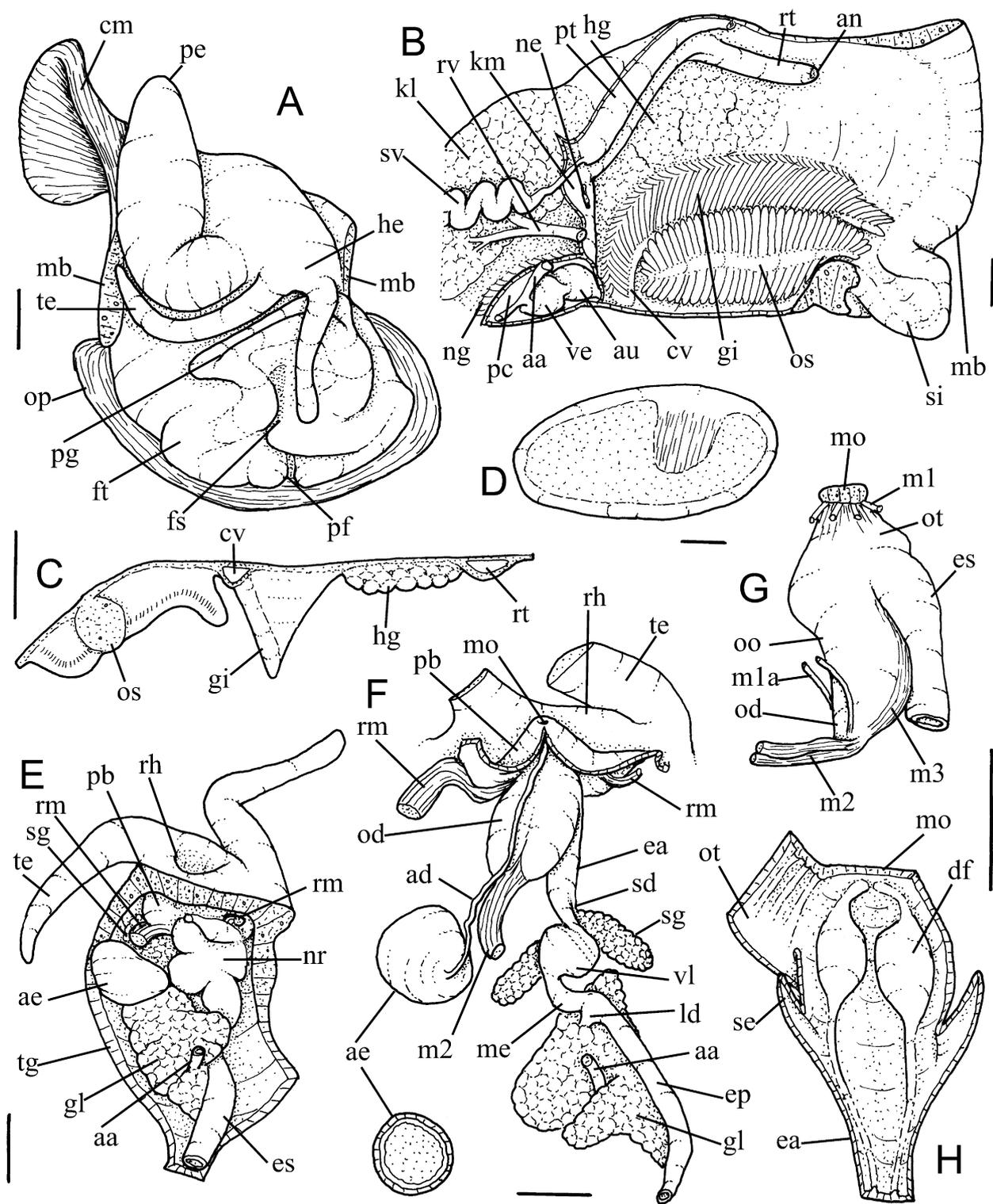


Figure 7. *Benthobia atafona* anatomy. **A.** Head-foot, male, frontal view. **B.** Pallial cavity roof and anterior region of visceral mass, ventral view, pericardium opened longitudinally. **C.** Pallial cavity roof, transverse section in middle level of osphradium. **D.** Opercular pad, operculum removed, dorsal view. **E.** Head and haemocoel, ventral view, foot and columellar muscle extracted. **F.** Foregut extended, a portion of head adjacent to rhynchostome also shown, ventral view, including a detail of a transversal section of accessory salivary gland. **G.** Buccal mass, lateral-left view. **H.** The same, ventral view, odontophore removed, ventral wall of oral tube deflected. Scale bars = 0.5 mm.

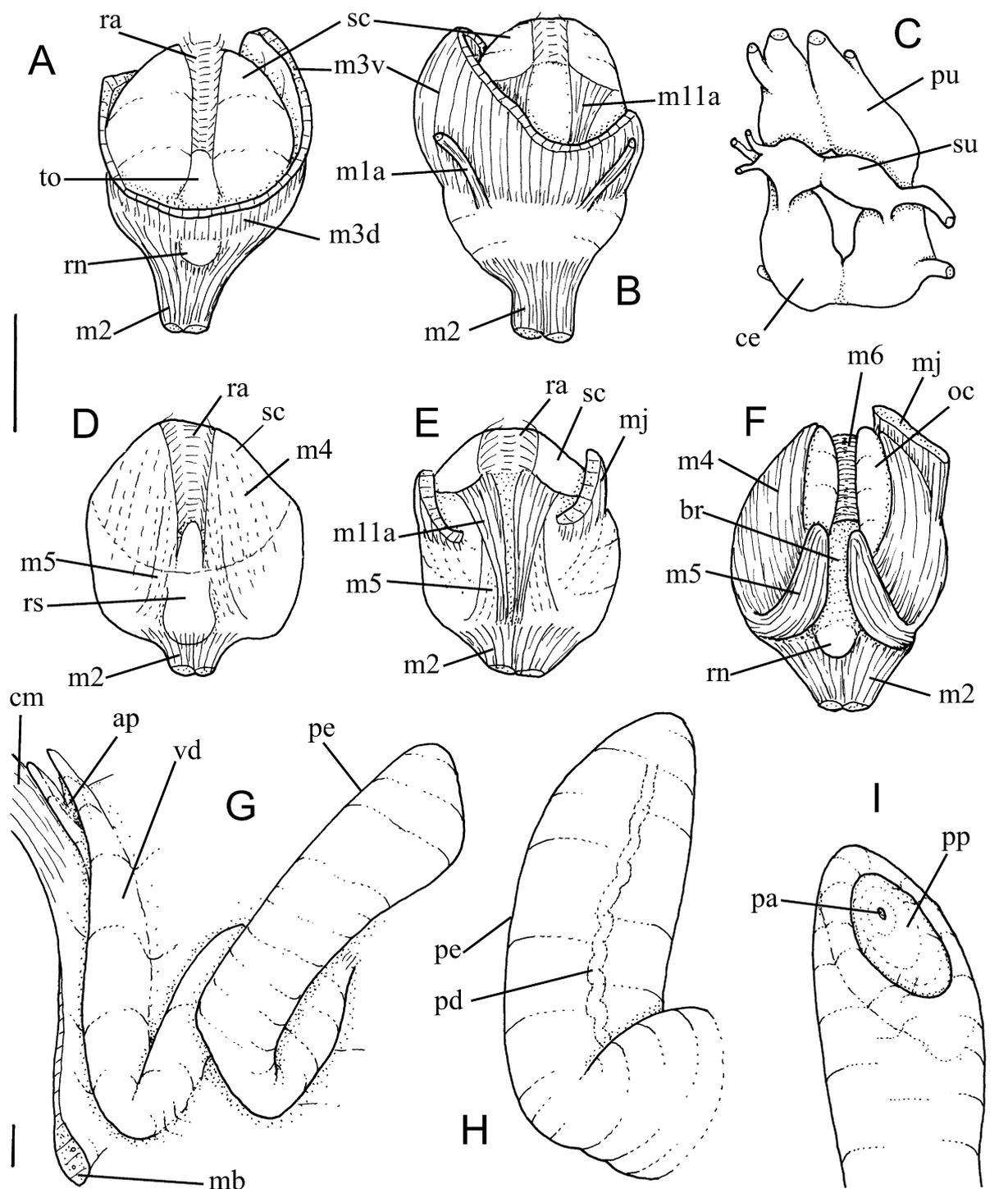


Figure 8. *Benthobia atafona* anatomy. **A.** Odontophore, dorsal view. **B.** The same in ventral view. **C.** Central nervous system, ventral view. **D.** Odontophore, dorsal view, first layer of muscles and membranes removed. **E.** The same, ventral view, some structures seen by transparency. **F.** Same, dorsal view, most superficial muscles and membranes removed, both cartilages deflected, radular sac only partially shown, radula extracted. **G.** Penis and adjacent structures of head-foot, dorsal view, penis partially deflected. **H.** Penis as *in situ*, dorsal view. **I.** Penis, detail of distal half, ventral view. Scale bars = 0.25 mm.

relation to upper (i.e. closer to suture) series; spiral furrow slightly inconstant and interrupted, located between middle and lower thirds of body whorl. Protoconch broad, flat, eroded; about two convex, smooth whorls. Teleconch of up to four whorls, first whorls with dome-shaped profile. Spire broad, wide, of about half body whorl length, spire angle about 80°. Aperture broad, elliptical, a little longer than half of spire length. Peristome white,

glossy. Outer lip with sharp edge, weakly projected; anal region with broad, shallow, sub-terminal notch. Siphonal notch poorly defined, narrow. Inner lip concave, callus low, broad. Umbilicus absent. Some specimens greatly eroded (Fig. 3C), with only inner shell layers remaining.

Head-foot (Fig. 9A): Characters very similar to those of preceding

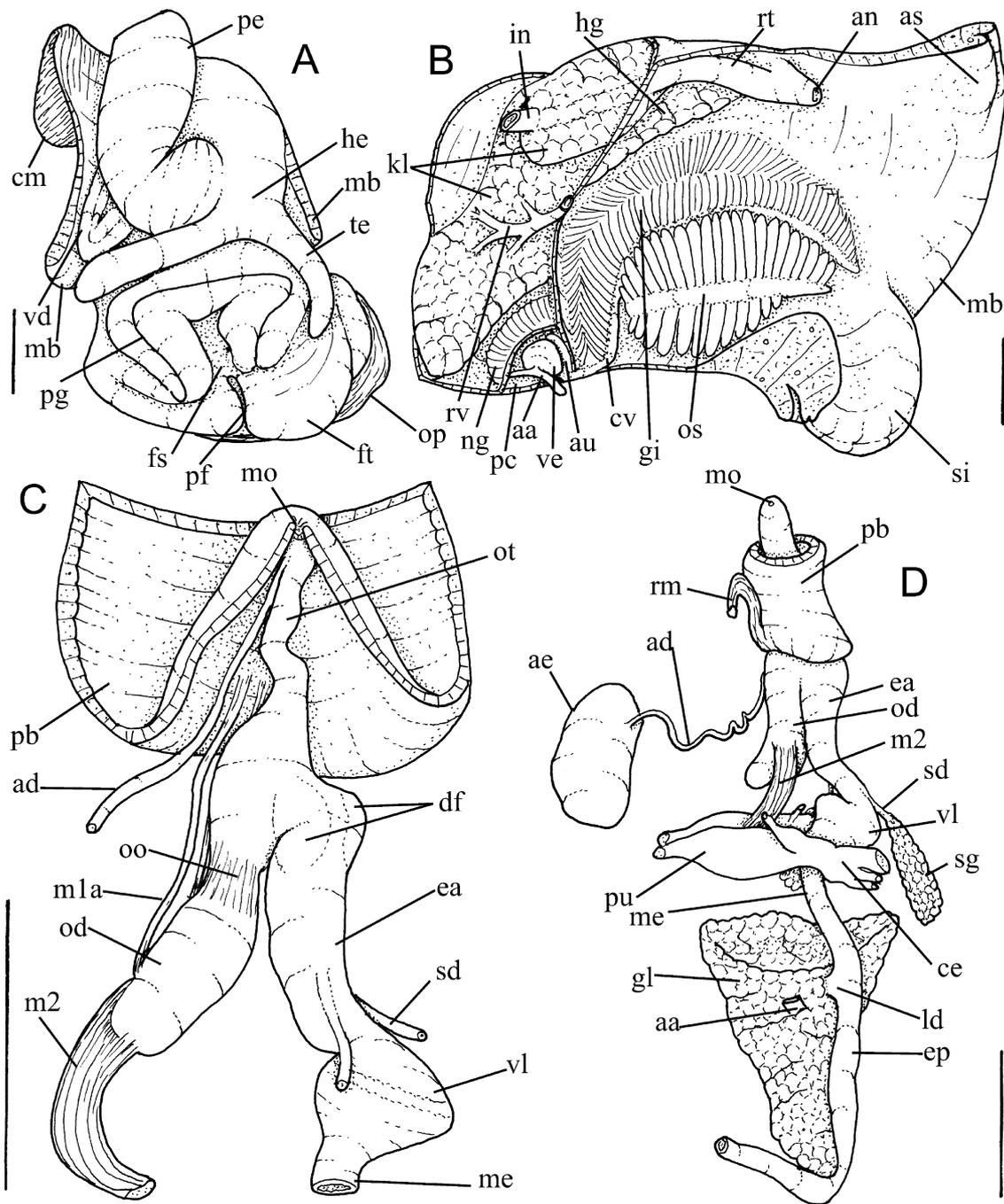


Figure 9. *Benthobia complexirhina* anatomy. **A.** Head-foot, male, frontal view. **B.** Pallial cavity roof and anterior region of visceral mass, ventral view, pericardium opened longitudinally, ventral membrane of kidney removed. **C.** Anterior region of foregut, extended, lateral-left view, proboscis opened longitudinally. **D.** Foregut extended, lateral-left view, nerve ring also shown. Scale bars = 1 mm.

B. atafona species, including lack of eyes, thick edges of pedal gland furrow, and posterior notch of foot sole. It differs by thicker edges of pedal gland furrow, producing a broad, thick anterior border of foot; attachment of operculum by a more symmetrical horseshoe shaped structure (Fig. 10B).

Operculum (Fig. 3F, G): Similar features to preceding *B. atafona* species, but with more elliptical outline (lacking upper corner).

Mantle organs (Figs 9B and 10A): Similar to those of *B. atafona*, with main differences as follows. Siphon somewhat broader and longer. Anal siphon slightly more developed. Osphradium

broader, with more rounded outline; monopectinate anterior portion also present. Osphradial filaments taller, each one with deep notch in apical region, surrounded by thin rod; left filaments slightly smaller than right ones, their notch shallower (Fig. 10A). Gill filaments taller, their distal half narrower and curved to right.

Circulatory and excretory systems (Fig. 9B): Characters closely similar to those of preceding species, including strong curved ctenidial vein in its connection with auricle, a relatively small heart and large afferent renal vessel coming from haemocoel. Renal lobe single, U-shaped, dorsal branch broader, thick and covering most

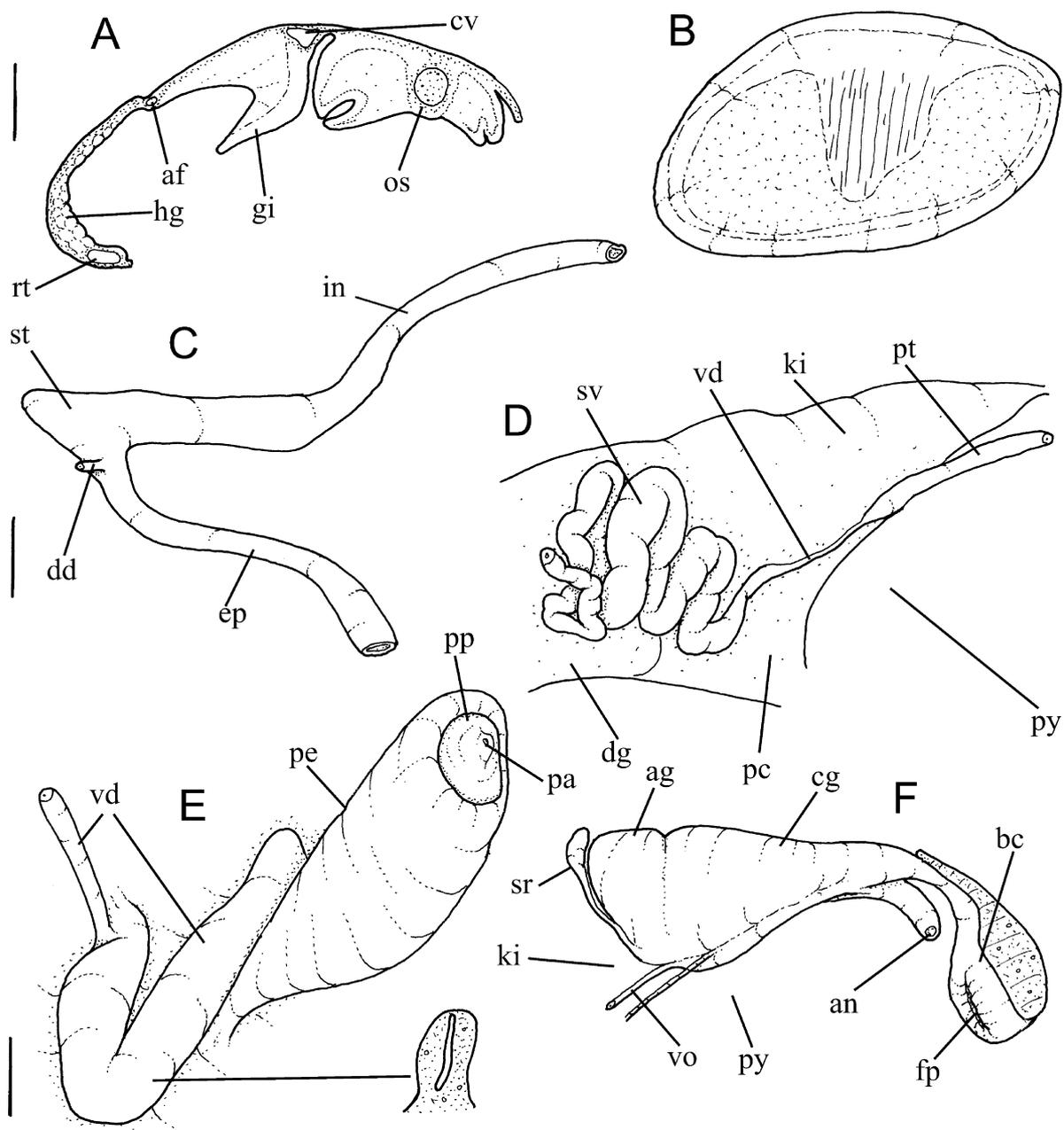


Figure 10. *Benthobia complexirhina* anatomy. **A.** Pallial cavity roof, transverse section at middle level of osphradium. **B.** Opercular pad, operculum removed, dorsal view. **C.** midgut, seen as *in situ*, ventral view. **D.** Anterior region of visceral mass, male, ventral view, emphasizing male genital structures. **E.** Penis and adjacent structures of head-foot, dorsal view, penis partially deflected, a detail of a transverse section of indicated region of vas deferens also shown. **F.** Pallial oviduct as *in situ*, ventral view, some adjacent structures also shown. Scale bars = 0.5 mm.

of dorsal surface of kidney chamber; ventral branch smaller, surrounding anterior half of intestine (its portion passing through kidney). Renal lobe indistinctly furrowed, inner surface almost smooth, except for a mosaic of shallow furrows. Nephridial gland broader.

Visceral mass: As for *B. atafona*.

Digestive system (Figs 9C, D and 10C): Foregut features similar to those of *B. atafona*, including short proboscis, unpaired accessory salivary gland, odontophoral muscles, dorsal folds of buccal mass, valve and gland of Leiblein (Figs 9C, D). Differences include the following: oral tube and tube of odontophore longer (Fig.

9C), with thicker walls. Accessory salivary gland longer antero-posteriorly, its duct originated sub-terminally (Fig. 9D). Radular teeth (Fig. 6A), similar to those of *B. atafona*, differences include: rachidian broader (about 80% of total radular width) and shorter, with about 10 tall cusps of almost equal size; lateral tooth with distal portion proportionally most slender. Posterior oesophagus narrow, long, inserting sub-terminally in left edge of stomach (Fig. 10C). Stomach situated about one whorl posterior to pallial cavity, somewhat narrow, long and flat. Duct to digestive gland small, situated at entry of oesophagus to stomach, turned towards posterior and ventral. A broad, blind and sac-like gastric portion lies posterior to oesophageal insertion. Remainder of stomach long, of uniform width along its length, about one-eighth of adjacent

visceral mass width, situated longitudinally at about one-quarter of whorl; walls thin, inner surface iridescent, smooth. Stomach gradually narrows, lacking clear separation from intestine. Intestine curving gradually towards right and ventrally, passing through digestive gland and ventral surface of kidney. Rectum short (less than half pallial cavity length). Anus simple, with short siphon, situated in middle of pallial cavity length (Figs 9B and 10F).

Male genital system: General morphological features similar to those of *B. atafona*. Remarkable features as follows: seminal vesicle larger and more intensely coiled (Fig. 10D), colour yellowish and iridescent; its middle portion notably broader. Seminal vesicle gradually narrowing about one-quarter whorl posterior to pallial cavity, running obliquely towards anterior and right, on columnellar muscle; suddenly expands in pallial cavity forming prostate (Fig. 10D). Prostate gland narrow, long, running along right floor of pallial cavity, no detectable aperture. Prostate gradually narrows after a length equivalent to 1/3 of pallial cavity length and becomes a narrow vas deferens. This becomes a broad, tall and thick-walled ejaculatory tube (Fig. 10E). Ejaculatory tube forming a zigzag preceding penis (Figs 9A, 10E); its angle at penial base particularly taller and protruded on floor of cavity. Penis somewhat similar to that of *B. atafona*, with same twisted structure (Fig. 9A) and dome-shaped, broad, sub-terminal papilla (Fig. 10E). Penis differs by blunt distal end, and by slightly tall penial duct aperture.

Female genital system (Fig. 10F): Visceral structures equivalent to those of males. Visceral oviduct very narrow, running in mid-ventral surface of visceral mass in its region preceding pallial cavity; inserting sub-terminally in left region of pallial oviduct, between albumen and capsule glands. Seminal receptacle small, balloon-like, situated in posterior region of pallial oviduct, bulging into kidney. Seminal receptacle duct narrow, long, running towards left, inserting in albumen gland a short distance from visceral oviduct. Albumen gland white, occupying about one-third of pallial oviduct, separated from capsule gland by deep, septum-like furrow. Capsule gland a continuation of albumen gland, yellowish, flat, pair of glandular laminae thick, occupying remaining two-thirds of pallial oviduct. Vaginal groove running along left edge of capsule gland, from insertion of visceral oviduct to vestibule. Capsule gland gradually narrows, becoming thin walled, narrow vestibule, running along right edge of pallial cavity at level of anus, inserting into bursa copulatrix. Bursa copulatrix terminal, a continuation of pallial oviduct, marked by sudden enlargement of vestibule, situated in floor of pallial cavity. Bursa walls thick, muscular, forming a hemisphere; aperture an open slit turned to left, edged by radial folds.

Distribution and habitat: Tasman Basin, Australia. Mostly in *Globigerina* ooze, 914–4411 m depth (living specimens 1436–4411 m depth).

***Benthobia tornatilis* new species**
(Figs 3H–JF, 4A–F, 6B and 11)

Types. Holotype: MNHN, shell (13.0 × 7.6 mm); type locality: 22°24' S 159°33' E, Coral Sea, Australia, 780–930 m depth, (R.V. *Coriolis*, Musorstom 5, stn 313). Paratypes: AMS 157289, 1 shell (13.0 × 9.0 mm), 32°58.8' S 152°41.6' E, off Newcastle, New South Wales, Australia, 951–1150 m depth (R.V. *Tangaroa*, stn U223); MNHN, 2 shells, 18°26' S 155°12' E, Mellish Reef, Coral Sea, 1100 m depth, (R.V. *Coriolis*, Corail 2, stn DW172); MNHN, 1 shell, 21°20' S 158°02' E, 1000 m depth (R.V. *Coriolis*, Musorstom 5, stn 321); MNHN, 3 shells, 21°19' S 158°00' E, 975 m depth (Musorstom 5, stn 322); MNHN, 1 shell, 23°06' S 166°46' E, 908 m depth (Bathus 3, stn CP844); MNHN, 1 shell, 23°47' S 169°49' E, 735–755 m depth (Bathus 3, stn DW795); MNHN, 2 shells,

23°48' S 169°49' E, 751–755 m depth (Bathus 3, stn DW794); MNHN, 1 shell (12.7 × 8.4 mm), 23°49' S 169°48' E, 685–715 m depth (Bathus 3, stn DW790); MNHN, 1 shell (12.2 × 7.9 mm), 23°39' S 167°59' E, Ride de Norfolk, New Caledonia, 650–730 m depth (R.V. *Alis*, Bathus 3, stn DW809); MNHN, 1 shell (12.9 × 8.1 mm), 24°44' S 170°08' E, 770–830 m depth (Bathus 3, Stn DW776); MNHN, 1 shell (12.3 × 7.6 mm); 13°49' S 179°56' E, South West Pacific Ocean, 700–715 m depth (R.V. *Alis*, stn DW635); MNHN, 1 shell, 9°10.4' S 159°53' E, Solomon Islands, 749–799m depth (Stn CP 1751 ADN).

Etymology: The specific epithet refers to the rounded shape of the shell, from the Latin *tornatilis*, meaning beautifully rounded.

Diagnosis: Shell fusiform, spire broadly pointed. Surface smooth, sculptured by single series of subsutural, axial, short threads on three first whorls of teleoconch, which disappear gradually on body whorl. Spire angle of about 60°. Aperture slightly longer than half of total shell length. Siphonal canal narrow, longer and broader. Spiral furrow of body whorl indistinct. Operculum with an upper corner. Osphradium filaments simple, tall, symmetrical, with narrow base. Anterior monopectinate portion of osphradium shorter. Radular rachidian tooth arched, bearing about eight stubby, tall, pointed cusps, pair of more lateral cusps smaller than remaining central cusps. Seminal receptacle situated in dorso-posterior region of pallial oviduct. Bursa copulatrix narrowly attached to pallial floor.

Shell (Figs 3H–J and 4A–E): Up to 13 mm, white, obese, fusiform. Outer surface opaque, smooth, growth lines weak. Sculptured by subsutural axial, short threads of regular size on first three whorls of teleoconch, these becoming fainter and disappearing gradually, with last 1.5 whorls lacking subsutural sculpture; spiral furrow indistinct (Fig. 4A–C), situated between middle and lower thirds of body whorl, but almost absent in most specimens (Figs 3H–J and 4D,E). Protoconch mammillate, hemispherical, small; about two convex, smooth, glossy whorls. Teleoconch of up to five whorls, first whorls with well-marked profile. Spire broadly pointed, of about half body whorl length, spire angle about 60°. Body whorl becoming highly inflated. Aperture broad, elliptical, slightly longer than half of total shell length. Peristome white, glossy. Outer lip with sharp edge, not projecting; anal region simple, lacking sub-terminal notch. Siphonal canal poorly defined, somewhat narrow. Inner lip concave, callus low, somewhat broad. Umbilicus absent.

Head-foot (Fig. 4F): Similar to that of *B. atafona*.

Operculum: Similar to that of *B. atafona*.

Mantle organs (Fig. 11A, B): Similar features to those described for *B. atafona*, with following differences: Siphon longer and broader; its base, at right, forming a tall fold separating anterior region of gill from that of osphradium. Anal siphon more developed. Osphradial filaments taller, symmetrical (left filaments in relation to right ones), tip rounded, base narrow (Fig. 11B). Monopectinate portion of osphradium shorter. Gill somewhat straightened. Gill filaments similar to those of *B. complexirhyna*.

Digestive system: Foregut similar to that of *B. atafona*. Differs by the following (Figs 4F and 11C): proboscis proportionally longer (Fig. 4F). Accessory salivary gland proportionally larger and longer. Gland of Leiblein larger, occupying almost half of haemocoel volume. Oral tube narrower and longer, of about same length as odontophore. Radula similar to that of *B. atafona*, with following differences (Fig. 6B): rachidian slightly longer, arched in its central region, with about 60% of total radular width, about eight tall, pointed cusps, pair of more lateral cusps

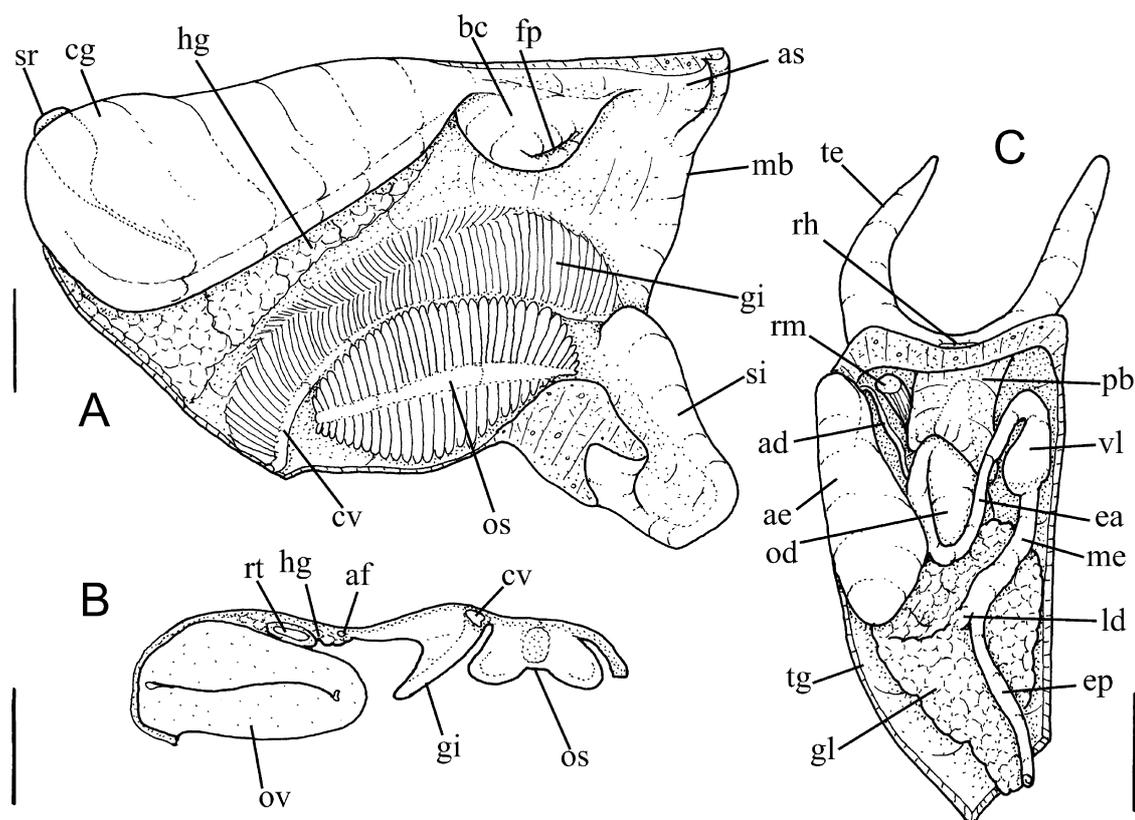


Figure 11. *Benthobia tornatilis* anatomy. **A.** Pallial cavity roof, female, ventral view, also showing pallial oviduct, seminal receptacle seen by transparency. **B.** The same, transverse section at middle level of osphradium. **C.** Head and haemocoel, ventral view, foot and columellar muscle removed. Scale bars = 1 mm.

smaller than central cusps; lateral tooth with a broader base, narrowing gradually, becoming triangular

Female genital system: Pallial oviduct similar to that of *B. complexirhyna*, but differing by the following (Fig. 11A): seminal receptacle situated dorsal to albumen gland (instead of posterior). Albumen and capsule glands thicker. Vestibule shorter. Bursa copulatrix inserted mostly at right edge of pallial cavity, and weakly in floor of pallial cavity. Bursa with aperture situated in anterior region, with cavity turned towards anterior.

Distribution and habitat: South West Pacific Ocean, from Coral Sea to off New South Wales, Australia. From 650 to 1150 m depth (live specimens in 951–1150 m).

***Benthobia tryonii* Dall, 1889**
(Figs 4H–J and 5A–D)

Benthobia tryonii Dall, 1889: 132, pl. 35, fig. 6 (holotype USNM 93441 off Cape Fear, South Carolina, USA, 32°40'00" N 76°40'30" W, 1337 m depth). Abbott, 1974: 249; fig. 2718. Bouchet & Warén, 1985: 249 figs 665–668. Vermeij, 1997: 1001.

Lacuna cossmanni Locard, 1897: 493, pl. 22, figs 4–9 (two syntypes of MNHN25°01' S 16°55' W, 2638 m depth). Bouchet & Warén, 1985: 249 (in synonymy).

Diagnosis: Shell obese, spire pointed and small. Sculpture small, short riblets confined to subsutural region, practically absent in body whorl. Spire angle about 80°. Aperture about three-quarters of total shell length. Siphonal canal narrow, forming a shallow canal.

Shell (Figs 4H–J and 5A–D): Up to 12 mm, white, obese, fusiform. Outer surface opaque, smooth, growth lines weak. Sculptured by low, subsutural, short, axial threads of regular size on first three whorls of teleoconch, becoming faint and disappearing gradually towards last whorl, where subsutural sculpture is weak, irregular and sometimes lacking; spiral furrow shallow, situated between middle and lower thirds of body whorl, absent in some specimens (Fig. 4H–J). Protoconch mammillate, hemispherical, small; about three convex, smooth, glossy whorls. Teleoconch of up to four whorls, first whorls with profile well-marked by suture. Spire broadly pointed, with about half body whorl length, spire angle about 80°. Body whorl becoming larger uniformly with spire. Aperture broad, elliptical, about half of total shell length or slightly shorter. Peristome white, glossy. Outer lip with sharp edge, not projecting; anal region with a shallow sub-terminal notch. Siphonal canal well defined, narrow, projecting forwards. Inner lip concave, rounded, callus low, flat, broad. Umbilicus absent. Other details in Dall (1889).

Operculum: Based on Bouchet & Warén (1985; fig. 668): outline elliptical, corner located at middle of upper edge. Other details as in *B. tornatilis*.

Radula: Based on Bouchet and Warén (1985; fig. 667): rachidian wide, occupying about 50% of total radula width, with seven long, slender, pointed cusps of approximately equal size; lateral tooth arched, tip pointed, base broad, triangular.

Measurements: MNHN (stn 68A13.3): 11.6 × 7.5 mm MNHN; (stn 68A13.14): 10.2 × 7.0 mm MNHN; (stn 165): 9.6 × 6.2 mm MNHN.

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Distribution and habitat. North Atlantic, from Azores to Gulf of Mexico, 713–2085 m depth.

Material examined. MNHN, 1 shell, 25°39' N 96°11' W, Gulf of Mexico, 713 m depth (stn 68A13.3); MNHN, 1 shell, 25°39.5' N 95°49.5' W, 960 m depth (stn 68A13.14); MNHN, 1 shell, 28°13.5' N 87°04' W, 1200–800 m depth (stn 66A9.xv); MNHN, 1 shell, 27°01.3' N 94°43.5' W, 1399 m depth (stn 69A11.7); MNHN, 1 shell, 37°33' W 25°58' W, SW of São Miguel, Azores, 2085–2050 m depth (Jean Charcot–Biacores 1971, stn 165). Additional material examined from photographs sent by USNM: USNM 824174, 1 shell with eroded spire, 37°46'10" N 70°27'52" W, off Virginia, USA, 4038 m depth (R/V *Advance II*, stn 013); USNM 832910, 1 eroded shell, 38°04'14" N 70°26'23" W, 3700 m depth (stn 009); 3 syntypes USNM 93441 (Fig. 4H–J), 32°40'00" N 76°40'30" W, Cape Fear, South Carolina, USA, 1337 m depth (R/V *Albatross*, stn 2678).

Benthobia sima new species (Figs 4G, 5E–I, 6C and 12)

Holotype. MNHN, shell (9.1 × 6.7 mm), type locality: 11°44' S 47°35' E, SE Glorieuses, Madagascar, 3716 m depth (French Benthedi Expedition 1977, stn 87).

Etymology. The specific epithet refers to the broad shape of the osphradium, from the Latin *simus* or *simatus*, meaning flat-nosed.

Diagnosis. Shell obese, spire low. Sculptured by growth lines and a subsutural spiral furrow. Spire angle about 100°. Aperture large, more than 80% of total shell length, outer lip broadly projecting. Siphon broad, weakly delimited. Spiral furrow well developed, producing a small tooth in outer lip. Operculum with an upper corner. Osphradium very broad (occupying about half of pallial cavity area), strongly asymmetrical, with simple filaments. Radula with very narrow rachidian, with about nine well spaced, slender cusps. Retractor muscle of odontophore (m2) not attached to radular sac. Seminal receptacle absent. Bursa copulatrix widely attached to pallial floor.

Shell (Figs 4G and 5E–H): Up to 9.1 mm, white, obese, turbiniform. Outer surface opaque, somewhat irregular, growth lines well marked. Sculpture totally absent, except for a spiral subsutural furrow in last whorl. Protoconch and spire greatly eroded. Teleoconch of four whorls. Spire low, of about one-quarter body whorl length, spire angle about 100°. Peristome white, glossy. Outer lip with sharp edge, amply projected; anal region simple, lacking sub-terminal notch. Siphonal canal poorly defined, broad and spacious. Inner lip concave, callus low, broad. Umbilicus absent.

Note. The following description is based on a single dried and re-hydrated female, incompletely extracted.

Head-foot. Characters similar to those of *B. atafona*.

Operculum (Fig. 5I): Closely similar to that of *B. atafona*, except in being slightly broader in middle region.

Mantle organs (Fig. 12A, D): Organization similar to that of *B. atafona*, with following differences: siphon longer and broader; its base, at right, forming a low fold separating anterior regions of gill and osphradium. Anal siphon more developed. Anterior end of osphradium and gill close to each other. Osphradium broad, occupying almost half of pallial cavity roof area. Osphradium filaments low and asymmetrical, right filaments with about double the number of left ones; right filaments with a rounded projec-

tion covering ctenidial vein. Anterior monopectinate portion of osphradium short. Gill filaments curved towards right, with a strongly concave right edge; tips pointed.

Circulatory and excretory systems (Fig. 12A): General construction of both very similar to those described for *B. complexirhyna*.

Digestive system (Fig. 12B,C): Foregut features similar to those of *B. atafona*. Distinctive attributes as follows: left proboscis retractor muscle the same size as right one. Oral tube and tube of odontophore longer. Salivary glands with glandular tissue up to its entrance into anterior oesophagus wall, just anterior to valve of Leiblein (duct not visible). Accessory salivary gland large (about same size as remaining foregut), pear-shaped. Pair of odontophore muscles m2 (retractor of buccal mass) separated from radular sac (not surrounding it as remaining species). Radula (Fig. 6C) with rachidian tooth very short and broad (about 80% of total radular width), bearing about nine well spaced, slender cusps; lateral teeth slender. Stomach not seen; posterior oesophagus and intestine running close to each other. Intestinal course similar to that of *B. complexirhyna*. Anus situated slightly more anterior than that of *B. atafona* (Fig. 12A).

Female genital system (Fig. 12A): Pallial oviduct with characters similar to those of *B. complexirhyna*, with notable exceptions: seminal receptacle absent. Vestibule preceding level of anus. Bursa copulatrix widely attached to pallial cavity floor. Bursal aperture broad, turned towards left.

Distribution and habitat. Off Madagascar. From 1190 to 3716 m depth.

Additional material examined. USNM 717352, 1 shell examined only by photo (Fig. 4G), c. 65 km WSW off Tulear, Madagascar, 23°43' S 43°25' E, 1190 m depth (A. Braun, stn 363K).

DISCUSSION

In a review of the genera of the family Pseudolividae, Vermeij (1998) accepted the position of the genus *Benthobia* in this family, based on the radular morphology (provided by Bouchet & Warén, 1985) and characters of the anatomy (provided by Kantor, 1991). In the present study, further details of the anatomy are described, providing an additional set of characters (probable apomorphies), which are included in the generic diagnosis given above.

All samples of *Benthobia* have previously been accepted as belonging to the single species *B. tryonii*, collected in deep waters around the world. However, thorough examination of shell characters and anatomy indicates that the samples found in different parts of the world should be regarded as distinct species (Fig. 13). Most of the similarities and differences among the species are listed in the descriptions and diagnoses. The following discussion explores some of the more significant characters.

A comparison of major characters among the five species studied is summarized in Table 1. Although the shells of the five species are similar, they can easily be separated by means of the following characters. The spire is small and pointed in *B. atafona*, larger and broadly pointed in *B. complexirhyna*, *B. tornatilis* and *B. tryonii*, but low and broad in *B. sima*. The spire angle is also different, it is about 60° in *B. atafona* and *B. tornatilis*, about 80° in *B. complexirhyna* and *B. tryonii*, and about 100° in *B. sima*. The aperture is about half of the total length of the shell in *B. atafona*, while it is slightly longer in *B. complexirhyna* and *B. tornatilis*, about 75% of the total length in *B. tryonii* and more than 80% in *B. sima*. The siphonal canal on the outer lip is normally weak in *Benthobia* species, but *B. complexirhyna*, *B. tornatilis* and *B. tryonii* have a somewhat narrow and differentiated canal, while *B. atafona* and

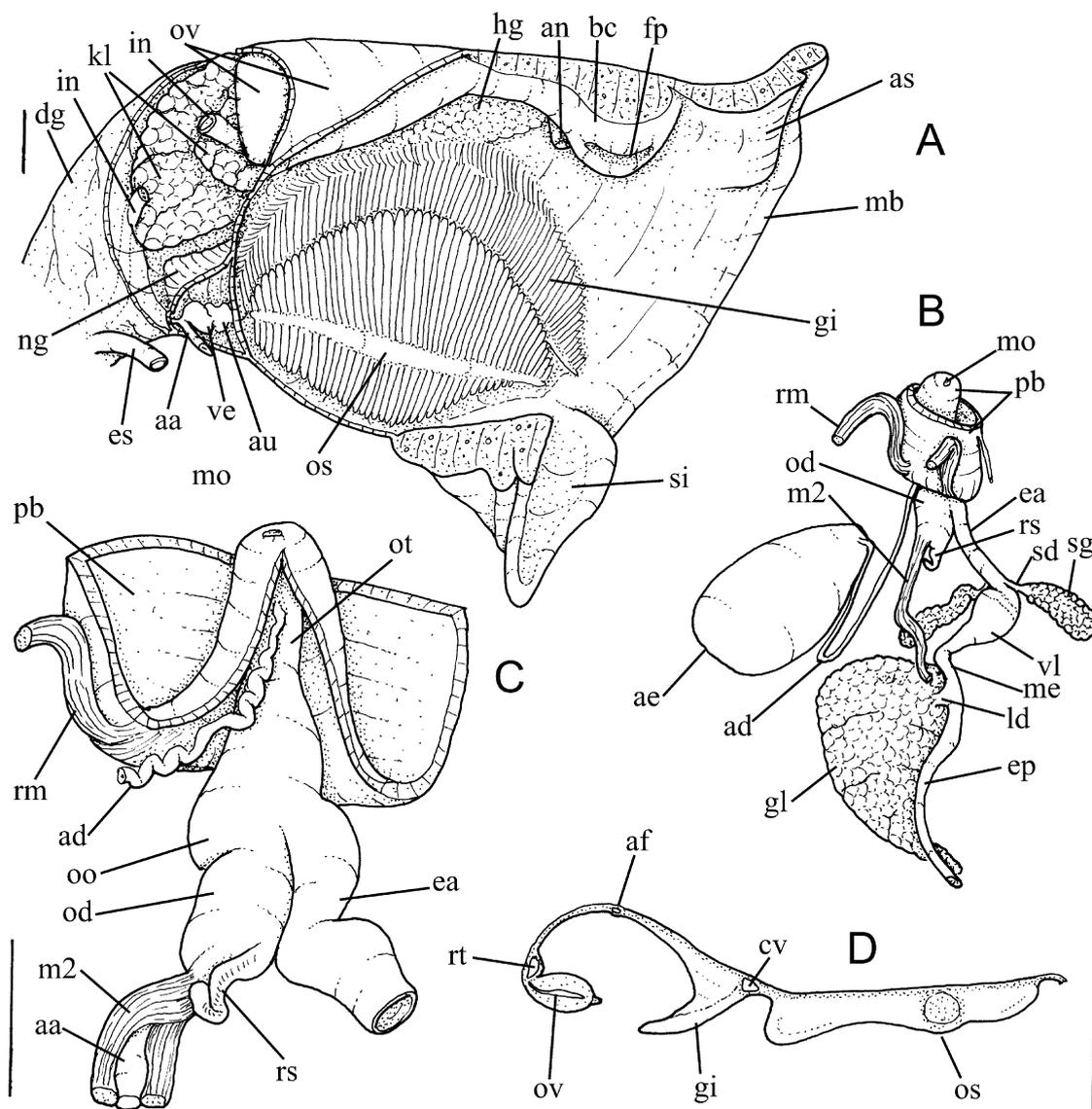


Figure 12. *Benthobia sima* anatomy. **A.** Pallial cavity roof and anterior region of visceral mass, ventral view, pericardium and kidney opened longitudinally. **B.** Foregut extended, lateral-left view. **C.** The same, detail of anterior region, proboscis opened longitudinally. **D.** Pallial cavity roof, transverse section at middle level of osphradium. Scale bars = 0.5 mm.

B. sima have a spacious and broad siphon that is poorly defined. The operculum of *B. complexirhina* has a unique elliptical outline, while the remaining species possess an upper corner (the operculum of *B. tryonii* was not examined). The osphradium is also an important source of comparative data; all the *Benthobia* species possess a short monopectinate anterior portion. However, the osphradium of *B. complexirhina* differs in having filaments with a notch in their distal region, that of *B. atafona* is narrower, that of *B. sima* is broader, while that of *B. tornatilis* is symmetrical (with reference to left and right filaments). The foreguts of all species are very similar. The main distinguishing feature is the retractor muscle of the buccal mass (m2) of *B. sima*, which is not attached to the radular sac. The radula is also different in some details of the rachidian, including form, number and relative size of cusps. The pallial oviduct is also different in the three species for which female specimens were available; *B. complexirhina* has the seminal receptacle located posterior to the remainder of the pallial oviduct, in *B. tornatilis* it is situated dorsal to the posterior end of remaining pallial oviduct, while *B. sima* lacks a seminal recep-

tacle. The bursa copulatrix of *Benthobia* is unique in being situated at the end of the pallial oviduct, as its continuation, and is also attached to the floor of the pallial cavity. However, the structure is narrowly attached to the floor in *B. tornatilis*, while in the other two species it is broadly attached.

The anatomical analysis in this study was limited by available material. For some species representatives of both sexes were unavailable; some specimens were dry (and were rehydrated for examination) and, in the case of *B. tryonii*, no soft parts were available. Examination of the USNM material (*B. sima* and the type specimens of *B. tryonii*) was limited to photographs. Despite these impediments, the quantity and quality of the morphological differences were sufficient to differentiate the species.

Although short, the proboscis is of the normal pleurembolic type (Figs 7E, F, 9C, D, 11C and 12B, C). *Benthobia atafona* exhibits a shorter proboscis than its congeners. The buccal mass is positioned at the base of the proboscis, connected to the mouth by means of a long oral tube. The buccal mass is always close to the mouth, even when the proboscis is extended (Fig.

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4F). This character agrees with Kantor's (1991) description of a basal location of the odontophore within the proboscis. Other aspects of Kantor's description of *Benthobia* are also in agreement with those presented here, mainly regarding the foregut, and the distinguishing character of the unpaired and massive accessory salivary gland.

The species *Nux alabaster* Barnard, 1960 (Fig. 14), from Atlantic coast of South Africa, has been considered a synonym of *B. tryonii* (Bouchet & Warén, 1985). In shell shape and other characters, *N. alabaster* shows some differences from the species described herein. The most similar species is *B. complexirhina*, from which

Nux differs by the broader spire, longer aperture and lack of sculpture. From the other South Atlantic species, *B. atafona*, it differs in its taller spire, lack of spire nodes, and an operculum with more elliptical outline. It differs from the African *B. sima* by the taller spire, lack of a spiral furrow on the last whorl and weaker siphonal area. Those differences, coupled with the different shape of the operculum (with an upper broad projection, Fig. 14B; Barnard, 1960: fig. 2) and the shorter cusps of the radular rachidian (Barnard, 1960: fig. 2), preclude a secure synonymy of *Nux alabaster* with any *Benthobia* species. For these reasons, besides the lack of any information on internal anatomy, the

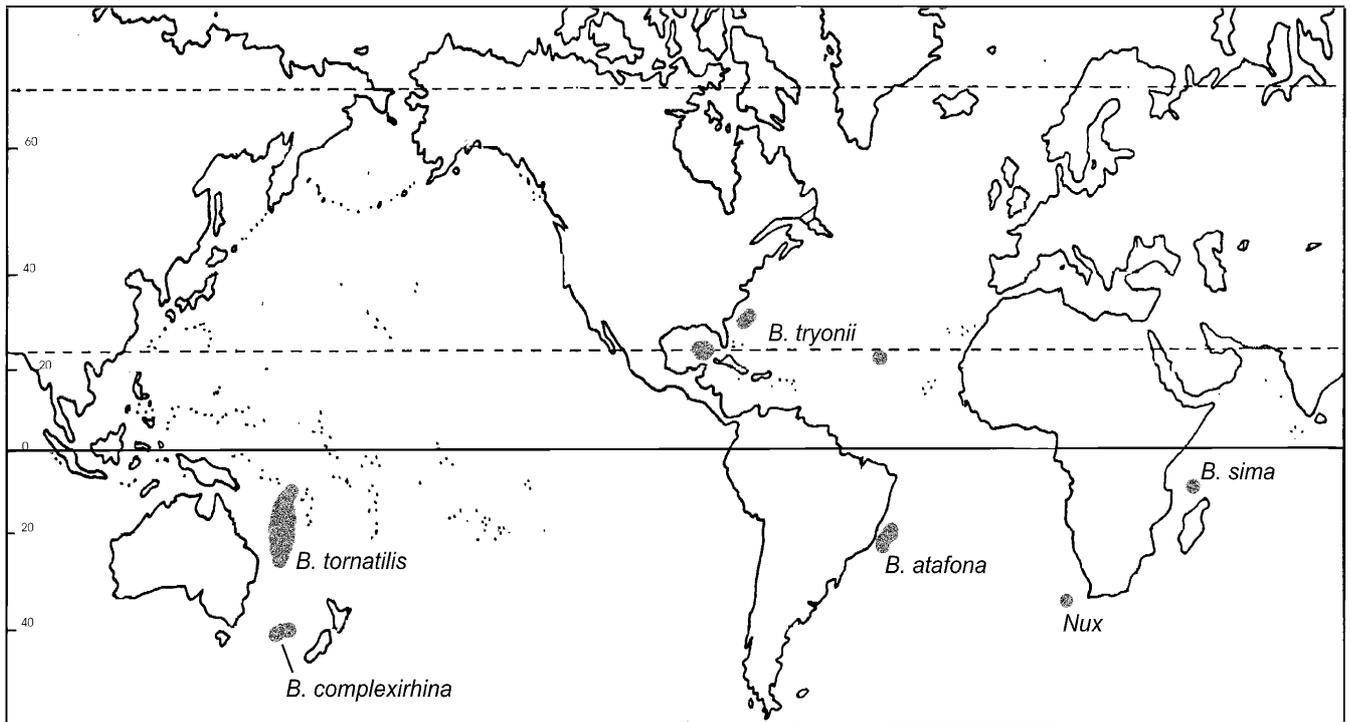


Figure 13. World map showing the known distribution of *Benthobia* species and *Nux alabaster*.

Table 1. Comparison of characters among the five studied species of *Benthobia*.

Character	<i>Benthobia atafona</i>	<i>Benthobia complexirhina</i>	<i>Benthobia tornatilis</i>	<i>Benthobia tryonii</i>	<i>Benthobia sima</i>
Distribution	SE Brazil	Tasman Basin, Australia	SW Pacific Ocean	N Atlantic Ocean	Off Madagascar
Spire form	Small, pointed	Larger, broadly pointed	Larger, broadly pointed	Larger, broadly pointed	Low, broad
Approximate spire angle	60°	80°	60°	80°	100°
Aperture total length	Half	Little longer than half	Little longer than half	About 75%	More than 80%
Shell siphonal canal	Broad	Narrow	Narrow	Narrow	Broad
Operculum outline	Upper corner	Elliptical	Upper corner	Upper corner	Upper corner
Osphradium filament notch	Absent	Present	Absent	?	Absent
Osphradium width (relative to pallial roof)	1/3	—	—	?	—
Osphradium symmetry	Absent	Absent	Present	?	Absent
(m2) Retractor muscle of buccal mass	Attached to radular sac	Attached to radular sac	Attached to radular sac	?	Free from radular sac
Radular rachidian approximate number of cusps	6	9	6	7	10
Approximate width of rachidian/radula width	70%	80%	60%	50%	80%
Seminal receptacle location	?	Posterior to remaining pallial oviduct	Dorsal to remaining pallial oviduct	?	Absent
Bursa attachment to pallial floor	?	Wide	Narrow	?	Wide

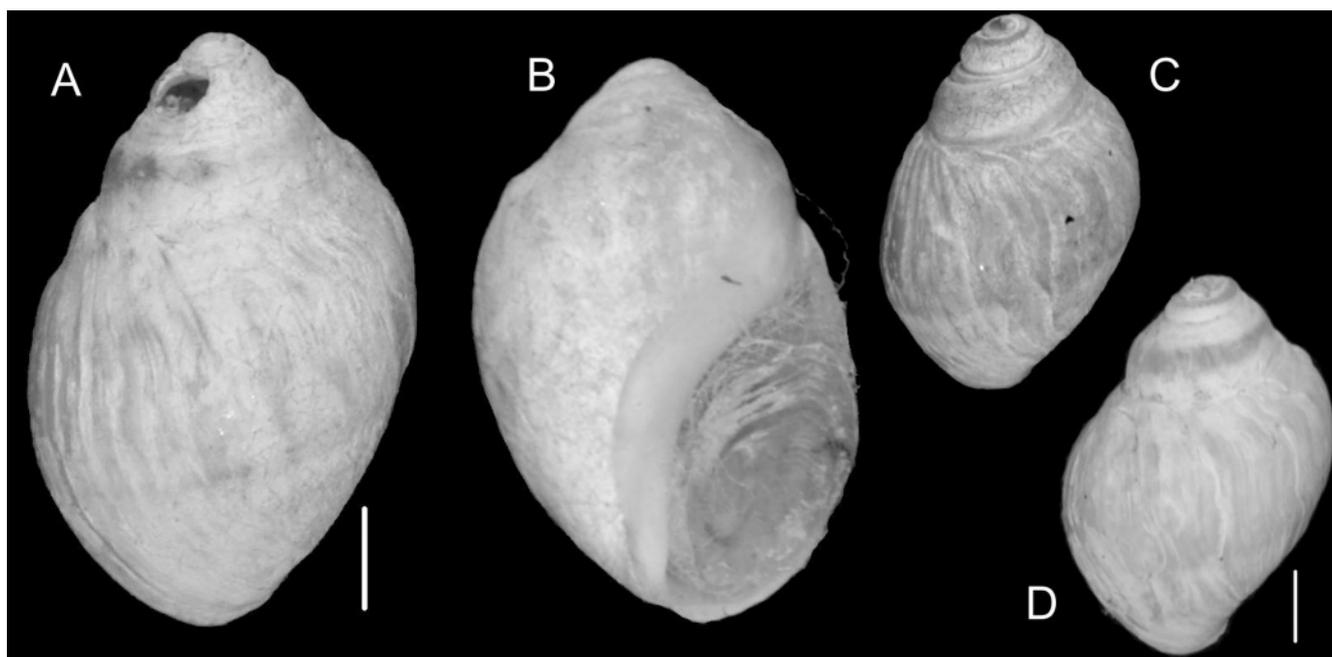


Figure 14. *Nux alabaster* type material. A, B. Holotype (SAM A9715), dorsal and frontal views. C, D. Shells of paratypes (SAM A9827). Scale bars = 2 mm.

genus and species *Nux alabaster* is herein considered valid, until further material becomes available for study. In fact, when Barnard described *Nux alabaster*, its similarity with *Benthobia tryonii* was pointed out. However, as noted by Bouchet & Warén (1985), the single reason for the generic separation is the fact that *Nux* has a rachiglossate radula, while *Benthobia* was considered a nematoglossate cancellariid at that time. Nevertheless, undoubtedly *Nux* is a close related taxon to *Benthobia*, as shown by the shell, opercular and radular resemblances.

It is apparent that there is no precise definition of the family Pseudolividae. The single character is perhaps the presence of what Vermeij (1998) called the 'pseudolivid groove', i.e. a spiral furrow running between the middle and lower thirds of the body whorl, producing a small tooth at the outer lip. However, this kind of furrow has been found in species belonging to other families, such as Olividae (e.g. *Ancilla* Lamarck, 1801), Fasciolaridae (e.g. *Leucozonia* Gray, 1847) and Buccinidae (e.g. *Babylonia* Schlüter, 1838), and may be a remarkable convergence. A parallel study is being performed with other pseudolivid taxa to confirm the monophyly of the family to clarify this question. The stronger shoulder of the shell of *B. complexirhina* resembles that of the pseudolivid genus *Fusulculus* Bouchet & Vermeij, 1998; however, the relationship between these two genera is still unclear.

The foregut characters of *Benthobia* are typical for neogastropods, as shown by the pleurembolic proboscis, the presence of a gland of Leiblein, presence of accessory salivary gland and salivary glands free from the nerve ring. Additionally, the presence of a valve of Leiblein and of the stenoglossate radula are indicative of a muricoidean (*sensu lato*) position of the genus. The accessory salivary gland of *Benthobia* is unique among the muricoideans, in being massive, with thin muscular walls, and unpaired. However, as also noted by Kantor (1991: 39) the structure may be homologous with the accessory salivary glands of the other muricoideans, based on its position and ventral insertion in the oral tube. Another interesting feature is the valve of Leiblein, which lacks an oblique furrow, such as has been found in most valves I have examined.

The characters of the radular teeth of *Benthobia* resemble those of Muricidae and Olividae. However, there are some

features of other structures that are not found in species of those families, such as the monopectinate portion of osphradium, the reduction (to one?) in number of accessory salivary glands, special arrangement of muscles in opercular pad attachment to the operculum, closure of the pallial sperm ducts and terminal position of the bursa copulatrix. These characters are not shared with other genera within the Pseudolividae either.

Specimens assigned to *Benthobia tryonii* studied by Kantor (1991) were collected in the southwestern part of the North Atlantic (one specimen) and northwestern Indian Ocean (two specimens). The figured shell (Kantor, 1991: fig. 1F, G) resembles that of *B. sima*, and may belong to this species if the specimen is from Indian Ocean. This is the reason for the absence of Kantor's citation in the synonymy of *B. tryonii*. Some anatomical data reported by Kantor (1991) are also different from the species described here (Kantor, 1991: figs 14, 15A and 16), such as the form of the gill filaments and the morphology of the radular rachidian, which has few, low and broader cusps. This may indicate that he studied an undescribed species. I had no access to that material and therefore cannot analyse the situation adequately.

Due to the great depths inhabited by *Benthobia* species, specimens may show some degree of shell erosion, which can be very intense (Fig. 3C). Highly eroded specimens are sometimes difficult to identify. The best ways to identify these species should be based on geographic location (Fig. 13) and on proportions of normally preserved shells.

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