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Anatomy of *Bullia laevissima* from Cape Town, South Africa

(Mollusca, Caenogastropoda, Nassariidae)

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The morpho-anatomy of *Bullia laevissima* (Gmelin, 1791), a marine snail from South Africa, is investigated in detail. It has a dome-shaped shell, with sinuous ribs along the surface of the three initial whorls. Other external characters include the lack of eyes, and a flat foot with a pair of small epipodial tentacles. Radular characters are a comb-like rachidian tooth, and lateral teeth bearing three small inner cusps. The gland and valve of Leiblein are absent, the posterior esophagus is very broad if compared to other congeners. Other similarities and differences with other congeners are also discussed herein. These morpho-anatomical characteristics are discussed in the light of the current knowledge on other *Bullia* species, and differences show that diversity of the genus is undeniable, even in closely related species.

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Introduction

The rachiglossan family Nassariidae Iredale, 1916, belongs to the neogastropod superfamily, the Buccinoidea (Brown 1982). It comprises a number of small to medium-sized marine snails with a worldwide distribution (Harasewych 1998). *Nassarius* Duméril, 1805, and its close relatives tend to be restricted to muddy environments, though a few species shelter among loose rocks and sand (Kilburn & Rippey 1982). Sandy beach snails are common in both hemispheres, with the richest diversity in the Arabian Sea and Bay of Bengal (Subba Rao 2003). They occur in temperate, subtropical and tropical waters. Their taxonomy, especially the status of the alleged genera and subgenera, is still far from a resolution and the distribution of most species is poorly understood. New species continue to be described (e. g. Abbate & Cavallari 2013, Zhang & Zhang 2014, Kool & Galindo 2014), and the taxonomy of the known species needs to be revised (Brown 1982, Cernohorsky 1984, Simone & Pastorino 2014).

The genus *Bullia* Gray, 1834 was erected by Gray (in Griffith, 1834) for the purpose of distinguishing a group of species he thought were intermediate between *Buccinum* and *Terebra*. Since the original description, the genus concept shows some taxonomic problems, among them its poor anatomical definition. The most recent and comprehensive revisions of these genera were published by Allmon (1990). Several genera within the Nassariidae were synonymized or validated according to subsequent authors, i. e. *Dorsanum* Gray, 1847 has been regarded as a junior synonym of *Bullia* (Adam & Knudsen 1984). *Dorsanum* is sometimes considered valid, but restricted to the type species, *D. miran* (Bruguière, 1789). Simone and Pastorino (2014) morphologically compared *D. miran* to *Bullia granulosa* (Lamarck, 1822), seeking an anatomical definition to solving the taxonomic and phylogenetic placement of closely

related genera. Nevertheless, a wider discussion on *Bullia* and *Dorsanum* is still lacking.

The present paper provides a more holistic anatomical description of *Bullia laevissima* (Gmelin, 1791) with discussion limited to data published so far. However, it is part of a wider project aiming to review the taxonomy and phylogeny of the Nassariidae, which includes the species studied herein as one of the *Bullia* representatives.

Material and methods

A list of material examined follows the species description. Shells were broken prior to soft part extraction. Specimens were immersed in 70 % ethanol and dissected by standard techniques under a stereomicroscope. The terminologies of Arnold (1965) and Simone (2011) were employed for shell characterization and anatomy, and Diver's (1939) whorl counting method was applied. Radula details were examined under Scanning Electronic Microscope (SEM) at the Museu de Zoologia da USP (MZSP). The preparation of the material included the isolation of the radula during dissection and subsequent immersion in a ¾ filtered water, ¼ sodium hypochlorite solution for cleaning. The resulting cleaned piece was attached to a stub with the aid of a conductive adhesive tape, and spur-coated with gold. SEM images include a panoramic view and two photos with details of the central and lateral teeth. Drawings were made under a stereomicroscope with the aid of a camera lucida.

Abbreviations used in anatomical drawings

aa, anterior aorta; *ae*, anterior esophagus; *ag*, albumen gland; *an*, anus; *au*, auricle; *ca*, common aorta; *ce*, cerebral ganglion; *cg*, capsule gland; *cm*, columellar muscle; *cv*, ctenidial vein; *es*, esophagus; *et*, epipodial tentacle; *fp*, female pore; *ft*, foot; *gc*, cement gland; *gi*, gill; *go*, gonads; *hd*, head; *it*, intestine; *kd*, kidney; *m1–m11*, odontophore muscles; *me*, medium esophagus; *mj*, julgal muscle; *mo*, mouth; *mt*, mantle; *ne*, nephrostome; *nr*, nerve ring; *oc*, odontophore cartilage; *om*, odontophore muscles; *os*, osphradium; *pb*, proboscis; *pc*, pericardium; *pd*, penis duct; *pe*, posterior esophagus; *pn*, penis; *pg*, anterior furrow of pedal glands; *pl*, stomach plicae; *po*, pallial oviduct; *pu*, pleural ganglion; *ra*, radula; *rh*, rhinchostome; *rm*, retractor muscle of proboscis; *rt*, rectum; *sd*, salivary duct; *sf*, siphon; *so*, salivary duct opening; *st*, stomach; *te*, tentacle; *vd*, vas deferens; *ve*, ventricle; *vg*, vaginal atrium; *vo*, visceral oviduct.

Institutional abbreviations

MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
KZN KwaZulu-Natal Museum, Pietermaritzburg, South Africa

Taxonomy

Family Nassariidae

Genus *Bullia* Gray, 1834 in Griffith & Pidgeon

Type species: *B. semiplicata* Gray in Griffith & Pidgeon, 1834, by monotypy.

Bullia laevissima (Gmelin, 1791)

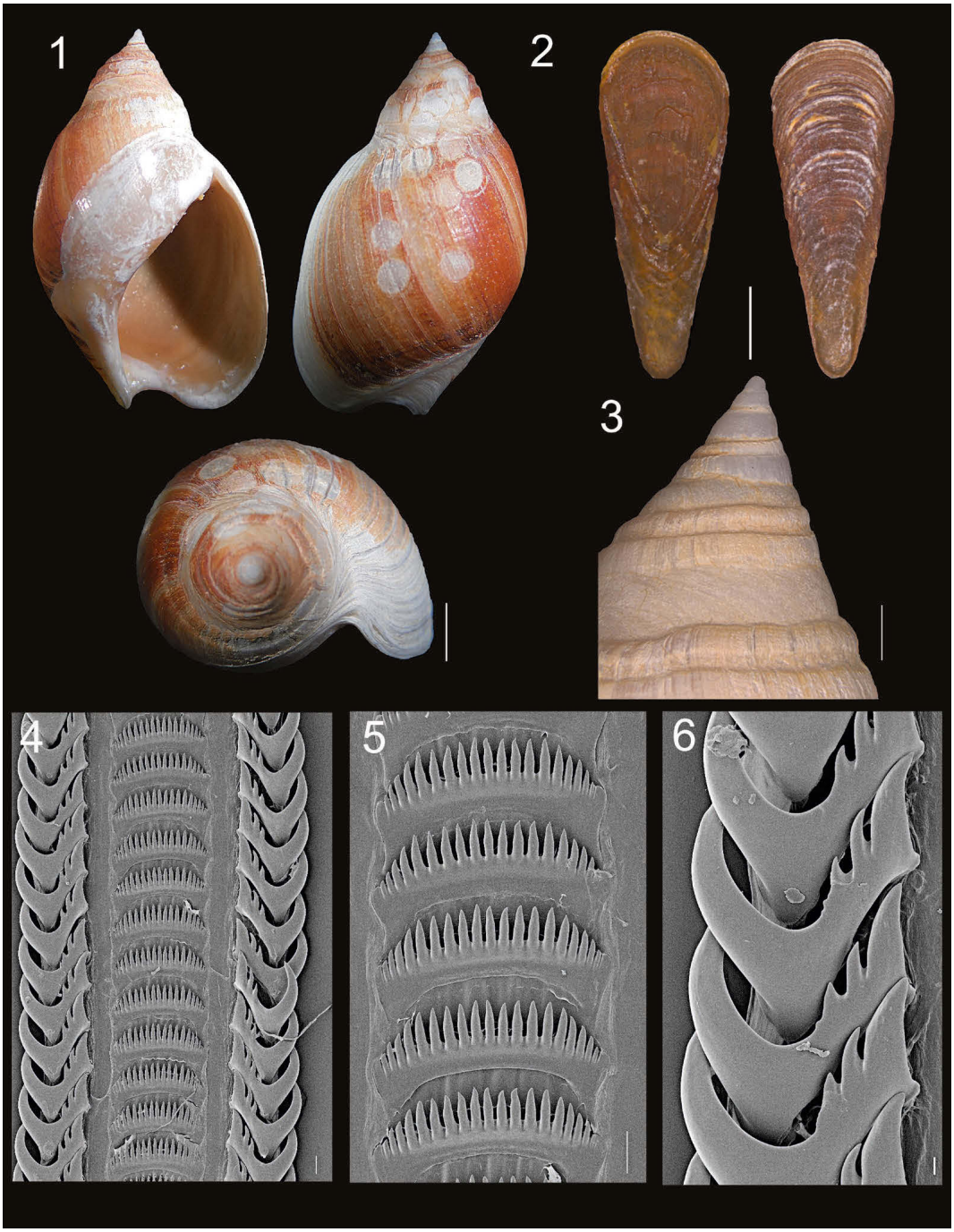
Figs 1–26

Buccinum laevissimum Gmelin, 1791: 3027.
Buccinum laevigatum Lamarck, 1822: 269.
Bullia sowerbyi Turton, 1932: 138-173.
Bullia laevissima Pacaud, 1833; Carr, 1967: 106; Willows, 1973: 187; Brown, 1961: 629; 1971; 1979: 573; 1982: 309-361; Trueman & Brown, 1976: 365; 1989: 129; Dye, 1980:108; Cernohorsky, 1984: 22; Cockcroft, 2002: 491; Kruger, 2005.

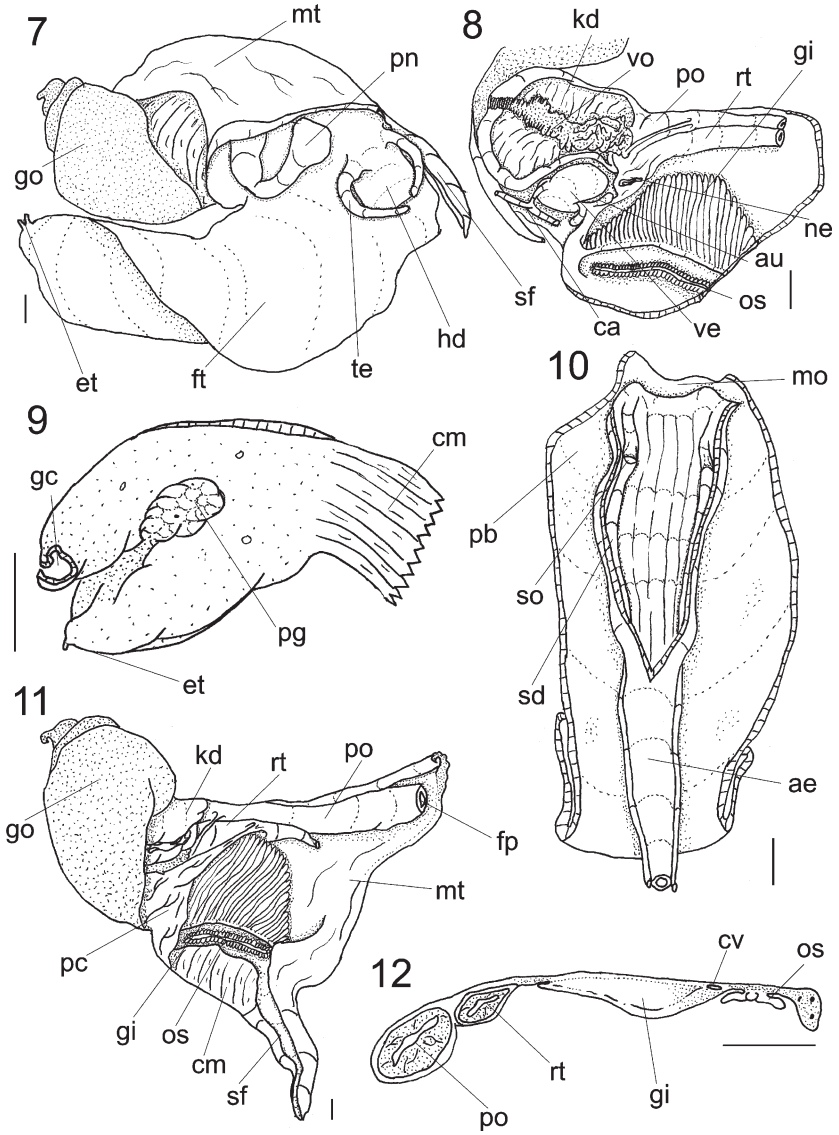
Description

Shell (Figs 1, 3)**.** Dome-shaped, twice as long as wide, with 9 convex whorls; colour uniform bright pale orange. Protoconch wide 4.2 mm, smooth, dome-shaped, white, with three whorls; transition hardly indicated. Teleoconch sculpture composed of two subsutural spiral ribs per whorl along surface of three first whorls (Fig. 3), remaining whorls with numerous axial growth markings along entire surface. Spire with shallow sutures, spire angle ~20°, shoulder absent. Aperture roughly as tall as wide, elliptical, typically with convex area at posterior end, terminally thicked; length ~½ of shell length. Anal notch weakly indicated. Outer lip thin and smooth. Columella straight, without folds. Siphonal canal like a sinus shape. Umbilicus absent.

Head-foot (Figs 7, 9)**.** Pallial cavity covering ⅓ of total animal length; muscular siphon located on left, length ~⅕ of head-foot length. Head protruded, socket-like; tentacles well-separated from each other, elongated and narrow, twice as long as head; eyes absent. Foot large, occupying whole body whorl (retracted), flat, bearing a pair of small metapodial tentacles; pedal gland located in central region of anterior edge of foot (Fig. 9), forming a groove, extending from dorsum of foot (propodium) to sole. Opercular pad occupying ~1/30 of dorsal area of foot, oval. Penis originated in right lateral region, posterior to cephalic base, at level of mantle edge. Columellar muscle wide and broad, two whorls long. Haemocoel short and wide, extending dorsally along center of foot and columellar muscle, 1.5 × as long as wide (Fig. 13).



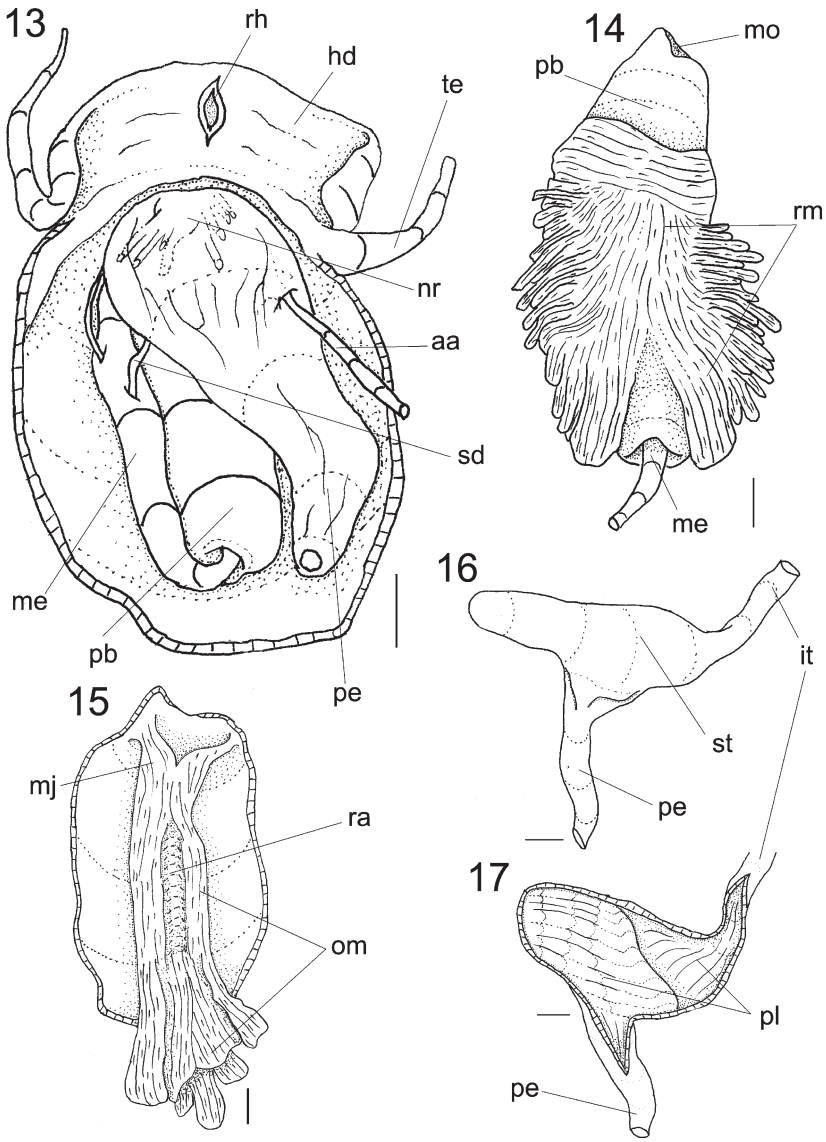
Figs 1–6. *Bullia laevissima*, KZN S3741, shell, operculum and radula: **1.** Shell ♀ apertural, dorsal and apical views (L 41.7 mm), scale bar = 1 cm. **2.** Operculum inner and outer views, scale = 2 mm. **3.** Protoconch and fist teleoconch whorls, lateral view, scale bar = 1 mm. **4.** SEM of radula: panoramic view of middle portion, scale bar = 100 µm. **5.** Same, detail of central teeth, scale bar = 100 µm. **6.** Same, detail of lateral teeth, scale bar = 30 µm.



Figs 7–12. *Bullia laevissima* anatomy, KZN S3741: **7.** Complete specimen extracted from shell (operculum removed), anterior-right view. **8.** Reno-pericardial region, ventral view, some adjacent structures also shown. **9.** Foot of female, sectioned longitudinally. **10.** Foregut, ventral view, mostly opened longitudinally. **11.** Pallial cavity roof, ventral view, and visceral mass. **12.** Pallial cavity roof, transverse section at middle level of osphradium. Scales = 2 mm.

Operculum (Fig. 2)**.** Small, oval, horny, pale brown; occupying 1/5 of aperture. Nucleus terminal, inferior. Outer surface with normal concentric growth lines, forming undulations. Scar oval, occupying about 2/3 of inner surface, located close to edge of foot.

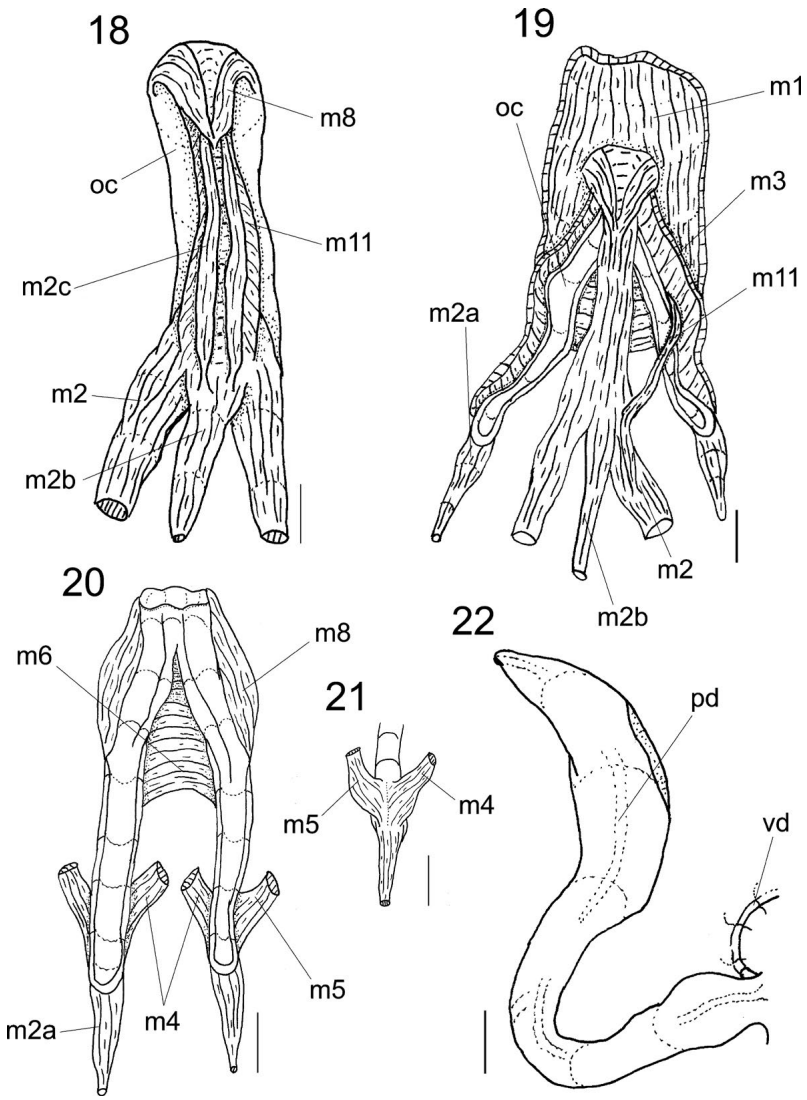
Mantle organs (Figs 8, 11, 12)**.** Mantle cavity covering ~1 whorl. Siphon width 1/5 of mantle cavity width, length 1/3 of mantle cavity length. Right base of siphon low, width same as mantle edge width; left base ending gradually. Osphradium long and narrow, elliptical, length 1/3 of pallial cavity length, width ~1/5 of its width. Osphradial filaments short, width similar to mantle edge. Ctenidial vein (efferent branchial vessel) uniformly narrow along its length. Gill elliptic, occupying ~80 % of length and width of



Figs 13–17. *Bullia laevissima* anatomy: **13.** Head and haemocoel, ventral view, foot and columellar muscle removed. **14.** Proboscis, ventral view, retractor muscles shown. **15.** Anterior foregut opened longitudinally, odontophore as in situ. **16.** Stomach and associated structures, digestive gland removed. **17.** Same in longitudinal section. Scales = 2 mm.

pallial cavity. Anterior end of gill rounded, ending gradually, inserted directly into pallial cavity. Gill filaments subtly increasing in size in middle region, decreasing at posterior end. Posterior end of gill rounded, located in posterior region of mantle cavity, inserted into pericardium. Gill filaments triangular, occupying ½ of pallial cavity height, apex rounded, at middle portion, slightly tilted to right; right and left edges of filament straight; space between gill and right pallial organs about ⅓ of gill width. Hypobranchial gland inconspicuous. Right side of pallial cavity almost entirely filled by gonoducts. Rectum short and thin, occupying ~⅛ of pallial cavity. Anus siphoned, distance between anus and mantle border ½ of total pallial cavity length. Anal gland absent.

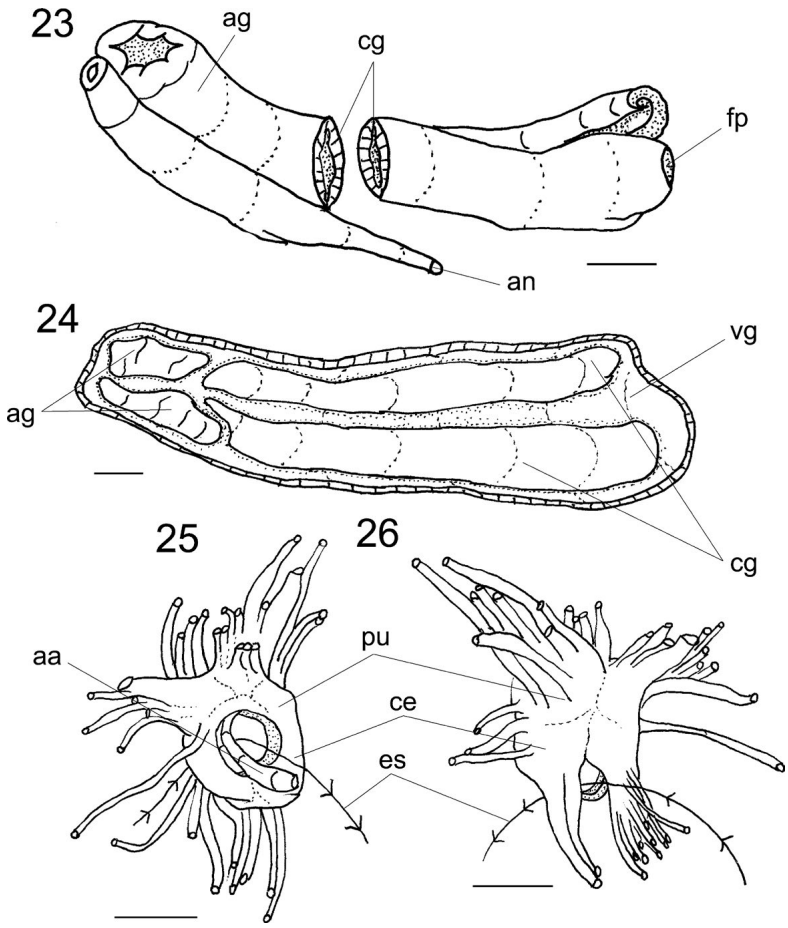
Visceral mass (Figs 7, 8, 11)**.** About 3 whorls posterior to mantle cavity. Digestive gland dark beige,



Figs 18–22. *Bullia laevissima* anatomy: **18.** Odontophore, ventral view, superficial layer of membrane and muscles removed. **19.** Odontophore ventral view, superficial muscles dissected. **20.** Odontophore cartilage, ventral view, some adjacent muscles shown. **21.** Detail of origin of *m4*, *m5* and *m2a* in posterior end of cartilage dorsal view. **22.** Penis ventral view, penis duct shown by translucency. Scales = 2 mm.

occupying ~80 % of visceral mass, encircling stomach. Gonad orange with small black spots, located on columellar surface, posterior to stomach. Seminal vesicle of males located in anterior portion of gonad, ~1/2 of its size. Kidney occupying ~1/3 of visceral mass volume, located on right side of anterior visceral end. Stomach small, located half whorl in front of pallial cavity.

Circulatory and excretory systems (Fig. 8)**.** Reno-pericardial region occupying 1/3 of whorl, on right margin of last whorl of visceral mass, adjacent to mantle cavity; oval shaped. Pericardium occupying 1/4 of reno-pericardial region, posterior to gill; situated on left anterior margin of visceral mass. Auricle reniform, anterior to ventricle; with three connections: on upper right side with kidney, on anterior right side with gill, and on posterior left side with ventricle. Ventricle three times as large as auricle,



Figs 23–26. *Bullia laevissima* anatomy: **23.** Pallial oviduct, ventral view, transversely sectioned in its middle level. **24.** Same, ventral view, opened longitudinally. **25-26.** Nerve ring, ventral and dorsal views. Scales = 2 mm.

with common aorta in left posterior margin. Aorta wide, located along postero-left region of ventricle. Kidney occupying 1/5 of pallial cavity, renal lobe single, solid, with glandular transverse folds along its ventral surface; efferent renal vessel located at its right portion. Nephridial gland present, but not seen in detail. Nephrostome small, transverse slit, located in anterior region of membrane between kidney and pallial cavity.

Digestive system (Figs 10, 13–21)**.** Mouth longitudinal, narrow. Proboscis short and wide, occupying about 80 % of haemocoel. Rhynchodeal wall thick and muscular, involving 2/3 of proboscis. Strong retractor muscles covering about half of proboscis; pair of thick retractors, originated on dorsal surface of foot, inserted into posterior end surface of proboscis. Salivary glands (Fig. 13) located at anterior portion of haemocoel, occupying ~1/4 of haemocoel volume, entirely involving nerve ring, middle esophagus and anterior portion of proboscis. Salivary ducts very narrow, except for short proximal region running completely attached to anterior esophagus wall and, more anteriorly, inside dorsal folds of buccal cavity (Fig. 10); opening very small (Fig. 10), in anterior-middle region of dorsal folds of buccal cavity. Valve and gland of Leiblein absent. Accessory salivary glands absent. Anterior esophagus broader; walls muscular, with strong dorsal internal longitudinal folds, occupying entire length of proboscis. Middle esophagus slender, diameter half of anterior esophagus diameter, and approximately of same length; posterior esophagus ~80 % of total haemocoel volume, broad, tapering posteriorly; anterior end rounded and expanding about twice diameter of posterior end, covered by membrane also involv-

ing nerve ring, differentiation between middle and posterior esophagus clear. Stomach oval, as blind sac, located half whorl posterior to kidney; inner surface entirely pleated, typhlosole absent; digestive gland ducts not analysed in detail.

Odontophore and buccal mass muscles: *mj*, thick pairs of perioral muscles connected on both sides, dorsal and ventral, surrounding odontophore cartilages; *m1*, jugal muscles, some hypertrophied in anterior region, forming a "second wall" on proboscis inner wall; *m2*, pair of strong protractor muscles of buccal mass, originating on inner surface of proboscis, running along entire odontophore, inserting in anterior region of odontophore cartilages; *m2a*, pair of retractor muscles of buccal mass, originating on dorsal surface of haemocoel, inserting at end of posterior margin of odontophore cartilages; *m2b*, pair of dorsal retractor muscles of buccal mass, elongated, length ~80 % of odontophore length, originating in posterior median edge of cartilages, extending in parallel across edges of radula, inserting along anterior ventral surface of subradular membrane; *m2c*, ventral double, thin muscle auxiliary of m2, originating on ventral medial fibers of *m2b*, running covering *m11*; *m3*, long and cylindrical muscle forming outer wall of odontophore, with transverse fibers; *m4*, pairs of strong radular dorsal tensor muscles covering almost entire surface of posterior portion of odontophore cartilages, inserting into subradular membrane; *m5*, pair of auxiliary dorsal tensor muscles of radula, originating inside edges of cartilage, adjacent to *m4* insertion; *m6*, horizontal muscle, thick, connecting ventral edges of cartilages, running ~1/3 of their length; *m8*, pair of small elliptical muscles, ~1/3 of total length of odontophore, originating at anterior end of odontophore cartilages, running along ventral surface of odontophore, inserting on anterior ventral surface of cartilages; *m11*, pair of ventral tensor muscles of radula elongated, about 1/3 of total odontophore length, originating at ventral-posterior end of cartilages, crossing ventrally entire odontophore, inserting into ventral posterior surface of radula. Additional odontophore structures: *br*, subradular membrane, thin, strong and translucent, along entire length of radular ribbon, covering inner surface of odontophore cartilages; *oc*, odontophore cartilages, about 3 times as long as wide, inner ventral surface concave, ~1/6 of anterior end fused with each other, ~1/2 of anterior region, concave, involving radular ribbon; *rs*, radular sac thin-walled, cylindrical, located at posterior end of radula; *nr*, radular nucleus width ~1/2 of radular sac width.

Radular teeth (Figs 4, 5, 6)**.** Rachidian tooth wide, comb-like, occupying about half of radular width; base curved, width ~3× its length; ~20 triangular, sharp pointed cusps of similar size, except for some diminishment towards the side; lateral tooth hook-like, with four cusps, base broad (equivalent to 1/2 of rachidian base width), obliquely disposed; main lateral cusp widely curved inwards, about as long as base; secondary cusp approximately half size of main lateral cusp, divided into three smaller cusps decreasing in size towards center; radula ribbon equal between males and females; jaws absent.

Male genital system (Fig. 22)**.** Visceral structures not seen in detail. Vas deferens narrow, simple, straight, running along ventral surface of kidney up to pallial cavity. Prostate totally closed (tubular), running thought right mantle edge, at ~2/3 of total pallial cavity length. Vas deferens anterior to prostate, straight, running immersed into integument of dorsum, next to mantle border and penis base. Penis slender, length ~1/4 of total head-foot length, dorso-ventrally flattened and with wide point at anterior half; base curved, apical region pointed. Penial duct straight, running through center of penis, closed (tubular). Penial aperture apical, very small.

Female genital system (Figs 23, 24)**.** Visceral oviduct narrow, sinuous, running along ventral surface of kidney in first whorl of visceral mass, located in front of pallial cavity. Posterior region of pallial oviduct protruding into kidney, occupying almost entire length of pallial cavity and 1/4 of its width. Albumen gland posterior, whitish, thick-walled, occupying ~1/5 of pallial oviduct. Capsule gland ~4/5 of oviduct, elongated, orange, thick-walled. Vaginal atrium anterior to capsule gland occupying ~1/6 of oviduct; walls thick, muscular, female genital pore wide, distal end blunt. Bursa copulatrix absent. Cement gland of females rounded, located in medium region of mesopodium close to edge of foot, inner space wide, duct short (Fig. 9).

Central nervous system (Figs 25, 26)**.** Nerve ring located in ventral basal proboscis region, occupying ~1/18 of haemocoel volume, highly concentrated. Ganglia mostly fused, hard to distinguish from each other, somewhat asymmetrical. Pairs of pleural and cerebral ganglia fully fused with each other. Pedal ganglia and sub-esophageal ganglion not seen in detail. Esophageal aperture broad, occupying about half of ventral surface of nerve ring. Statocysts not seen.

Shell measurements (length a width in mm): KZN S3741; 1♂ 43.6 × 24.2; 1♀ 41.7 × 25.3.

Distribution. South Africa.

Habitat. Fine sand bottoms, infratidal.

Material examined. 1♂, 1♀, South Africa: Cape Town; False Bay, 34°11.2'S 18°35.8'E, 40 m depth (Coll. Sardinops Vessel, dredged, Station CD 4, 10.iv.1991).

Discussion

The supra-generic taxonomy of the nassarids include a "*Bullia* group" suggested by Brown (1982). However, its validity has been considered doubtful by Allmon (1990) and Haasl (2000), stating that some characters are shared by other groups, e. g. the lack of last columellar fold. Additionally, the relationship among fossil buccinoids and the "*Bullia* group" are not well resolved. Species belonging to this genus are morphologically very diverse, but they share some anatomical characters. *B. laevissima* shares several anatomical characters with the type species *B. semiplicata* Gray, 1834, as the broad and flat foot, absence of eyes, a pair of epipodial tentacles, atrium and ventricle of the same proportion and size, gill filament shape, and absence of a bursa copulatrix. Conchologically, *B. laevissima* differs from the type species (Cernohorsky 1984: 25, fig. 91) in lacking the turreted outline and in lacking a rounded shoulder above the aperture (Barnard 1959: 132 fig. 271–m). Anatomically *B. laevissima* differs from *B. granulosa* (Simone & Pastorino 2014) by the dome-shaped outline of the shell, a protruded head with smaller tentacles distant from each other, a proportionally much smaller operculum, a wider gill if compared to the roof of the pallial cavity, smaller osphradium, absence of a valve and gland of Leiblein (Fig. 13), a shorter proboscis, and more powerful retractor muscles. Though the radulae have the same basic configuration, the lateral teeth of *B. laevissima* present four cusps as described by Barnard (1959) (Fig. 6), whereas in *B. semiplicata* and *B. granulosa* the lateral teeth are bicuspidate (Simone & Pastorino 2014, Barnard 1959 – respectively).

This set of differences shows that the genus *Bullia* has some diversity of anatomical features. The significance and taxonomical implications of these differences and similarities are still under analysis as a part of an ongoing wider study on Nassaridae. In any case, the present study already underlines a hypothesis where the monophyly of the subfamily Bullinae and *Bullia* are possibly debatable after a more thorough analysis, resulting in a new phylogenetic and taxonomic arrangement.

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