F.E. Wells, D.I. Walker and G.A. Kendrick (eds) 2005. *The Marine Flora and Fauna of Esperance, Western Australia.* Western Australian Museum, Perth.

# Anatomy and morphology of *Stephopoma nucleogranosum* Verco, 1904 (Caenogastropoda: Siliquariidae) from Esperance Bay, Western Australia

**Rüdiger Bieler[1] and Luiz Ricardo L. Simone [1, 2]**

[1]Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2496, U. S. A. Email: bieler@fieldmuseum.org

[2]Museu de Zoologia da Universidade de São Paulo, Caixa Postal 42494, 04299-970 São Paulo, SP, Brazil. Email: lrsimone@usp.br

**Abstract** – Anatomy and morphology of *Stephopoma nucleogranosum* Verco, 1904 (type species of the nominal genus *Lilax* Finlay, 1926), from waters off Esperance, south coast of western Australia, are described and compared to the other two congeneric species known from Australia, *S. tricuspe* (Mörch, 1861) and *S. abrolhosense* Bieler, 1997. Similar in most features, including protoconch sculpture, radular dentition, and pallial-cavity-brooding of few egg capsules, the three species differ substantially and remarkably in their complex morphology of opercular setae. The opercular pad projection, a pedal structure that produces the elaborate opercular setae is discussed. The first detailed descriptions of the nervous system and odontophoral musculature of a siliquariid are given.

**Key words**: Cerithioidea, nervous system, odontophore, operculum, protoconch

## INTRODUCTION

*Stephopoma* Mörch, 1860, is a member of the Siliquariidae, a group of sessile cerithioidean snails closely related to the Turritellidae (Morton, 1951, 1953). Most members of that family, including its type genus *Siliquaria* Schumacher, 1817 (a junior synonym of *Tenagodus* Guettard, 1770) live embedded inside sponge tissue and have shell slits that allow water exchange with the canal system of the host sponge (e.g., Bieler, 2004). *Stephopoma* species do not have such shell modifications and their attached postlarvel shells (teleoconchs) resemble those of the not-closely related vermetid genus *Dendropoma* Mörch, 1861. Ten named species of *Stephopoma* are currently recognized worldwide (Bieler, 1997). Three of these are known to occur in Australia, including *S. tricuspe* (Mörch, 1861) from New South Wales, *S. nucleogranosum* Verco, 1904, from South Australia, and *S. abrolhosense* Bieler, 1997, from Western Australia. The last is known to date only from the Houtman Abrolhos Islands, an archipelago representing the southernmost coral reef communities in the Indian Ocean.

Published anatomical information for the family Siliquariidae has been sparse (e.g., summary by Healy and Wells, 1998), with interpretation of siliquariid conditions based almost exclusively on the excellent study by Morton (1951) of *Stephopoma roseum* (Quoy and Gaimard, 1834) and *Pyxipoma weldii* (Tenison Woods, 1876), the latter a species with a shell slit. The discovery of

a *Stephopoma* species off Esperance, on the south coast of Western Australia – here identified as *S. nucleogranosum* Verco, 1904 – provided the opportunity for in-depth anatomical investigation and to further explore the morphological characters of the *Stephopoma* species in the context of other recent anatomical investigations of *S. abrolhosense* and western Atlantic species of *Tenagodus* (Bieler, 1997, 2004). Special focus is placed on the complex structures of the opercular setae (that provide species-specific characters in this group), the pedal structure that builds them, and on the nervous system and odontophoral musculature, which had not been explored for this family.

## MATERIALS AND METHODS

Collecting took place during the 12th International Marine Biological Workshop in Esperance Bay (Western Australia, Southern Ocean). The *Stephopoma* specimens were obtained with rhodolith (crust-forming coralline red algal) nodules by local fishing boat and bucket dredge in 33 m depth at 33°56.933'S, 122°01.611'E (FMNH/RB-1859, 19-II-2003). The animals became available during the final phase of the workshop when observations on living material were no longer possible. Three specimens were directly fixed in 100% ethanol and another three specimens were relaxed by chilling in a household refrigerator assisted by the addition of magnesium sulfate crystals (Epsom salts) to their seawater supply, fixed in Bouin's solution, and later transferred to 70% ethanol. About 15 other animals (plus additional empty shells), attached to rhodolith nodules and heavily fouled by coralline algae (compare Figure 1), were whole-preserved in 70% ethanol. For anatomical study, specimens were extracted from their shells and dissected immersed in fixative under a stereomicroscope. Air-dried protoconchs, radulae, and opercula were coated with gold, and observed and photographed using an AMRAY 1810 scanning electron microscope at FMNH. The material is deposited in the Field Museum of Natural History, Chicago (FMNH 301981), and the Western Australian Museum, Perth (WAM S 13498).

The following abbreviations are used in text and figures: **aa**, anterior aorta; **af**, afferent gill vessel; **an**, anus; **au**, auricle; **bg**, buccal ganglion; **br**, subradular membrane; **ca**, capsules; **ce**, cerebral ganglion; **cg**, capsule gland; **cm**, columellar muscle; **cv**, ctenidial vein; **dd**, duct to digestive gland; **df**, inner folds of dorsal wall of buccal mass; **dg**, digestive gland; **ea**, oesophageal aperture; **eg**, supra-oesophageal ganglion; **en**, endostyle; **es**, oesophagus; **fg**, food groove; **ft**, foot; **gf**, gastric folds; **gi**, gill; **gp**, gastric posterior projection; **gs**, gastric shield; **he**, head; **in**, intestine; **jw**, jaw; **ki**, kidney; **m1** to **m11**, odontophore muscles; **mb**, mantle border; **me**, mantle empty region; **mj**, jaw and peribuccal muscles; **mo**, mouth; **mp**, mantle border papilla; **oc**, odontophoral cartilage; **op**, operculum; **or**, opercular pad projection; **os**, osphradium; **ov**, oviduct; **oy**, ovary; **pc**, pericardial chamber; **po**, pedal ganglion; **pp**, propodium; **pr**, pleural ganglion; **py**, pallial cavity; **ra**, radular ribbon; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sc**, subradular cartilage; **sd**, salivary gland duct; **se**, salivary gland aperture; **sg**, salivary gland; **sn**, snout; **sp**, septum separating odontophore from oesophagus; **ss**, style sac; **st**, stomach; **su**, suboesophageal ganglion; **te**, cephalic tentacle; **tg**, integument; **tn**, three-dimensional network of muscles/connective tissue filling hemocoel; **to**, odontophore tissue on radular ribbon preceding buccal cavity; **ty**, typhlosole; **ve**, ventricle; **vo**, visceral oviduct.

## RESULTS

### Systematics

The collected material is here identified as *Stephopoma nucleogranosum* Verco, 1904, originally described from Backstairs Passage, South Australia, from 16–23 fathoms (29–42 m).

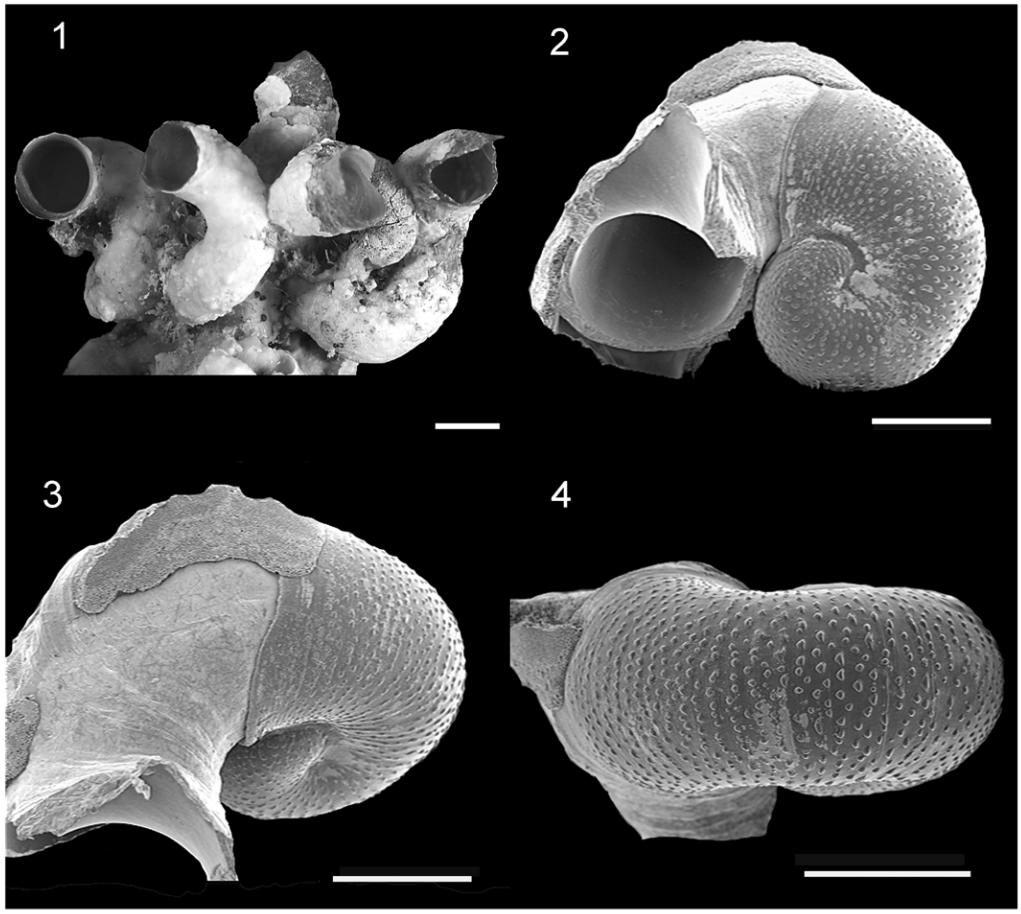
**Siliquariidae Anton, 1838**

***Stephopoma* Mörch, 1860**

***Stephopoma nucleogranosum* Verco, 1904**

Selected citations:

*Stephopoma nucleogranosum* Verco, 1904: 143, pl. 26, figs. 11–13 (shell, opercular setae); —



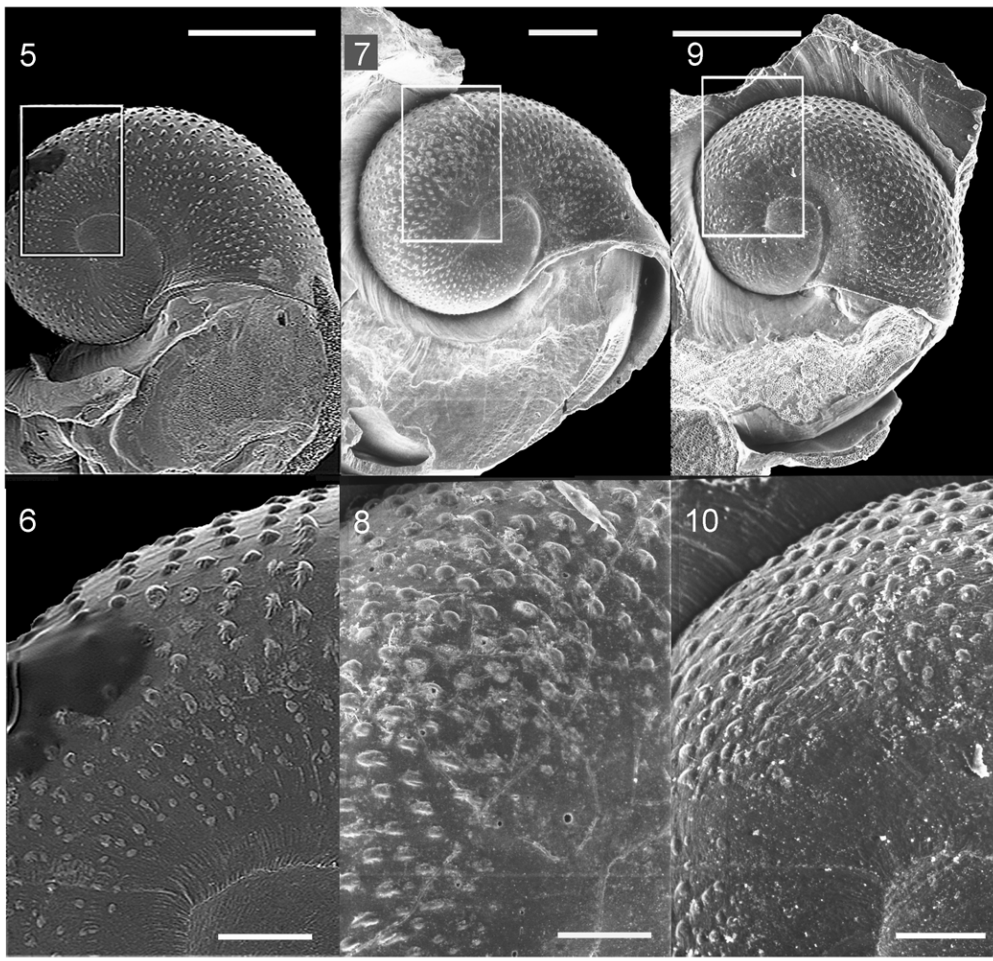

**Figures 1–4** *Stephopoma nucleogranosum* Verco, 1904, shell (Esperance Bay, FMNH 301981): **1**, cluster of specimens (5 visible) attached to rhodolith nodule; heavily fouled by coralline algae except for new growth near apertures; **2**, base of protoconch, with early teleoconch broken away; **3**, oblique view of protoconch base showing slightly sinuous peritreme at fluted protoconch aperture; **4**, side view of protoconch with pattern of fine pustules. Scale bars: **1** = 3 mm; **2–4** = 500 μm.

Morton, 1951: 22 ff., fig. 18 (protoconch), 26 (shell); — Morton and Keen, 1960: 28 ff., fig. 9 (after Morton, 1951); — Bieler, 1997: 262–263, figs. 15–17 (shell and protoconch SEM).

*Tenagodus (Stephopoma) nucleogranosum*, — Healy and Wells, 1998: 720.

## Description

**Shell – teleoconch** (Figure 1): More-or-less regular coil of 2.0 to 2.5 piled-up whorls attaching to substratum; last whorl overlapping preceding whorl with somewhat broadened and lateral flange and extending into openly coiling (in largest specimens corkscrew-like) thin-shelled feeding tube; diameter of shell coil in reproductive females about 6 mm; maximum inner diameter of slightly oval to circular aperture 3.8 mm; outer dorsum of whorl (corresponding to

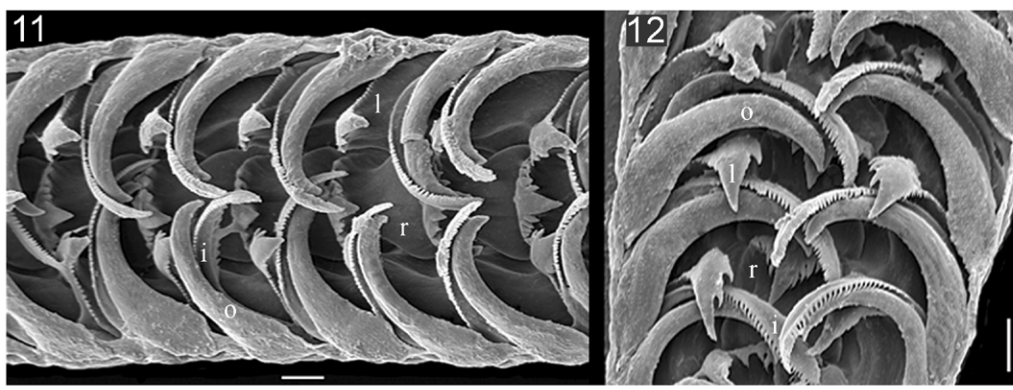



**Figures 5–10** Protoconch and early teleoconch whorl (above) and detail of protoconch sculpture (below) of Western and South Australian *Stephopoma* specimens: **5–6,** *S. nucleogranosum* from Esperance Bay (FMNH 301981); **7–8**, *S. nucleogranosum* from South Australia (AMS C.092660); **9–10**, *S. abrolhosense* from Houtman Abrolhos (Paratype, FMNH 279603). Scale bars: **5, 7, 9** = 500 μm; **6, 8, 10** = 100 μm.

umbilical keel on regularly coiled shell) sometimes with somewhat scaly ridge; sculpture of fine longitudinal striae crossed by densely placed irregular growth lines, often with irregular repair marks. Milky-white to reddish tan.

**Shell – protoconch** (Figures 2–6): Depressed helical coil of about 1.5 rapidly expanding whorls, nautilus-shaped with somewhat fluted aperture; translucent caramel brown, with top of whorl colourless; 1.30 to 1.37 mm (to 1.46 including South Australian material) in maximum diameter. Sculpture: embryonic whorl initially nearly smooth; after first half-whorl (demarcated by fine growth marks on upper side) with distinct pattern of well-defined pustules; pustules smaller (and blending into fine spiral striations) near suture and in protoconch umbilicus; pustules roughly aligned with growth lines and relatively evenly spaced, more crowded and fading in size near protoconch apertural lip; approximately 65–70 "rows" of well-defined pustules on upper side; about eight pustules in 100 x 100 µm area in region shown in Figure 6.

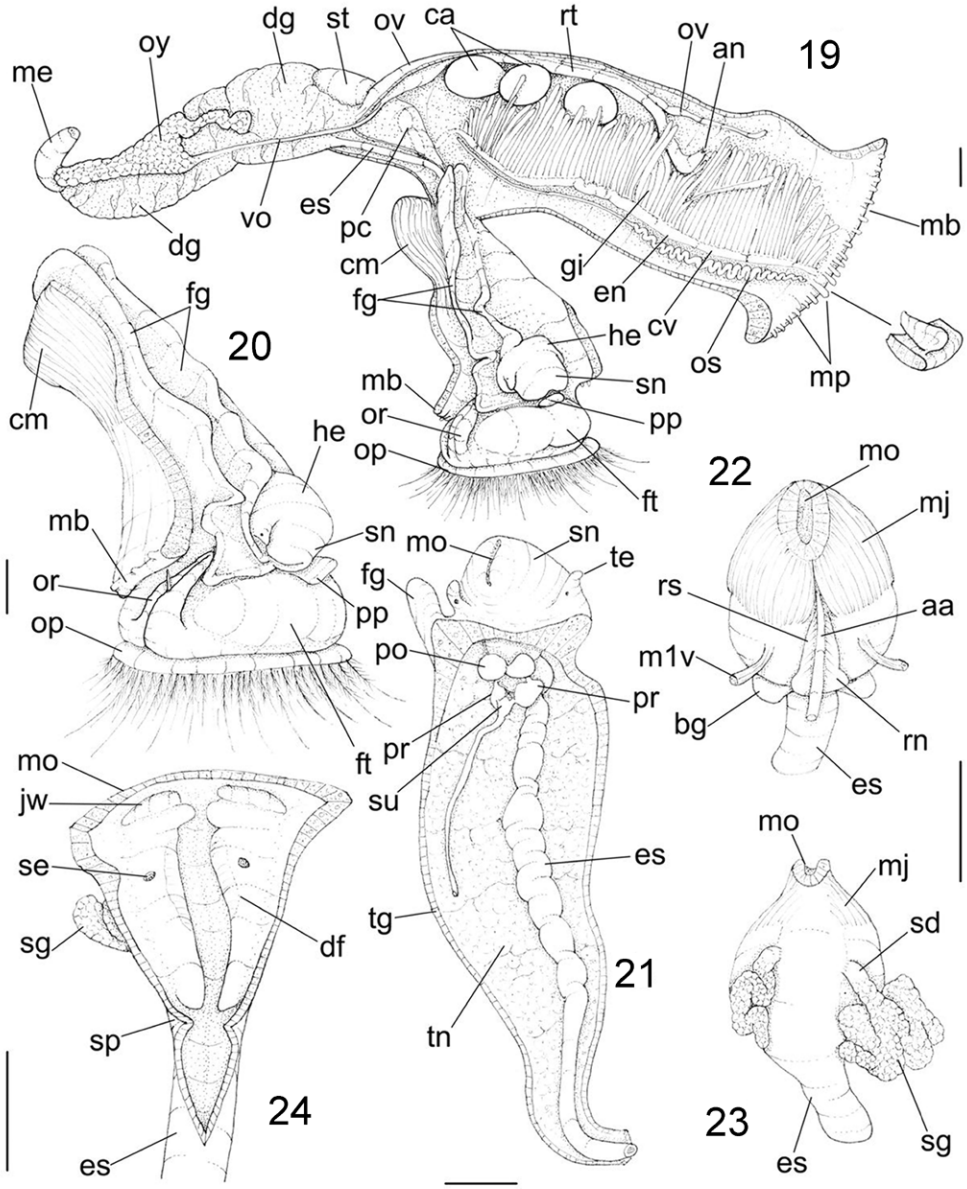
**Head-foot** (Figures 19–21, 33–36; based on alcohol-preserved material). Head bulging, spherical, about half size of foot. Snout broad, stubby, widely conical, with mouth as vertical slit in ventral-terminal surface. Cephalic tentacles triangular, very short (about 1/3 of snout length), at each side of snout base. Eyes very small, immersed in ventral region of tentacle bases (Figures 21, 36). Colour overall beige, with dark brown (almost black) snout region, except for area surrounding mouth opening (Figure 36); foot and mantle edge greyish tan (Figure 34). Foot occupying about 1/3 of total cephalo-pedal volume. Propodial projection located in ventral region of snout (Figures 19, 20: pp), dorso-ventrally flat, about as long as snout width, with distal tip squared. Pedal sole region broadly bulging (Figures 19, 20, 34: ft). Opercular pad almost as wide as foot, ovoid (about 2 mm maximum diameter), attachment to operculum covering nearly entire inner surface. Opercular pad projection about as long as head, conical (Figures 19, 20, 33–35: or), at right edge of opercular pad just posterior to pedal sole; ventral surface with longitudinal, deep furrow, which sometimes envelopes an opercular seta (Figures 33, 34). Columellar muscle broad and thick, about four times as long as foot; originating in ventral surface of shell as thick fold, gradually thickening toward opercular pad and foot, and ultimately reaching about 2/3 of head-foot thickness. Food-groove large, occupying about half of pallial floor width, edges tall and relatively thick, inner furrow broad (Figures 19, 20, 34: fg); starting abruptly in posterior end of pallial cavity, running on right side of pallial floor toward right side of head, where left fold




**Figures 11–12** *Stephopoma nucleogranosum*, part of radular ribbon: **11,** mid-radular region; **12**, relatively newly formed teeth at beginning of radular ribbon. Abbreviations (teeth): r, rachidian; l, lateral; i, inner marginal; o, outer marginal. Scale bars: 10 µm.


**Figures 13–15** Opercular setae of Australian *Stephopoma* species, showing closed side of lamella: **13**, *S. abrolhosense* from Houtman Abrolhos (FMNH 279606); **14**, *S. nucleogranosum* from Esperance Bay (FMNH 301981); **15**, *S. tricuspe* from Sydney (AMS C.092660). Scale bars: 100 μm.


**Figures 16–18** Opercular setae of Australian *Stephopoma* species, showing open side of lamella; major branching points visible as hollow tubes: **16**, *S. abrolhosense* from Houtman Abrolhos (FMNH 279606); **17**, *S. nucleogranosum* from Esperance Bay (FMNH 301981); **18**, *S. tricuspe* from Sydney (AMS C.092660). Scale bars: 100 μm.



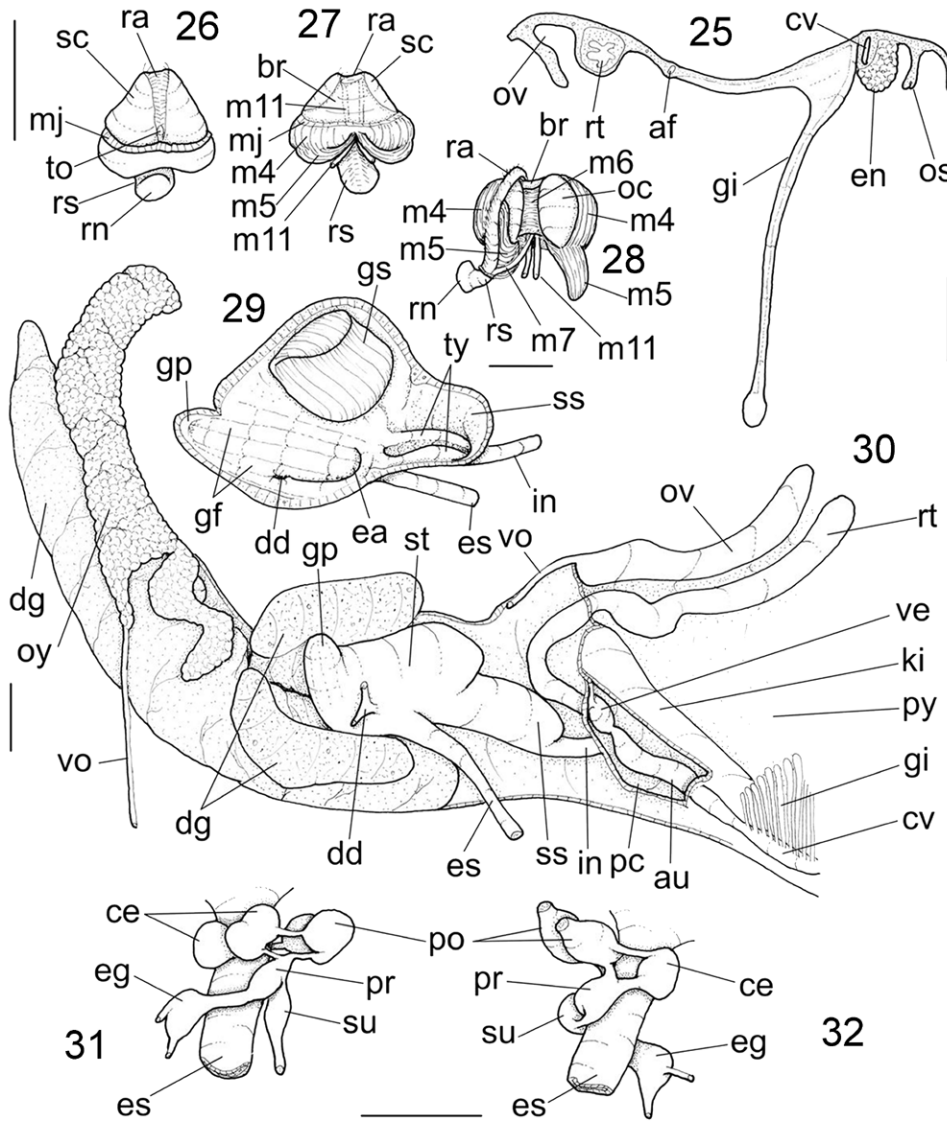

**Figures 19–24** *Stephopoma nucleogranosum* Verco, 1904; anatomy: **19**, female extracted from shell, right view; pallial cavity walls partially removed, sectioned along both sides, head-foot deflected to expose pallial cavity floor; inner surface of pallial roof exposed, showing 3 egg capsules *in situ*; a detail of larger mantle border papilla also shown; **20**, head-foot, oblique right view, note opercular seta enveloped by opercular pad projection (or); **21**, head and hemocoel, ventral view, foot and columellar muscle removed; **22**, buccal mass, ventral view; **23**, same, dorsal view, right salivary gland (sg) partially deflected and uncoiled; **24**, dorsal wall of buccal mass, ventral view, odontophore removed, inner surface exposed, anterior oesophagus partially sectioned longitudinally. Scale bars: 0.5 mm.

surrounds snout base and right fold forms wider flap projecting outward and contouring anterior edge of pedal sole; both folds tapering out close to mouth (Figures 20, 36). Hemocoel wide, about ¾ of head-foot width; internally filled by three-dimensional network of muscles and connective tissue fibres, traversed by oesophagus and nerves (Figure 21).

**Operculum**. Brown, circular chitinous curved dish, concave side exposed, overlapping edge of foot and completely filling aperture; multispiral; each successive whorl with fringe of tall complex setae projecting externally, somewhat perpendicular to opercular plane (Figures 14, 17, 19, 20, 33–35), increasing in size toward outer rim to about 1 mm; opercular seta consisting of folded lamella (with edges rolled-in; open toward opercular nucleus) rising from narrow stalk, inner surface glossy; main spine a direct continuation of stalk, without sharp bend, showing continuation of open lamellar slit; upper part of heavily bristled shaft giving rise to forked spines (Figures 14, 17), with longest reaching about a third of main spine length; free end of main spine about three times as long as bristle-bearing shaft above narrow stalk. Operculum usually heavily fouled.

**Mantle organs** (Figures 20, 25, 30). Pallial cavity long, occupying somewhat more than half of body length, of uniform width. Mantle edge thick, with series of small papillae on internal surface of mantle border; papillae taller in left-dorsal region, just anterior to gill end. Each papilla forming a projected flap, not digitiform (more evident in taller ones; Figure 19: mp). Osphradium on left side of pallial cavity, ridge-like, slightly shorter than total pallial cavity length; anterior end a short distance from mantle edge, near base of taller papillae; posterior end some distance from posterior end of pallial cavity. Anterior half of osphradium broader and tightly meandering, posterior half about three times thinner, running more or less straight. Osphradium in form of tall and thin fold, with distal edge broader than basal region and dark pigment along middle region of distal edge (Figure 25: os). Gill length approximating osphradium length; anterior end slightly anterior to that of osphradium, posterior end slightly posterior. Ctenidial vein close to, and to right of, osphradium, somewhat narrow. Endostyle covering length of ctenidial vein and narrow portion to left (Figure 25: en); about twice as tall and three times broader than ctenidial vein. Endostyle touching left edge of gill filaments at right but well separated from osphradium at left. Gill filaments with broad bases occupying an area equivalent to half of that of pallial cavity roof. Gill filaments tall and slender (about twice as long as basal width), narrowing abruptly a short distance from their pallial insertion (Figures 19, 25: gi); filament tip broader, spherical. Afferent gill vessel very narrow, situated along right gill edge. Between afferent gill vessel and rectum a narrow area (about ¼ of gill base width). Rectum relatively wide (about ¼ of gill base width), running along right edge of pallial cavity, suddenly (at about final third) curving left toward gill edge (Figure 19: rt). Anus simple, small, opening toward anterior right. Pallial oviduct compressed between rectum and right edge of pallial cavity, described below.

**Visceral mass** (Figures 19, 30). Shorter than half of animal length, not filling all available shell space at posterior end. Short portion of posterior apex lined by unfilled mantle. Digestive gland occupying most of visceral mass, pale green, with minute superficial black spots. Ovary along ventral surface of visceral mass, somewhat flat, compressing digestive gland and of about same length (other details below). Stomach voluminous, occupying almost entire anterior quarter of visceral mass, except for ventral area filled by digestive gland tissue. Pericardium and kidney form anteriormost visceral structures, both very long and narrow. Pericardium located at left, between stomach and posterior gill region. Kidney immediately to right of pericardium (more details below).




**Figures 25–32** *Stephopoma nucleogranosum*; anatomy: **25**, pallial cavity, transverse section at level of anterior third of osphradium; **26**, odontophore, dorsal view; **27**, same, ventral view; **28**, same, dorsal view, subradular cartilage and membrane removed, radular ribbon and odontophore cartilages deflected, left muscles still inserted in radula, right muscles separated from radula and deflected; **29**, stomach, ventral view, sectioned longitudinally, inner surface exposed; **30**, posterior end of pallial cavity and visceral mass, ventral view, anterior region of digestive gland (dg) sectioned and deflected to show stomach, posterior region of gonad artificially separated from adjacent digestive gland, ventral wall of pericardium removed; **31**, central nervous system (nerve ring) and adjacent oesophagus, dorsal and obliquely right view; **32**, same, ventral and obliquely left view. Scale bars: 0.5 mm.

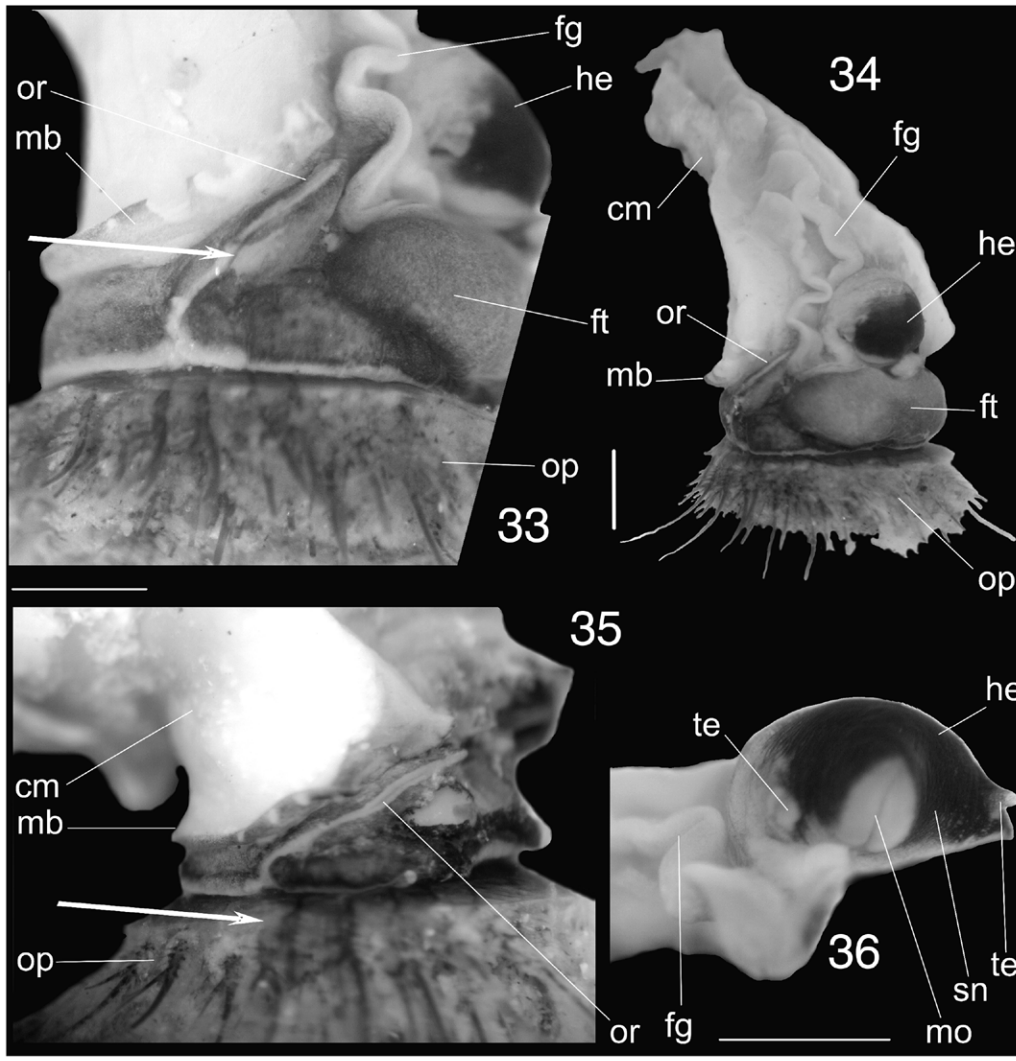
**Circulatory and excretory systems** (Figures 19, 30). Pericardium relatively small (about 1/8 to 1/10 of visceral mass), located obliquely as anterior boundary of visceral mass, mostly exposed in pallial cavity roof; posterior region lying ventrally to stomach and initial region of intestine; anterior region just posterior to posterior end of gill. Auricle narrow and long, in anterior 2/3 of pericardium, with dorsal-right surface attached to pericardial inner surface. Connection between auricle and gill via ctenidial vein free from gill filaments for distance equivalent to half of auricle length. Ventricle very small, posterior to auricle. Both aortae very narrow, originating in posterior-ventral region of ventricle. Kidney solid, filled with yellowish-white tissue; renal area about same size as pericardium; transversal section triangular; about half exposed in pallial cavity. Nephrostome not seen.

**Digestive system** (Figures 21–24, 26–30). Oral tube short and broad, walls mostly of longitudinal muscle fibres. Jaw muscles immerse in oral tube walls; relatively thick in lateral region, gradually thinning towards dorsal surface and median line (Figures 22, 23: mj). Jaw plates very thin, broad laterally and short antero-posteriorly (Figure 24: jw); located in dorsal surface of oral cavity, close to mouth lips. Dorsal folds broad (Figure 24: df), originating from jaw region, gradually narrowing toward posterior, and abruptly ending in region just posterior to odontophore. Dorsal chamber (between both dorsal folds) smooth, shallow, of about same width as each dorsal fold; with dark brown pigment that also extends onto anterior half of dorsal folds. Salivary glands small, white, clustering in dorsal-posterior surface of buccal mass as two masses separated by relatively wide median space (Figure 23: sg); each salivary gland Y-shaped with distal branches similar-sized; each distal branch about twice as long as basal branch, somewhat convoluted, crowded, with rounded tip; basal branch about 1/3 of buccal mass length. Insertion of salivary glands at midlevel of dorsal surface of buccal mass, separated from each other by space equivalent to about 1/3 of buccal mass width. Salivary duct very short, running short distance to immerse in dorsal buccal mass wall. Salivary gland aperture (Figure 24: se) a short distance from salivary duct penetration into buccal mass dorsal wall, in anterior third of dorsal folds of buccal mass, at some distance from their median edge. Odontophore typical for cerithioideans, occupying most of snout and short portion of hemocoel posterior to it. Odontophoral muscles (Figures 22, 26–28): **m1**, jugal muscles, several small muscle fibres connecting odontophore outer surface with adjacent inner surface of snout and remaining hemocoel; **m1v**, small pair of ventral odontophore retractors muscles, originating in posterior-ventral region of snout, running toward anterior and median, inserting in mid-region of odontophoral ventral surface, next to radular sac (Figure 22); **m2** absent (pair of odontophore retractor muscles); **m4**, pair of main dorsal tensor muscles of radula; thick, surrounding outer surface of both cartilages, inserting in inner surface of subradular membrane, especially on tissue in radular ribbon preceding its exposed (in-use) area (Figure 26: to); **m5**, broad pair of accessory dorsal tensor muscles of radula, originating in posterior surface of m4 pair, running toward anterior and median, inserting in ventral surface of radular ribbon in relatively long region at level of exposed area of radula; **m6**, horizontal muscle, wide, thin, with about ¾ of odontophoral cartilage length; **m7**, pair of very small and thin muscles, originating in subradular membrane, in ventral region close to median line, covered by m6, running toward posterior, penetrating into radular sac, inserting fan-like into inner surface of radular sac at short distance from radular nucleus (Figure 28); **m11**, pair of narrow and slender ventral tensor muscles of radula, originating in ventral surface of hemocoel, at odontophore midlevel, running dorsally for short distance, penetrating into odontophore next to radular sac, approaching m7 origin externally, inserting along subradular membrane to distal edge of radula. Odontophoral non-

muscular structures: **oc**, pair of odontophoral cartilages, flat, oval, relatively short (Figure 28); **sc**, subradular cartilage, transparent, expanding in lateral regions of exposed area of radula, covering entire odontophore portion exposed in buccal cavity (Figures 26, 27); **to**, tissue located in radular ribbon in region preceding its exposed (in-use) area; part of m4 inserts in this tissue (Figure 26); **br**, subradular membrane, covering subradular cartilage internally and serving on ventral surface as flexible membrane permitting radular movement (Figure 27). Radular sac extending slightly beyond odontophore. Radular nucleus spherical, curved inward. Radula (Figures 11, 12) taenioglossate, small and narrow (length of ribbon about 640 μm, width of ribbon about 76 μm in largest animal observed); rachidian relatively broad (up to 22 μm) with strong pointed median cusp, flanked by about 5–7 shorter lateral cusps on either side; lateral tooth with 20 very fine cusps on outer side, somewhat stronger toward strong and pointed median cusp, on inner side of lateral tooth with about 5 cusps; slender inner marginal tooth long and pointed, with outline broadened and rounded by fringe of 40+ cusps on either side; slender outer marginal tooth curved talon-like, tapering to sharp terminal cusp. Oesophagus narrow, slightly wider in mid-portion along hemocoel, where becoming somewhat folded (Fig. 21: es); oesophageal inner surface mostly smooth. Oesophagus insertion on left side in mid region of stomach, in left base of posterior gastric projection (Figures 29, 30). Stomach occupying about half of visceral space in that part, placed a short distance from posterior end of pallial cavity, extending about one whorl; main gastric chamber wide and somewhat dorso-ventrally flattened (Figures 29, 30: st). Posterior gastric projection originating posteriorly from oesophageal aperture, running almost straight toward right as posterior stomach end, protruding weakly beyond gastric walls to right with rounded, short blind-sac (Figures 29, 30: gp). Duct to digestive gland single, small, located in mid-region between oesophageal aperture and gastric projection, bifurcating in T-fashion shortly after its origin (Figure 30: dd). Style sac projecting anteriorly from main gastric chamber, slightly shorter than chamber length and about half as wide; anterior limit rounded, touching pericardium (Figure 30: ss). Stomach inner surface mostly smooth (Figure 29), whitish-iridescent; 3–4 low wide folds running along posterior and lateral surfaces of posterior gastric projection, each fold similarly sized and close to each other, initiating gradually in oesophageal aperture and finishing abruptly in blind end; ventralmost fold surrounding aperture to digestive gland in mid region. Pair of typhlosoles running in left-anterior surface of style sac, separating intestinal from style sac portions (Figure 29: ty); typhlosoles connected at their origins just posterior to oesophageal aperture, with remaining regions somewhat tall, running in direction of intestine. Low transversal fold separating style sac from gastric main chamber, also running along anterior border of gastric shield. Gastric shield occupying about 1/3 of inner gastric surface, on right and ventral surfaces. Digestive gland described above (visceral mass). Intestine separating from style sac distal end on right side, running dorsally to posterior region of pericardium where forming short loop toward posterior, curving anteriorly in wider loop at right of style sac, surrounding right end of kidney (Figure 30: in); then exiting into pallial cavity, running along right edge as described above (mantle organs). Faeces a continuous bundle.

**Genital system**. **Male**. No male examined.

**Female**. Ovary described above (visceral mass). Visceral oviduct very narrow, running along ventral side of anterior third of visceral mass for about two whorls (Figure 30: vo). Visceral oviduct inserting in posterior end of pallial oviduct as simple aperture. Pallial oviduct occupying about 2/3 of pallial cavity length, running along right edge, externally to rectum (Figures 19, 30: ov). Pallial oviduct of about same width as rectum, comprised of single tall, glandular fold




**Figures 33–36** *Stephopoma nucleogranosum*; anatomy (photographs of preserved material): **33**, detail of region of opercular pad projection (or), showing one opercular seta enveloped (i.e., in the process of formation; arrow), right view; **34**, head-foot, oblique right-frontal view, specimen of Figure 33; **35**, detail of region of opercular pad projection (or) of another specimen, showing region of operculum where setae are added (arrow); **36**, detail of head and adjacent region of food groove, ventral view; note pigmentation. Scale bars: 1 mm.

forming deep furrow against outer surface of rectum, which appears to function as inner lamina of that pallial oviduct (Figure 25). Pallial oviduct narrowing gradually toward anterior end, ending abruptly. No detectable special chambers or glands.

Egg capsules bred inside posterior region of pallial cavity, between gill and right structures (rectum and oviduct) (Figure 19: ca). Up to three capsules per specimen, apparently unattached. Each capsule ovoid, with size roughly equivalent to animal's head. Capsule with rigid, somewhat flexible, transparent cover. No fully developed embryo or

young found. Content of largely uniform yolk, with set of large cells found concentrated on one side.

**Central nervous system** (Figures 21, 31, 32). Relatively well concentrated, located just posterior to buccal mass. All nerve ring ganglia distinct and similarly sized. Cerebral ganglia (ce) spherical, with approximately 1/6 of buccal mass size each; close to each other and united by very short, narrow commissure. Pedal ganglia (po) located on opposite side of oesophagus, somewhat dislocated to right, immersed in pedal musculature, roughly spherical, bluntly pointed ventrally; both pedal ganglia located very close to each other, united by very short and thin commissure; broad pair of pedal nerves originating from pedal ganglia. Cerebral and pedal ganglia united by narrow connectives, these somewhat shorter than ganglion diameter. Pleural ganglia (pr) somewhat elongated, located equidistant from other ganglia pairs, united with them by pair of connectives of about same length as cerebro-pedal connectives. Supraoesophageal ganglion (eg) about same size as other ganglia, located at dorsal-left side of oesophagus at short distance posterior to cerebral ganglia; single connective with right pleural ganglion, very broad (about 1/3 of ganglion width) and twice as long as ganglion. Suboesophageal ganglion (su) about same size as other ganglia, located on ventral side between and slightly posterior to both pleural ganglia; connected to pleural ganglia by short, narrow connectives; thick visceral nerve originating from suboesophageal ganglion, running posteriorly along right side of hemocoel.

**Distribution**. Southern coast of Australia (known from Esperance Bay and Backstairs Passage, see Discussion below). New Zealand records of this species refer to *Stephopoma roseum* (see Morton, 1951).

**Type material.** Verco (1904) described this species from Backstairs Passage (between Cape Jervis and Kangaroo Island), South Australia, from 16–23 fathoms [29–42 m]. The number of type specimens was not indicated ("many alive," p. 144). Syntypes are located in the South Australian Museum, Adelaide (SAM) and in the Australian Museum, Sydney (AMS C.019970, three specimens, *vidi*; see Bieler, 1997: figure 15).

## DISCUSSION

The material was identified as *Stephopoma nucleogranosum* Verco, 1904, originally described from about 100 km south of Adelaide in South Australia. It is one of the least known species of the genus (Bieler, 1997) and has been rarely cited in the literature. Most of these citations refer to New Zealand material, which Morton (1951) has shown to belong to *S. roseum*. Protoconch characteristics of S. *nucleogranosum* specimens from both regions match in detail: The horn-coloured to tan protoconch has about 65–70 transverse rows of tubercles per whorl in material from both locations (Figures 5–8). The protoconch diameter range of the Esperance material (1.30 to 1.37 mm) falls within that known for South Australian material (1.30 to 1.46 mm; Bieler, 1997). Opercular setae of South Australian material remain to be investigated in detail. However, Verco's description (1904: 144) as "... one part continues nearly in the same axis, and is the larger and longer; the other stands out at an angle and generally divides into two" matches the Esperance material (Figures 14, 17).

All three Australian *Stephopoma* species (*S. nucleogranosum, S. tricuspe* (Mörch, 1861) and *S. abrolhosense* Bieler, 1997; Figures 5–10) have finely pustulated protoconchs, a feature also shared with the South African species *S. lacunosum* (Barnard, 1963) (see Bieler, 1997). The species differ substantially in the composition and relative proportions of the opercular setae (compare Figures 13–18). The Western Australian *S. abrolhosense* has a comparatively short

bristled shaft area, which forms a spined crown region from which, after a distinct bend, the very long main shaft continues (Figures 13, 16). *Stephopoma tricuspe*, described from New South Wales, and South African *S. lacunosum*, have a comparatively shorter free main spine and the secondary spine is forked toward the tip, not at the base as seen in *S. nucleogranosum*.

In contrast to earlier published statements based on light microscopy (Morton and Keen, 1960; Barnard, 1963), Bieler (1997) found that scanning electron micrographs of *Stephopoma* radulae revealed a surprisingly uniform organization among the studied species (*S. abrolhosense*, *S. tricuspe, S. lacunosum*, *S. levispinosum* Bieler, 1997). The data here presented for *S. nucleogranosum* confirm the same pattern: These species have a small taenioglossate radula with a rachidian tooth that bears a strong triangular median cusp flanked by 5–6 short fine cusps on either side; broad lateral teeth, each with a strong median cusp flanked by short cusps on either side (fewer and larger on the side facing the rachidian); inner marginal teeth that are long and pointed, with their outlines broadened and rounded by fringes of numerous cusps on either side; and the outer marginal teeth curved and tapering into sharp talons without further dentition. The type species of *Stephopoma*, *S. roseum* (Quoy and Gaimard, 1834), remains to be reinvestigated: Morton (1951: figure 23; reproduced by Healy and Wells, 1998: figure 1589H) illustrated all lateral and marginal teeth as devoid of lateral cusps.

At least some anatomical data are now available for four *Stephopoma* species: *S. roseum* (described by Morton, 1951), *S. mamillatum* Morton and Keen, 1960 (with gross-morphological data), *S. abrolhosense* (as described by Bieler, 1997), and *S. nucleogranosum* (herein). All show very similar overall organization. The opercular pad projection (Figures 20, 33, 35), a pedal structure that forms the elaborate setae is here first described in functional detail. Some specimens were preserved with an opercular shaft inside the projection (Figures 20, 33 – arrow). Even for specimens with an empty opercular pad projection a functional link can be inferred, as the row of setal shafts begins immediately below the projection (Figure 35 – arrow). The projection appears to occur in this form also in other *Stephopoma* species. Morton and Keen (1960: 32) mentioned for *S. mamillatum* "a small unpaired triangular papilla" in the same position. It is possible that this also is the structure referred to as "pre-oral appendage" by Morton (1951: 26 ff.; for *Stephopoma roseum*), who found its function "difficult to determine exactly, but it appears to be employed in connection with both feeding and waste rejection". The opercular pad projection appears to be a functional necessity for forming the elaborate opercular setae in this group. Related genera with similarly complex setal structures (e.g., *Petalopoma* Schiaparelli, 2002) are in need of anatomical investigation.

Analysing the anatomical data of *Stephopoma nucleogranosum* in the context of a recent phylogenetic analysis of Cerithioidea (Simone, 2001), it appears that it shares most synapomorphies that were inferred for that superfamily. These include a papillate mantle border, the relative length and shape of the osphradium, a wide rectum, a posteriorly placed anus, the position of the aortae on the gastric style sac, a lateral origin of the accessory dorsal tensor muscles of the radula (m5), an insertion of the ventral tensor muscles of the radula (m11) separated from m4, a broad stomach, a single gastric duct to the digestive gland, and the isolation of the gonad from the digestive gland. Some cerithioidean synapomorphies are absent in this species (possibly because of its peculiar sessile mode of life), such as an odontophoral pair of small muscles accessory to the horizontal muscles (m12), the development of oblique faecal pellets, and the presence of an ovipositor. *Stephopoma* also shares synapomorphies in support of the branches that include Vermetidae and Turritellidae (nodes 2, 3 and 4 of Simone, 2001, fig. 440; Vermetidae therein considered a part of Cerithioidea). These include an

elongated shell shape (at least in the early whorls); deformation and attachment of the shell to the substratum, absence of determinate shell growth (formation of a lip) and canal, a reduction of the hypobranchial gland, a more posteriorly located insertion of the mantle in the ventral surface of the head-foot, a food groove, long and narrow ctenidial filaments, the loss of the retractor muscle pair of the buccal mass (m2), thick protractors of the odontophore (mj), hook-shaped marginal radular teeth, and the simplification of the pallial oviduct. The close relationship of Turritellidae and Siliquariidae, already inferred by Morton (1951: 39), is supported by shared characters such as the enlargement of the foot, the size and position of the gastric style sac, and pallial brooding.

Putative synapomorphies supporting *Stephopoma* [and, perhaps, closely related groups such as *Petalopoma*] (Morton, 1951; Morton and Keen, 1960; Bieler, 1997; this study) include the protoconch shape and pustulation, the complex opercular setae and the opercular pad projection producing them, the enlargement of the mantle papillae toward the anterior end of the ctenidium, the meandering anterior region of the osphradium, the shape of the salivary glands (two separated masses clustering in the buccal mass, in T-fashion), and the extreme simplification of the pallial oviduct into a single fold.

Brooding has now been described for several *Stephopoma* species and appears to be a common trait. *Stephopoma roseum* females maintain 10–15 single-egg capsule freely in the mantle cavity (Morton, 1951), *S. abrolhosense* was found to breed five to eight single-egg capsules (Bieler, 1997), and the current study found up to three capsules in *S. nucleogranosum* females. As was the case in the previously studied Western Australian species *S. abrolhosense*, all anatomically investigated animals of *S. nucleogranosum* were females. Morton (1951: 35) described males of *S. roseum* as lacking a prostate, "and the sperms leave the male aperture far back in the pallial cavity, being carried forward by cilia along the right margin of the food groove and discharged with the exhalant current." Hughes (1985) described and coarsely sketched a tentaculiform penis extending "from between the lobes of the foot" in *S. pennatum* from Pacific Panama. As he (1985: 323) explicitly described ejection of sperm from it, the structure cannot have been confused with the setae-producing opercular pad projection (unless the latter has multiple functions), and thus the presence of a cephalopodal penis in this otherwise aphallic group remains enigmatic.

## ACKNOWLEDGEMENTS

This study is a result of the successful 12th International Marine Biological Workshop in Esperance, organized by Fred Wells, Di Walker, and Gary Kendrick. Several participants (especially Anne Brearley and Justin McDonald) helped RB in his hunt for "wormsnails", both above and below the waterline. The present material was dredged by a local fisherman, Marcus Gray, who very kindly supported our activities. Prior taxonomic studies on this group were greatly aided by specimen loans arranged by Ian Loch (AMS) and Kathie Way (The Natural History Museum, London). Lisa Kanellos (PEET project scientific illustrator, FMNH) rendered the opercular setae drawings. Financial support for field collecting was provided by FMNH Zoology's Department's Marshall Field Fund. Laboratory research and LRS's postdoctoral research visit to FMNH was supported by U.S. National Science Foundation PEET DEB-9978119 award to RB and Paula M. Mikkelsen. Additional support was obtained from the Brazilian agency Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), processes 00/11357-7 and 03/02447-0.

## LITERATURE CITED

Barnard, K.H. (1963). Contributions to the knowledge of South African marine Mollusca. Part III. Gastropoda: Prosobranchiata: Taenioglossa. *Annals of the South African Museum* **47**(1): 1–199.

Bieler, R. (1997). *Stephopoma* (Caenogastropoda: Siliquariidae) from the Houtman Abrolhos Islands, Western Australia; with a review of the genus. *In* F.E. Wells (ed.). *The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia*: 255–280. Western Australian Museum, Perth.

Bieler, R. (2004). Sanitation with sponge and plunger: western Atlantic slit-wormsnails (Mollusca: Caenogastropoda: Siliquariidae). *Zoological Journal of the Linnean Society* **140**: 307–333.

Finlay, H.J. (1926). A further commentary on New Zealand molluscan systematics. *Transactions and Proceedings of the New Zealand Institute* **57**: 320–485, pls. 18–23 (volume "issued 10th March, 1927", article "issued separately, December 23rd, 1926").

Healy, J.M. and Wells, F.E. (1998). Superfamily Cerithioidea. *In* P.L. Beesley, G.J.B. Ross and A. Wells (eds), *Mollusca: The Southern Synthesis. Fauna of Australia vol. 5*: 703–733. CSIRO Publishing, Melbourne.

Hughes, R.N. (1985). Feeding behaviour of the sessile gastropods *Vermicularia pellucida* and *Stephopoma pennatum* (Turritellidae, Vermicularinae). *Journal of Molluscan Studies*, **51**: 320–325

Mörch, O.A.L. (1861). Review of the Vermetidae. Part I. *Proceedings of the Scientific Meetings of the Zoological Society of London,* 1861, part 2: 145–181, pl.25.

Morton, J.E. (1951). The structure and adaptations of the New Zealand Vermetidae Part II. The genera *Stephopoma* and *Pyxipoma*. *Transactions of the Royal Society of New Zealand* **79**(1): 20–42, pls. 4–7.

Morton J. E. (1953). *Vermicularia* and the turritellids. *Proceedings of the Malacological Society of London* **30**(3): 80–86.

Morton, J.E. and Keen, A.M. (1960). A new species of *Stephopoma* (Siliquariidae: Mesogastropoda) from the Eastern Atlantic Ocean. *Proceedings of the Malacological Society of London* **34**(1): 27–35.

Quoy, J.R.C. and Gaimard, J.P. (1834). Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M. J. Dumont d'Urville. Zoologie, Mollusques. 3(1): 1–366 (1834); Atlas: pls.1–107 [dates of plates not verified]. Paris, J. Tastu.

Schiaparelli, S. 2002. Taxonomy of the family Siliquariidae (Mollusca, Caenogastropoda) in eastern Atlantic Ocean and Mediterranean Sea: description of a new genus and a new species. *Italian Journal of Zoology* **69**: 245–256.

Simone, L.R.L. 2001. Phylogenetic analyses of Cerithioidea (Mollusca, Caenogastropoda) based on comparative morphology. *Arquivos de Zoologia* (São Paulo) **36**(2): 147–263.

Verco, J.C. (1904). Notes on South Australian marine Mollusca, with descriptions of new species, Part I. *Transactions of the Royal Society of South Australia* **28**: 135–145.