

MORPHOLOGY OF THE WESTERN ATLANTIC HALIOTIDAE (GASTROPODA, VETIGASTROPODA) WITH DESCRIPTION OF A NEW SPECIES FROM BRAZIL

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ABSTRACT

Haliotis aurantium, new species, is described from the southeastern coast of Brazil and compared morphologically with *Haliotis pourtalesii*, which inhabits the Gulf of Mexico and the Caribbean Sea. These species differ mainly in characters of the head, epipodium, metapodium and digestive system. The species are also compared anatomically with other species of *Haliotis* based on published descriptions and on comparative dissections of *H. lamellosa* and *H. tuberculata*.

INTRODUCTION

The finding of a haliotid in the western Atlantic excited considerable interest (Henderson, 1915; Harry, 1966; Klappenbach, 1968; Sarasua, 1968; Merrill & Petit, 1969; Guince, 1969; Nijssen-Meyer, 1969; Silva & Guerra, 1981; Martinez & Ruiz, 1994), although until now few specimens with soft parts have been found (Titgen & Bright, 1985).

All western Atlantic haliotid specimens have been identified as *Haliotis pourtalesii* Dall, 1881, with apparently in two disjunct populations, one from North Carolina to Cuba and other in Brazil (Rios, 1985; Titgen & Bright, 1985). These identifications were based only on shell characters, because no anatomical information has appeared to date. Photos and a brief description of the head-foot and color pattern of a specimen from the Gulf of Mexico were given by Titgen & Bright (1985).

Specimens from the two regions were carefully compared in their morphology, showing that, despite the similarity in their shells, the specimens from these regions are sufficiently distinct to be regarded as separated species.

Few papers provide anatomical information on haliotids (e.g., Freure, 1905; Crofts, 1929, 1937, 1955; Campbell, 1965; Russell & Evans, 1989). The present paper provides an anatomical description, as a basis for comparison between the two western Atlantic species, as well as for use in a future systematic rearrangement of the family, which has about 70 species in the single genus *Haliotis* Linné, 1758 (Abbott & Dance, 1983).

The complex history of the discovery of *H. pourtalesii* in waters near Florida and the loss of its type specimen have been discussed elsewhere (e.g., Foster, 1946; Titgen & Bright, 1985). Also there are misidentifications based on young specimens of other species (Abbott, 1974) and based on similar species occurring in Pacific waters (*H. dalli* Henderson, 1915; *H. roberti* McLean, 1969), demanding care in literature analysis.

MATERIAL AND METHODS

The specimens from Brazil are in the collection of the Museu de Zoologia da Universidade de São Paulo (MZSP), some of them collected by Instituto Oceanográfico da Universidade de São Paulo (IOUSP) in the project "Monitoramento Ambiental Oceânico da Bacia de Campos." The northern specimens are in the collection of the National Museum of Natural History (USNM) and Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML). Those with soft parts are preserved in 70% ethanol.

Two Brazilian and five northern specimens were available with soft parts for dissections, which were made using standard techniques. Some organs, such as the buccal mass and pallial organs, were dehydrated in ethanol series, stained with carmine, fixed and cleared in creosote. All drawings were made with the aid of a camera lucida. Shells, radulae and jaws were also examined using SEM in the Laboratório de Microscopia Eletrônica do Insti-

tuto de Biociências da Universidade de São Paulo. The shells were not coated with gold. Odontophoral muscles were examined by direct dissection, although the jugal muscles were not seen in detail. The nomenclature of buccal musculature follows Fretter & Graham (1962).

Anatomical comparison with other *Haliotis* is based on the literature (Fleure, 1905; Crofts, 1929, 1937, 1955; Fretter & Graham, 1962; Campbell, 1965, digestive system; Russell & Evans, 1989, circulatory system) and on comparative examination of two lots of the MZSP collection: MZSP 13340, *Haliotis tuberculata* Linné, 1758, 5 specimens in 70% ETOH from Trieste, Italy; MZSP 28202, *Haliotis lamellosa* Lamarck, 1822, 1 specimen in 70% ETOH from Trieste, Italy.

In the figures the following abbreviations are used: ac: anterior cartilages; af: accessory oesophageal fold; al: aperture of left oesophageal pouch; an: anus; ar: aperture of right oesophageal pouch; cm: main (right) columellar muscle; da: direct anterior radular tensors; dg: digestive gland; dr: direct radular tensor muscle; ef: efferent gill vessel; ep: epipodium; ff: dorsal epipodial flap; gc: gastric caecum; go: gonad; hz: horizontal muscle; if: intermediary epipodial flap; im: intertentacular membrane; in: intestine; ja: jaws; la: left auricle; lc: left columellar muscle; lg: left gill; lh: left hypobranchial gland; lk: left kidney; lm: lateral protractor muscle; lp: left oesophageal pouch; ma: main epipodial tentacle; mb: mantle border; mt: metapodium; nr: nerve ring; oa: outer approximator muscle of cartilages; od: odontophore; oe: oesophagus; om: ommatophore; os: osphradium; pc: posterior cartilage; pr: pigmented region of dorsal epipodial flap; pv: posterior ventral radular tensor muscle; ra: right auricle; rd: radula; rg: right gill; rh: right hypobranchial gland; rk: right kidney; rp: right oesophageal pouch; rs: radular sac; rt: rectum; sa: sorting area; sf: pigmented multipapillate tentacles surrounding ma; sl: pallial slit; sn: snout; sr: subradular membrane; st: stomach; tc: metapodial tentacle covered with long cilia; te: cephalic tentacle; tm: metapodial tentacle; ts: slit pallial tentacle; ty: gastric typhlosole; vp: ventral buccal protractor muscle; ve: ventricle; vf: ventral epipodial flap.

Abbreviations of institutions: MNRJ: Museu Nacional do Rio de Janeiro; MORG: Museu Oceanográfico da Fundação Universidade de Rio Grande; MZSP: Museu de Zoologia da Universidade de São Paulo; UMML: Marine Invertebrate Museum, Rosenstiel School of

Marine and Atmospheric Science, University of Miami; USNM: National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Haliotis aurantium, new species (Figs. 3–9, 11–13, 18–35)

Haliotis pourtalesii: Klappenbach, 1968: 1–2; Rios, 1970: 16, pl. 1; Silva & Guerra, 1971: 49–50, figs. 1–4; Rios, 1975: 11, pl. 1, fig. 4; Rios, 1985: 10, pl. 5, fig. 35; Rios, 1994: 22, pl. 5, fig. 39 (*non* Dall, 1881).

Types: Holotype, MZSP 28201, from type locality; paratypes: MZSP 18482, 1 shell, off Ubatuba, São Paulo, 24°07'S 44°06'W, 150 m depth; MZSP 19569, 2 shells, 22°27'6"S 40°30'W, off Cabo de São Tomé, Rio de Janeiro, Brazil, 95 m depth (11/ii/1969); MZSP 28391, 1 specimen, 21°05'S 41°19'W, east of Ponta do Ubú, Espírito Santo, Brazil, 48 m depth (E. C. Oliveira Fo. col., 1986).

Type Locality: Brazil, Rio de Janeiro, off Campos Bay (sta. 21), 22°06'06"S 40°08'38"W, 95 m depth (R. V. Astrogaroupa, 22/vii/1991).

Diagnosis

Minute southwest Atlantic species with unpigmented head-foot and mantle; two tentacles in mantle slit; epipodial tentacles randomly arranged; pair of large epipodial tentacles posteriorly; pair of metapodial tentacles sometimes present; lobed snout border; left pouch of buccal mass covering ventral surface of odontophore; several pairs of lateral radular protractor muscle.

Description

Shell (Figs. 3–7). Auriform, fairly thin, subelliptical, up to 15 mm in length, few more than three whorls (Fig. 4). Color of exposed areas from homogeneous vivid reddish orange in living specimens to pale yellow in eroded specimens. Protoconch (Fig. 5) of two whorls, low, sculptured by several minute, uniform, spiral threads. Spire small, low, submarginal, situated on posterior fourth of shell (Figs. 4, 7). Aperture subelliptical, nacreous. Base of shell concave with some lateral torsion. Columella with a sulcus inside raised parietal margin of aperture (Fig. 6). Three to four oval

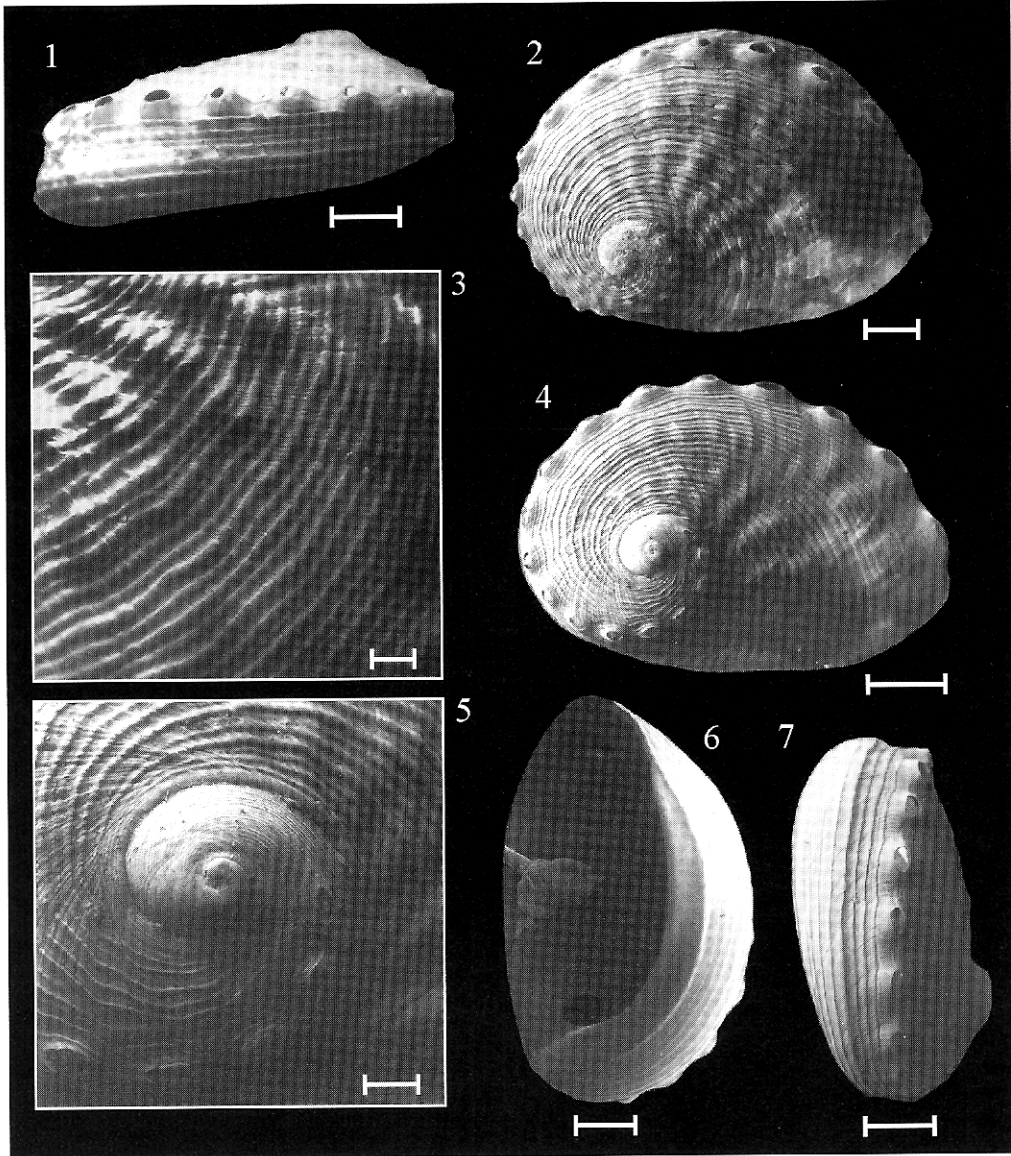


FIG. 1–7; shells in SEM. (1) and (2) left and dorsal view of *Haliotis pourtalesii* USNM 833627, scales = 2 mm; (3) detail of middle-outer region of body whorl of *Haliotis aurantium*, MZSP 18482, paratype, scale = 0.5 mm; (4) to (7) *Haliotis aurantium* holotype: (4) dorsal view, scale = 2 mm; (5) detail of protoconch, scale = 0.5 mm; (6) ventral view, scale = 2 mm; (7) left view, scale = 2 mm.

shell pores (tremata) open, preceded by several closed, all of them oval, with elevated margins (Figs. 4, 6, 7). Spiral sculpture of sharp, rather widely shaped cords, between which finer threads are occasionally intercalated (Fig. 3). About 30 cords and threads in area between suture and outer margin of

body whorl. Lateral portion of body whorl with three cords followed by strong, angular, peripheral ridge or carina (Fig. 7). Immediately below this, three or four more cords present (Figs. 6, 7). Axial sculpture consisting of radiating lamellae, which roughly correspond to pores in their position, considerably variable,

sometimes missing. Minute uniform axial cords between spiral cords occasionally present. Surface with very fine growth lines. No periostracum apparent.

Head-Foot. Head somewhat protruding (Fig. 21). Tentacles stubby, short, broad, covered with long cilia, pigmented by regular pale brown, successive transverse bands (Fig. 21). All other structures without pigment. Ommatophore well developed, in outer basal region of tentacles (Figs. 18, 19, 21), with dark, vesicular, opened eyes. Intertentacular membrane a semi-transparent, thin flap (Figs. 21, 26, 27) between the two cephalic tentacles, covering anterior region of snout and inner region of tentacles (Fig. 21). Snout well developed (Figs. 21, 25), cylindrical, broad, with irregular ventral margin. Foot large, about same size as shell aperture (Fig. 19), without pigment. Epipodium with many lobed tentacles (Figs. 19, 22, 23), without pigment, uniform in size, some of them covered with long cilia, apparently without special organization (Fig. 22); in posterior extremity of epipodium two epipodial tentacles larger and longer (Fig. 23), and a median area without tentacles (Fig. 23). In the holotype, a pair of long metapodial tentacles present on posterior border; dissected paratype without this structure. Main (right) columellar muscle very large, circular in section (Fig. 18). Secondary (left) columellar muscle very small (Fig. 25: lc).

Mantle border. Trifolded and simple, without pigment. Slit deep (Figs. 18, 20), with two tentacles covered with long cilia, one on the left-anterior border and other on the right-posterior border of slit (Figs. 18, 20).

Pallial cavity. Short, about half of body whorl (Fig. 20). Gills short, bipectinate, right gill shorter than left (Fig. 20). Afferent gill vessel in base of gill's insertion. Efferent vessel between two flaps of each gill leaflet, inserting in gill sub-terminally, anterior to posterior extremity of gill (Fig. 20). Hypobranchial glands present, left larger, with several transverse, uniform furrows; right much smaller, with three oblique furrows. Both hypobranchial glands situated at left of slit (Figs. 18, 20, 24). Rectum between both hypobranchial glands, slightly free in posterior half of pallial cavity; anus papillated near posterior extremity of slit (Figs. 20, 24).

Circulatory and excretory systems. Kidneys and pericardium situated ventrally, in mid-left side of animal just behind pallial cavity (Fig. 24). Left kidney short, broad, with a short

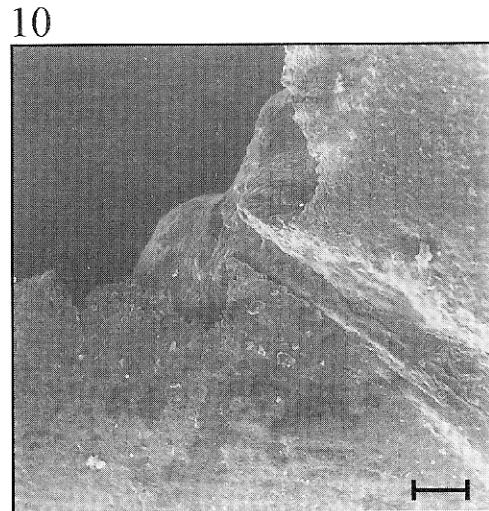
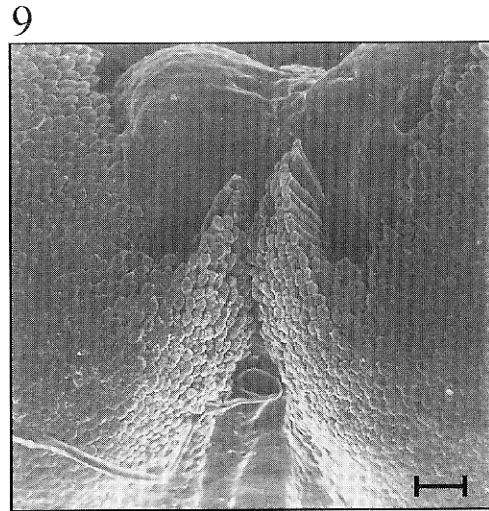
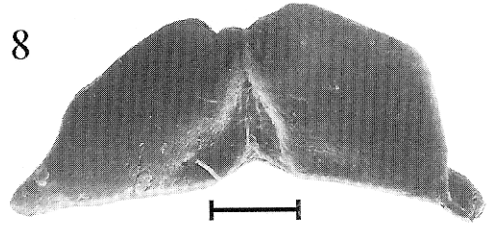
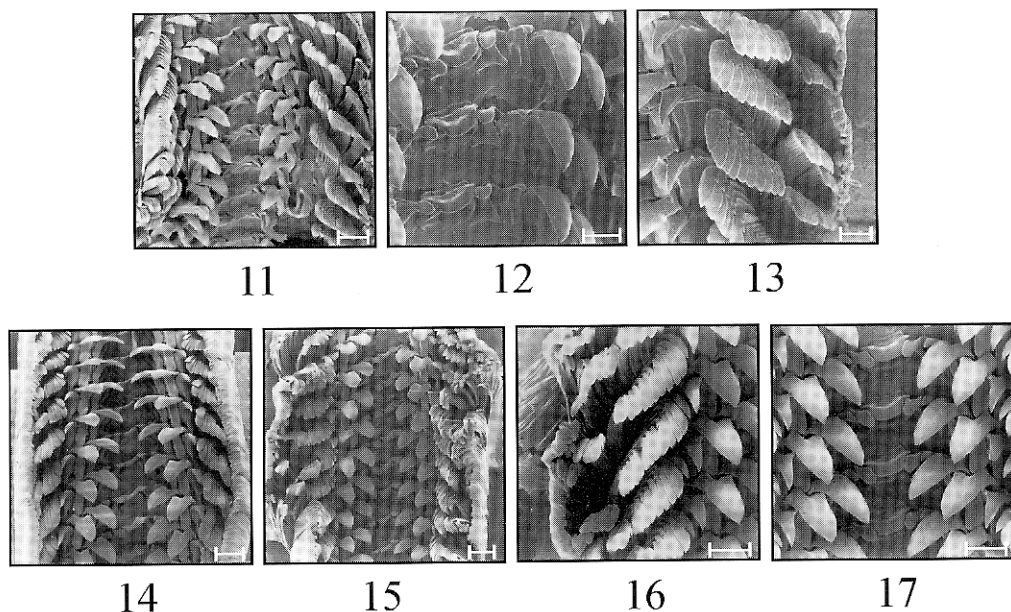


FIG. 8–13. Jaws and radula in SEM: (8) jaws of *Haliotis aurantium*, scale = 200 μm ; (9) detail of same, scale = 20 μm (10) detail of central region of jaws of *Haliotis pourtalesii*, scale = 50 μm ; (11) radula of *Haliotis aurantium*, scale = 100 μm ; (12) detail of same, central region, scale = 50 μm ; (13) detail of Fig. 11, marginal region, scale = 50 μm .

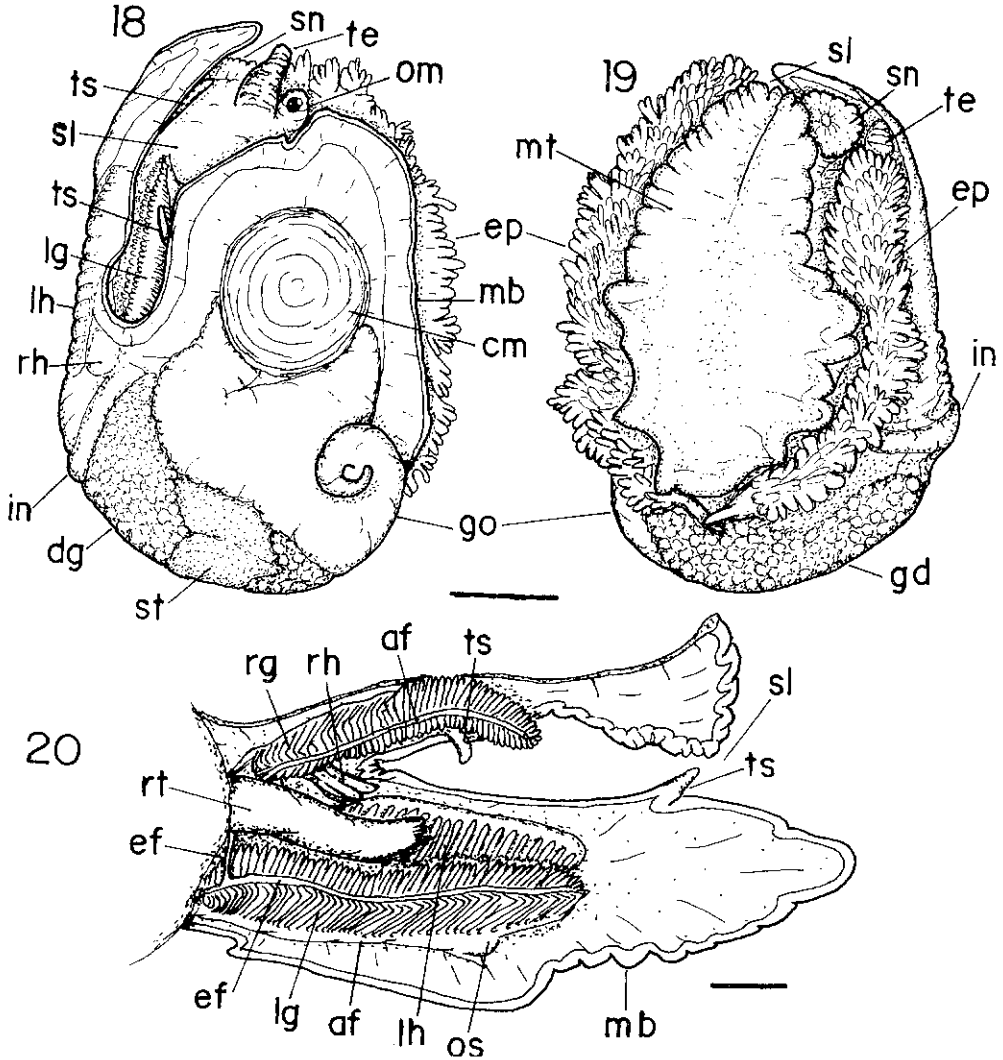


FIGS 14–17. Radulae of *Haliotis pourtalesii* in SEM: (14) USNM 833627, scale = 100 μ m; (15) UMM 30–8376, scale = 100 μ m; (16) detail of Fig. 14, marginal region, scale = 100 μ m; (17) the same, central region, scale = 100 μ m.

papillated nephrostome in ventral base of rectum. Right kidney long, thin, lying right margin of pallial cavity (Fig. 24), its nephrostome a longitudinal slit in its anterior extremity. Ventricle large, surrounding intestine; left auricle anterior to ventricle and right auricle ventral to it.

Digestive system. Mouth in snout, covered internally by pavement-shaped papillae (Fig. 28). Jaws two small plates (Figs. 8, 28), with rounded borders, situated in mid-dorsal region of mouth; median and anterior region of each plate with a small, sharp pointed projection (Figs. 8, 9). Buccal mass very large, complex; odontophore surrounded by two glandular oesophageal pouches (Figs. 25–27), both with inner surface covered by many tall villiform papillae (Fig. 28). Left pouch broad, short, covering ventral and lateral-left surfaces of odontophore. Right pouch narrow, long, beginning at right and running obliquely (Figs. 26, 27). Both pouches open in ventral-anterior region of oesophagus in two separated, tall, ring-like folds; a third short accessory fold also at this position (Fig. 28: af). Odontophore short, with very long radular sac, extending behind buccal mass and terminating near stomach (Fig. 25). Radula (Figs. 11–13): rachidian teeth broad,

short, each with a large curved terminal cusp and two lateral bolsters (Fig. 12); first lateral tooth with triangular base and small rounded cusp; second lateral tooth long, with a somewhat rectangular base and a lateral-terminal, hook-like cusp; third lateral tooth the largest, with a long, irregular, curved base, and a large, long, sharp cusp, of almost the same length as base; fourth and fifth lateral teeth similar to third, but narrow; fifth narrowest, sharply pointed. About 32 pairs of marginal teeth per row (Fig. 13), with a long stalk; main cusp rounded, curved, spoon-like, flanged on each side by two small, sharp secondary cusps; marginal teeth gradually decrease in size laterally. Odontophore muscles (Figs. 31–35) consisting of: pair of ventral buccal protractor muscles, with their origin in ventral-lateral inner surface of peribuccal wall, and their insertion in ventral lateral region of posterior cartilages (Figs. 31, 32: vb); pair of direct radular tensor muscles, their origin in mid-ventral region of posterior cartilages and insertion on lateral angles of ventral edge of radula (Figs. 31, 33, 34: dr); pair of muscles as outer approximator of cartilages, their origin in anterior surface of posterior cartilages and insertion in outer lateral surface of anterior cartilages



FIGS. 18 to 20. *Haliotis aurantium* n. sp. anatomy: (18) topography of the holotype specimen in dorsal view; (19) the same in ventral view, scale = 2 mm; (20) pallial organs, mantle deflected, inner-ventral view, scale = 1 mm.

(Figs. 33–35: oa); pair of small posterior ventral radular tensor muscles, their origin in ventral inner surface of peribuccal wall and insertion in mid-ventral region of radular sac (Figs. 31, 32: pv); several pairs of small lateral protractor muscles, their origin in dorsal inner surface of peribuccal wall and insertion in dorsal-mid surface of radula (Fig. 32; lm); pair of direct anterior radular tensors, their origin in ventral-dorsal surface of posterior cartilages and insertion in lateral borders of sub-radular membrane and ventral surface of radula up to mid

line, in a "M" shape (Fig. 33: da); and horizontal muscle, uniting ventral edge of both anterior cartilages (Figs. 31, 35: hz). Anterior odontophoral cartilages long, flattened, anteriorly sharp, posteriorly broad, with rounded borders (Fig. 35). Posterior odontophoral cartilages very short, elliptic, situated in outer posterior extremity of anterior cartilages (Fig. 35).

Oesophagus short, flattened tube (Figs. 25, 26), with about eight internal longitudinal folds (Fig. 28). Stomach very large, U-shaped, near mid line in posterior region of animal (Fig. 18).

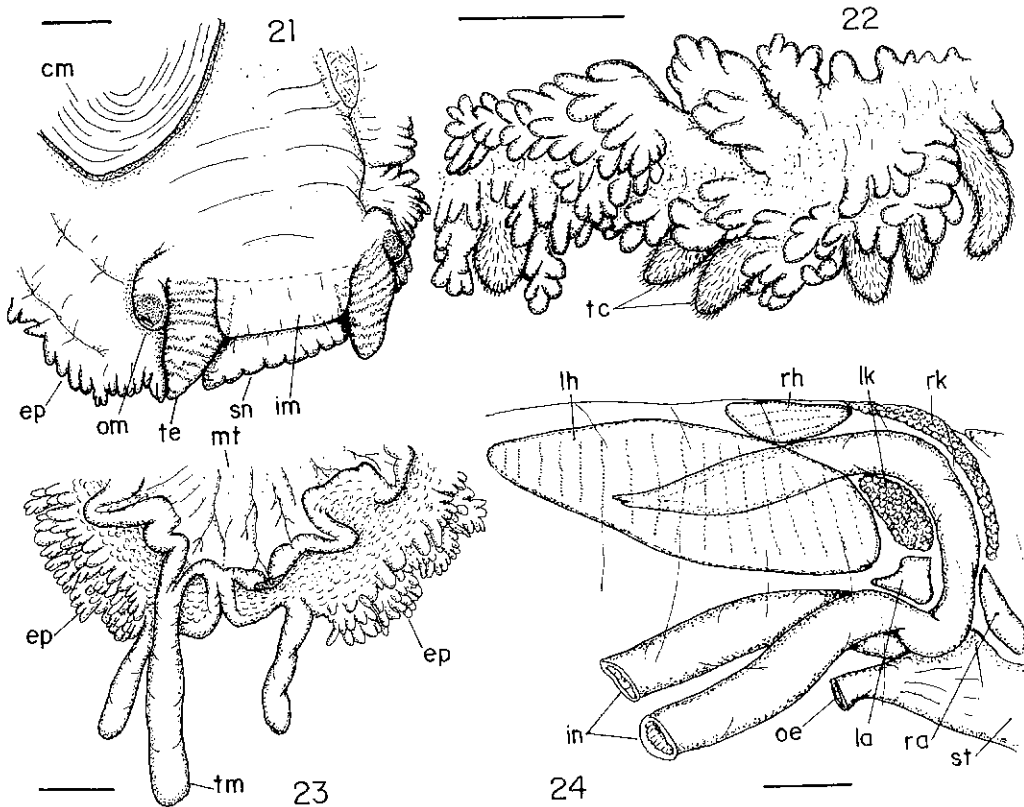


FIG. 21 to 24. *Haliotis aurantium* n. sp. anatomy: (21) detail of head, frontal view, mantle removed, scale = 1 mm; (22) detail of left-posterior fourth of epipodium, scale = 1 mm; (23) detail of posterior extremity of foot, ventral view, scale = 1 mm; (24) semi-diagrammatic drawn of cleared pericardial and nearby structures, ventral-right view, scale = 1 mm.

Oesophageal branch of stomach ventral, conical, with a very small caecum (Fig. 26). Internally oesophageal branch of stomach with mosaic of low, irregular folds near oesophagus opening (Fig. 30), where three longitudinal folds begin, two of them contouring posterior extremity of stomach, becoming weaker posteriorly; the third fold becoming larger and running to intestinal branch of stomach where it becomes weaker (Fig. 30: ty). Some radial muscle fibers in stomach wall originating between oesophageal and intestinal branches of stomach (Fig. 30: lc) and inserting in small left columellar muscle (Fig. 25: lc). Intestinal branch of stomach dorsal, conical, larger than oesophageal branch (Fig. 26); two typhlosoles running alongside gastric intestinal branch from caecum into intestine, one of them presenting in its mid region a series of oblique folds, differentiating a small sorting area (Fig. 29: sa). Other regions of stomach inner surface

smooth, covered by thin greenish cuticle (Figs. 29, 30). Intestine long, with thin transparent walls, running near right side of head, when it twists and returns to posterior region near stomach (Figs. 25, 27); in this posterior region, it is sigmoid, running through pericardium (Fig. 24) and exiting into pallial cavity (Figs. 20, 25, 26). Intestine and stomach full of gravel.

Digestive glands large, green, with mosaic of irregular brown spots on its surface (Figs. 18, 25) and occupying visceral mass ventral to gonad, surrounding stomach (Fig. 25).

Genital system. Very large ovary occupying all of spire and part of body whorl (Figs. 18, 25: go), pale cream in color. Ovary with three lobes (Fig. 18), one within spire, one posterior to main columellar muscle, the third in left side of this muscle (Fig. 18). Oviduct, which probably runs within right kidney, not seen. Ventral limit of gonad at the digestive gland and stomach (Fig. 25). Male not examined.

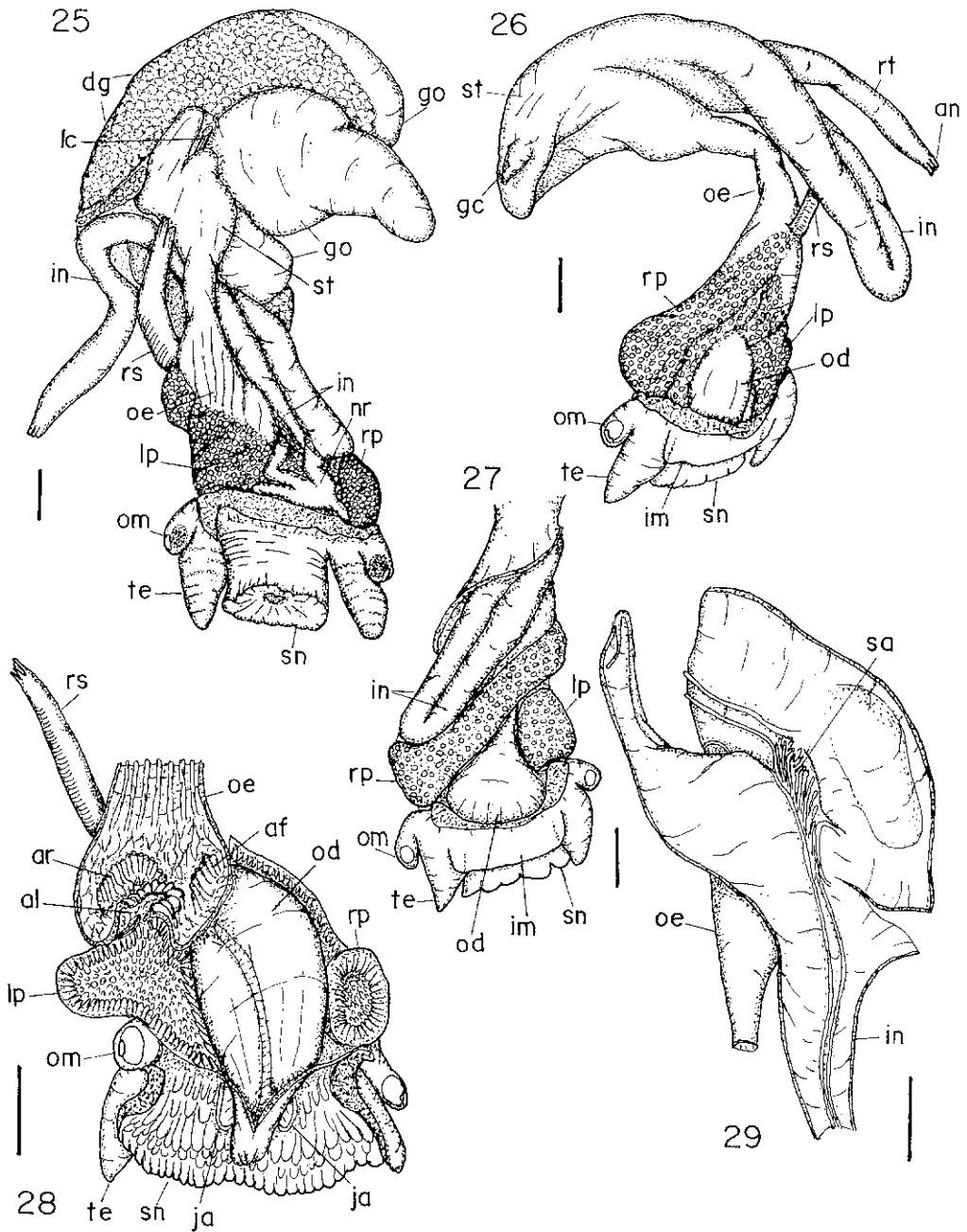


FIG. 25 to 29. *Haliotis aurantium* n. sp. anatomy: (25) cephalic organs and visceral mass, ventral view, foot and mantle removed; (26) extracted head and digestive ducts, right-dorsal view; (27) detail of anterior region of digestive system, dorsal view, head tegument partially removed; (28) snout, buccal mass and esophagus opened longitudinally, ventral view; (29) stomach opened longitudinally in intestinal branch. Scales = 1 mm.

Nervous system. Only circum-oesophageal region examined, agreeing closely with that described by Fleure (1905) and Crofts (1929) for *Haliotis tuberculata*.

Measurements (respectively length in mm, width in mm, number of whorls, of opened pores, of closed pores). Holotype, MZSP 28201: 12.9 by 8.7, 3.2, 4, 14; Paratypes: MZSP 18482: 15.0 by 10.5, 3.2, 3, 16; MZSP 19569: 13.2 by 9.0, 3.0, 4, 13 and 7.2 by 5.2, 2.1, 4, 8.

Habitat. From 77 to 150 m depth, on gravel, generally associated with *Laminaria* sp.

Etymology. The specific name refers to the orange color of the external shell surface (Latin, *aurantium*).

Material Examined. Types.

Material Available. BRAZIL; *Amapá*; MORG 15000, 1 shell, off Cabo Orange, 100 m (R. V. Almirante Saldanha, 30/xi/1988). *Espirito Santo*; MNRJ-HSL 6603, 2 specimens, off Vitória (lost); MORG 15930, 1 shell, off Vitória, 87 m (R. V. A. Saldanha, 24/iv/1969); MNRJ 3577, 20 shells, 20°37'05"S 39°59'00"W, 87 m (R. V. A. Saldanha, sta. DHN 2027, 24/ix/1971). *Rio de Janeiro*; MNRJ 3554, 14 shells, 21°56'05"S 40°07'00"W, 77 m (R. V. A. Saldanha, sta DHN 2012, 11/ix/1969); MNRJ 3578, 4 shells, off Cabo Frio, 23°05'00"S 40°05'00"W, 111 m (R. V. A. Saldanha, sta. DHM 2168); MORG 15931, 1 shell, off Cabo Frio, 90 m (R. V. A. Saldanha, 9/ix/1969); MORG 26226, 1 shell, off Cabo Frio (R. V. A. Saldanha, x/1986, on *Laminaria*); MORG 15929, 1 shell, off Cabo de São Tomé, 77 m (R. V. A. Saldanha, 11/iv/1969). *Rio Grande do Sul*; MORG 17467, 1 shell, off Conceição, 126 m (R. V. Mestre Jerônimo, 2/x/1972).

Haliotis pourtalesii Dall, 1881 (Figs. 1, 2, 10, 14–17, 36–45)

Haliotis (Padollus) Pourtalesii Dall, 1881: 79 [Gulf Stream near Florida Reefs, 180 m (31/iii/1869)] (described from memory).

Haliotis pourtalesii: Dall, 1889: 168; Henderson, 1911: 81 [neotype]; Cooke, 1914: 103; Henderson, 1915: 660, pls. 45, 46; Smith, 1937: 78, pl. 29, fig. 3; Foster, 1946: 38–40, pl. 22, figs. 1, 2; Parker, 1960; Harry, 1966: 207–208, pl. 30; Jung, 1968; Sarasua, 1968: 1–8, figs. 1, 2; Merrill & Petit, 1969: 117; McLean, 1969: 115; Guice, 1969: 140; Abbott,

1974: 18, fig. 30; Titgen & Bright, 1985: 147–152 figs. 1, 2; Abbott & Dance, 1983: 19, fig.; Ode, 1986: 69–73; Martinez & Ruiz, 1994: 63–64, figs. 1–2.

Type: Neotype USNM 271601 [3 miles off Sand Key, Florida, 49 m, 1913]

Diagnosis

Minute northwest Atlantic species with pigmented epipodium and metapodium; three tentacles in mantle slit; epipodial tentacles arranged in three layers around well-developed (main) tentacles; without large epipodial tentacles posteriorly; without metapodial tentacles; snout border papillated; ventral surface of odontophore free of pouches; only one pair of lateral radular protractor muscles.

Description

Shell. Figs. 1, 2.

Head-foot. Head somewhat protruding (Fig. 39). Tentacles long, narrow, covered with long cilia; pigmented by regular dark brown, successive, well-spaced transverse bands and a mid longitudinal band (Fig. 39). Dark brown spots abundant in dorsal and ventral epipodium faces and dorsal face of metapodium, scanty in metapodial sole. Ommatophore well developed, on outer basal region of tentacles, with dark, vesicular, open eyes (Figs. 36, 37, 39). Intertentacular membrane semitransparent, thin, covering anterior region of snout and inner region of cephalic tentacles (Fig. 39). Snout well developed, cylindrical, broad, with regular small, abundant papillae on its ventral border (Fig. 39). Foot large, about same size as shell aperture (Fig. 37). Epipodium with many tentacles (Fig. 37) arranged as follows (Fig. 41):(1) a dorsal flap (df) fringed by flattened, polytomic tentacles in a uniform zigzag pattern; regions nearest foot with dark pigment in dorsal and ventral faces (pr), other regions white; (2) intermediary flap (if) with conspicuous, large, white, sharp tentacles (called "main" tentacles), covered with long cilia (ma); bases of these main tentacles, which are ventral to pigmented region of superior flap (pr), surrounded by two (one on each side) large, multipapillated, dark-brown colored tentacles (sf); between these structures, many other short tentacles, with rounded tips, without pigment nor evident cilia; (3) ventral flap (vf) extremely rich in tentacles, some of them longer

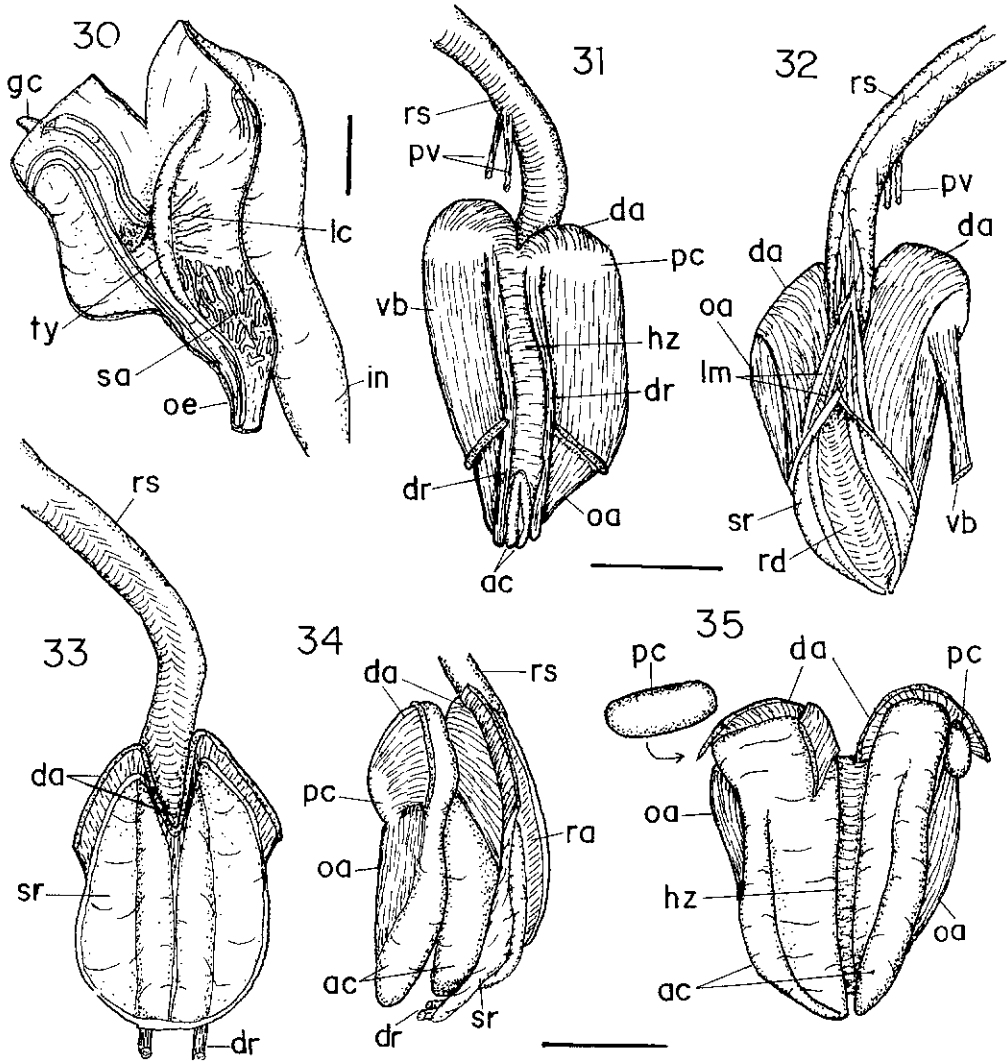


FIG. 30 to 35. *Haliotis aurantium* n. sp. anatomy: (30) oesophageal branch of stomach opened longitudinally; (31) ventral view of odontophore; (32) dorsal view of same; (33) ventral view of radular ribbon and subradular membrane showing the "M" in shape insertion of "da"; (34) lateral-right view of odontophore, direct anterior radular tensor muscle (da) partially sectioned; (35) dorsal view of odontophore with part of its muscles removed, right anterior cartilage deflected. Scales = 1 mm.

(tc), sharp, covered with long cilia, similar to but smaller than main tentacles; other tentacles short, without pigment, with rounded tips without evident cilia. Epipodium on each side beginning near snout and ending at posterior extremity of foot, where it unites with metapodial sole (Fig. 40); practically no region without tentacles. Number of main epipodium tentacles in each side from 10 to 12. Main columellar muscle very large, circular in section (Fig.

36). Secondary (left) columellar muscle very small, with some fibers attached to mid wall of stomach (Fig. 42: lc).

Mantle border. Trifolded, simple, depigmented. Slit deep, with three sharp tentacles covered with long cilia, two of them about mid region of the slit (one in each side), and the third in posterior extremity of slit (Figs. 36, 38).

Pallial cavity. Short, about half of body whorl (Figs. 36, 38). Gills somewhat long, bipecti-

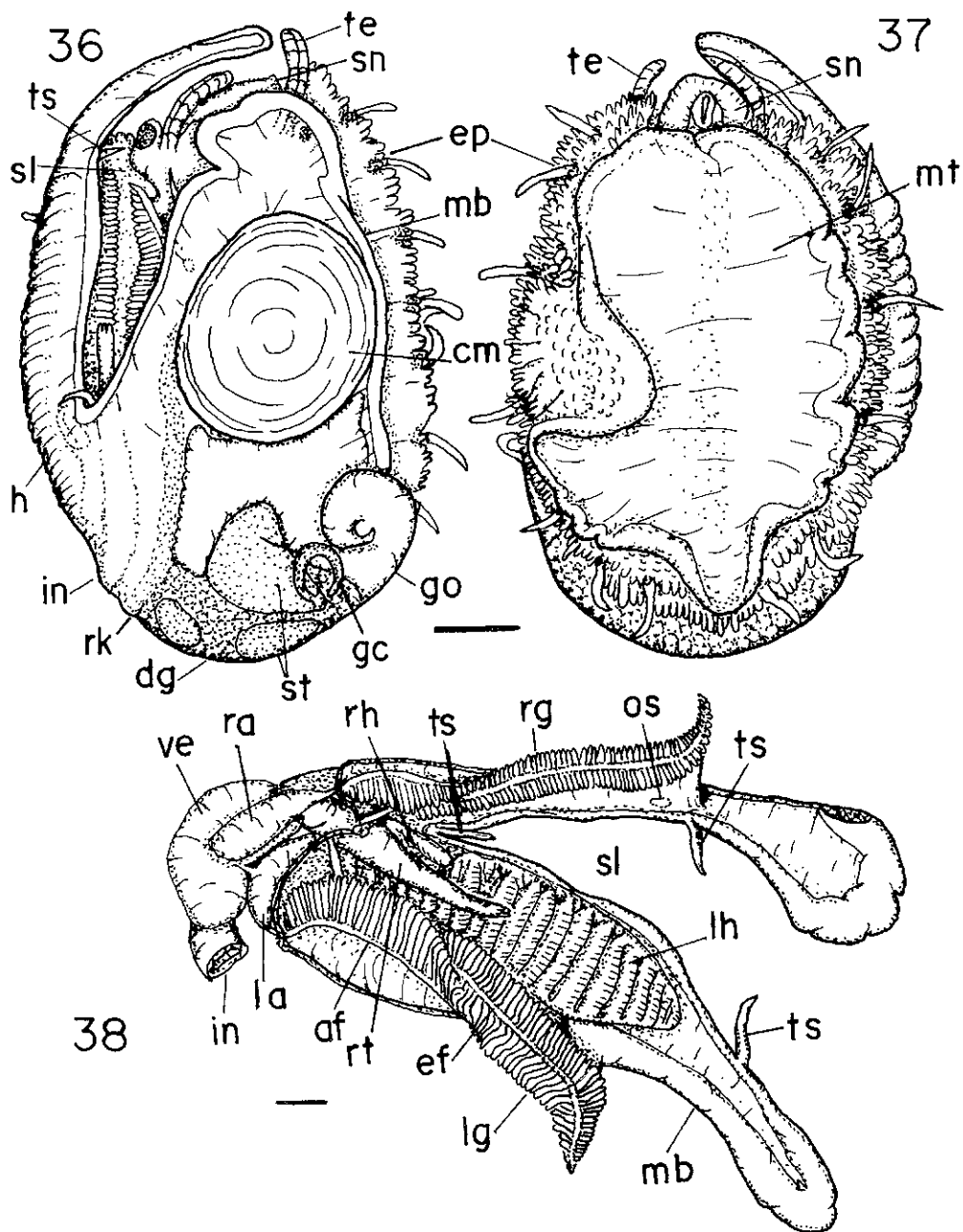


FIG. 36 to 38. *Haliotis pourtalesii* anatomy: (36) topography of the specimen USNM 833627 in dorsal view, scale = 2 mm; (37) same in ventral view, scale = 2 mm; (38) pallial organs, mantle deflected, inner-ventral view, scale = 1 mm.

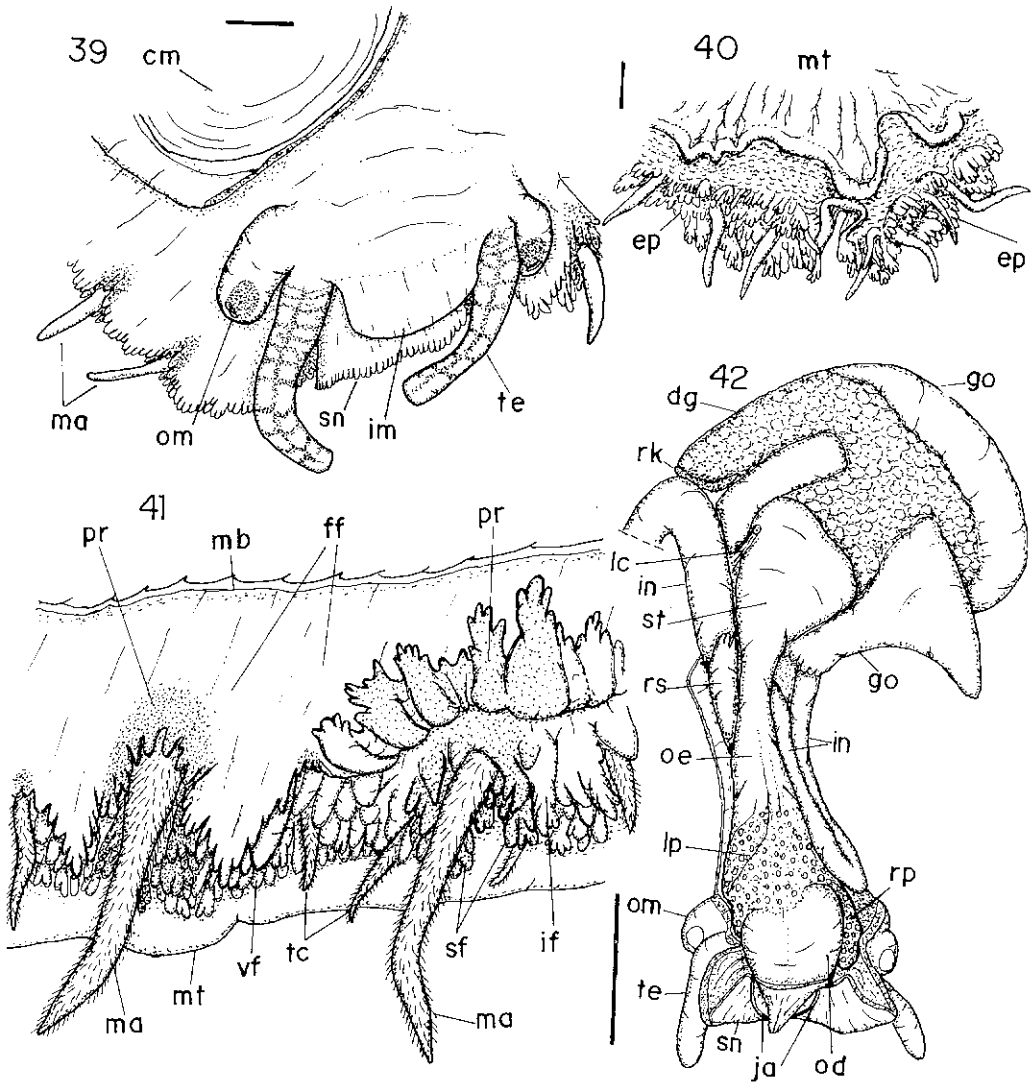


FIG. 39 to 42. *Haliotis pourtalesii* anatomy: (39) detail of head, frontal view, mantle removed, scale = 1 mm; (40) detail of posterior extremity of foot, ventral view, scale = 1 mm; (41) detail of left-posterior fourth of epipodium, scale = 1 mm; (42) cephalic organs and visceral mass, ventral view, snout opened longitudinally, scale = 1 mm.

nate; right gill somewhat shorter than left (Fig. 38). Afferent gill vessel in base of gill's insertion. Efferent vessel between two flaps of each gill leaflet, inserting in gill sub-terminally, anterior to posterior extremity of gill. Hypobranchial glands present, left very large (Fig. 38), with about 18 transverse, successive, uniform folds; right smaller, with two oblique, somewhat curved folds (Figs. 36, 38). Both hypobranchial glands at left of slit (Fig. 38).

Rectum lying between hypobranchial glands, slightly free in posterior half of pallial cavity; anus papillated, opening in posterior third of slit (Fig. 38).

Circulatory-excretory systems. Kidneys and pericardium in posterior left side of animal, just behind pallial cavity. These structures are very similar to those of the preceding species (Figs. 24, 38).

Digestive system. Mouth in snout, covered

internally by smooth walls (Fig. 42). Jaws two somewhat large plates (Fig. 42), brown, in mid-dorsal region of buccal cavity, lateral and anterior border with a sharp edge, median-anterior region with a sharp projection (Fig. 10). Buccal mass large, complex; odontophore (Fig. 42) surrounded, except in its ventral region, by two glandular pouches, both with inner surface covered by many tall, villiform papillae (Fig. 43). Left pouch broad, short, covering left side of odontophore. Right pouch narrow, long, running obliquely from right side of odontophore. Both pouches opening in ventral-anterior region of oesophagus in separate, tall, ring-like folds, that of left chamber more anteriorly (Fig. 43). Radular sac very long, running close to and attached to dorsal region of buccal mass and oesophagus (Fig. 42). Radula (Figs. 14–17): similar to that of preceding species, except for the marginal teeth, which have a much longer, sharp central cusp (Fig. 16); and in being more abundant, with about 40 pairs per row (Figs. 14, 15). Odontophore similar to that of preceding species (Figs. 44, 45), including cartilages and intrinsic muscles; except lateral protractor muscle of radula (Fig. 45: lp), which in *H. pourtalesii* is a single, larger pair.

Oesophagus short, flat (Fig. 42), with about ten internal longitudinal folds (Fig. 43). Stomach very large, U-shaped; walls irregular, with two ventral (oesophageal) and three dorsal (intestinal) chambers and a well-developed, narrow spiral caecum in right dorsal region of stomach, with about one whorl (Fig. 36: gc). Stomach and intestine of studied specimen with a large quantity of clear gravel and organic materials including foraminiferan shells and unidentified bristles.

Intestine, rectum and digestive gland characters similar to those of preceding species (Fig. 42).

Genital system. Gonad with only two lobes: a lobe within spire and another just posterior to main columellar muscle (Fig. 36). Ventrally, this gland terminates at the digestive gland and stomach (Fig. 42).

Measurements (respectively length in mm, width in mm, number of whorls, of opened pores, of closed pores). USNM 833627: 17.8 by 12.5, 3.2, 6, 18. UMML 30–8376: a) 20.1 by 13.0, 3.1, 5, 18; b) 17.6 by 11.3, 3.0, 5, 17; c) 9.9 by 7.0, 2.5, 5, 12; d) 21.6 by 15.0, 3.2, 5, 19; e) 19.6 by 13.0, 3.0, 5, 17; f) 13.7 by 9.9, 3.0, 6, 16; g) 12.9 by 9.1, 2.3, 5, 14.

Habitat. Depth from 50 to 160 m. In the literature, the habitat is referred to as bottoms

with rocks, stones sand and shell debris, or reef (Nijssen-Meyer, 1969).

Material examined: USNM 833627, 1 specimen, U.S.A., Gulf of Mexico, off Florida, 25°16'55"N, 83°37'47"W, 74 m depth (15/viii/1984). UMML 30–8376, 4 specimens + 5 shells, off VENEZUELA, 11°03'N 65°59'W, 69–155 m (R. V. Pillsbury sta. P-736, 22/vii/1968).

DISCUSSION

Haliotis pourtalesii and *H. aurantium* are atypical Haliotidae. Generally, haliotids are large gastropods, over 150 mm in length, whereas both these species are less than 25 mm. Haliotids generally are common and occur in shallow waters, whereas these species are rare and found in deep water (slope). However, both have the same general anatomical characters of the family, modified due to miniaturization.

Haliotis aurantium differs from *H. pourtalesii* in having: (1) a smaller size; (2) only two tentacles on the mantle slit (not three); (3) only transverse bands in the cephalic tentacles (without a longitudinal band); (4) foot without pigment; (5) epipodial tentacles of a simpler structure (see below); (6) a pair of larger tentacles on the posterior extremity of the epipodium and a proportionally large area with out tentacles posteriorly; (7) a pair of large tentacles on the posterior extremity of the metapodium sometimes present (absent in paratype) (Fig. 23: tm); (8) right gill much shorter than the left (in *H. pourtalesii* both gills are about the same size and are proportionally longer than in *H. aurantium*); (9) left hypobranchial gland with three folds (not two); (10) right hypobranchial gland proportionally smaller and with weaker transverse folds; (11) pericardial structures situated more anteriorly; (12) snout bordered by lobes (without small papillae); (13) marginal teeth with rounded main cusp (those of *H. pourtalesii* are sharp); (14) left pouch of the buccal mass covering the ventral surface of the odontophore (*H. pourtalesii* has this region free); (15) several pairs of small lateral protractor muscles of the radula (not one large pair); and (16) kidneys and pericardium more ventrally placed.

Both species show considerable shell variation, from specimens with well-developed axial ridges to specimens lacking them (e.g., the figures of Sarasua, 1968). There is also variation in the number of spiral ridges, which

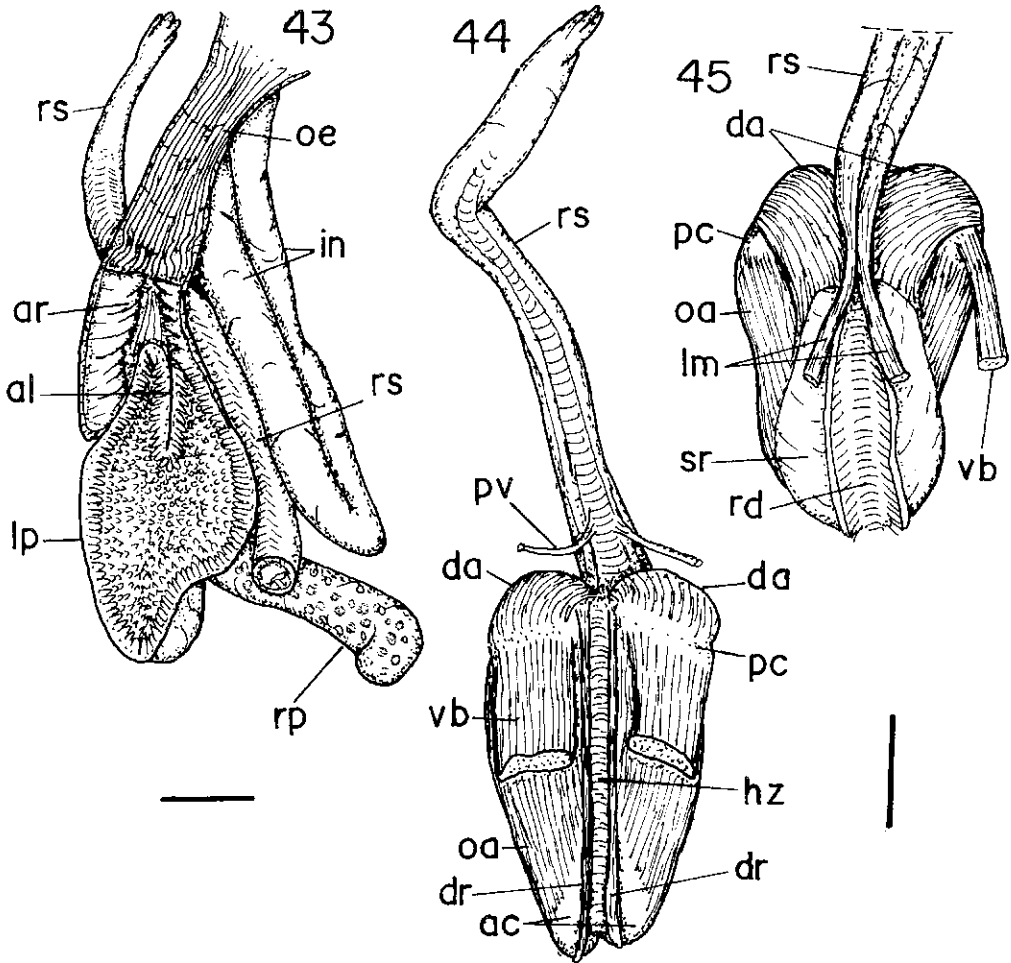


FIG. 43 to 45. *Haliotis pourtalesii* anatomy: (43) anterior region of digestive system, odontophore removed, left pouch (lp) and oesophagus opened longitudinally; (44) ventral view of odontophore; (45) same in dorsal view. Scales = 1 mm.

apparently increases with shell growth. Between the spiral ridges, shells sometimes have delicate axial and uniform threads (Fig. 3). Shared shell characters of these species are small size (up to 25 mm), the reddish-orange color of the exposed areas, and the prominent borders of the tremata. A possible difference between the species is the number of open pores; in specimens of *H. aurantium*, they varied from 3 to 4, whereas *H. pourtalesii* had from 5 to 6 open pores. Analysis of more specimens is necessary to establish whether this is consistent. Comparative examination of available shells, as well as those figured in the literature, no shell character exclu-

sive of a species was found. Thus, it is difficult to separate them using only the shell, although, if a specimen is found from North Carolina to the Caribbean Sea it is probably *H. pourtalesii*, whereas if collected in Brazil (from Espírito Santo to Rio Grande do Sul), it is probably *H. aurantium*. This criterion was used in the synonymic list, but the anatomical study of specimens from all localities was not undertaken and perhaps examination of additional specimens could modify this concept. In both areas, a considerable number of specimens were found. Between these areas shells have been recorded from three localities: off Surinam (Nijssen-Meyer, 1969), off Para

River (Rios, 1975) and off Maranhão (Kemp & Matthews, 1968). Although this could be due to transportation, further sampling in these areas should clarify the distribution of these taxa. Dr. Mello (Museu de Malacologia of the University of Pernambuco), has not obtained haliotids from dredge samples in the northeastern coast of Brazil (pers. comm.).

The epipodial tentacles of *H. aurantium* (Fig. 22) differ from those of *H. pourtalesii* (Fig. 41) in being entirely unpigmented and in having no specific arrangement around the main tentacles. The characters of the epipodial tentacles of *H. pourtalesii* have some similarity to those of the Mediterranean *H. lamellosa* and *H. tuberculata*, (pers. obs), but these differ from *H. pourtalesii* in having only two epipodial tentaculated flaps, the main tentacles inserting dorsally in the dorsal flap; the ventral flap has a similar organization to the dorsal one, but its main tentacles are smaller, ventrally inserted, and situated between the main tentacles of the dorsal flap. *Haliotis tuberculata* has a practically straight epipodium, with three or four small undulations between the main tentacles (Crofts, 1929: pl. 1); *H. lamellosa*, in contrast, has two strong undulations between the main tentacles. Epipodial tentacle characters have been used in haliotids by Owen, et al. (1971) for separating seven eastern Pacific abalone species, and even their hybrids. Using the good figures of that paper, it is clear that the species studied herein differ considerably from those taxa.

Haliotis aurantium and *H. pourtalesii* differ anatomically from *H. tuberculata* (Fleure, 1905; Crofts, 1927, 1937, 1955; person. obs.) and from *H. lamellosa* (pers. obs.) in several characters: the cephalic tentacles possess spots (not of uniform color); the intertentacular membrane simple and free in its lateral margins (*H. lamellosa* has minute lobes in lateral margins, and in *H. tuberculata* the lateral regions are attached to omatophores); as well as the other characters of epipodial tentacles (noted above); the epipodium of Atlantic species begins abruptly near the snout (in the Mediterranean species, there is a coiled expansion in each side, which partially covers the snout); gill proportionally shorter and with fewer leaflets; hypobranchial glands proportionally smaller and simpler (those species have strong and tall folds, *H. pourtalesii* has low folds and *H. aurantium* only furrows); rectum only covered by tegument (both Mediterranean species have the posterior region of the rectum covered on both sides by the hy-

pobranchial glands); anus long and papilliform (*H. tuberculata* and *H. lamellosa* have a short, broad anus); stomach shorter with clear delimitation; and gastric spiral caecum much shorter (which also differentiates it from *H. cracherodii*, see Campbell, 1965). With regard to the tentacles of the mantle slit, *H. pourtalesii*, *H. tuberculata* and *H. lamellosa* are similar in having three tentacles in somewhat the same disposition; *H. aurantium* has only two (there is no tentacle situated just in angulated posterior extremity of slit).

The auriform shell with tremata, the complex tentaculate epipodium and the lack of an operculum, are known synapomorphic characters of the Haliotidae within the Vetigastropoda. At least three additional synapomorphies are offered here: (1) the insertion in the stomach of some fibers of the right retractor muscle, (2) the insertion in a "M" shape of the direct radular anterior muscle, and (3) the intertentacular membrane of the head ("head pleat" of Crofts, 1927).

Schremp (1981: 1125, pl., fig. 1) called a Pliocene haliotid found in the Imperial Formation of California *Haliotis pourtalesii*. Because this identification is based only on the shell, this specimen might instead be the Pacific *Haliotis roberti* McLean, 1969, considered a synonym by that author.

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