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A new species of *Thaisella* (Neogastropoda: Muricidae) from Caribbean Guatemala, with accounts on the anatomy and taxonomy of the genus in the Western Atlantic

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Abstract. *Thaisella guatemalteca* is a new species with type locality in Puerto Barrios, Department of Izabal, Caribbean (Atlantic) coast of Guatemala. Its anatomical attributes are described. The main intention is to provide data for a future re-evaluation of a possible complex of species that inhabit different estuarine regions along the Western Atlantic, of which this species is part. The new species can be easily distinguished by its small size, well-developed anal canal, simple sculpture, stubby periumbilical keel, and an orange aperture bearing poorly developed riblets. Anatomically, the set of distinctive features include an anal flap at the mantle edge, elongated radular teeth, strong asymmetry of salivary glands, a lack of accessory salivary glands, a pair of gastric ducts to the digestive gland, a relatively small and simple penis, and a pallial oviduct lacking a bursa and other chambers. The significance of these findings is still obscure because these characters are unknown in allied species, but provisionally, the genus *Thaisella* appears to be exclusively American (mostly Atlantic), always associated with an estuarine environment, and possessing geographically restricted species.

Key words. Anatomy, morphology, Rapaninae, taxonomy, new species.

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Introduction

The genus *Thaisella* Clench, 1947 (Muricidae, Rapaninae), type species by original designation *Purpura trinitatensis* Guppy, 1869, is sometimes considered a subgenus of *Thais* Röding, 1798. It is mainly characterized by the presence of a strong and stubby keel surrounding a pseudoumbilicus (Clench 1947: 69, Claremont et al. 2011).

The genus *Thaisella* encompasses just six species, which are usually associated with an estuarine environment. In the Western Atlantic, only three species are recognized as valid: 1) *T. coronata* (Lamarck, 1816), which actually was described from Senegal, West Africa, but has been reported to occur at some locations in northern South America and southeastern Brazil; 2) *T. trinitatensis*, with type locality in Trinidad, but with records from Guatemala to southern Brazil, including a synonym, *T. brujensis* (Smith 1946: 61, as subspecies of *T. coronata*), from the Atlantic side of the Canal Zone, Panama (Bruja Point); and 3) *T. mariae* (Morretes 1954), from southern São Paulo to northern Santa Catarina, Brazil (Marini 1988).

Despite the current taxonomy, the identification of Western Atlantic *Thaisella* is not easy, as several different conchological phenotypes occur, including variants with restricted distributions. Most of the identifiable samples came from estuarine areas, with some samples showing great tolerance, for a neogastropod, to freshwater and, for example, occurring even in rice plantings of Marajó Island, Pará, Brazil (unpublished data). All these euryhaline samples are the subject of ongoing comparative and taxonomical study to possibly show that each of the isolated estuarine regions of the Brazilian coast could harbor an exclusive species. As such, only the three species mentioned above are so far formally described. A similar study documented the division of species of a related genus, *Stramonita* Schumacher, 1817, which occurs only in fully marine, stenohaline habitats. That study described the Brazilian population previously known as *S. haemastoma* Linné, 1767 as *S. brasiliensis* Claremont & Reid, 2011 (Claremont et al. 2011).

The present paper is based on samples, collected by the naturalist José Coltro Jr. and his team, of a population that supposedly represents *Thaisella trinitatensis* at its northern distributional limit along the Caribbean coast of Guatemala (Clench 1947). The distinctive conchological and anatomical characters that are reported, and which define the new species, will serve as the basis for future

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comparisons with samples collected from other areas.

As typical muricids, *Thaisella* are predators, preying on other shelled invertebrates. They have an ability to penetrate the shells of their prey by means of the accessory boring organ (ABO), a gland located in the anterior region of foot sole. The ABO is used to perforate the shell of prey, allowing the subsequent introduction of the proboscis for prey consumption. The ABO has been theorized to be homologous to the cement gland (or ventral pedal gland), which occurs only in females of most neogastropods and higher apogastropods (Simone 2011).

Material and Methods

The specimens were fixed in 70% EtOH and deposited in the Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP). Dissections were performed by standard techniques, a stereomicroscope, with the specimen immersed in fixative. For the extraction of soft parts, some shells were broken. All drawings were made with the aid of a camera lucida. Most dissection steps were digitally photographed. Radulae of three specimens were also examined in a scanning electron microscope in the Laboratório de Microscopia Eletrônica do Museu de Zoologia da USP. All specimens were dissected. The holotype of *Thaisella trinitatensis* is also illustrated (Figs 14–16) to allow comparisons of the shell.

In the figures, the following abbreviations are used: **aa**, anterior aorta; **ae**, anterior esophagus; **af**, afferent gill vessel; **ag**, albumen gland; **al**, anal flap of mantle border; **an**, anus; **ap**, female aperture; **au**, auricle; **bg**, buccal ganglion; **bm**, buccal mass; **br**, subradular membrane; **bv**, blood vessel; **ce**, cement gland and accessory boring organ (ABO); **cg**, capsule gland; **cm**, columellar muscle; **cp**, cerebro-pleural ganglion; **cv**, ctenidial vein; **dd**, duct to digestive gland; **df**, dorsal inner folds of buccal mass; **dg**, digestive gland; **di**, diaphragmatic septum; **es**, esophagus; **ey**, eye; **fs**, foot sole; **ft**, foot; **gd**, duct of gland of Leiblein; **gi**, gill; **gl**, gland of Leiblein; **gm**, gill muscle; **ha**, haemocoel; **hg**, hypobranchial gland; **in**, intestine; **jw**, jaw and peribuccal muscles; **kd**, kidney dorsal lobe; **ki**, kidney; **km**, membrane between kidney and pallial cavity; **m1**–**m6**, buccal mass and odontophore muscles; **mb**, mantle border; **md**, muscles at base of odontophore connecting it with proboscis; **me**, middle esophagus; **mj**, peribuccal muscles; **mo**, mouth; **ng**, nephridial gland; **ne**, nephrostome; **nr**, nerve ring; **oa**, opercular pad; **oc**, odontophore cartilage; **od**, odontophore; **op**, operculum; **os**, osphradium; **ot**, oral tube; **ov** pallial oviduct; **oy**, ovary; **pb**, proboscis; **pc**, pericardium; **pd**, penis duct; **pe**, penis; **pg**, pedal gland furrow; **po**, posterior esophagus; **pt**, prostate gland; **pu** pedal ganglion; **ra**, radula; **rm**, proboscis retractor muscle; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **rv**, afferent renal vessel; **ry**, rhynchostome; **sa**, salivary gland aperture; **sb**, subesophageal ganglion; **sc**, subradular cartilage; **sd**, salivary duct; **sg**, left salivary gland; **si**, siphon; **sp**, supraesophageal ganglion; **sr**, right salivary gland; **st**, stomach; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **vd**, vas deferens; **ve**, ventricle; **vf**, ventral buccal platform; **vl**, valve of Leiblein; **vo**, visceral oviduct.

Systematics

Thaisella guatemalteca new species

Figures 1–13, 17–36

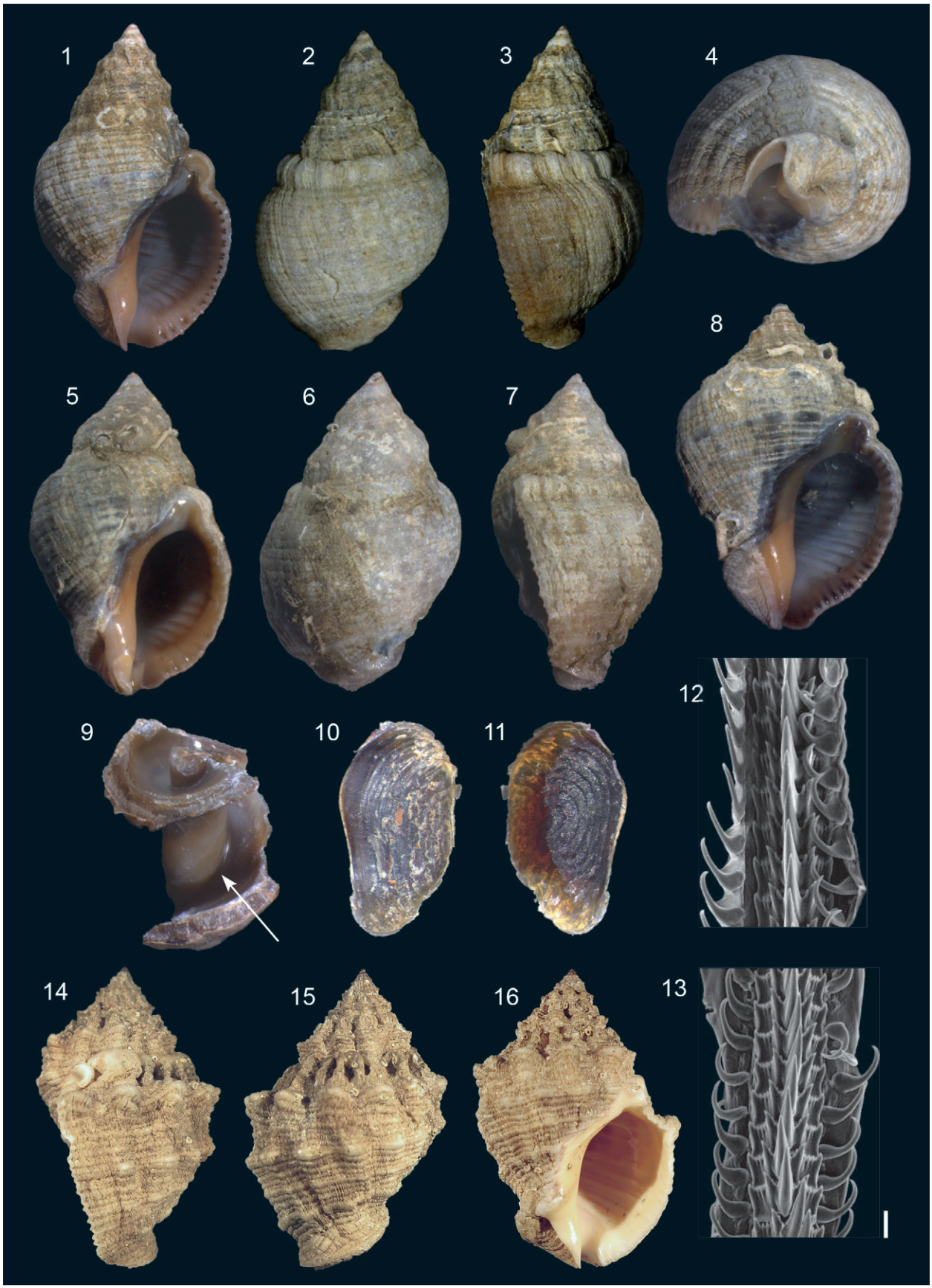
Thais (Thaisella) trinitatensis — Clench 1947: 69–71 (part) (non Guppy, 1869).

Types. Holotype MZSP 121000. Paratypes: MZSP 116688, 4♂, 5♀ from type locality.

Type locality. Guatemala: Department of Izabal: Puerto Barrios, 15° 44′ 29.52″ N, 88° 35′ 58.72″ W (José Coltro Jr. collector, vi.2014).

Diagnosis. Size small (less than 30 mm), anal canal well developed, sculpture simple, almost obsolete spiral cords; periumbilical keel stubby; subsutural scales absent or restricted to final ¼ whorl; aperture orange, bearing poorly developed riblets. Anal flap at the mantle edge; radular teeth mostly elongated; salivary glands strongly asymmetric; accessory salivary glands absent; pair of gastric ducts to digestive gland; small and simple penis; pallial oviduct lacking bursa and other chambers.

Shell (Figs 1–9). Size up to 30 mm, outline elliptical, fusiform. Spire conic, as long as aperture. Up to 6 slightly convex whorls. Color uniform brownish gray. Protoconch eroded, not seen. Sculpture relatively uniform spiral cords, interspaces very narrow, distal edge flattened, about 15 on last whorl, 5 or 6 on penultimate whorl; subsutural furrow shallow, located c. ⅕ whorl below suture (Figs 2, 3, 6, 7); in larger specimens last ¼ whorl of space between subsutural furrow and adjacent suture filled by weakly developed scales (Figs 3, 7), forming anal canal at aperture (Figs 1, 5, 8). Umbilicus flanked at left by stubby, strong carina (Figs 1, 4, 5, 8), with anterior ⅓ of inner lip as right edge; shallow and wide furrow between umbilical carina and dorsal surface of last whorl (Fig. 4). Aperture elliptical, slightly prosocline (Fig. 3, 7), as long as spire, c. ½ shell width, roughly twice as long as wide. Anal and siphonal canal of approximately same width, c. ⅕ aperture width at middle (Figs 1, 5, 8); inner surface glossy, orange to reddish orange, interior of outer lip with c. 10 spiral riblets, well-spaced, uniformly distributed, disappearing at some distance from outer lip, occluded by elongated callus lying parallel to outer lip edge. Outer lip with c. 16 small teeth, uniformly distributed, extending slightly beyond lip; interspaces between successive teeth about their same width, normally possessing brown pigment (Figs 1, 8); anal and siphonal canals lacking teeth



Figures 1–13. *Thaisella guatemalteca* shells. **1–4.** Holotype, MZSP 121000 (length, 28.7 mm). **1.** Frontal view. **2.** Dorsal view. **3.** Right view. **4.** Anterior view. **5–7.** Paratype MZSP 116688-1 (length, 27.8 mm). **5.** Frontal view. **6.** Dorsal view. **7.** Right view. **8.** Paratype MZSP 116688-2 (length, 22.9 mm), frontal view. **9.** Fragment of columella of paratype MZSP 116688-2, arrow showing siphonal groove. **10.** Operculum, outer view (length, 8.3 mm). **11.** Same, inner view. **12.** Radula in SEM, detail of middle region. **13.** Same, another specimen, scale bar = 20 µm. **14–16.** Holotype of *Thaisella trinitatensis* MCZ 177755 (Museum of Comparative Zoology, Harvard University) (length, 45.1 mm). **14.** Right view. **15.** Dorsal view. **16.** Frontal view.

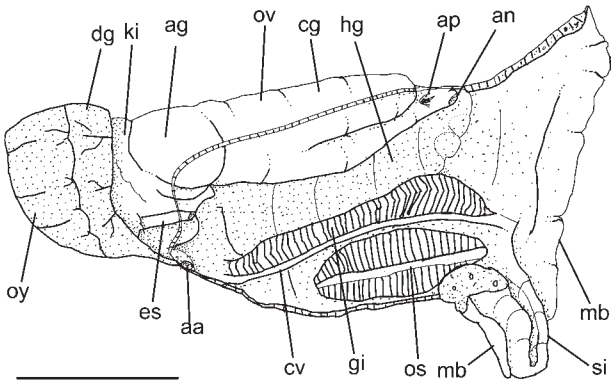


Figure 17. *Thaisella guatemalteca*, pallial cavity, ventral view, adjacent region of visceral mass also shown. Scale bar = 5 mm.

on edges. Inner lip gradually concave, simple, smooth; callus narrow, weakly extending beyond aperture. Wide furrow along anterior margin of columella (Fig. 9: arrow), corresponding to left component of columellar muscle.

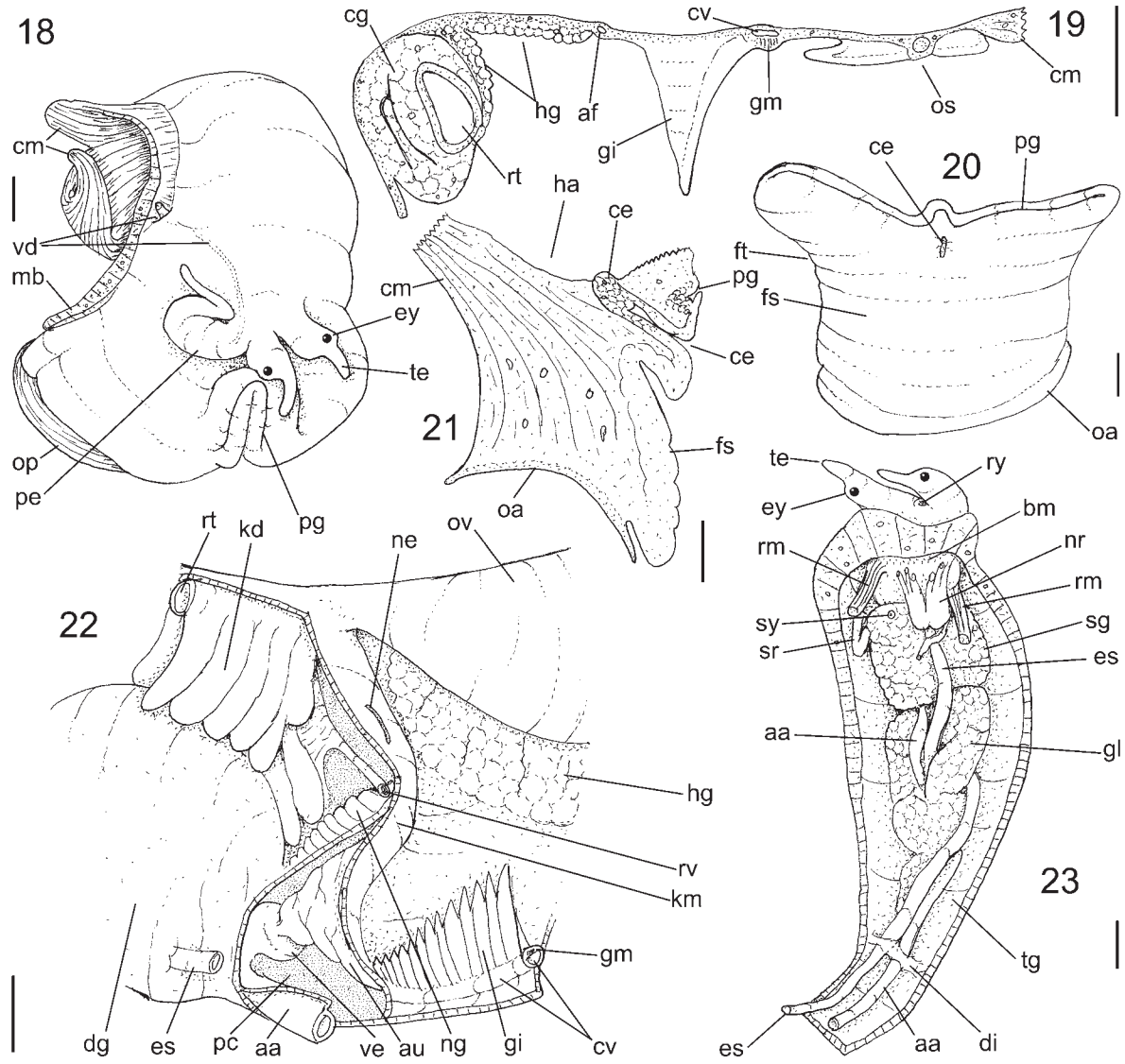
Head-foot (Figs 18, 20, 21). Head not protruded, small (c. ¼ local head-foot width). Tentacles stubby, broad, flat, basal half clearly broader than distal half; length c. ⅓ local width of head-foot, close to each other (Figs 18, 23: te). Eyes dark, small, situated in middle region of outer edge of tentacles (ey). Rhynchostome as small, transverse slit; located between, slightly ventral to tentacles (Fig. 23: ry). Foot large, wide, c. ½ whorl in length. Anterior furrow of pedal glands (pg) spans anterior foot edge. Columellar muscle thick, c. ¾ whorl long, posterior region bifid (Fig. 18: cm), left component slightly longer and narrower than right. Haemocoel long, c. 5× longer than wide, c. ⅓ width of adjacent head-foot (Fig. 23); diaphragmatic septum thin, located posteriorly at haemocoel. Accessory boring organ (ABO) very narrow and relatively deep (c. ¼ foot thickness), more developed in females, because of association of cement gland (Fig. 21: ce), with no clear distinction between them.

Operculum (Figs 10, 11). Suboval, planar, occupying entire aperture. Superior edge rounded; inferior edge broadly pointed, internally turned; inner and outer edges somewhat uniformly rounded. Outer surface opaque, mostly smooth; conspicuous scales parallel to inner edge. Nucleus in middle level of outer margin. Inner scar occupying about 70% of inner surface, somewhat dislocated internally; scar bearing concentric, somewhat uniform undulations. Outer margin glossy, uniformly wide along operculum length of c. ¼ opercular width.

Mantle organs (Figs 17, 19). Pallial cavity length c. 1 whorl. Mantle border simple, slightly thick. Siphon (si) width c. ⅓ free portion of mantle edge, c. ¼ whorl long; siphonal base low, simple (Fig. 17: si). Osphradium (os) elliptical, osphradium length c. ⅓ of pallial cavity length, osphradium width c. ⅓ of pallial cavity roof width. Osphradium leaflets low (height c. ¼ their width); tip bluntly pointed, turned externally; right filaments slightly longer and more pointed than left filaments (Fig. 19: os). Anterior end of osphradium well-separated from gill, reaching half-way across base of siphon. Osphradium nerve inserting in osphradium ganglion approximately in its middle region. Area between osphradium and gill narrow. Ctenidial vein (cv) narrow, uniformly wide along its length. Ctenidial longitudinal muscle covering c. ¾ of ctenidial vein ventral surface (Figs 19, 22: gm). Gill elongated, narrow, c. 85% of pallial cavity length, c. ¼ its width. Anterior end of gill pointed; gill increasing somewhat abruptly towards posterior; uniformly wide along most its length except for slightly broader anterior quarter (Fig. 17: gi). Posterior end of gill pointed, close to posterior end of pallial cavity and pericardium (Fig. 22: gi). Gill filaments triangular, c. ½ pallial cavity height, their apices almost central, feebly turned to right, left and right edges straight. Afferent gill vessel very narrow, edging gill right margin. Area between gill and right pallial organs about as wide as gill. Hypobranchial gland (hg) relatively thick, surface uniform, pale to dark purple; covering most of area between gill and right pallial structures and part of them (Fig. 19: hg). Right edge of pallial cavity mostly filled by gonoducts. Rectum narrow, running in right edge of cavity dislocated to left by gonoducts (Fig. 19: rt). Pallial gonoducts described below. Anus (an) sessile in females (Fig. 33), slightly siphoned in males (Fig. 34), located posteriorly to mantle border at c. ¼ length of pallial cavity (Fig. 17).

Visceral mass (Figs 17, 21). Of about 3.5 whorls posterior to pallial cavity. Somewhat triangular, narrowing abruptly. Digestive gland pale beige, surrounding stomach, extending from first whorl to kidney-pericardium. Gonad orange, situated in columellar and right surfaces of digestive gland, extending from first whorl to half whorl posterior to stomach.

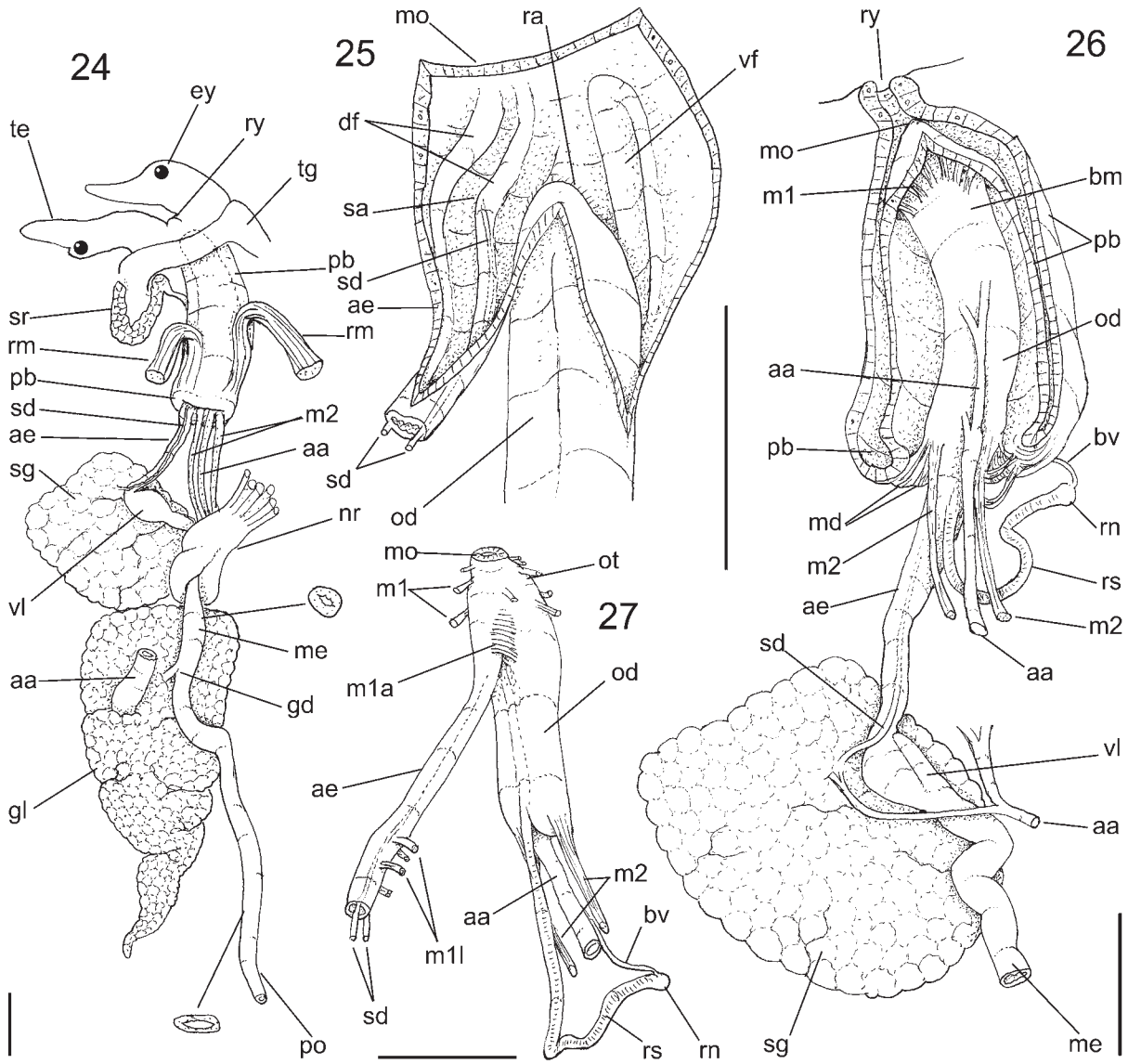
Circulatory and excretory systems (Fig. 22). Reno-pericardial region somewhat triangular, with wider region right, c. ⅓ whorl; forming anterior end of visceral mass, partly exposed to pallial cavity. Heart occupying c. ⅓ left reno-pericardial region, situated just posterior to gill in anterior-left limit of visceral mass. Auricle (au) anterior to ventricle, connected to ctenidial vein in its left-anterior side, and to reno-pericardial aperture in right side, attached to anterior pericardium wall with pallial cavity. Ventricle (ve) spherical, connected to aortas in its posterior-left side. Aortas narrow, anterior aorta (aa) c. 2× size of posterior aorta, running parallel to esophagus. Kidney with somewhat elliptical outline. Renal lobe (kd) single, mostly solid; thick, septum-like, transverse glandular folds; all connected to rectum; efferent renal vessel (rv), coming from haemocoel, narrow; renal lobe cream, surface strongly transversally folded, filling c. ½ kidney inner space, not connected to ventral renal surface. Nephridial gland (ng) with c. ⅕ width of renal lobe, triangular in section; covering most of membrane



Figures 18–23. *Thaisella guatemalteca* anatomical details. **18.** Head-foot, male, frontal view. **19.** Pallial cavity roof, transverse section in middle level of osphradium. **20.** Extending foot, female, ventral view. **21.** Foot, female, transverse sagittal section. **22.** Region between pallial cavity and visceral mass, ventral view, ventral wall of kidney and pericardium removed. **23.** Head-foot, ventral view, foot and columellar muscle removed, haemocoelic structures seen as in situ. Scale bars = 1 mm.

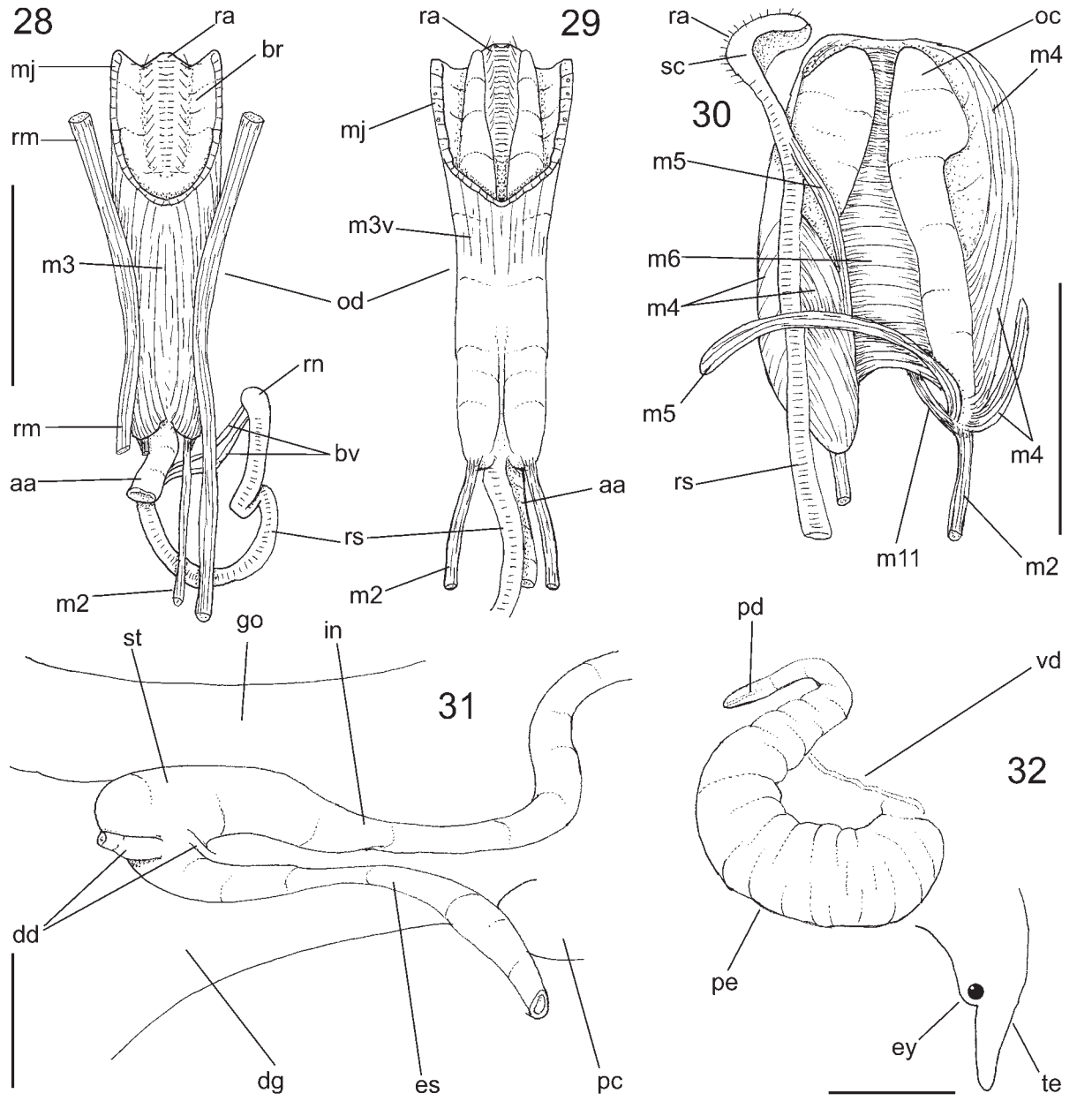
between kidney and pericardium, being wider dorsally. Nephrostome as small slit situated in left side of membrane between kidney and pallial cavity (Fig. 22: ne).

Digestive system (Figs 19–27). Rhynchostome located between both tentacles (Figs 23, 24: ry). Proboscis wide and short (c. ⅓ length and width of haemocoel), outer walls thickly muscular (Figs 23, 24). Pair of ventral retractor muscles of proboscis (rm) narrow, origin in dorsal surface of foot concentrated in right region just ventral to head (Fig. 23), running mostly embedded in inner proboscis wall, with some fibers protruding anteriorly (Fig. 28). Mouth single, central at proboscis tip. Oral tube short (c. ⅙ proboscis length) and broad, walls weakly muscular (Fig. 27: ot). Ventral smooth platform running at middle level of ventral oral tube surface (Fig. 25: vf). Pair of dorsal folds gradually appearing in dorsal inner surface of oral tube, running longitudinally towards posterior (Fig. 25: df). Surface between both dorsal folds smooth, equivalent to their width. Odontophore c. ½ length of proboscis (Fig. 26: od). Odontophore and buccal mass muscles (Figs 27–30): mj, pair of peribuccal muscles, thick layers of muscles connected at both sides of anterior-outer margin of odontophore cartilages (Figs 28, 29), running embedded in buccal mass dorsal wall; m1, jugal muscles, several pairs of small and short fibers connecting buccal mass with adjacent inner surface of proboscis (Fig. 26); m1a, small pair of lateral jugal muscles, connecting laterally anterior connection between esophageal origin and odontophore (Fig. 27); m2, pair of retractor muscles of buccal mass, origin in ventral middle level of



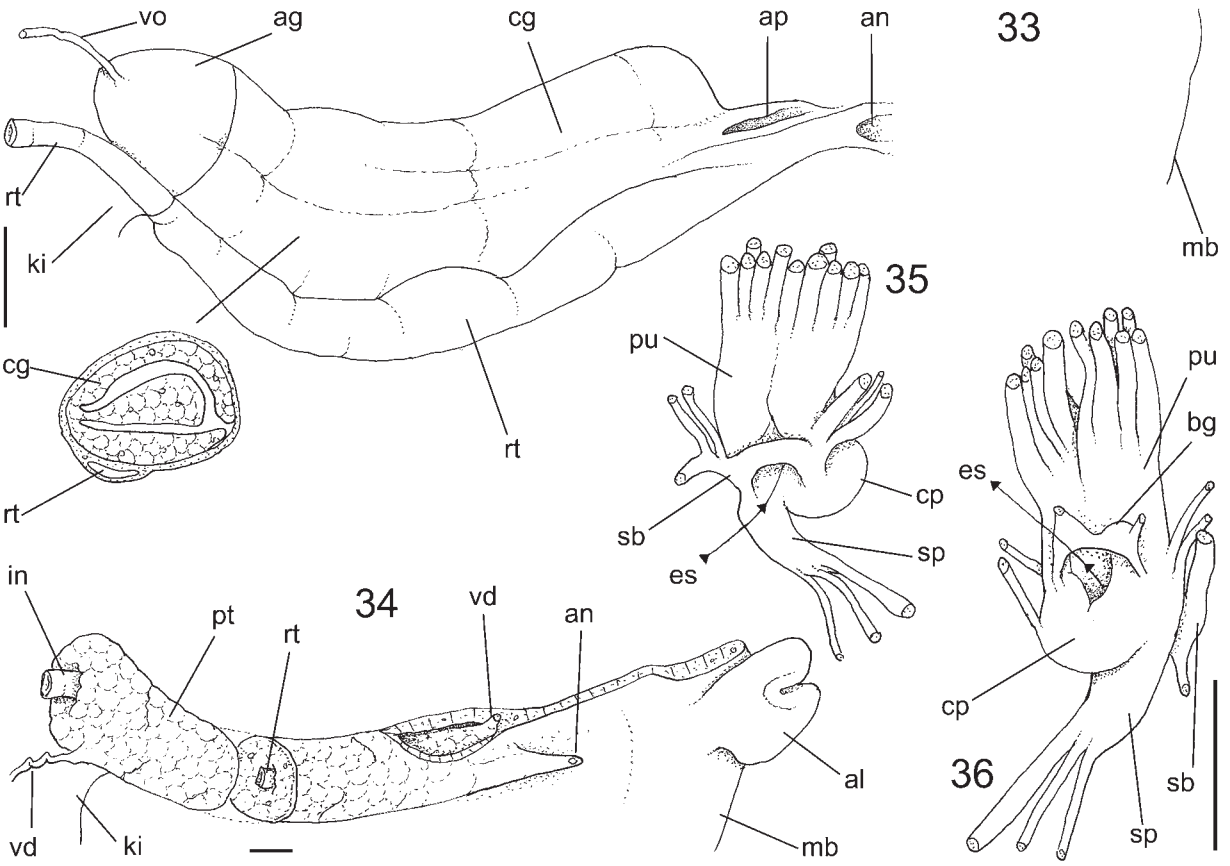
Figures 24–27. *Thaisella guatemalteca* anatomical details. **24.** Foregut, ventral view, most structures uncoiled, transverse section in two indicated levels of esophagus and topology of head also shown. **25.** Buccal cavity, right view, mostly opened longitudinally, esophagus slightly deflected. **26.** Foregut, ventral view, most structures uncoiled, contracted proboscis (pb) opened longitudinally. **27.** Buccal mass, right view, esophagus (ae) deflected. Scale bars = 1 mm.

surface of haemocoel (dorsal surface of foot sole), just posterior to proboscis retractor muscles, running longitudinally towards anterior and dorsal (Fig. 24), small portions crossing through nerve ring, entire insertion in posterior end of both odontophore cartilages (Figs 27–30); m3, thin, superficial, longitudinal, ventral muscular layer, originating in ventro-posterior region of odontophore, running anteriorly, spreading in oral tube (Fig. 28); m3v, dorsal portion of m3 connected to esophageal origin (Fig. 29); m4, pair of large, broad dorsal tensor muscles of radula, originating in outer surface of posterior end of cartilages, along c. ½ length of cartilage, covering most of cartilage surface, inserting most in subradular membrane (Fig. 30); m5, pair of auxiliary dorsal tensor muscle of radula, thin, originating in median edge of cartilages in posterior end, running towards medial and anterior, inserting along radular sac ventral portion crossing odontophore (somewhat on opposite side of m4; Fig. 30); m6, horizontal muscle, relatively thin, connecting ventral edge of both cartilages, anterior region just in anterior end of cartilages, extending c. 95% length of cartilages (Fig. 30); m11, pair of thin and narrow ventral tensor muscles of radula, origin in median-posterior end of odontophore cartilages (Fig. 30), dorsally to m5 origin, running towards anterior at some distance from median line, inserting along anterior surface of ventral region of subradular membrane. Other non-muscular odontophore structures: br, subradular membrane, thin, translucent, strong, most connected to m4 pair lateral and anterior edges, covering inner surface subradular cartilage (Fig, 28); oc, pair of odontophore cartilages, slightly flattened, long (c. 6× longer than wide), claviform, anterior



Figures 28–32. *Thaisella guatemalteca* anatomical details. **28.** Odontophore, ventral view. **29.** Same, dorsal view, radular sac only partially shown. **30.** Same, dorsal view, superficial layer of muscles and membrane removed, both cartilages deflected, radular sac removed to left, right muscles deflected to show cartilage (oc), left muscles still connected to radula. **31.** Midgut, ventral view, topology of some adjacent structures also indicated. **32.** Penis and adjacent structures, dorsal view. Scale bars = 1 mm.

end bluntly pointed, anterior ¼ clearly broader, bulging dorsally, posterior ¾ slender, narrowing gradually, posterior end rounded. Radular sac narrow and long (c. ⅕ width of odontophore, 2× length of buccal mass) (Figs 27, 28). Radular nucleus slightly expanded, connected to local portion of anterior aorta by pair of narrow vessels (Fig. 28: bv). Radular teeth (Figs 12–13): rachidian wide, occupying c. 60% width of radular ribbon, rectangular; 3 main central, pointed cusps turned posteriorly, central cusp as long as rachidian width, pair of secondary cusps c. ½ size of central cusp, bearing small cusp in middle level of their inner edge; pair of lateral cusps almost at lateral edge, c. ¼ size of central cusp; 3 small cusps between lateral and central cusps, c. ¼ of size of lateral cusp. Pair of lateral teeth narrow, slender, hook-like; base rounded, c. ¼ of rachidian width; cusp long, weakly curved, as long as rachidian; tip sharply pointed, turned posteriorly. Salivary glands strongly asymmetrical; right gland small (c. ⅒ volume of haemocoel), narrow, located in right-anterior side of haemocoel, close to base of right tentacle (Fig. 24: sr); left gland large (c. ¼ volume of haemocoel) situated just posterior to valve of Leiblein and anterior to nerve ring (Figs 24, 26: sg); pair of ducts very narrow; attaching to anterior esophagus at some distance



Figures 33–36. *Thaisella guatemalteca* anatomical details. **33.** Pallial oviduct, ventral view, some adjacent structures also shown, including topology of mantle border (mb), transverse section in indicated level of oviduct also shown. **34.** Pallial portion of male structures, ventral view, transverse section artificially done in middle level of prostate (pt), some adjacent structures also shown. **35.** Central nervous system (nerve ring), ventral view. **36.** Same, dorsal view. Scale bars = 1 mm.

anterior to valve of Leiblein (Fig. 26: sd), gradually becoming embedded in anterior esophageal wall (Fig. 25: sd), running along dorsal folds (df); salivary aperture at middle level of inner edge of dorsal folds (Fig. 25: sa). No accessory salivary glands.

Anterior esophagus relatively wide and long (Figs 26, 27: ae), with about same length as proboscis, inner surface smooth with a pair of low and narrow longitudinal folds in anterior region (Fig. 25: df). Valve of Leiblein weakly wider than surrounding esophagus, anterior half rounded, posterior half conical (Fig. 26: vl), oblique bypass present as narrow furrow. Middle esophagus about same width as anterior esophagus (Figs 24, 26: me), c. ½ its length; wall uniformly thick glandular. Gland of Leiblein occupying c. ⅓ volume of haemocoel, anterior region broad and flat, gradually tapering posteriorly, posterior end very narrow, sharply pointed (Figs 23, 24: gl). Duct of gland of Leiblein (gd) narrow, situated at some distance from gland anterior end. No "gland framboise" (see Simone 2011). Posterior esophagus narrow, walls thin, about same length as anterior esophagus (Figs 24, 31: po) inner surface with 7 or 8 narrow, longitudinal folds; uniformly wide along its length.

Stomach a simple curve (Fig. 31: st), width equal to esophagus, located c. ⅓ whorl posterior to kidney, immersed in digestive gland. Inner surface smooth, simple. Paired ducts to digestive gland simple, posterior duct situated in posterior gastric curve, about same intestinal width, running towards posterior; anterior located in intersection esophagus-intestine, c. ½ width of posterior duct, turned anteriorly and slightly left (Fig. 31: dd). Intestine as wide as esophagus, almost straight, running along right region of visceral mass anterior, crossing through ventral region of renal lobe (Fig. 31: in). Digestive gland, rectum, and anus described above.

Genital system. Male. Visceral vas deferens running from testis (described above) along middle region of visceral last whorl, on columellar surface. Seminal vesicle scantly coiled, located in mid-ventral region of last whorl of visceral mass only running in weak zigzag (Fig. 34: vd). Vas deferens narrow, simple and straight along ventral wall of kidney, exiting to pallial cavity in its middle-posterior edge. Prostate gland c. ½ length of pallial cavity, c. ⅒ its width (Fig. 34: pt); walls glandular, iridescent, narrowing gradually towards anterior lacking clear separation from remaining anterior vas deferens. Rectum narrow, running along prostate middle region (Fig. 34: rt). Vas deferens crossing to pallial floor in region just posterior to anus,

lying attached to floor surface, almost straight up to penis base (Figs 18, 32: vd); pallial vas deferens entirely closed (tubular). Penis with c. ⅙ pallial cavity volume, broader in basal and middle regions, somewhat flattened; base curved; apical region c. ⅓ length of penis, narrowing abruptly, normally curving away from basal and middle region (Figs 18, 32: pe); apical papilla narrow, c. ⅛ length of penis and width of base. Penis duct c. 1/20 larger width of penis, weakly coiled, running along central penis region (Fig. 32: pd), opening at papilla tip.

Female (Figs 17, 33). Visceral structures similar to those equivalent of males. Visceral oviduct very narrow, inserting at left side of ventro-posterior region of albumen gland (Fig. 33: vo). Pallial oviduct massive (Fig. 17: ov), c. ⅔ length of pallial cavity and c. ⅓ its width. Albumen gland (ag) irregularly spherical, flat, walls thick, white; c. 1/4 total length of pallial oviduct; inner duct broad and flat, continuous to that of capsule gland. Capsule gland (cg) long (c. ⅔ length of pallial oviduct), as wide as albumen gland, widely connected to it; walls thick glandular, with central, tall, glandular, longitudinal fold (Fig 33: section detail), pale beige. Capsule gland anterior end narrowing abruptly, forming short region (c. ⅛ length and width of pallial oviduct) with thinner walls, as female aperture (Figs 17, 33: ap). Bursa copulatrix lacking. Female aperture antero-posteriorly elongated, located close and posterior to anus (Fig. 33: ap).

Central nervous system (Figs 35, 36). Located in anterior region of haemocoel, at proboscis base (Figs 23, 24: nr). Nerve ring volume c. 1/20 volume of haemocoel. Ganglia highly concentrated. Pair of cerebral and pleural ganglia totally fused (cp). Pair of pedal ganglia (pu) widely connected with each other and to remaining main ganglia as large as cerebro-pleural pair. Supraesophageal ganglion (sp) close to nerve ring, c. ½ size of a pedal ganglion. Subesophageal ganglion (sb) as part of ring connecting ventrally both cerebro-pleural ganglia. Pair of buccal ganglia (bg) close to each other and to dorsal surface of nerve ring. Statocysts not found.

Measurements (in mm). Holotype: 28.7 × 18.0; paratype MZSP 116688-1: 27.8 × 17.6 (Figs 2–4)

Geographic distribution. Only known from the type locality.

Habitat. Intertidal rocks, estuarine. On dark-colored rocks that reach high temperature with insolation.

Material examined. Types.

Discussion

The generic attribution of *Thaisella guatemalteca* is based mainly on the presence of the well-developed ridge that borders the umbilical region and forms a strong and stubby keel surrounding a pseudoumbilicus (Clench 1947: 69, Claremont et al. 2011) (Figs 1–8). Additionally, *Thaisella* is characteristic of estuarine environments, which has not been emphasized previously.

Thaisella guatemalteca can be distinguished easily from *T. trinitatensis* (Figs 14–16) by its much simpler sculpture. The main sculpture consists only of spiral, uniform cords lacking any sign of scales on and between them (Figs 1–8), which are clearly present in *T. trinitatensis*. *Thaisella guatemalteca* also lacks the set of strong transverse subsutural region scales present in *T. trinitatensis* (Figs 14, 15). Closely spaced scale-like features may be present in larger specimens of *T. guatemalteca*, in the region preceding the aperture (Figs 2, 3, 7), and they form a small carina flanked by a shallow groove, which runs parallel to the superior suture (Figs 2, 3, 6, 7). This carina corresponds to the anal notch in the aperture (Figs 1, 5, 8). The anal notch is in the same plane of the aperture lips in *T. guatemalteca* (Figs 3, 7) but elevated in *T. trinitatensis* (Fig. 14). This elevation of the anal notch of *T. trinitatensis* forms during shell growth the distinguishing subsutural scales. The size also differentiates these species, as *T. guatemalteca* is not larger than 30 mm, while *T. trinitatensis* easily reaches 50 mm, comparing specimens with the same number of whorls. The operculum of *T. guatemalteca* is slightly more elongated (Figs 10–11) than that of *T. trinitatensis* (Clench 1947: fig. 32-2).

Thaisella guatemalteca also differs from *T. coronata*, from the tropical Eastern Atlantic, and from *T. kiosquiformis* (Duclos, 1832), from West Panama, in lacking the development of the subsutural scales. Additionally, it differs from *T. coronata* in having a more elongated spire, and from *T. kiosquiformis* in a having shorter spire with a shallower suture.

Thaisella mariae appears to be the southernmost species of the genus, and was redescribed by Marini (1988), revalidating the species that had been in the synonymy of *Thais haemastoma* (presently *Stramonita brasiliensis*). *Thaisella guatemalteca* differs from *T. mariae* mainly in lacking high nodes in the sculpture and having a subsutural carina and more developed anal notch at aperture. Both species are similar in size and color. *Thaisella mariae* appears to be the species with higher freshwater tolerance, occurring in low salinity in estuaries between the states of São Paulo and Paraná, where it seems to be endemic. Prior treatment as a synonym of *S. brasiliensis* was based on the similarity with some variants of that species, which is highly variable in shell attributes, as well as on unfamiliarity with the biology of *T. mariae*.

Comparing several lots of both *Thaisella* and *Stramonita*, shell variability appears low in *Thaisella*. Shell variation obviously exists but not to the same degree as in *Stramonita*.

Thaisella guatemalteca has some distinctive anatomical features when compared to other muricids (Harasewych 1984, Vermeij & Carlson 2000, Domínguez-Ojeda et al. 2015). Distinctive is the absence of accessory salivary glands, which are present in other muricids. On the other

hand, in *T. guatemalteca* the pair of salivary glands are clearly asymmetric. The left salivary gland is located close to the nerve ring, and has a normal shape (Figs 23, 24: sg), while the right one (sr) is small and displaced in the anterior-right corner of the haemocoel. Possibly this division of both salivary glands compensates for the loss of the accessory salivary glands. Most muricids possess the framboise gland (Pastorino 2002), which appears to be a vestige of the ventral esophageal gland of some higher caenogastropods, of which the gland of Leiblein is the homologue (Simone 2011). The framboise gland appears to be absent in the rapanines, and *T. guatemalteca* is not an exception. Another unique feature of *T. guatemalteca* is the simplicity of the pallial oviduct, lacking developed ingesting gland and bursa copulatrix. Only the albumen and capsule glands are distinguishable, with a tall inner longitudinal fold in the former (Fig. 33). Given the present level of knowledge, it is not possible to determine whether the anatomical distinctions of *T. guatemalteca* are consistent with species, genus or subfamily levels. No complete anatomical information is available for any other *Thaisella* species, and it is weak even in Rapaninae as a whole (Harasewych 1984). The penis of *T. guatemalteca* is similar to that of *T. mariae* (Marini 1988: fig. 3) but differing in having much a shorter terminal papilla. The rachidian has the cusps much more elongated in *T. guatemalteca* than in *T. mariae* (Marini 1988: fig. 8); in fact, it resembles the rachidian cusps of *Semiricinula bozzettii* (Houart & Héros 2013: fig. 8C).

The present description contributes to the complex biology of the genus *Thaisella*, whose species are enigmatically adapted to the estuarine environment. The data suggest that descriptions are needed for more species within the genus, which encompasses a set of endemic species, related to the evolution of estuarine clusters along the coast of Central and South America.

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