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Review of *Pugilina* from the Atlantic, with description of a new species from Brazil (Neogastropoda, Melongenidae)

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ABSTRACT

The anatomy of Brazilian and African specimens of *Pugilina morio*, a supposedly amphi-Atlantic species, is described in detail in this paper. Two different entities are recognised. The first is the true *Pugilina morio*, which is now restricted to the western African coast, from Senegal to Congo. The remaining species is *Pugilina tupiniquim* sp. n., described herein as the single Brazilian melongenid species known so far, distributed from the Caribbean to Brazil (Pará to Santa Catarina states). The two species showed important anatomical discrepancies, and differ in the position of the tentacles, size of the neck, diameters of the aortas, diameter of the posterior oesophagus, and other features described below. A bursa copulatrix and rachidian teeth bearing a central cusp are both exclusive to *P. morio*.

KEY WORDS: Mollusca, Neogastropoda, anatomy, Melongenidae, Brazil, Africa, new species.

INTRODUCTION

Members of the family Melongenidae (Neogastropoda) commonly live in muddy and sandy bottoms, with some taxa predominantly inhabiting estuaries and bays. Though frequently referred to as scavengers, melongenids are active predators of bivalves and other gastropods (Morton 1953; Hathaway & Woodburn 1961). Males tend to be smaller and reach sexual maturity before females (Kumar *et al.* 1988; Matthews-Cascon *et al.* 2011). Melongenids had their radiation and diversity apogee in the Upper Cretaceous, but such diversity has gradually decreased since then (Taylor *et al.* 1980). The vast majority of recent melongenid species were described in the first half of the eighteenth century (Bayer 1952), including pre-Linnaean taxa. The family encompasses two subfamilies: Melongeninae, with a global, primarily Tropical distribution represented in this paper by *Pugilina morio* (Linnaeus, 1758); and Busyconinae, which is restricted to temperate waters of the northeastern Atlantic (Harasewych 1998), and is now regarded as a subfamily of Buccinidae (Bouchet *et al.* 2005).

Melongenids are similar to Buccinidae and Fascioliariidae in general appearance and anatomical organisation, and are grouped with them within Buccinoidea (Kantor 1996). A long, narrow head with short tentacles and distal rhynchostome is unique to melongenids, but other exclusive anatomical attributes are reported in the literature, such as the absence of the valve and gland of Leiblein, an extremely long and narrow proboscis with a set of exclusive retractor muscles, and the presence of a typhlosole in the stomach (Kosyan & Kantor 2004).

The single melongenid species occurring in Brazil known so far, *Pugilina morio* (Linnaeus, 1758), inhabits low salinity areas such as intertidal mud flats and mangroves close to river mouths. It supposedly occurs in the western Atlantic from the Caribbean to Brazil. Interestingly, it is reported as an amphi-Atlantic species that also occurs on the western African coast (Abbott 1974), where its type locality was established by subsequent designation (Clench & Turner 1956).

In this paper a comparative anatomical study of samples of *P. morio* belonging to both sides of the Atlantic is conducted. The anatomical distinctions between the African samples (the true *P. morio*) and the western Atlantic samples allow for the recognition of two different entities. The new western Atlantic species is formally described below.

MATERIAL AND METHODS

A list of examined specimens follows each species description. Shells were broken prior to soft-part extraction. Specimens were immersed in 70% ethanol and dissected by standard techniques under a stereomicroscope. The terminologies of Arnold (1965) and Simone (2011) were employed for shell characterisation, and Diver's (1939) whorl counting method was applied for all our specimens. Radula details were examined under scanning electronic microscope (SEM) at the Instituto de Biociências da Universidade de São Paulo (IBUSP) and the Museu de Zoologia da USP (MZSP).

Abbreviations used in anatomical drawings: *aa*, anterior aorta; *ab*, albumen gland; *ae*, anterior oesophagus; *an*, anus; *au*, auricle; *br*, subradular membrane; *ce*, cerebral ganglion; *cg*, capsule gland; *cl*, cement gland; *cm*, columellar muscle; *cv*, ctenidial vein; *dd*, duct to digestive gland; *df*, dorsal fold of buccal mass; *dg*, digestive gland; *dv*, vas deferens; *ep*, posterior oesophagus; *es*, oesophagus; *fp*, female pore; *fs*, stomach folds; *ft*, foot; *ge*, suboesophageal ganglion; *gi*, gill; *go*, gonads; *gp*, pleural ganglion; *hg*, hypobranchial gland; *in*, intestine; *kd*, kidney; *ml–mll*, odontophore muscles; *mb*, mantle border; *me*, medium oesophagus; *mj*, jugal muscle; *mo*, mouth; *mp*, mouth papilla; *mt*, mantle; *nc*, neck; *ne*, nephrostome; *ng*, nephridial gland; *nr*, nerve ring; *oa*, opercular insertion; *oc*, odontophoral cartilage; *od*, odontophore; *og*, osphradium ganglion; *os*, osphradium; *ov*, pallial oviduct; *pa*, posterior aorta; *pb*, proboscis; *pd*, penial duct; *pe*, penis; *pg*, anterior furrow of pedal glands; *pp*, penial papilla; *pr*, propodium; *pt*, prostate; *ra*, radula; *rm*, retractor muscle of proboscis; *rn*, radular nucleus; *rs*, radular sac; *rt*, rectum; *rv*, afferent renal vessel; *ry*, rhynchostome; *sd*, salivary duct; *se*, siphon base fold; *sf*, siphon; *sg*, salivary gland; *st*, stomach; *sv*, seminal vesicle; *te*, tentacle; *tf*, typhlosole; *tg*, tegument; *ve*, ventricle; *vg*, vaginal atrium; *ye*, eye.

Institutional abbreviations

MNHN – Muséum national d'Histoire naturelle, Paris, France;
 MNRJ – Museu Nacional do Rio de Janeiro, Brazil;
 MZSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

TAXONOMY

Class Gastropoda
 Order Neogastropoda
 Family Melongenidae

Genus *Pugilina* Schumacher, 1817

Type species: *Pugilina fasciata* Schumacher, 1817 (= *Murex morio* Linnaeus, 1758) by monotypy.

Pugilina tupiniquim sp. n.

Figs 1–3, 6, 8, 10, 11–34, 37

Pugilina morio: Clench & Turner 1956: 185–186 (partim) (figs 69, 109); Rios 1970: 93 (pl. 26); 1985: 104 (partim) (pl. 35, fig. 457); 1994: 131 (partim) (pl. 41, fig. 563); 2009: 247 (partim) (fig. 619);

Abbott 1974: 221 (partim); Matthews-Cascon *et al.* 2011: 48–50 (pl. A–E); de Azevedo *et al.* 2012: 786–792 (non Linnaeus, 1758).

Etymology: The specific name is from the native Tupi language, and refers to the homonymous Brazilian indigenous tribe.

Diagnosis: Shell with well-developed shoulder and entire inner surface of outer lip lirate. Teleoconch sculpture consisting of spiral cords along entire surface and nodules along middle level of whorls, more conspicuous on body whorl. Gill elongated with triangular filaments, bursa copulatrix absent. Cephalic region with long neck, with two small ventral tentacles on distal end. Rachidian tooth with two similar-sized pointed cusps with a vestigial cusp between them. Penis apical papilla present.

Description:

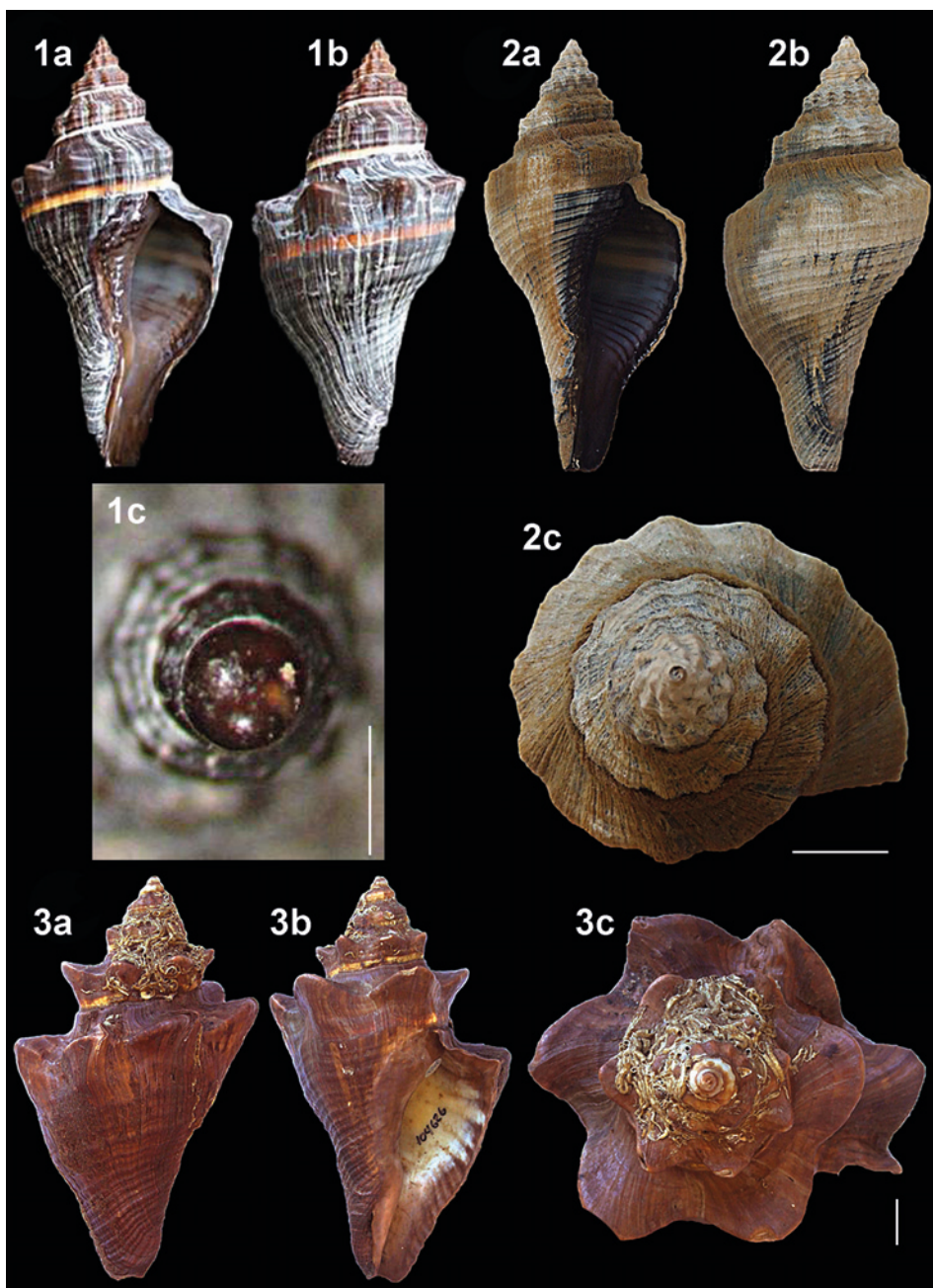
Measurements (length \times width in mm). Holotype: 81.4×41.3 ; Paratypes: 81.10×37.2 ; 83.6×36.1 ; 88.5×40 ; 89.7×31.6 .

Shell (Figs 1–3). Fusiform, \sim twice as long as wide, with about 10 convex whorls; colour dark brown with narrow yellowish spiral line. Protoconch with three whorls, smooth; colour reddish brown to amber (Fig. 3), transition well marked. Periostracum light brown, thick, hairy. Teleoconch sculpture consisting of spiral cords along entire surface; nodules along middle level of whorls, more conspicuous on body whorl. Spire angle $\sim 50^\circ$. Aperture elliptical, length $\sim \frac{1}{3}$ of shell length, width $\sim \frac{1}{2}$ shell width, normally with well-developed shoulder; entire inner surface of outer lip lirate. Anal notch small, located at posterior end of aperture. Outer lip thin and smooth, with low and wide spiral folds congruent with teleoconch sculpture. Columella straight, without folds. Siphonal canal short, length $\sim \frac{1}{4}$ of shell length.

Head-foot (Figs 11, 13, 34). Live animal black. Pallial cavity covering $\frac{2}{3}$ of total animal length, leaving cephalic region and penis exposed in males; large muscular siphon located on left, length $\sim \frac{1}{3}$ of head-foot length. Cephalic region with long neck with two small ventral tentacles on distal end; eyes located on outer side of head, anterior to tentacles. Foot large, occupying whole body whorl (retracted), slightly cylindrical; pedal gland located in central region of anterior edge of foot, forming a groove, extending from dorsum of foot (propodium) to sole. Cement gland present in females, located in medium region of mesopodium. Opercular pad occupying $\sim 80\%$ of insertion area, bearing concentric circles resembling a fingerprint. Penis originated in right lateral region, posterior to cephalic base, at same level of mantle edge. Columellar muscle wide and broad, occupying about a whorl and a half in length. Haemocoel long and narrow, extending dorsally along centre of columellar muscle.

Operculum (Fig. 8). Dark brown, corneous, oval, occupying entire aperture; nucleus terminal. Outer surface concave, opaque; inner and outer edges thin, top edge and bottom edge acuminate, outer surface lightly marked by concentric circles. Inner surface reddish brown, convex, shiny; outside edge thick, inner edge thin. Opercular scar well defined, occupying $\sim 80\%$ of inner area.

Mantle organs (Figs 15–16). Mantle cavity covering one whorl. Siphon width $\frac{1}{2}$ of mantle cavity width, length $\frac{1}{4}$ of mantle cavity length. Right base of siphon high, width about twice mantle edge width; left base gradually ending. Osphradium small, elliptical, length $\sim \frac{1}{3}$ of pallial cavity length, width $\sim \frac{1}{3}$ of its width. Osphradial filaments



Figs 1–3. *Pugilina tupiniquim*: shell. (1) Holotype MZSP: 73487, (a) apertural and (b) dorsal views (L=120 mm); protoconch, (c) apical view, scale bar = 2 mm; (2) Paratype MZSP: 116299, (a) apertural, (b) dorsal and (c) apical view (L=80 mm), scale bar = 9 mm; (3) Paratype (a) dorsal, (b) apertural and (c) apical view (L=110 mm), scale bar = 7 mm.

short, width $\sim 1/4$ of mantle edge width. Middle-anterior portion of osphradium separated from gill by small crease. Ctenidial vein (efferent branchial vessel), uniformly narrow throughout its length. Gill elongated, occupying $\sim 80\%$ of mantle cavity length and $\sim 1/3$ of its width. Anterior end of gill rounded, gradually ending, inserted directly into pallial cavity. Gill filaments subtly increasing in size towards posterior region. Posterior end of gill rounded, located in posterior region of mantle cavity and inserted into pericardium. Gill filaments triangular, occupying $\sim 1/3$ of pallial cavity height, apex central, slightly tilted to right; right edge of filament rounded; left edge triangular. Space between gill and right pallial organs about half of gill width. Hypobranchial gland light brown, thin, with uniform surface, covering half the length of the space between the gill and right pallial organs. Right side of pallial cavity almost entirely filled by gonoducts. Rectum thick, occupying $\sim 1/8$ of pallial cavity. Anus siphoned, distance between anus and border of mantle $\sim 1/3$ of total pallial cavity length. Anal gland absent.

Visceral mass (Fig. 19). ~ 2 whorls posterior to mantle cavity. Digestive gland dark beige, occupying $\sim 80\%$ of visceral mass, encircling stomach. Gonads orange with small black spots, located on columellar surface, posterior to stomach. Seminal vesicle of males located in anterior portion of gonads, $\sim 1/2$ of its size. Kidney with $\sim 1/3$ of visceral mass volume, located on right side of anterior visceral end.

Circulatory and excretory systems (Fig. 12). Reno-pericardial region occupying $\sim 1/3$ of whorl, on right margin of visceral mass, adjacent to mantle cavity; shape triangular, wider on right side compared to left margin. Pericardium occupying $\sim 1/2$ of reno-pericardial region, posterior to gill; situated on left anterior margin of visceral mass. Auricle triangular, anterior to ventricle; with three connections: on upper right side with kidney, on anterior right side with gill, and on posterior left side with ventricle. Ventricle twice as large as auricle, connected at its left posterior margin with common aorta. Aortas thick, anterior aorta twice as thick as posterior aorta. Renal lobe single, solid, with glandular transverse folds along its ventral surface; efferent renal vessel located at its right portion; colour pale-beige. Nephridial gland elliptical, width $\sim 1/3$ of renal lobe width, $3\times$ as long as wide, covering entire membrane between kidney and pericardium. Nephrostome as small, transverse slit, located in anterior region of membrane between kidney and pallial cavity.

Digestive system (Figs 14, 17–25, 28, 35, 37). Mouth transverse, narrow, with rounded papilla on its anterior end. Proboscis thick and long, occupying about half of haemocoel. Rhynchodeal wall thin and membranous, involving entire proboscis. Proboscis wall mostly thick and muscular. Five retractor muscles, three thinner originating from buccal mass, inserted on proboscis wall; pair of thick retractors, originated on dorsal surface of foot, inserted into posterior dorsal surface of proboscis. Odontophore and buccal mass muscles: *mj*, thick pairs of perioral muscles connected on both sides, dorsal and ventral, surrounding the odontophore cartilage; *m1*, jugal muscles, several small short muscles connecting odontophore surface to inner wall of proboscis; *m2*, two pairs of strong protractor muscles of buccal mass, originating on inner surface of proboscis, running along entire odontophore, between *m2b* muscles, inserting in anterior region of odontophore cartilages; *m2a*, couple of small retractor muscles of buccal mass, originating on dorsal surface of haemocoel, inserting at end of posterior margin of odontophore cartilages; *m2b*, pair of dorsal retractor muscles of buccal

mass, elongated, $\sim 80\%$ of odontophore length, originating in posterior medial edge of cartilages, extending in parallel across edges of radula, inserting along anterior ventral surface of subradular membrane; *m3*, long and cylindrical muscle forming outer wall of odontophore, with transverse fibres; *m4*, pairs of strong radular dorsal tensor muscles covering almost entire surface of posterior portion of odontophore cartilages, inserting into subradular membrane; *m5*, pair of auxiliary dorsal tensor muscles of radula, originating inside edges of cartilage, in front of *m4* insertion; *m6*, horizontal muscle, thin, almost membranous, connecting ventral edges of cartilages, running $\sim 80\%$ of their length; *m8*, pair of small elliptical muscles, $\sim 1/4$ of total length of odontophore, originating at anterior end of odontophore cartilages, running along ventral surface of odontophore, inserting on anterior ventral surface of cartilages; *m11*, pair of ventral tensor muscles of radula elongated, about 80% of total odontophore length, originating at ventral-posterior end of cartilages, crossing ventrally entire odontophore, inserting into ventral posterior surface of radula. Additional odontophore structures: *br*, subradular membrane, thin, strong and translucent, along entire length of radular ribbon, covering inner surface of odontophore cartilages; *oc*, odontophore cartilages, $\sim 4\times$ as long as wide, inner ventral surface concave, $\sim 1/5$ of anterior end fused with each other, $\sim 1/3$ of anterior region, concave, involving radular ribbon; *rs*, radular sac thin-walled, cylindrical, located at posterior end of radula; *rn*, radular nucleus width $\sim 1/2$ of radular sac width.

Radular teeth (Fig. 6). Rachidian tooth occupying $\sim 1/3$ of radula width, aligned and imbricated; base and apex rectangular with two similar-sized pointed cusps with a vestigial cusp between them, slightly angled; lateral teeth width about half width of rachidian and higher (about $3\times$ as high), base large, about half length of cusps, with two pointed cusps of differing size: a larger internal cusp and a smaller external one. *Salivary glands* (Fig. 17) located at anterior portion of haemocoel, occupying $\sim 1/4$ of haemocoel volume, involving entirely nerve ring, middle oesophagus and anterior portion of proboscis. Salivary ducts thin, slender, running in parallel to anterior oesophagus towards oral tube, presenting a dilated muscular bulb immersed in anterior oesophagus wall in the region preceding salivary aperture; bulb with about half length of oral tube, terminal region curved perpendicularly (Fig. 14); salivary openings located in dorsal wall of oral tube, in its posterior third. Valve and gland of Leiblein absent. Accessory salivary gland absent. Anterior oesophagus long and thin; walls muscular, two strong dorsal internal longitudinal folds, dilatation in anterior portion, occupying entire length of proboscis. Middle oesophagus slender, diameter half of anterior oesophagus diameter, and about half length; posterior oesophagus $\sim 80\%$ of total haemocoel length, tapering posteriorly; anterior end rounded and expanding about twice diameter of posterior end, differentiation between middle and posterior oesophagus clear (Fig. 18). Stomach reniform, located half whorl posterior to kidney; inner surface entirely pleated, possessing conspicuous fold in midline (typhlosole); two digestive gland ducts, one inserted in posterior dorsal surface, other inserting near oesophageal insertion.

Genital system. Male (Figs 26, 27). Seminal vesicle located on columellar surface of last visceral mass whorl, surrounded by gonad and occupying $\sim 1/4$ of total gonad length. Vas deferens narrow, simple, straight, running along ventral surface of kidney up to pallial cavity. Prostate totally closed (tubular), running through right mantle edge, at $\sim 2/3$ of total pallial cavity length. Vas deferens anterior to prostate, straight, running immersed

into tegument of animal dorsum next to mantle border and penis base. Penis length $\sim 1/2$ of total head-foot length, slightly flattened; base curved, apical region rounded and narrower than base. Apical papilla $\sim 1/6$ of penis length. Penial duct straight, running through centre of penis, closed (tubular), opening at papilla tip.

Female (Figs 29, 31). Pallial oviduct occupying $2/3$ of pallial cavity length and $1/3$ of its width. Albumen gland posterior, relatively spherical, whitish, thick-walled, occupying $\sim 1/4$ of pallial oviduct. Capsule gland $\sim 1/2$ of oviduct, elliptical, orange, thick-walled. Vaginal atrium anterior to capsule gland occupying $\sim 1/4$ of oviduct; walls thick, muscular, female genital pore sessile. Bursa copulatrix absent.

Spawning (Fig. 10). Capsules 10–15 mm long and 8–14 mm wide, containing 50–170 eggs. Capsules elliptical, yellowish and opaque, with output pore in their posterior region.

Central nervous system (Figs 32, 33). Nerve ring located in ventral basal proboscis region, occupying $\sim 1/4$ of haemocoel volume, highly concentrated. Ganglia mostly fused, hard to distinguish, somewhat asymmetrical. Pairs of pleural and cerebral ganglia fully fused with each other. Pedal ganglia as large as cerebro-pleural ganglia. Sub-oesophageal ganglion posterior, near the nerve ring. Statocysts not visualised.

Holotype ♂: BRAZIL. Ceará: Caucaia, estuary of Ceará River, 03°41'50.20"S 38°35'20.56"W, intertidal, ix/2011, Abbate, Simone & Lima coll. (MZSP 101902).

Paratypes: 13 specimens, same data as holotype (MZSP 116299); BRAZIL: Sergipe: Aracaju, 10°56'S 37°02'W (MZSP 104626).

Additional material examined. BRAZIL: Rio Grande do Norte: Rio do Fogo (Tavares col., xi/2009), Praia de Zumbi, MZSP 96942, 1 ♂; Foz do Rio das Conchas, MZSP 96928, 2 ♀; Porto do Mangue, MZSP 99884, 5 specimens. Paraíba: João Pessoa, Cabo da Ponta do Seixas, MZSP 41434, 3 specimens (Souza col., vii/1998), MZSP 45275, 4 specimens (Simone, 2005). Alagoas: Passo do Camaragibe, MZSP 94774, 12 specimens (Santana col., x/2009), MZSP 102909, 5 specimens (Tavares col., 27/x/2011); Barra do Camaragibe (Santana col., ix/2009), MZSP 91643, 6 specimens, MZSP 91653, 1 ♂. Bahia: Alcobaça, MZSP 73487, 1 ♀ (Bianchi col., x/2004); Itapagibe, MNRJ 7472, 10 specimens; Nova Viçosa, Ilha da Coroa Vermelha, MNRJ 8301, 4 specimens (Egipe col., i/1995). Espírito Santo: Aracruz, Praia de Santa Cruz, MZSP: 97217, 4 specimens (Abbate & Lima, i/2013).

Distribution: Caribbean and Brazil: from Pará to Santa Catarina.

Habitat: Estuarine muddy substrates at river mouths, shallow waters, sometimes over rocks, stumps and piers.

Pugilina morio (Linnaeus, 1758)

Figs 4, 5, 7, 9, 34–36, 38–44

Ancient synonymy see Dautzenberg (1921: 112–117). Complement:

Murex morio Linnaeus, 1758: 753; 1767: 1221; Hanley, 1855: 300.

Fusus brevis Müller, 1766 (pl. 11, fig. 4) [non-binominal].

Fusus morio: Röding 1798: 120.

Fusus aethiops Röding, 1798: 120.

Fusus deplanatus Röding, 1798: 121.

Fusus coronatus Lamarck, 1803: 321; 1816: 7 (pl. 430, fig. 4); Deshayes, 1832: 156.

Neptunea aethiops Link, 1807: 118.

Murex bandarius Perry, 1811 (pl. 1, fig. 5).

Murex bandatus Perry, 1811 (pl. 1, fig. 4).

Pugilina fasciata Schumacher, 1817: 216.

Pyrula morio: Reeve 1847 (pl. 1, fig 3).

Melongena morio: Tryon 1881: 111 (pl. 43, figs 228–229).

Semifusus morio: Dautzenberg 1910: 204.

Melongena (*Pugilina*) *morio*: Dautzenberg 1921: 112.

Pugilina morio: Clench & Turner 1956: 185–186 (partim); Rios 1970: 93, 1985: 104 (partim), 1994: 131 (partim), 2009: 247 (partim); Abbott 1974: 221 (partim) (Fig. 2439); Bodin *et al.* 2013: 150–157.

Type locality: Gorée Island, Senegal (SD by Clench & Turner, 1956: 185).

Diagnosis: Shell with delicate spiral sculpture on the body whorl and internal surface of the outer lip and short siphonal canal. The species showed a conchological uniformity, exhibiting only non-shouldered shells. Gill large with rounded filaments, pallial oviduct with bursa copulatrix. Cephalic region with small neck, with two small dorsal tentacles on distal end. Rachidian tooth with three pointed similar-sized cusps. Penis apical papilla absent.

Measurements. 80 mm avg.

Shell (Figs 4, 5). Fusiform approximately 3× as long as wide, with ~8 convex whorls. Protoconch not observed (eroded). Sculpture consisting of spiral cords along entire surface and rounded nodules along middle level of whorls. Spire angle ~60°. Aperture elliptical, length ~¼ of shell length, width ~⅓ of shell width, without prominent shoulder. Anal notch well defined, located at posterior end of aperture.

Head-foot (Figs 34, 40). Live animal not visualised, fixed animal dark beige. Mantle thick, covering ~⅔ of animal length, leaving cephalic region and part of penis exposed in males. Siphon large, muscular, located on the left, length ~½ of head-foot length. Cephalic region with small neck, with two small dorsal tentacles on distal end.

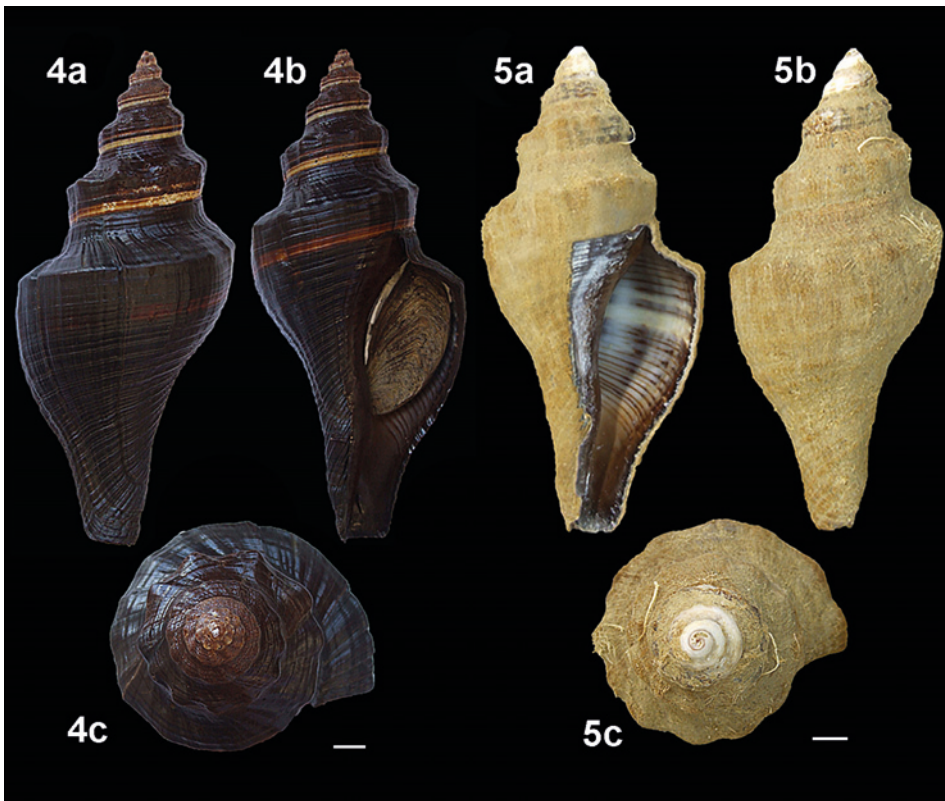
Operculum (Fig. 9). Similar to *P. tupiniquim*.

Mantle organs (Figs 36, 41, 43). Siphon general morphology similar to that of *P. tupiniquim*, differing by being longer (length ½ of mantle cavity length). Osphradium length ~⅓ of pallial cavity length and width ~¼ its width. Osphradial filaments short, width ~⅓ mantle edge width. Fold between gill and osphradium absent. Ctenidial vein thin (efferent branchial vessel), uniformly narrow throughout its length. Gill elongated and voluminous, occupying ~90% of pallial cavity length and ¼ of its width. Anterior end of gill rounded, gradually ending, inserted directly into pallial cavity. Gill filaments rounded, occupying ~⅓ of pallial cavity height; right and left edge of filament rounded. Space between gill and pallial organs size similar to gill filament length. Hypobranchial gland dark brown, thick, with uniform surface, covering half the length of the space between the gill and right pallial organs. General morphology of right side of the pallial cavity similar to *P. tupiniquim*, entirely filled by gonoducts. Rectum thick, about half the diameter of the pallial oviduct. Anus siphoned and peduncled, distance between anus and border of mantle ~⅓ of total pallial cavity length.

Visceral mass. Similar to visceral mass of *P. tupiniquim*.

Circulatory and excretory systems (Fig. 36). Characters and topology similar to *P. tupiniquim*. Aortas very thin, with similar calibre; connection between ventricle and common aorta with dilated, bulb-shaped region.

Digestive system (Figs 35, 38, 40, 42). Mouth transverse presenting a pointed papilla on its anterior end. Proboscis thin and medium-sized, occupying ~⅓ of haemocoel. Rhynchodeal wall and retractor muscles of proboscis similar to those of *P. tupiniquim*. Odontophore and buccal mass muscles *mj* to *m11* and subradular membrane very similar to those described for previous species. Only exception is the odontophore cartilage (*oc*), with ⅓ of anterior end fused.



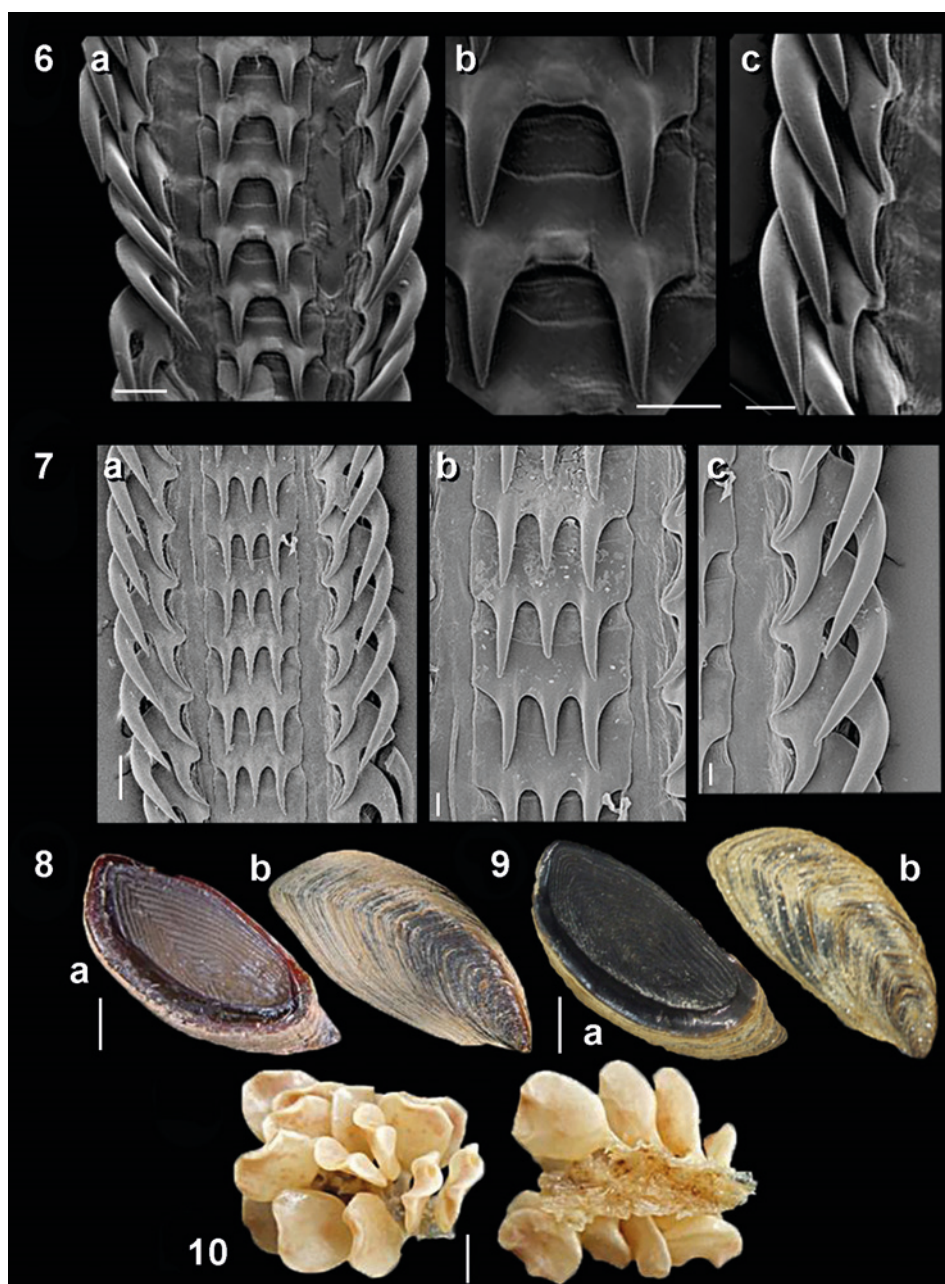
Figs 4–5. *Pugilina morio*: shell. (4) MNHN (a) dorsal, (b) apertural, and (c) apical view (L = 160 mm), scale bar = 9 mm; (5). MNHN (a) apertural, (b) dorsal and (c) apical view (L = 80 mm), scale bar = 5 mm.

Radular teeth (Fig. 7). Rachidian tooth width $\sim \frac{1}{3}$ of radula width; with three pointed, similar-sized cusps, each cusp as long as base width; outer cusps slightly arched externally; lateral teeth similar to those of *P. tupiniquim*. Anterior and middle oesophagus similar to previous species except for length, about $2.5\times$ length of anterior oesophagus; posterior oesophagus length $\sim 90\%$ of total haemocoel length, tapering posteriorly; anterior end rounded and very expanded, about $3\times$ larger in diameter than posterior end. Stomach similar to previous species.

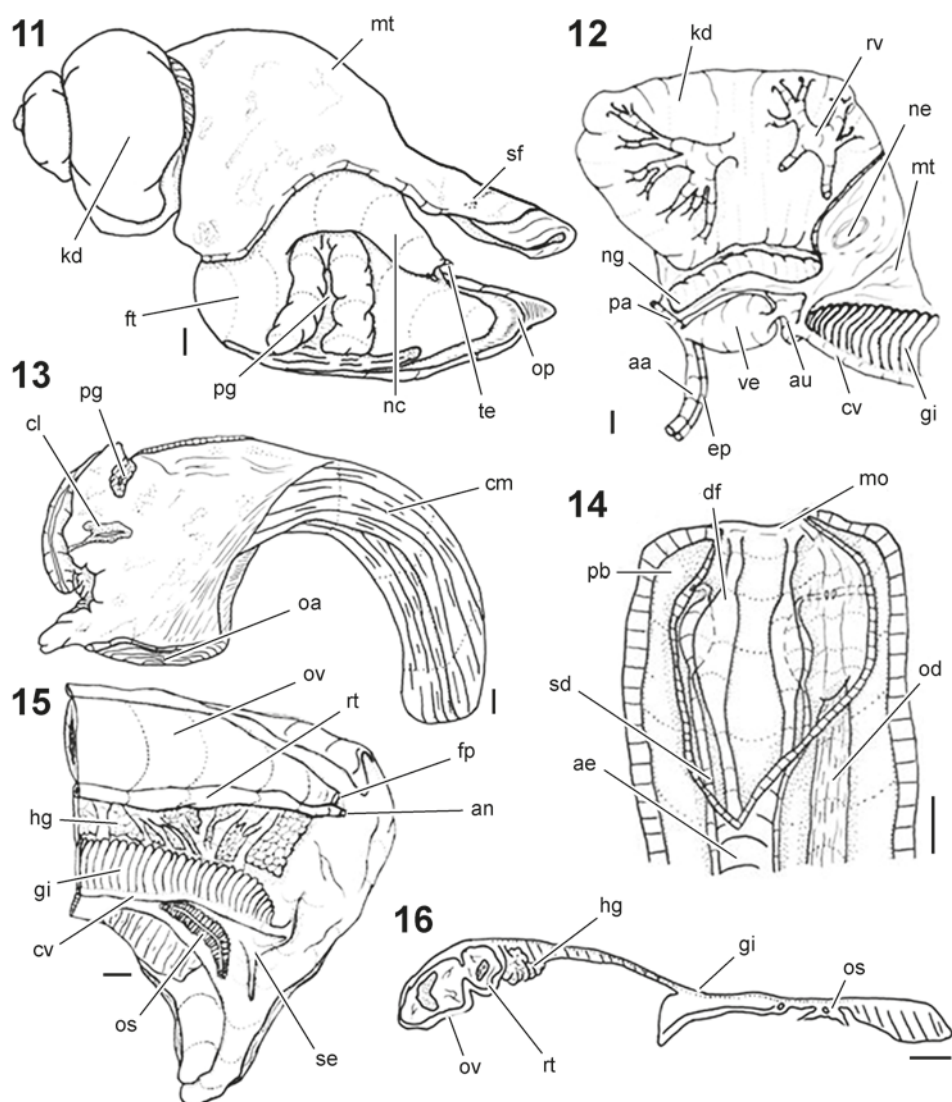
Genital system. Male (Fig. 44). Seminal vesicle and vas deferens similar to *P. tupiniquim* in anatomical features and location. Penis cylindrical, length $\sim \frac{1}{3}$ of total head-foot length, base curved, apical region rounded, narrower than base. Apical papilla absent. Penial duct straight, running through centre of penis, closed (tubular); opening located in concavity on left side of apical region.

Female (Fig. 39). Pallial oviduct occupying $\sim \frac{1}{3}$ of pallial cavity length and $\sim \frac{1}{4}$ of its width. Albumen gland posterior, spherical, whitish, thick-walled, occupying $\sim \frac{1}{4}$ of pallial oviduct. Capsule gland occupying $\sim \frac{1}{2}$ of oviduct, elliptical, orange, thick-walled; female genital pore not pedunculated. Bursa copulatrix present, with thick muscular walls.

Central nervous system. Similar to the previous species.



Figs 6–10. *Pugilina tupiniquim* and *Pugilina morio* radula, operculum and spawning: (6) *P. tupiniquim* MZSP: 91653, radula: (a) panoramic, (b) central and (c) lateral view, scale bars: (6a = 100 μ m, 6b, c = 50 μ m); (7) *P. morio*, MNHNP, radula, (a) panoramic, (b) central and (c) lateral view, scale bars: (7a = 100 μ m, 7b, c = 30 μ m); (8) *P. tupiniquim*, operculum (a) inner and (b) outer views, scale bar = 5 mm; (9) *P. morio*, operculum (a) inner and (b) outer views, scale bar = 5 mm; (10) *Pugilina tupiniquim*, spawning, scale bar = 5 mm.

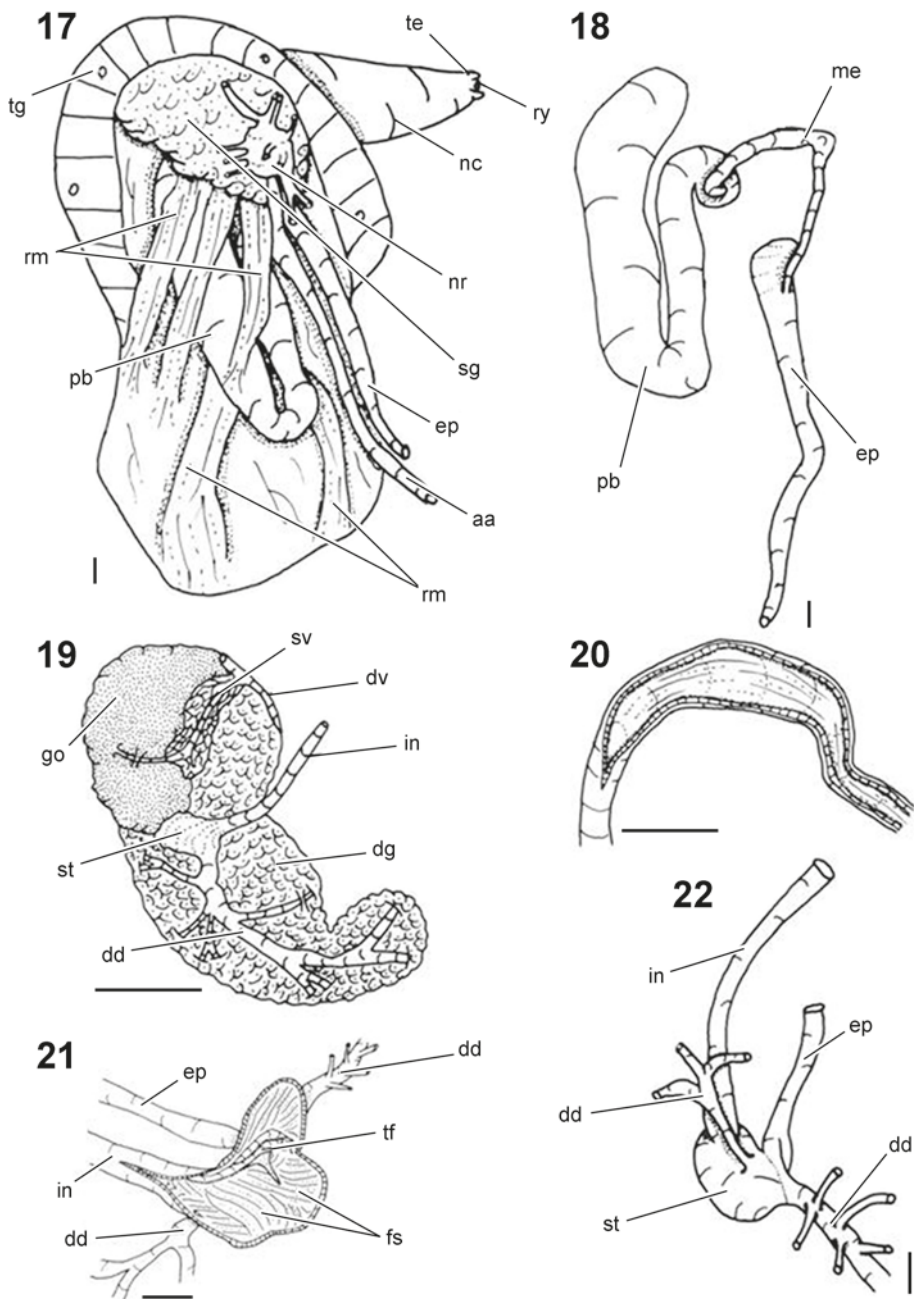


Figs 11–16. *Pugilina tupiniquim*: (11) complete specimen extracted from shell, anterior-right view; (12) renopericardial region, ventral view, some adjacent structures also shown; (13) foot of female, sectioned longitudinally; (14) anterior foregut, ventral view; (15) pallial cavity hoof, ventral view; (16) pallial cavity roof, transverse section at middle level of osphradium. Scale bars = 2 mm.

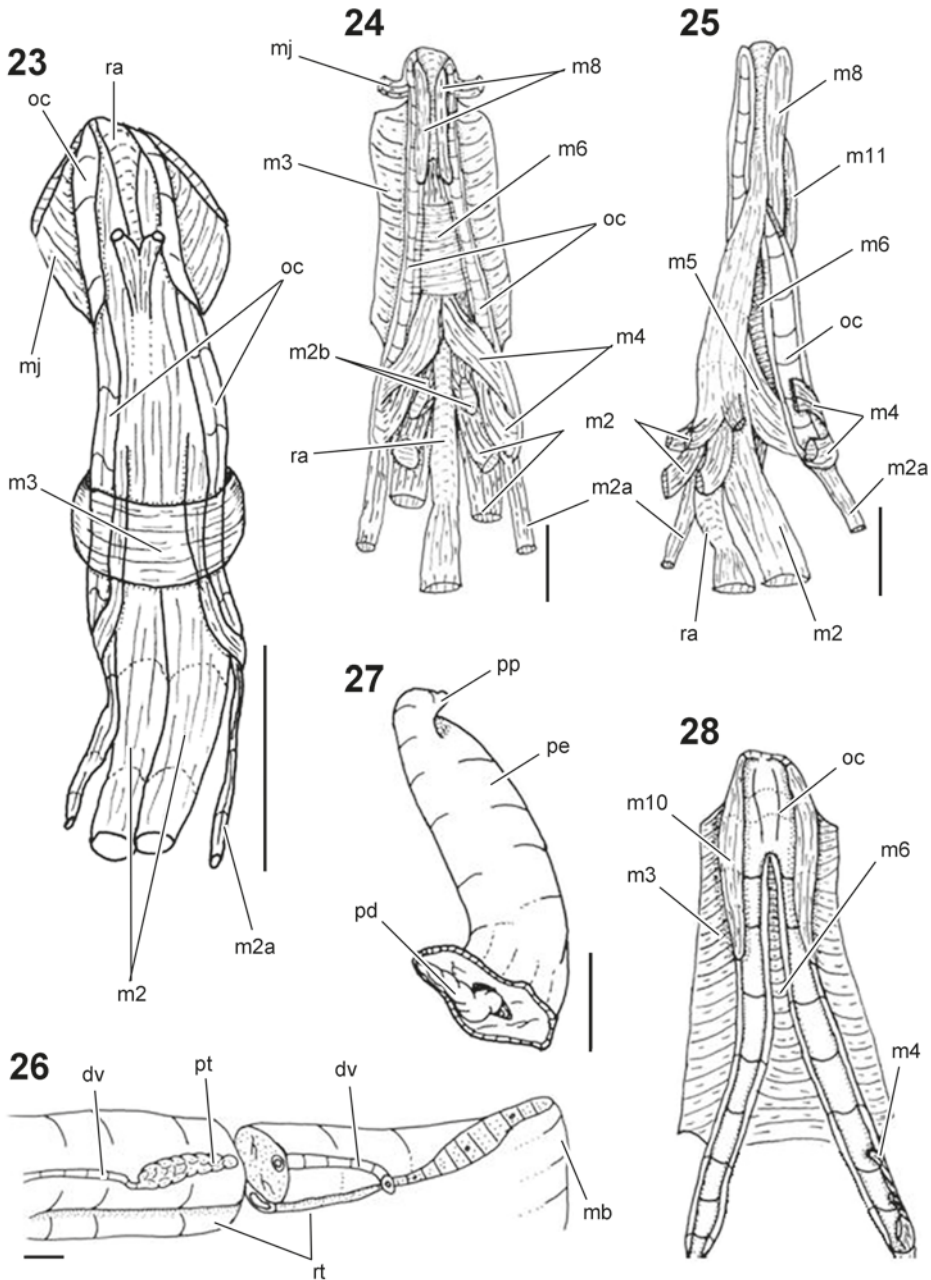
Material examined: Unknown locality, MNHN 51722, 2 shells (Lamarck collection, identified as *Hemifusus coronatus*). AFRICA: MNHN 51721, 1 shell (Lamarck collection). SENEGAL: *Dakar, Gorée Island*, 14°40'N 17°23'W, MZSP: 99901, 1 specimen ♀ (J Coltro col., ii.2011); *Ouaran*, MNHN, 1 specimen ♂ (Bouchet col., 1973). SÃO TOMÉ AND PRÍNCIPE: *Gulf of Guinea*, MZSP 99989.

Distribution: Western African coast, from Senegal to Congo.

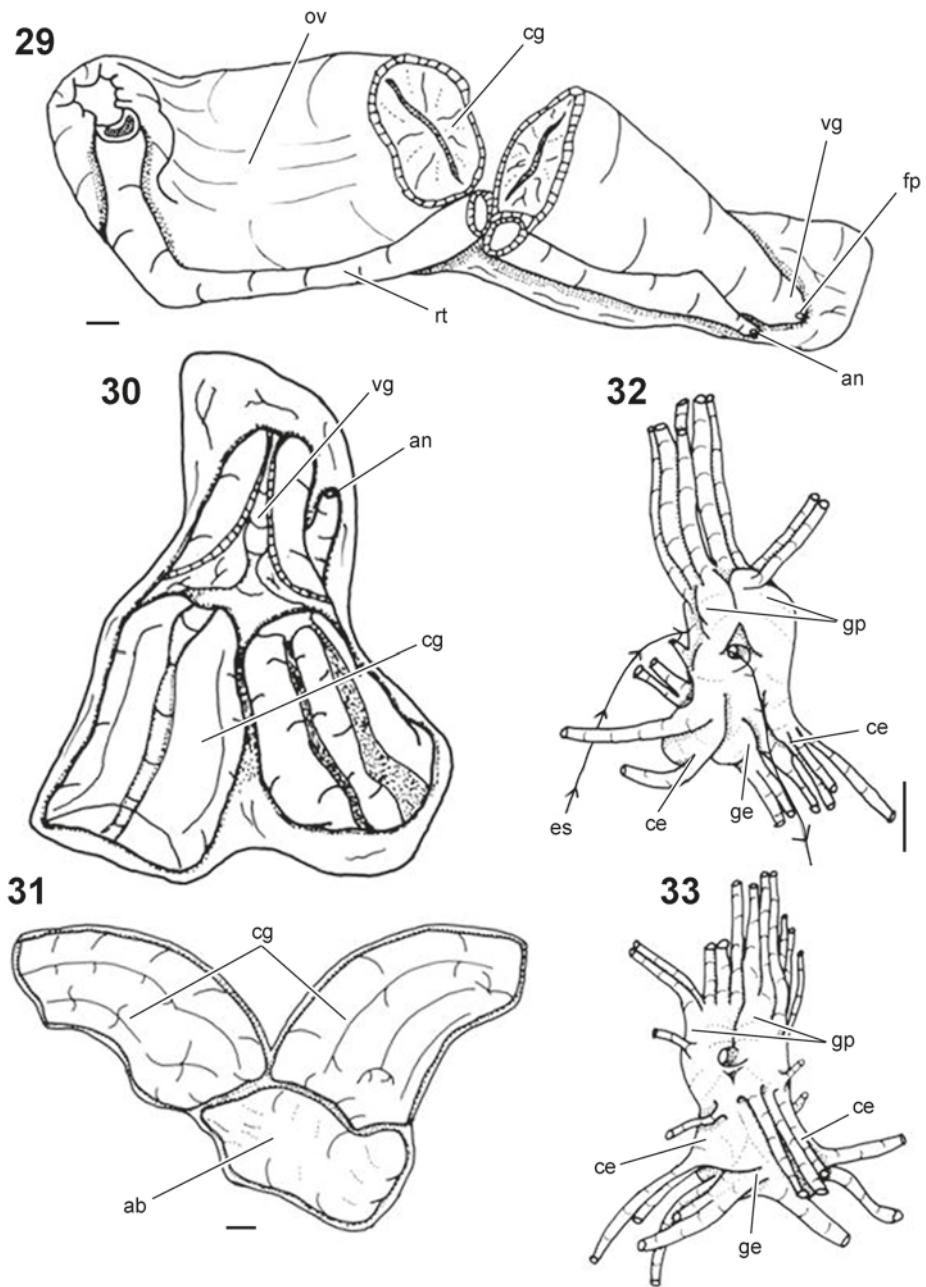
Habitat: Muddy flats and sandy beaches.



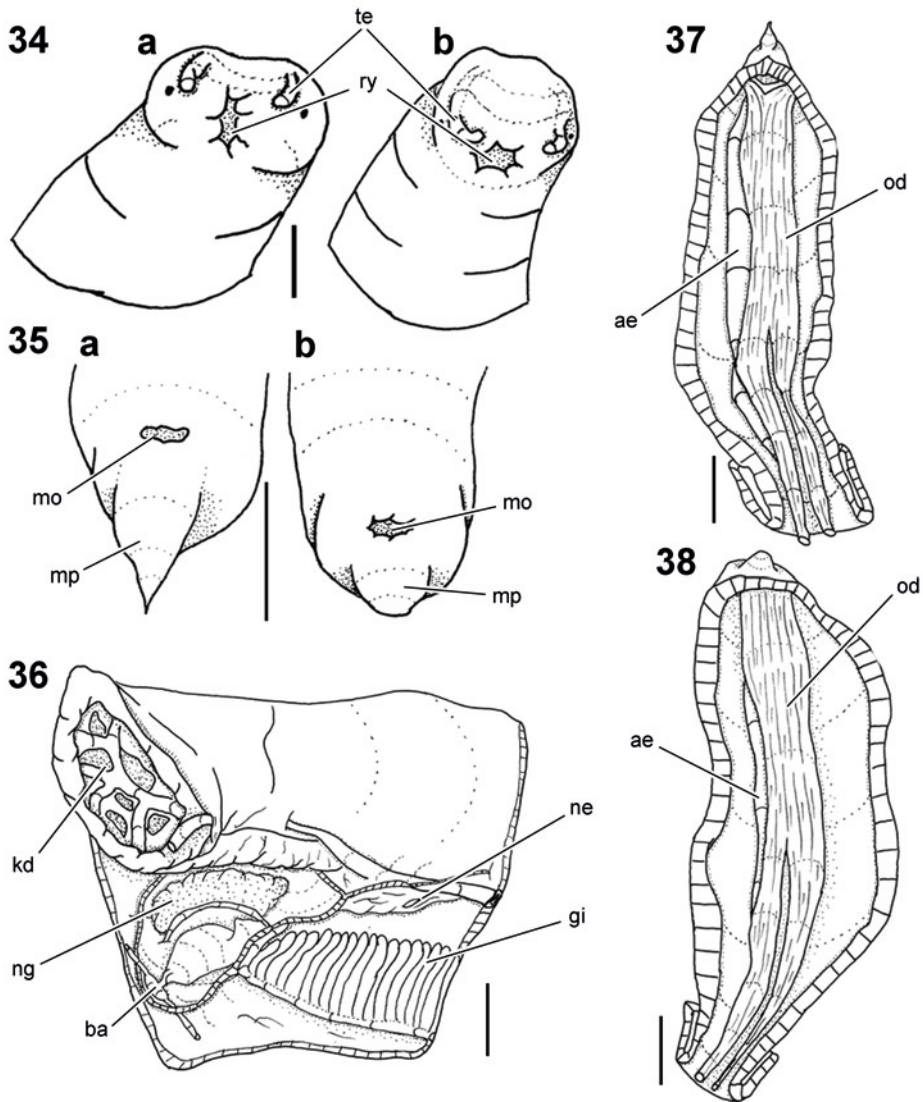
Figs 17–22. *Pugilina tupiniquim*: (17) head and haemocoel, ventral view, foot and columellar muscle removed; (18) proboscis, medium and posterior oesophagus, ventral view; (19) visceral mass; (20) detail of medium oesophagus; (21) stomach longitudinal section; (22) stomach and associated structures, digestive gland removed. Scale bars = 2 mm.



Figs 23–28. *Pugilina tupiniquim*: (23–24) odontophore, ventral view; (25) odontophore ventral view, left structures, partially deflected right; (26) detail from the right region of pallial cavity, male; (27) penis ventral view; (28) odontophore cartilage ventral view. Scale bars = 2 mm.



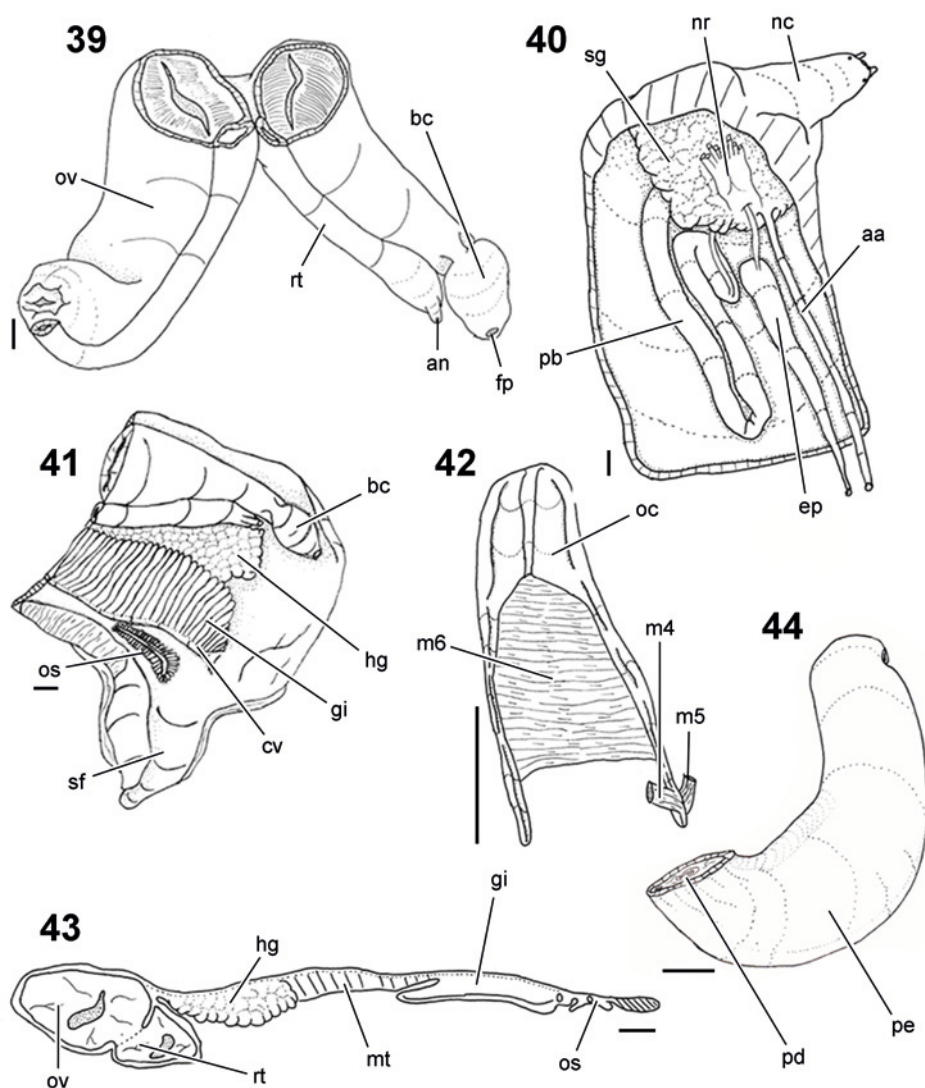
Figs 29–33. *Pugilina tupiniquim*: (29) pallial oviduct, ventral view, transversely sectioned; (30–31) pallial oviduct, ventral view, transversal cut; (32–33) nerve ring, ventral and dorsal view respectively. Scale bars = 2 mm.



Figs 34–38. *Pugilina tupiniquim* and *Pugilina morio*: (34a) *P. morio*; (34b) *P. tupiniquim*, head, details of tentacles positions; (35a) *P. morio*; (35b) *P. tupiniquim*, mouth papilla; (36) *P. morio*, reno-pericardial region, ventral view, some adjacent structures also shown; (37) *P. morio*, anterior foregut ventral view; (38) *P. tupiniquim*, anterior foregut ventral view. Scale bars = 2 mm.

DISCUSSION

None of the type localities of the synonyms of *Pugilina morio* were designated in their original descriptions (Rosenberg 2011). Clench and Turner's (1956) revision of *P. morio* contained a detailed history of the issue. The main intention of those authors was to establish a type locality for *P. morio*, because Linnaeus (1758) also did not provide any in the original description. Nine years later, in the twelfth edition of *Systema Naturae*,



Figs 39–44. *Pugilina morio*: (39) pallial oviduct, ventral view, transversal cut; (40) head and haemocoel, ventral view, foot and columellar muscle removed; (41) pallial cavity hoof, ventral view; (42) odontophore cartilage, ventral view, fused region detail, *m4*, *m5* and *m6* maintained; (43) pallial cavity roof, ventral view, transverse section at middle level of osphradium; (44) penis ventral view. Scale bars = 2 mm.

Linnaeus (1767) mentioned Adanson (1757), a paper devoted to the fauna of Senegal, under the species' entry. This led Clench and Turner (1956: 185) to subsequently designate Gorée Island, Senegal as the type locality.

Despite some degree of variation, it is possible to establish some conchological differences between the species studied herein, such as the more delicate spiral sculpture on the body whorl and internal surface of the outer lip in *P. morio* when compared to the more robust sculpture of *P. tupiniquim*. Similarly, *P. morio* exhibits a shorter siphonal

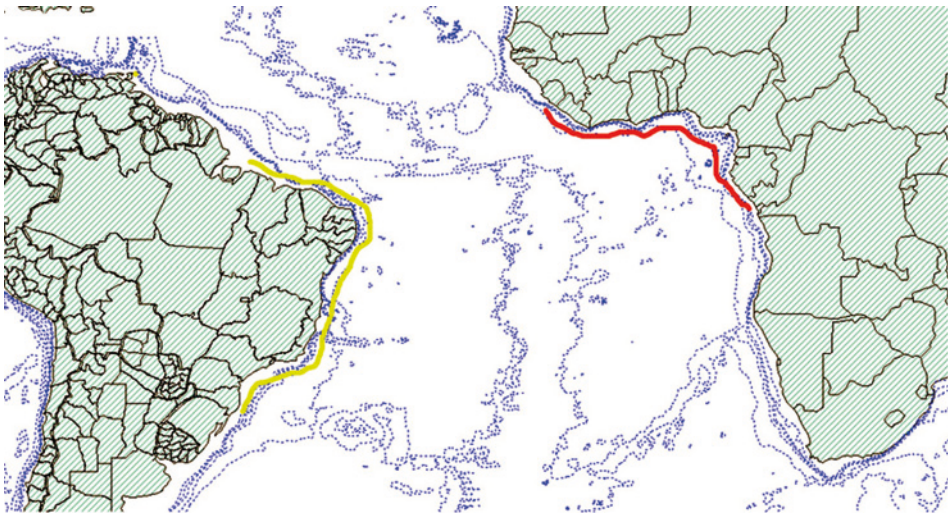


Fig. 45. Geographic distribution — yellow line: *P. tupiniquim*; red line: *P. morio*.

canal. Nonetheless, *P. tupiniquim* shows an overall greater variation in shell shape and sculpture (Figs 1–3), mainly regarding its prominent shell shoulder, than the African species. *P. morio* showed a conchological uniformity in all studied specimens, exhibiting only non-shouldered shells. This conclusion, however, is based on a limited number of *P. morio* specimens, and further samplings may reveal more. The more detailed analysis of anatomical structures, plus the wide distance between their occurrences further endorses the specific separation, which may also be associated with the short duration of their embryogenesis. The outbreak of *T. tupiniquim* occurs in the later veliger stage, somewhere between seven and eight weeks after oviposition; the veliger remains swimming around the capsule for 24 hours, and then begins crawling across the bottom (Matthews-Cascon *et al.* 2011). Considering the brief free-swimming time of the larvae, the amphi-Atlantic migration that has been inferred in the literature (e.g. Dautzenberg 1921: 117), and consequently a genetic flow between African and Brazilian populations, seems highly unlikely. The presence of subfossil samples of *Pugilina* on both sides of the Atlantic does not make any anthropic transportation hypothesis (e.g. Dautzenberg 1921) more credible, though *Pugilina morio* and *P. tupiniquim* are certainly sister species.

Regarding pallial structures, the gill is slightly larger with rounded filaments in *P. morio*, and smaller with triangular filaments in *P. tupiniquim*. The pallial oviduct presents a bursa copulatrix in *P. morio*, which is absent in *P. tupiniquim*. There are additional anatomical differences between both species, which involve almost all remaining somatic regions, such as the neck length, tentacle position, and bicuspidate rachidian teeth in *P. tupiniquim* (with a vestigial cusp at the centre) present in all studied specimens (as opposed to tricuspidate teeth in *P. morio*), the degree of fusion of the odontophore cartilages (much higher in *P. morio*), and the presence of a bulb in the common aorta in *P. morio*. Despite the anatomical differences, it is also important to emphasise that a distinction in habitat was also detected. The Brazilian species occurs preferentially in plains under the influence of tides in estuaries, in very low salinity areas. In contrast, the African species was also found on sandy beaches but in places with no presence

of rivers. These data also indicate that they are two distinct species: *P. morio* with a geographical distribution in the eastern Atlantic, and *P. tupiniquim* in the western Atlantic.

We so far and tentatively consider the Caribbean population to belong to the new *P. tupiniquim*. However, it is important to emphasise that we have not examined Caribbean samples, and future studies could change this scenario. The given synonymic list is the most complete in the present knowledge, as the consulted literature suggested that all of the *P. morio* synonyms would be from Africa, a conclusion taken from old literature (Dautzenberg 1910, 1921). This fact led us to create a new epithet, instead of resurrecting any synonyms. As mentioned above, the occurrence of *P. tupiniquim* in the south Caribbean area is doubtful, as the radula of a specimen from Tobago Island shows more robust teeth; its rachidian has three cusps like *P. morio*, but the central cusp is reduced, resembling the bicuspid condition of *P. tupiniquim* (Clench & Turner 1956, fig. 96–6).

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