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ANATOMY OF *NERITINA ZEBRA* FROM GUYANA AND BRAZIL (MOLLUSCA: GASTROPODA: NERITIDAE)

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Abstract Neritina zebra *is a common brackish water gastropod living on muddy bottoms with poorly known morphological characters. The morphology, including the variety of colour and pattern of shells, and the anatomy are described. We mainly analyzed the animals collected in the estuary of the Ceará river, Ceará, Brazil, from "Parque Estadual do rio Cocó", and specimens from other places deposited in institutional collections, from French Guyana (topotypes) to São Paulo. A complete anatomical description is performed, including illustration and discussion main concerned to systematics. Amongst the more important anatomical data are: heart diotocardian; kidneys solid; anterior esophagus with pair of ventral esophageal pouches; odontophore with 4 cartilages and 2 horizontal muscles (m6, m6a); males with penis dorsal-right to snout, bearing a terminal papilla; pallial oviduct triaulic, possessing 3 pallial apertures.*

Key words: Neritina zebra, *Neritimorpha, morphology, shell, anatomy, Brazil*

INTRODUCTION

The gastropod group Neritimorpha Golikov & Starobogatov 1975 (= Neritopsina Cox & Knight 1960) has undergone a huge adaptive radiation (Kano *et al*., 2002). Normally considered inside the archaeogastropod clade (e.g., Haszprunar, 1985, 1988) the taxon has been considered amongst the more modified members, even as a sister group of the Apogastropoda (Caenogastropoda plus Heterobranchia) (Ponder & Lindberg, 1997; Ponder *et al*., 2007). Despite several important studies on the neritimorphs (e.g., Bourne, 1908; Morton & Yonge, 1964; Little, 1972; Kano *et al*., 2002; Tan & Clements, 2008) doubts still remain about their identity and internal organization. One of the main reasons for this confusion is the lack of morpho-anatomical data on its representatives, which raises the need for molecular approaches (e.g., Spencer *et al*., 2007).

The Neritimorpha are a highly diverse and important group, with representatives in several habitats (Tan & Clements, 2008). They are normally detritivores and herbivores that inhabit aquatic (seawater or freshwater) and terrestrial environments (Ponder & Lindberg, 1997). Freshwater and terrestrial invasions have been suggested (Ponder & Lindberg, 1997; Kano *et al*., 2002) to have occurred at least four times during Mesozoic (Bandel & Kiel, 2003). Despite some few species living in deep waters, most marine species lives in shallow water, intertidal or supratidal (Andrzej & Przemyslaw, 2005). The most diverse family is Neritidae, commonly called nerites. This is exclusively aquatic, with representatives from marine to freshwater environments, some species being able to migrate through different levels of salinity (Goodwin, 2005).

The following can be evoked as the main morphological characters of the Neritidae: globose shell with few whorls, short spire (Hyman, 1967), lack of columella (Ponder & Lindberg, 1997); calcareous operculum (Haynes, 1988); epipodium absent; one left bipectinate gill; rhipidoglossate radula; reduced or absent right auricle with single kidney, which serves also as a gonoduct (Hyman, 1967; Ponder & Lindberg, 1997). This family also displays a complex female system, with two or three gonopores (Hyman, 1967). Nerites can be highly polymorphic, the shells of some species showing a huge variety of colours and patterns (Tan & Clements, 2008).

The family Neritidae is represented on the Brazilian coast by five species: *Nerita ascensionis* Gmelin 1791, *Nerita fulgurans* Gmelin 1791, *Nerita tesselata* Gmelin 1791, *Neritina virginea* (Linnaeus 1758) and *Neritina zebra* (Bruguière 1792) (Rios, 1994, 2009). In this area, these animals can be found forming aggregates in estuarine roots and

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trees, constituting dense and extended populations (Matthews-Cascon *et al.*, 1990).

Neritina zebra is considered herein. The species occurs from Suriname to Cabo Frio (Rio de Janeiro) and is common on mudbanks in brackish waters (Rios, 1994, 2009) being tolerant of pollution. The species endures limnetic and euryhaline environments (Fernandes, 1990). It is used as food and a source of income for riverside communities (e.g., in the state of Pará), its shell being also employed to prepare wattle-and-daub cement, together with other ingredients, such as water and clay (Andrade, 1984). Despite the human importance, little is known regarding its anatomy. Studies previously made are restricted to characteristics of the shell, operculum and radula (Russell, 1941; Calvo, 1987; Haynes, 1988; Matthews-Cascon *et al.*, 1990; Mienes, 1991; Rios, 1994, 2009). The present study aims to fill a gap in the knowledge of this species and amplifies knowledge of a typical representative of the Neritimorpha.

Material and Methods

A complete list of material examined follows the species description. Most material, both shells and 70% ethanol preserved specimens, were deposited in the malacological collection "Prof. Henry Ramos Matthews" of the Universidade Federal do Ceará — (CMPHRM) UFC; and in the Collection of Mollusks of the Museu de Zoologia da Universidade de São Paulo — MZSP.

Living individuals had been collected manually in the intertidal zone of the mangrove in the Ceará river, (03°44′11.1″S 038°37′23.6″W), during spring tides between March and October 2007; and on the State Park of Cocó River (Parque Estadual do Rio Cocó), Fortaleza, CE (S 03º45′06.5″ W 038º29′00.0″), on July 2008. Some specimens were frozen and, later, preserved in 70% ethanol solution. Others were anesthetized and later put in 70% ethanol.

Dissections were performed under a stereomicroscope by standard techniques, with the specimens immersed under seawater or fixative. Digital photos of each step of the dissection were obtained, as well as drawings aided by a camera lucida. A scanning electron microscope (SEM) was employed to view the protoconch and radula in the Laboratório de Microscopia Eletrônica of MZSP.

In all figures, the following abbreviations are used: **ac**, accessory cartilage immersed in m6; **af**, afferent gill vessel; **ag**, albumen-capsule gland; **am**, male aperture; **an**, anus; **ap**, female aperture; **ar**, right auricle; **au**, left auricle; **ax**, annexed gland; **bc**, bursa copulatrix; **bd**, bursa copulatrix duct; **bf**, buccal dorsal fold; **bg**, buccal ganglion; **br**, subradular membrane; **bv**, blood vessel; **cc**, cerebral commissure; **ce**, cerebral ganglion; **cg**, capsule gland; **cm**, columellar muscle; **cf**, cephalic lappet; **co**, collar vessel; **cs**, reinforcement sac; **cv**, ctenidial vein or efferent gill vessel; **dc**, dorsal chamber of buccal mass; **dd**, duct to digestive gland; **df**, dorsal folds of buccal mass; **dg**, digestive gland; **ed**, enigmatic duct; **es**, esophagus; **fs**, foot sole (mesopodium); **ft**, foot; **ga**, gill's anterior projection or suspensory membrane; **gd**, gonopericardial duct; **gi**, gill; **gm**, gill muscle; **go**, gonad; **fp**, female pore; **he**, haemocoel; **in**, intestine or intestinal loop in haemocoel; **ir**, insertion of m4 in radular sac; **jw**, jaws; **ki**, kidney; **lg**, labial ganglion; **m1-m12**, odontophore muscles; **ma**, muscular attachment to operculum; **mb**, mantle border; **mc**, buccal sphincter; **mf**, muscle fibers; **mg**, male pallial gonoduct; **mj**, jaw and peribuccal muscles; **ml**, lateral muscle of buccal mass; **mo**, mouth; **ne**, nephrostome; **nr**, nerve ring; **nv**, nerve; **oa**, opercular apophysis; **oc**, anterior odontophore cartilage; **od**, odontophore; **of**, ophthalmic/tentacular nerve; **om**, ommatophore; **op**, opercular pad; **ot**, oral tube; **pc**, pericardium; **pd**, pedal ganglion; **pe**, penis; **pl**, pleural ganglion; **pn**, pedal nerve; **po**, posterior odontophore cartilage; **pp**, penis distal papilla; **pt**, prostate; **py**, pallial cavity; **ra**, radula; **rm**, snout retractor muscle; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **rv**, efferent renal vessel; **sg**, salivary gland; **sm**, gastric muscle; **sn**, snout; **sp**, spermatophore; **sr**, seminal receptacle; **st**, stomach; **sv**, seminal vesicle; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **ts**, testis; **va**, vaginal opening; **vd**, vas deferens; **ve**, ventricle; **vg**, visceral ganglion; **vo**, visceral oviduct; **vr**, vaginal duct connecting capsule gland with duct of bursa copulatrix.

Institutional abbreviations: CMPHRM: malacological collection "Henry Ramos Matthews", Universidade Federal do Ceará; MNHN, Museum National d'Histoire Naturelle, Paris; MZUSP, Museu de Zoologia da Universidade de São Paulo.

SYSTEMATICS

Neritina zebra (Bruguière 1792)

(Figs 1–33)

Nerita zebra Bruguière 1792: 126 [Cayenne, French Guyana].

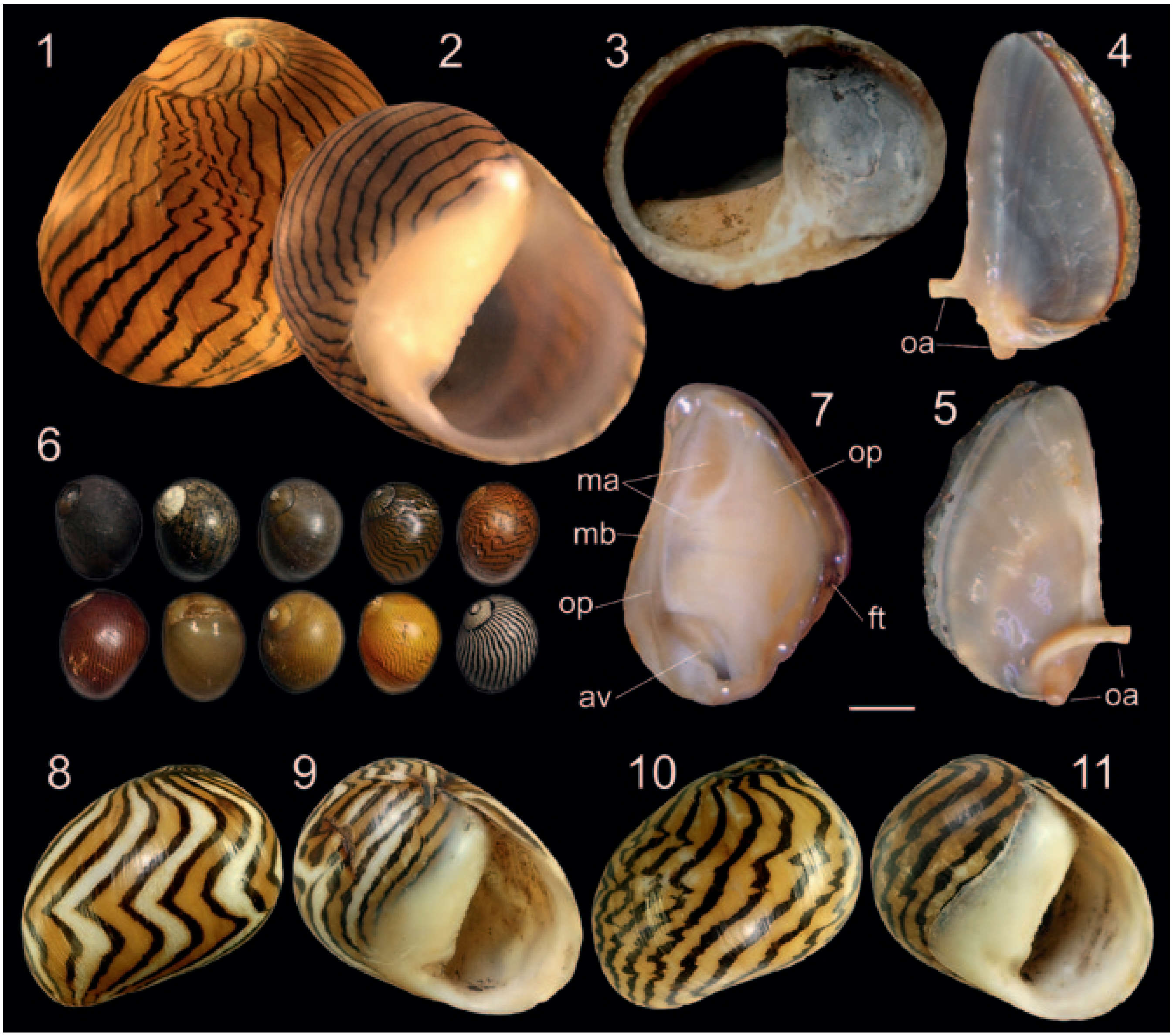
Nereina lacustris Cristofori & Jan 1832: 4 [Brazil].

Nerita sobrina Récluz 1846: 119–120 [Cayenne?]; Martens, 1877: 117.

Neritina zebra: Couturier, 1907: 169; Russell, 1941: 390–391 (pl. 4, figs. 1–2); Olsson & McGinty, 1958: 11; Calvo, 1987: 31; Matthews-Cascon, Pinheiro & Matthews, 1990: 53; Mienis, 1991: 14–17; Prado, 1998: 3 (fig. 31); Barroso & Matthews-Cascon, 2009: 137–142.

Neritina (Vitta) zebra: Rios, 1994: 46 (pl. 16, fig. 160), 2009: 76 (fig. 178).

Types: MNHN, 2 syntypes (examined, Figs 8–11).



Figures 1–11 *Neritina zebra* anatomy. 1) ordinary shell, CMPHRM 2673, dorsal view, maximum diameter = 18.2 mm; 2) same, apertural view; 3) broken shell showing peri-apertural region, inner-dorsal view, maximum diameter = 17.1 mm; 4) operculum, outer view; 5) same, inner view; 6) examples of shell variation, dorsal views, specimens about 15 mm, respectively CMPHRM 2096, CMPHRM 2427, CMPHRM 2426, MZSP 28204, MZSP 1953, MZSP 1953, MZSP 15291, CMPHRM 2090, MZSP 369, MZSP 3367; 7) opercular pad, dorsal view, operculum just removed; 8–11) two syntypes, MNHN, specimens with periostracum partially eroded; 8–9) syntype 1, dorsal and apertural views, maximum diameter = 22.0 mm; 10–11) same for syntype 2, maximum diameter = 19.5 mm. Scale (4, 5, 7) = 2 mm.

Description

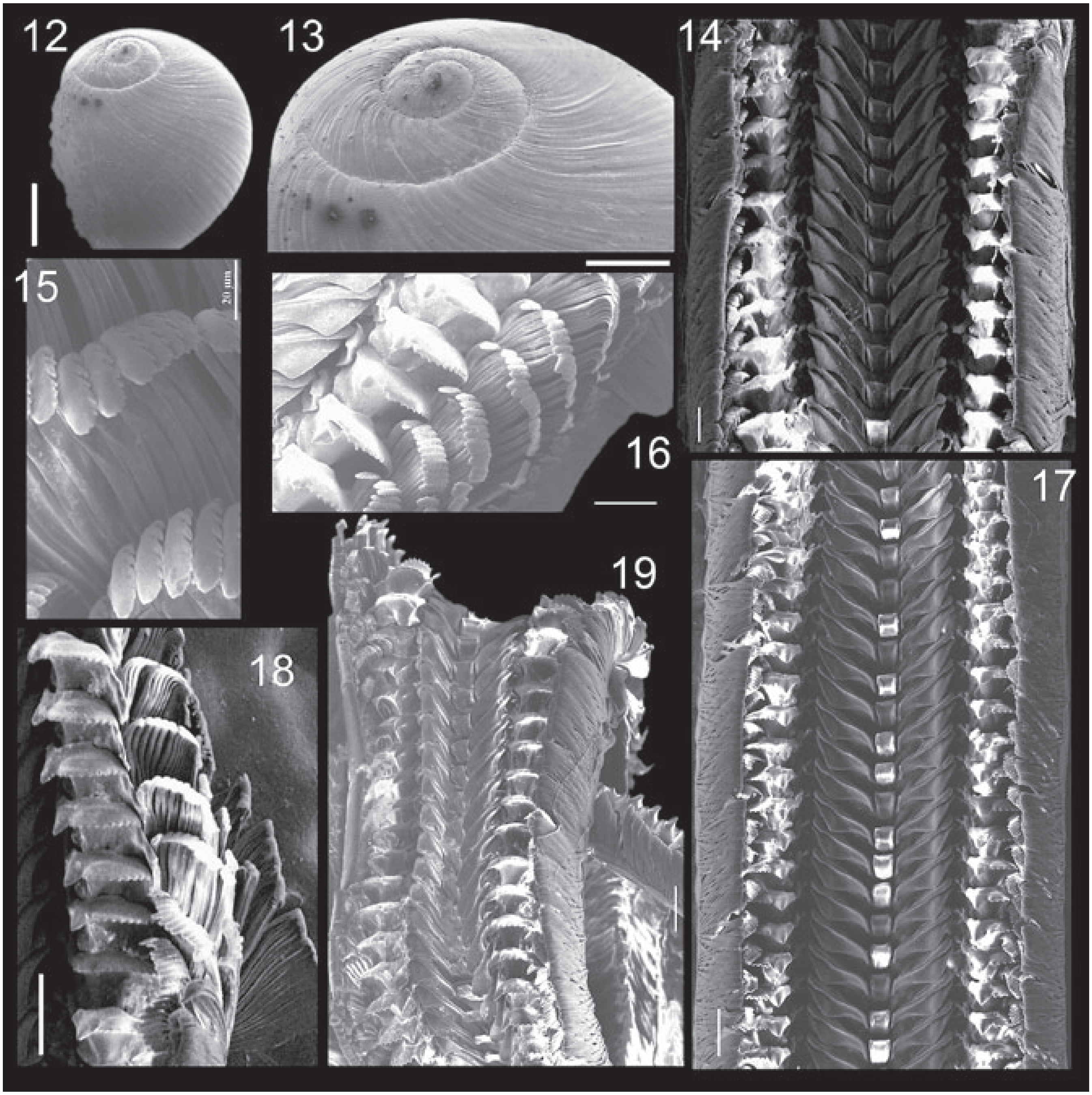
Shell (Figs 1–3, 6) Globose, glossy, length about 25 mm. Protoconch with 1.5 whorls; teleoconch with up to 3.5 whorls. Protoconch generally eroded in elder specimens. Periostracum rather thin, beige, translucent. Colour varying from yellow to dark brown, with black axial stripes of several patterns and thicknesses. Stripes varying from straight, curved to zigzag, or absent. Suture weakly marked; sometimes with fine dark lines along it. Body whorl smooth, representing ~90% of length. Aperture semilunar, reaching around 2/3 of the body whorl. Outer lip with thin margin, internally thickened, forming callus in which operculum fits. Inner lip with wide denticle in lower region, representing about 1/6 of inner lip length; followed by row of 4 to 14 smaller, somewhat uniform denticles. Parietal region smooth, convex, whitish to dark-yellow. Columella forming transversal septum, dividing inner space in two, anterior and posterior chambers.

Head-foot (Figs 21, 23, 31) Commonest colour dark brown with black transverse lines. Length about ¾ whorl; about as wide as aperture. Head with about half of head-foot width. Tentacles long and thin, with black longitudinal stripes. Eyes located on distal end of ommatophores, located close and external to tentacles. Snout about as broad as head, about twice broader than long; ventral, peribuccal surface plane, flanked by thin edges extending weakly beyond snout wall, somewhat pointed laterally; mouth located in center, flanked by protruded, circular oral fold. Special arrangement of integument folds, as siphons or lobes, located in both sides of head (Figs 21, 23: cf), left fold about as long as snout and with ~1/4 is width; right fold with ~1/3 left siphon size. Foot oval and very thick, with dark colour and black small spots and stripes, sole lacking pigmentation. Furrow of pedal gland restricted to about half of anterior foot edge.

Opercular pad (Fig. 7) Covering most of operculum inner surface; attachment restrict to anterior half, being about three times wider than long; attachment with somewhat similar-sized three regions, right and middle regions two different arranged muscular insertions, left region composed by deep furrow relative to opercular apophysis (Fig. 7: av). Columellar muscles of different sizes, separated by concavity of about ¼ head-foot width. Right columellar muscle positioned more dorsally, length equivalent to 1/3 of that of foot; origin oblique, weakly broader than middle portion, in area equivalent to 1/3 of that of operculum. Left columellar muscle with about half of right muscle length and weakly thinner than that, directed more ventrally; origin with equivalent area of that of right muscle, but narrower and transversely longer, turned to left.

Operculum (Figs 4, 5) Calcareous and smooth, with bifurcated apophysis. Occupying entire shell aperture. Outer surface with clear growth lines; colour varying from bluish black to light brown. Nucleus sub-terminal. Inner edge almost straight, with two somewhat equidistant low projections; inferior projection wide, superior projection corresponding to apophysis. Outer edge semi-circular, with cutting, flaccid border; inferior edge thickened by callus located inferiorly to nucleus; superior edge bluntly pointed. Inner surface glossy, pale beige; scar weakly visible, occupying about ¾ of inner area. Apophysis superior element curved, gradually increasing from inner to outer sides, with about half of opercular width; projecting about ¼ of its length beyond opercular inner edge. Apophysis inferior element with about 1/3 of length of superior element, stubby; tip blunt, flattened, tuned ventrally and to left; about 1/3 of its length projected beyond inferior opercular edge; tip weakly broader than middle portion. Pair of shallow, broad furrows flanking inner surface of outer edge.

Mantle cavity (Figs 20, 22, 23) Length about ¾ whorl; around twice as long as wide. Mantle border dark coloured, thick without indentation, with several minute folds at edge. Gill bipectinate, almost as long and pallial cavity and about 1/5 of its width; gradually narrowing, up to sharp pointed end; located on left side; about half of its length attached to pallial roof at left, and about 1/3 at right; anterior half mobile, projected forwards sustained by left suspensory membrane. Gill filaments semi-circular, same sized in both sides, about twice wider than tall; afferent and ctenidial vessels similar-sized, each with about 1/6 of gill width, both vessels possessing pair of gill muscles (Fig. 20: gm), each with about 1/8 of vessel's size; these gill muscles running all along



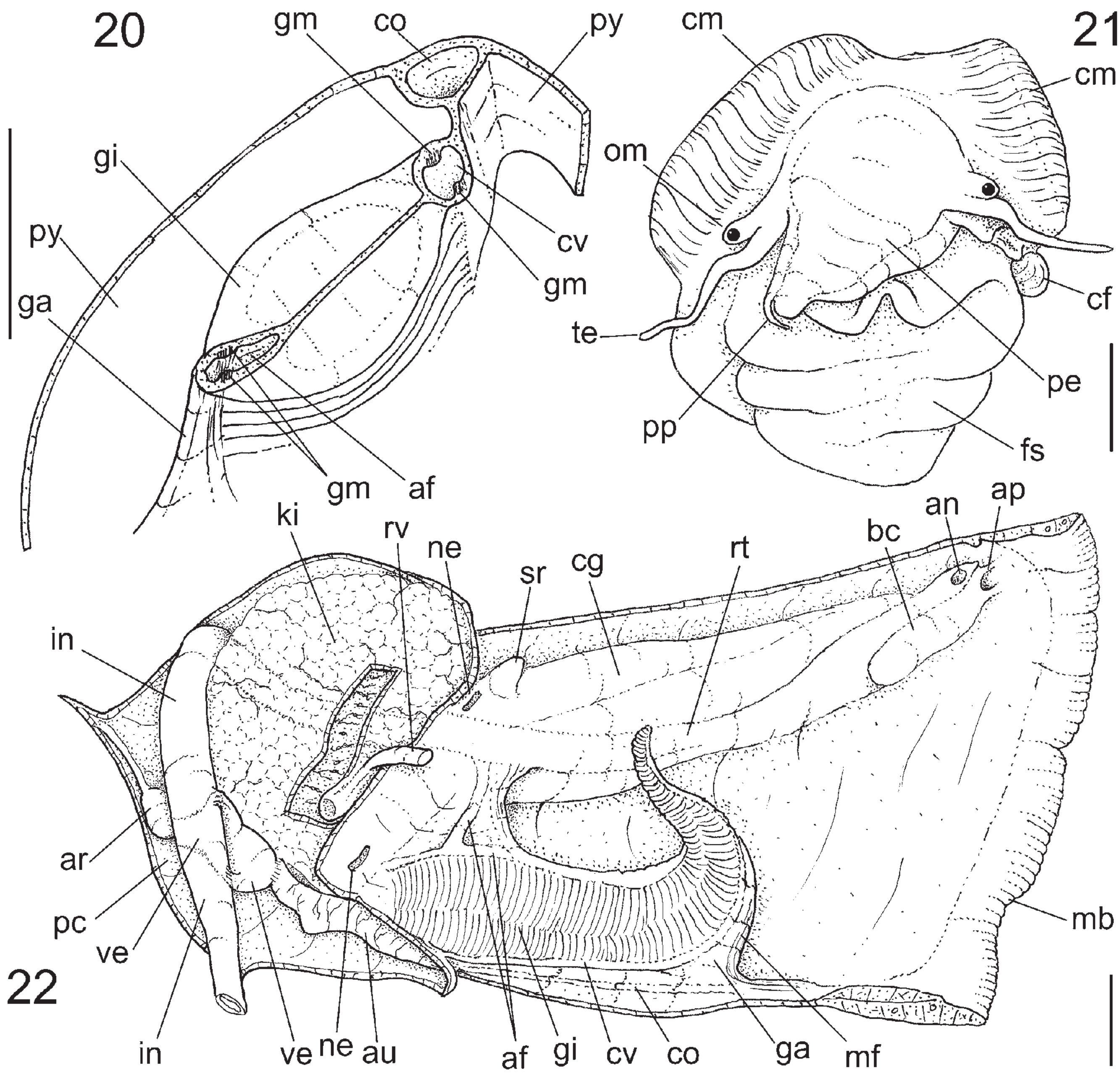
Figures 12–19 *Neritina zebra* SEM of hard parts: 12) shell of young specimen, scale = 1 mm; 13) same, detail of spire; 14) radula, whole view of a portion, scale = 100 µm; 15) detail of inner marginal teeth, scale = 20 µm; 16) detail of lateral and inner marginal teeth, scale = 100 µm; 17) panoramic view of a portion of another specimen, scale = 100 µm; 18) detail of lateral and marginal teeth, scale = 100 µm; 19) panoramic view of a bended portion, a third specimen, scale = 100 µm.

gill length. Ctenidial vein connected to adjacent left pallial cavity edge by membrane possessing well-developed collar vessel in its intersection with mantle (Fig. 20: co). Osphradium minute, difficultly seen, located in front of base of suspensory membrane, in front of anterior end of left columellar muscle. Rectum with about 1/6 of pallial cavity width. Anus sessile, located close to mantle. No clear hypobranchial gland or vessels.

Visceral mass (Figs 22, 23) Forming a single, spherical mass, lacking spiral conformation. Fills the entire shell's spiral cavity, ~1/3 shell volume. Reno-pericardial structures located anteriorly, occupying ~1/4 visceral volume. Stomach located in right-ventral side, occupying ~1/4 visceral volume. Digestive gland greenish beige, covering dorso-posterior surface of stomach, occupying ~1/6 visceral volume. Gonad brown, located in dorso-left region, occupying ~half of visceral volume.

Circulatory and excretory systems (Fig. 22) Pericardium somewhat lozenge-like, located behind posterior end of gill, also encroaching dorsally posterior-left ¼ of gill; volume equivalent to 1/10 of pallial cavity. Left (anterior) atrium about 5 times longer than wide, connected to posterior end of ctenidial vein in distance ~1/5 of posterior end of gill. Right (posterior) auricle with about 1/5 of anterior auricle's size, located in opposed side of intestine, weakly directed towards posterior and right. Ventricle about as long as and about 1.5 times wider than anterior auricle, attached to rectum only in its dorsal half (Fig. 22: ve). Pair of kidneys solid, pale beige, positioned adjacent to rectum, in its region passing through pericardium and about ¼ of pallial cavity towards anterior, protruding about half inside pallial cavity. Both kidneys asymmetrical, left kidney with about ¼ of right kidney; both running close attached to rectum. Efferent renal vessel (Fig. 22: rv) single, connected to pair of concavities if renal tissue, each one located at some distance from efferent renal vessel insertion. Each nephrostome simple, right nephrostome located about half way between posterior end of pallial cavity and mantle border; left nephrostome located somewhat more posterior than right nephrostome. Internally no special chamber of nephrostome.

Digestive system (Figs 22–29) Mouth circled by fine, narrow, radial folds on oral fold described above. Buccal mass pyriform, located just posterior to mouth, connected to it by wide, thick muscular walled oral tube (Figs 24, 27: ot). Buccal mass occupying ~¼ of haemocoel. Odontophore occupying ~3/4 of buccal mass volume. Oral cavity occupying anterior half of buccal mass; pair of jaw plates very small and thin (Fig. 25: jw), each one with about 1/6 of adjacent width of buccal mass, about three times wider than long; dorsal oral fold extending entire dorsal half (Fig. 25: bf) at short distance anterior to jaws, about twice taller than thick. Buccal dorsal chamber (Fig. 25: dc) somewhat shallow, anterior edge rounded, running towards posterior gradually disappearing in level posterior to buccal mass; occupying about half of adjacent width of esophagus; possessing pair of low longitudinal folds located somewhat equidistant from each other and from chamber lateral edges (Fig. 25: df). Esophageal origin located in middle level of buccal mass dorsal surface (Fig. 26); width circa of ¼ of adjacent width of buccal mass. Odontophore muscles: **m1**, several pairs of small jugal muscles, more concentrated close to mouth (Fig. 24); **m1d**, pair of narrow and thin jugal dorsal retractor muscles (Fig. 26), originating in antero-dorsal region of snout, running posteriorly close to odontophore dorsal surface, inserting in posterior-dorsal region of odontophore; **ml**, pair of lateral muscles, narrow and somewhat thick, working as buccal retractors and dilatators, originating in middle level of snout lateral walls, composing four pair of muscles of similar size (Fig. 27), each one with about 1/3 of odontophore length, running to different insertions, a dorsal pair inserting in dorsal region of mouth, two pairs inserting in oral tube close to buccal sphincter (mc), posterior pair penetrating lateral wall of odontophore, inserting in middle level of dorso-lateral surface of anterior cartilages (Figs 28, 29); **mc**, buccal sphincter, composed by circular fibers mainly placed in dorsal and lateral walls of oral tube (Figs 26, 27), with about ¼ oral tube length; **mj**, narrow and thin pair of jaw muscles, originating in latero-anterior surface of anterior cartilages (Fig. 29), running towards external and dorsal, penetrating into oral tube, splaying in it in region of jaws; **m2**, pair of main retractors of buccal mass absent; **m3l**, pair of longitudinal superficial muscles covering lateral and part of dorsal surface of odontophore (Figs 25, 26), originating in posterior-lateral corner of anterior cartilages (Fig. 28) about half as thick as cartilages, running towards anterior ant dorsal, penetrating in dorsal wall of buccal mass, gradually splaying um to buccal sphincter, touching its pair in median line (Fig. 26); **m3d**, pair of narrow protractor muscles of buccal mass, originating in dorsal wall of snout close to median line, running dorsally distance equivalent to 1/3 that of odontophore (Fig. 26), inserting in lateral surface of posterior cartilage (Figs 28, 29); **m4**, pair of main dorsal tensor muscles of radula. Originating in



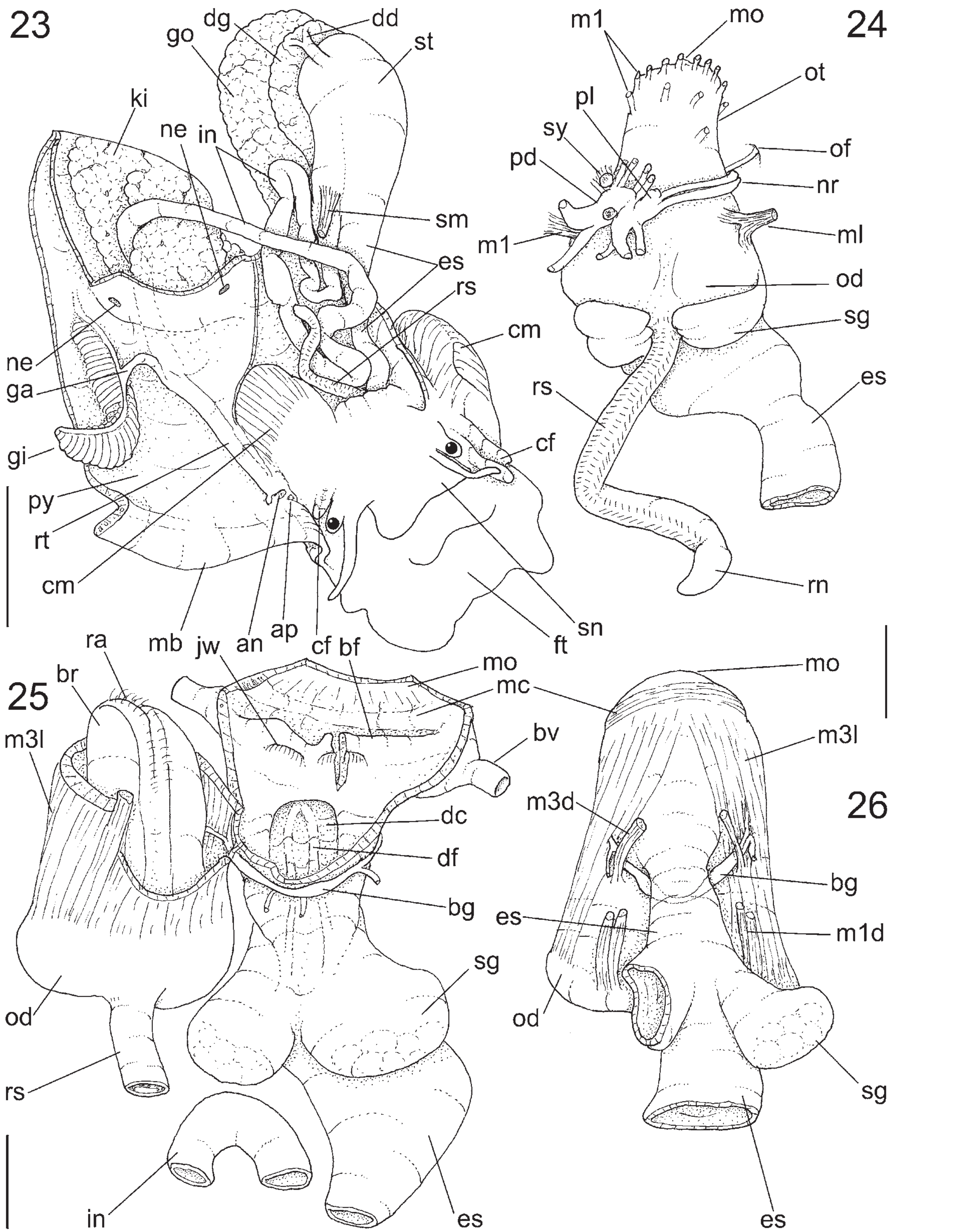
Figures 20–22 *Neritina zebra* anatomy: 20) pallial cavity, transverse section on its middle level; 21) head-foot, male, frontal view; 22) pallial cavity and annexed region of visceral mass, inner-ventral view, gill slightly deflected, a band of ventral region of renal wall artificially removed. Scale = 2 mm.

dorsal surface of posterior cartilages (Figs 28, 29) almost as thick as cartilages, running dorsally about 1/3 of odontophore length covering posterior cartilage, inserting in radular ribbon in its region preceding oral cavity (Fig. 29: ir); **m5**, pair of secondary dorsal tensor muscles of radula, with about half of m4 pair size and similar features, located more medially (Figs 28, 29), inserting in radular ribbon more ventrally than m4 insertion; **m6**, horizontal muscle, connecting ventral edge of both anterior cartilages, with about 2/3 of anterior cartilages length and about 1/5 their width, weakly narrower anteriorly (Figs 28, 29), anterior end in level of anterior end of anterior cartilages, small cartilaginous tissue accumulated in posterior quarter (Fig. 29: ac); **m6a**, accessory horizontal muscle, with similar features of m6 but with about 1/6 its length, and as wide as m6 posterior portion, separated from m6 distance equivalent to its length, located in middle way between posterior end of m6 and posterior end of anterior cartilages (Figs 28, 29); **m7**, pair of narrow and thin muscles originated in middle region of m4 median surface, running dorsally penetrating into radular sac, splaying in it in region of m4-m5 insertion (Fig. 29); **m8**, pair of approximator muscles of cartilages, about as thick as cartilages, connecting middle portion of median surface of anterior cartilages (about 1/3 of this surface) (Fig. 28) with posterior-medial surface of posterior cartilage (Figs 28, 29), average distance equivalent to half anterior cartilage length; **m10**, pair of ventral protractor muscles of buccal mass, originating in ventral wall of mouth, running towards posterior along almost entire odontophore length narrowing gradually (Fig. 27), inserting in odontophore ventro-posterior surface, in ventro-posterior corner of anterior cartilages (Fig. 28); **m11**, pair of ventral tensor muscles of radula, originating in same region of m10 origin (Fig. 28), weakly medially, narrow and thin, running anteriorly flanking m6 (Fig. 29), each one inserting as two bundles in subradular membrane in its ventro-anterior region (Fig. 28). Odontophore non-muscular structures: pair of anterior cartilages with about same odontophore length and about 1/3 its width, anterior end bluntly pointed medially (Figs 28, 29), about three times longer than wide, about six times longer than thick; posterior end flat; pair of posterior cartilages elliptical, with about 1/8 anterior cartilages length and almost their same width, located posteriorly and weakly external to anterior cartilages; subradular cartilage, expanding in buccal cavity beyond radular ribbon at about half radular ribbon width. Complex net of buccal mass vessels and nerves as shown in Figs 25–27.

Radula (Figs 15–19) Rachidian tooth rectangular, about twice as longer than wide, width ~1/12 of total radular ribbon; cutting edge poorly defined, cuspless, marked only by subterminal thickness (Figs 14, 17, 19). First lateral tooth obliquely disposed (outer edge located at level of preceding rachidian), with about rachidian length and about four times wider; cutting edge smooth, as longitudinal fold flanking proximal edge, median edge flanking rachidian, abruptly curving externally up to outer edge, performing another abrupt curve; inner half somewhat taller and narrower than lateral half; secondary triangular edge located in lateral half, turned opposite to cutting edge (Figs 14, 17, 19). Second lateral tooth sigmoid, ~20 times smaller than first lateral, located edging outer border of first lateral (Fig. 24). Third to fifth lateral teeth forming a single block (Figs 16, 18), base with about twice rachidian width and its same length; cutting edge about twice taller than base, about three times wider than rachidian; cutting edge bearing strong subterminal cusp turned inwards; single small cusp located in inner edge of this subterminal cusp, sometimes absent; about eight secondary cusps along outer edge, sometimes similar-sided and 15–20 times smaller than subterminal cusp (Figs 16, 18), sometimes cusps gradually decreasing in size from medial to lateral (Figs 14, 17); cutting edge continuing along lateral border as smooth tall fold (Fig. 18). Marginal teeth from 20 to 30 pairs per row; base long, somewhat flat, rod-like, ~20 times longer than wide; terminal region spoon-like, flanked in both sides by 6–8 pairs of small cusps (Fig. 15); each marginal tooth with about twice rachidian length and about 1/10 rachidian width; marginal teeth gradually decreasing from medial to lateral, being more marginal teeth approximately half-sized in relation to more medial teeth (Figs 14–18). Pair of salivary gland as two hollow pouches located covering posterior surface of odontophore (Figs 24–26), bearing glandular tissue in their postero-ventral inner surface; connection to esophagus somewhat wide, duct with about half of gland width. **Esophagus** with flaccid, thin, translucent walls, compressed by adjacent intestinal loops; width approximately equivalent to half buccal mass width; inner surface smooth, lacking glands or folds (Figs 23–26).

Stomach Balloon-like, walls flaccid, thin, translucent, no clear separation from (dorsal-left) esophageal insertion and (ventral-right) intestinal origin; duct to digestive gland located in ventral surface of posterior gastric wall (Fig. 23: dd); gastric inner surface simple, lacking folds except for transverse septum separating esophageal and intestinal regions.

Gastric muscle (Fig. 23: sm) Originating from columellar septum in small area, running posteriorly flanking intestine; inserting in region of intestinal origin in stomach.

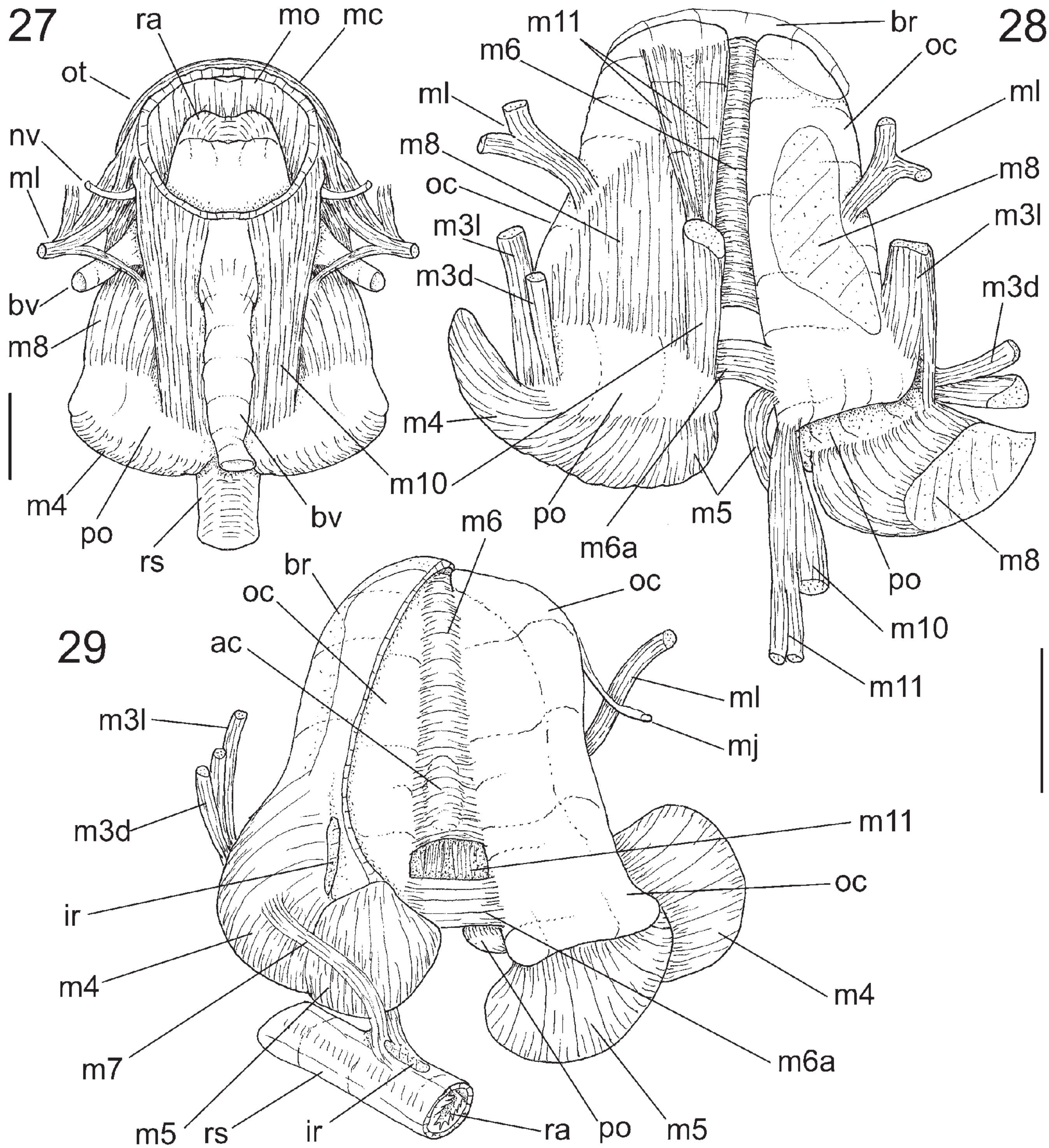


Figures 23–26 *Neritina zebra* anatomy: 23) head-foot, female, with part of visceral mass and pallial cavity sectioned and deflected to right (left in fig.), head-food in dorsal view, pallial cavity in ventral-inner view, midgut loops as in situ; 24) buccal mass and adjacent structures, ventral view; 25) same, ventral view, odontophore partially removed and deflected to left, longitudinal section artificially done in buccal fold in level of right jaw plate, place of haemocoelic intestinal loop also shown; 26) buccal mass, dorsal view. Scales: 23=5 mm; 24–26=1 mm.

Intestine Possessing two loops (Fig. 23), second loop about twice larger than first look, reaching haemocoel in region close to buccal mass (Fig. 25); intestinal walls thin, flaccid and simple. Rectum crossing dorsally visceral mass through kidney (Fig. 22). Pallial rectum and anus described above.

Reproductive system, male (Fig. 32) Visceral vas deferens convolute, short narrow region individualized from anterior region of testis. Seminal vesicle forming spherical mass between visceral and pallial cavities, just anterior to right kidney, with ~1/10 of visceral volume; bearing several, intense loops, those more proximal narrow, those more distal gradually becoming broad, sometimes possessing spherical nodulations, of dark brown colour. This nodular terminal portion of seminal vesicle running in right region of pallial cavity in wide zigzag; in middle level of pallial cavity inserting in very narrow gonopericardial duct (Fig. 32: gd); after this vas deferens running short distance, inserting in annexed gland. Annexed gland (ax) amorphous, with equivalent size as spherical portion of seminal vesicle; located in middle level of ventral surface of pallial spermoduct. Prostate as balloon-like sac, occupying most of pallial spermoduct, with about same pallial cavity length, about 1/6 pallial cavity width; its posterior end rounded, protruding into right kidney, gradually becoming narrower, in its region anterior to annexed gland abruptly narrowing; anterior third about 4 times narrower than remaining prostatic regions; aperture simple, sessile, just at right from anus; prostate inner surface smooth, thinly glandular. From genital aperture to penis base no clear furrow (Fig. 21). Penis located in dorsal-right surface of snout (Figs 21, 31), base almost as wide as snout base, gradually narrowing towards anterior and ventral, covering dorsal surface of snout; generally extending twice snout length beyond snout anterior end. Penis somewhat triangular, solid, about twice wider than thick; pair of shallow furrows flanking both sides, being left furrow weakly deeper; both furrows converging in penis tip, up to base of terminal papilla (Figs 21, 31: pp). Penis papilla from five to ten times longer than wide, cylindrical, tapering towards pointed tip; length ~1/8 that of penis; curved to left.

Reproductive system, female (Figs 22, 33) Visceral oviduct very narrow, running in middle region of visceral ventral surface. Gonopericardial duct with length ~1/6 of visceral width, connected to visceral oviduct in its anterior end; similar characters than visceral oviduct. Visceral oviduct inserting just anterior to right kidney in posterior end of large albumen-capsule gland, in left posterior, small, weakly spiral projection of that gland. Albumen-capsule gland with ~80% of length of pallial cavity and ~25% its width, located edging its right surface; ~4 times longer than wide, about twice wider than thick; posterior and middle thirds of similar width, narrowing gradually in anterior third; interiorly composed mostly by pair of thick glandular laminas. Seminal receptacle very small, balloon-like, located in right-posterior corner of albumen-capsule gland; with ~1/100 of that gland volume; duct of similar characters of visceral oviduct, running towards left distance equivalent to 1/3 of that of albumen-capsule gland width; inserting in that gland just at right from insertion of visceral oviduct. Enigmatic duct (ed) with similar characters as visceral oviduct, running longitudinally along albumen-capsule gland ventral surface at ~60% its length; anterior end with narrow aperture; posterior end inserting in seminal receptacle duct between its middle and left thirds. Bursa copulatrix (bc) spherical, weakly attached dorso-ventrally, located posteriorly to albumen-capsule gland protruding dorsally to right kidney; with ~1/4 albumen-capsule gland volume; its duct cylindrical, with same length of remaining pallial oviduct and ~1/10 id width; duct posteriorly running at left from pallial oviduct, gradually crossing ventrally to right in anterior third, opening in small, simple papilla located anteriorly and at right from anus (va). Vaginal duct (vr) with similar characters as visceral oviduct in some specimens, and very irregularly convolute in others, originated between middle and posterior thirds of albumen-capsule gland ventral surface; running towards anterior distance ~1/2 pallial oviduct length; inserting in right surface of duct of bursa copulatrix, in region preceding its anterior quarter. Reinforcement sac (cs) with ~1/4 pallial oviduct length and ~1/3 its width; located in anterior left region of pallial oviduct, flanking albumen-capsule gland anterior end. Vaginal atrium simple, connecting albumen-capsule gland and reinforcement sac with genital



Figures 27–29 *Neritina zebra* odontophore: 27) ventral view, superficial layer of membranes and muscles removed; 28) dorsal view, both anterior cartilages somewhat deflected, right structures partially removed and deflected (mainly m8) in order to show inner structures; 29) same, ventral view, left-posterior structures (right in Fig.) deflected, subradular membrane (br) and radular sac (rs) only partially shown. Scale = 1 mm.

aperture (ap). Genital aperture simple, sessile, located anteriorly and at left from anus.

Central nervous system (Fig. 30) Nerve ring located just posterior to mouth, surrounding anterior region of buccal mass (Fig. 24). Pair of cerebral ganglia locates in opposed sides of mouth; each one with about same size of oral tube width. Cerebral commissure with ~1/4 ganglia width, and ~1/2 odontophore width; flanking dorsal surface of oral tube. Labial ganglia located close to inner-anterior side of cerebral ganglia, with ~1/6 of their volume; labial commissure with ~1/4 cerebral commissure width and about its same length; flanking ventral surface of oral tube. Pair of cerebro-pleural and cerebro-pedal connectives running close from each other ventrally and anteriorly; length equivalent to that of cerebral commissure. Pleural and pedal pair of ganglia with equivalent size as cerebral ganglia; both located very close to each other and to median line (commissure very short); pleural ganglia located weakly dorsal and more anterior than pedal ganglia; pair of pleuro-pedal connectives very short. Pair of statocysts located ventrally and anteriorly to pedal ganglia, relatively close to median line; volume ~1/4 pedal ganglia.

Measurements (N= 40, in mm)
Minimum diameter 14.34–20.59 (av. 16.84)
Maximum diameter 14.70–21.52 (av. 17.79)

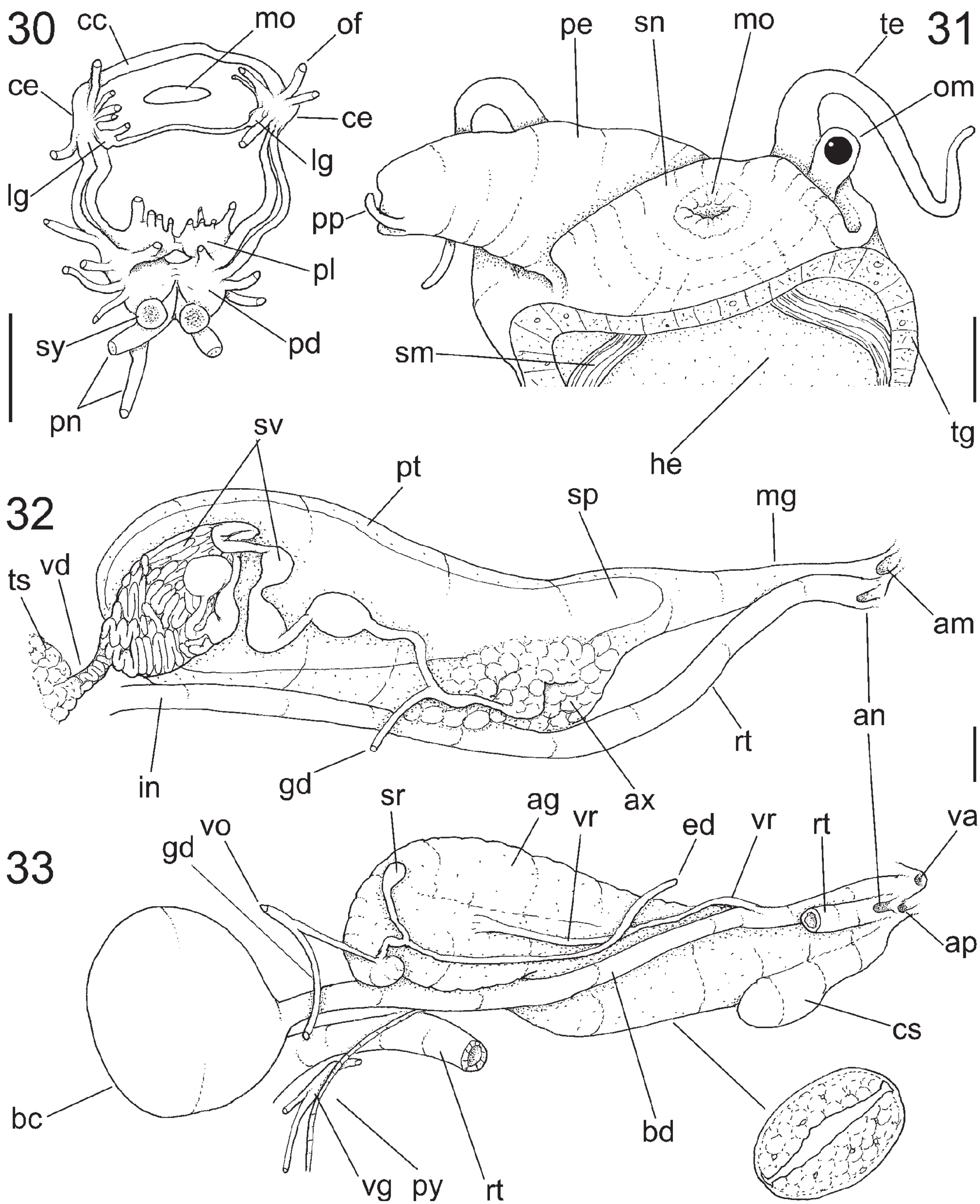
Distribution From French Guiana to Rio de Janeiro.

Habitat Estuarine, on intertidal muddy bottoms.

Material examined (s=shell/s; spm= specimen/s) French Guyana: Cayenne, MNHN, 2♂, 1♀. Brazil: Amapá – Maracá-Jipioca, Siriubal, Estação Ecológica, MZSP 28204, 7 s, (Fernandes col, 27.x.1995); Pará – Belém, Rio Guamá, UFPA, CMPHRM 2667, 6 s (Belúcio col.vi.2008), CMPHRM 2670, 8 s (Lobato col.), MZSP 24397, 7 s, (Amaral col., 1944), MZSP 33700, 2 s (Oliveira col., 1954), Mosqueiro, MZSP 35609, 7 s, (Vanin col., 11.ii.1996), MZSP 54337, 28 spm, (Mourgues col.. 11.ii.1984), Parque do Museu Emílio Goeldi, MZSP 36895, 1 s (Vanzolini col., 21.i.1974), Abaetetuba, MZSP 24394, 4 s (Exp. DZ, 5–7.vi.1958), Vigia, MZSP 24395, 17 s (Oliveira col., 7.viii.1979), MZSP 24396, 9 spm (Julieta col., xii.1978), Iguarapé-Mirim, Vila Maiauatá, Iguarapé Oruzinho, MZSP 24398, 25 s (EPA col., 27.viii.1970), Ilha do Marajó, MZSP 33673, 7 s (Camargo col., ii.1967), MZSP 81103, 1 s (Simone col., 1972), Itapua, Vigia, Baixo Salgado, MZSP 45114, 12 s (vii.1978); Ceará – Aquiraz, Rio Pacoti, CMPHRM 2090, 1 s (Sousa col., 1986), Fortaleza, MZSP 83539, 2 s (Simone col., 1981), Parque do Cocó, CMPHRM 2096, 8 s (Rocha-Barreira col., 5.vi.2005), CMPHRM 2564, 3 ♀ (Barroso col.. 25.vii.2008), Porto do Mucuripe, CMPHRM 2738, 1 s (vi.2002), Manguezal do rio Ceará, MZSP 87779, 13 spm (Barroso col., 13.viii.2007), Caucaia, Manguezal do rio Ceará (Barroso col.), CMPHRM 2424, 6 s (20.vii.2005), CMPHRM 2425, 1 s (15.ix.2005), CMPHRM 2426, 1 s (15.ix.2005), CMPHRM 2427, 3 s (17.x.2005), CMPHRM 2428, 1 s (1.ii.2006), CMPHRM 2428, 1 s (1.ii.2006), CMPHRM 2566, 10 s (iii.2008), CMPHRM 2568, 3 ♂ (iii.2008), CMPHRM 2569, 30 s (2007), CMPHRM 2672, 3 ♀ (27.iii.2008), CMPHRM 2673, 3 ♀ (iv.2007); Fortim, Praia do Canto da Barra (Rocha-Barreira & Araújo col., 13.xii.2001), CMPHRM 2746, 2 s, CMPHRM 2750, 2 s, São Gonçalo do Amarante, Terminal Portuário do Pecém, CMPHRM 2671, 6 s (Rabay col., 2.vii.2008); Camocim, Rio Camocim (Bianchi col.), MZSP 65186, 2 s (ix.2002), MZSP 69312, 25 spm (Bianchi col. Femorale, ix.2002), MZSP 72044, 5 s (i.2003); Bahia – MZSP 369, 15 s (Bicego col., v-vii.1996), Canavieiras, MZSP 1953, 21 s, Cachoeira, Rio Paraguaçu, MZSP 24399, 24 s (M. Roxo col., 1939), MZSP 24401, 16 s (Bicego col. v-vii.1986); Ilha de Itaparica, MZSP 26850, 1 s (Farani & Cristina col.), MZSP 33834, 4 s (J. Vaz col., xi.1974), Salvador, MZSP 79651, 9 s (Ferreira col., i.1979); Alagoas – channel between Lagoa Manguaba & Lagoa Norte, MZSP 17428, 3 s (Cardoso col., 1952); Espírito Santo – Piúma, MZSP 59074, 3 s (Guimarães col., 20.vii.1976); Rio de Janeiro – São João da Barra, Atafona, MZSP 15293, 2 s (vii.1963), MZSP 87733, 13 spm (vii.1963); São Paulo – Iguape, MZSP 17420, 1 s, MZSP 24400 6 s (Wachet col., xi.1901).

Discussion

Characteristically for Neritimorpha, the shell of *Neritina zebra* lacks a columella (Fig. 3), a consequence of the re-absorption of the inner walls of the shell (Fretter & Graham, 1962; Bandel & Kiel, 2003; Andrzej & Przemyslaw, 2005). Consequently, *N. zebra* shows morphological modifications relative to that such as shape of visceral mass (rounded, instead of spiraled), and the shape of the columellar muscles (Figs 21, 23). Unequal development of the left and right columellar muscles, such as observed in this study (Fig. 21), appears to be connected to the peculiar development of the shell and the significance of the semilunar operculum (Bourne, 1908) (Figs



Figures 30–33 *Neritina zebra* anatomy: 30) nerve ring, ventral view, topology of mouth also indicated; 31) head, male, ventral view, foot removed, inner haemocoelic structures extracted; 32) male, pallial gonoducts and anterior portion of visceral gonoducts as in situ, ventral view, some adjacent structures also shown; 33) same, female, with transversal section of indicated level of capsule gland also shown, part of rectum removed. Scale = 1 mm.

4, 5). Processes of re-absorption of calcareous material, in different degrees, are not rare in gastropods (Hyman, 1967).

Typical for the genus *Neritina*, there is great variation in colour and patterns of the shells in *N. zebra* (Matthews-Cascon *et al*., 1990), which can be shown in the Figs 1, 6, 8–11. Colour and pattern are genetically determined and polymorphic, and have evolved under disruptive selection for crypsis (Berger, 1983; Stanley, 1988). A strange bicoloured banded shell is present in syntype 1 (Figs 8–9), which is not found in syntype 2 (Figs 10–11). This has been interpreted as caused by erosion of the periostracum. This conclusion is based on the examation of the apertural region of the shell of both specimens (Figs 9. 11), which show more clearly erosion of the periostracum.

The shells of *Neritina zebra* have different pigmentation patterns if compared with other Neritidae. The species exhibits oblique lines that originate from traveling waves of pigment production. In this type of pattern, an existing pigmented region, if touched by a growing mantle gland, can initiate a traveling wave of pigment production on the newly formed portion of the shell. Other species of Neritidae have different patterns, such as staggered dots (e.g. *Neritina natalensis* (Reeve 1845)), parallel and oblique lines (e.g. *Neritina communis* (Quoy & Gaimard 1832)) and parallel lines with tongues (e.g. *Neritina virginea*). These tongues are gaps in a pattern of parallel lines caused by temporary interruptions in synchronous oscillations (Meinhardt, 2009).

The pair of asymmetrical columellar muscles is another distinctive feature of neritids, which is also found in the present species (Fig. 21) and in closely related ones (Little, 1972; Martins *et al*., 2002: fig. 7).

The heart of *N. zebra* has a pair of auricles, with the right auricle relatively reduced (Fig. 22). A reduced right atrium is common in other nerites (Bourne, 1908; Hyman, 1967; Little, 1972; Estabrooks *et al*., 1999). Following this trend, a monotocardic condition, i.e., total absence of right atrium, is found in terrestrial neritimorphs such as Helicinidae (Little, 1972).

The small size of the jaw plates of *Neritina zebra* (Fig. 21: jw) appears to be another characteristic of family Neritidae (Hyman, 1967; Ponder & Lindberg, 1997).

The radular teeth of *Neritina zebra* (Figs 14–19) have similar characters to those described by Calvo (1987), except for the number of cusps present in the fifth pair of lateral teeth. According to Calvo (1987), the number of cusps of the fifth pair varies from 9 to 19. However, the number found here ranged between 13 and 15 (Fig. 18). Nevertheless, variation in the number of cusps on the lateral tooth of radulae in Neritidae might be caused by age (Russel, 1941). Comparing the radular attributes of *N. zebra* with those of the sympatric *N. virginea* (Martins *et al*., 2002: figs. 9–12) a close similarity is indicated. The radula of *N. zebra* has as differences the more squared rachidian, and a weaker basal reinforcement of the first lateral teeth.

Reproductive characters have been advocated as the only morphological characteristics useful for the diagnosis of all clades in Neritimorpha (Kano *et al*., 2002, Berry & Kumar, 2009). However, it is possible that alternative structures have been little explored. Remarkably, except for Neritopsidae and Hydrocenidae, which have monoaulic females (i.e., a sole genital opening), in the other families of Neritimorpha, the females are usually diaulic, with two genital openings. This has been considered an apomorphic condition. This is despite some genera of Neritidae having a third opening, the enigmatic duct, as is the case with *N. zebra*. The enigmatic duct appears to function in the elimination of materials not used in the reproductive process, being related to the spermatic sac and seminal receptacle (Fretter, 1984). The pallial gonoducts of *N. zebra* females are considerably different from most others so far described (Fig. 33). For example, *N. zebra* differs from *Neritilia rubida* (Pease 1865) and from *Platynerita rufa* Kano & Kase 2003 (Kano & Kase, 2003: fig. 5) in lacking a spermatophore sac (which is enormous in those species), in lacking a posterior vaginal opening, in having a reinforcement sac, in having a much longer capsule gland antero-posteriorly, etc. The large bursa copulatrix of *N. zebra* may be homologous to the spermatophore sac of those two species, differing in possessing the terminal balloon-like enlargement and in being more anteriorly situated. On the other hand, the lack of a spermatophore sac in *zebra* is shared with limpet-like freshwater neritids such as *Septaria* spp. (Haynes, 1996). Species of *Septaria* from southeast Asia and the Pacific islands, although lacking a spermatophore sac, produce complicated spermatophores. Others do not produce spermatophores but have a spermatophore sac, while others have neither a spermatophore sac nor spermatophores (Haynes, 1996). This is a fascinating subject for future studies.

A massive penis with a lateral groove is present in males of the Phenacolepadidae and Neritidae, not having been observed in other Neritimorpha (Kano *et al.*, 2002). Males of *N. zebra* in the present study had grooved penises on the right side of the cephalic region. This penis allocation shows that it is not homologous to the penis of other gastropods, which are located behind the right cephalic tentacle. A similar penis is found in *Neritina virginea*, but that of *N. zebra* is independent of the snout (Fig. 31), while that of *N. virginea* is a prolongation of the right side of the snout's anterior end (Martins *et al.*, 2002: fig. 6; pers. obs.). This difference appears indicative of convergence.

A set of morphological characters exclusive of the Neritimorpha suggest that the taxon is monophyletic. The characters are: a globose, low-spired shell shape, with re-absorption of the columella; a calcareous operculum with apophysis; the bifurcate position of both columellar muscles; the presence of single pallial organs; and the high complexity of the pallial structures of the reproductive system, which normally allow internal fertilization and the production of egg capsules.

Nereina lacustris, one of the junior synonyms of *N. zebra*, is the type species of the genus *Nereina* Cristofori & Jan 1832, by monotypy. Based on this, *N. zebra* should be referrable to *Nereina*. Although it is older than *Vitta* Mörch 1852, *Nereina* has an early homonym (*Nereina* Mandelstam 1957, an arthropod), so *zebra* has mostly been referred to *Neritina* Lamarck 1816 or *Neritina (Vitta)* (see synonymy). As a wider analysis of the systematics of *Neritina*-like species is still lacking, a more conservative approach was adopted here, with *zebra* placed in *Neritina*.

Neritina lineolata Lamarck 1816 has been considered a synonym of *N. zebra* by some authors (e.g., Russel, 1941: 390). However, other authors consider the species a synonym of the closely related Florida species, *N. usnea* (Röding 1798) (e.g. Rosenberg, 2010). *Neritina usnea* has the same shape and similar colour pattern to *N. zebra*, differing by its more delicate transverse, zigzagged dark bands (which are sometimes absent) and by the almost freshwater environment preferred (Tunnell *et al.*, 2010: 127). Another closely related species is *N. sobrina* Récluz 1846, which occurs in the Pacific coast of South America. Certainly, comparative studies of samples of these taxa will be required to clarify the significance of these similarities.

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