ISSN 0738-9388

Volume: 56 THE FESTIVUS ISSUE 3

A New *Drymaeus* in the Region of Itapebi, Bahia, Brazil (Eupulmonata, Bulimulidae)

Luiz Ricardo L. Simone [1] & Alain Celzard [2]
[1] Museu de Zoologia da Universidade de São Paulo (MZUSP) São Paulo, SP, Brasil
lrsimone@usp.br ORCID: http://orcid.org/0000-0002-1397-9823
[2] Université de Lorraine, CNRS, IJL, F-88000 Epinal
alain.celzard@univ-lorraine.fr ORCID: https://orcid.org/0000-0003-0073-9545

ABSTRACT *Drymaeus nigroflavus* is a newly described species found in the region of Itapebi, Bahia, Brazil, near the Jequitinhonha River. This species is characterized by its whitish shell adorned with dark, spiral bands that are uniform and spaced apart. Its genital system exhibits a very short penis and bursa copulatrix, as well as a spermoviduct with a wide, coiled uterus and a very narrow prostate, among other anatomical idiosyncrasies.

KEY WORDS New species, Gastropoda, *Drymaeus nigroflavus*, Anatomy, Brazil

INTRODUCTION

Some less-studied regions of Brazil, such as Southeast Bahia, have revealed intriguing malacological discoveries, largely uncovered by a team of collectors led by the naturalist José Coltro Jr., and in particular the talented collector Weslley Vailant-Mattos.

This paper reports one of these discoveries, a new species of the genus *Drymaeus* Albers, 1850 (type species *Helix hygrohylaea* d'Orbigny, 1835, SD by Pilsbry, 1898) (Orthalicoidea, Bulimulidae). The genus comprises approximately 230 species (MolluscaBase, 2024), distributed from southern Florida to Patagonia. Because of the considerable number of species within the genus, it is not surprising that it has been subdivided (Salvador *et al*., 2023). However, despite this large number, species of *Drymaeus* and its relatives have been found to be relatively endemic to restricted areas, and new species continue to be discovered and described, including with regard to anatomical aspects (Simone & Salvador, 2016; Simone & Amaral, 2018; Simone *et al*., 2020).

The present paper introduces another *Drymaeus* species, presenting both conchological and anatomical characteristics. Conchological comparisons are primarily limited to species with banded shells, as this is the main characteristic that distinguishes the new species from most others. On the other hand, anatomical comparisons are more extensive, given that relatively few species are known in these aspects. The anatomical features of the new species are compared with those of congeners known at this level, as well as with some species from other allied genera.

MATERIAL AND METHODS

A complete list of examined material is given in the species description. The samples were donated to the Museu de Zoologia da Universidade de São Paulo (MZSP) as dry shells or already fixed unrelaxed in 70% ethanol. The dissections were performed by standard techniques, with the specimens immersed in

ISSN 0738-9388

alcohol and examined under dissecting stereomicroscopes. All drawings were done with the aid of a camera lucida, and most drawings are normally based on several specimens. Photos of all dissection steps were taken using a digital camera coupled to the microscope. SEM examinations were performed in a Zeiss device of the Laboratory of Electronic Microscopy of the MZSP. This institution also houses the type material.

ABBREVIATIONS

aa, anterior aorta; **ac**, albumen chamber; **ad**, albumen gland duct; **ag**, albumen gland; **an**, anus; **as**, accessory albumen chamber; **au**, auricle; **bc**, bursa copulatrix; **bd**, bursa copulatrix duct; **bg**, buccal ganglia; **br**, subradular membrane; **bv**, blood vessel; **ca,** carrefour; **ce**, cerebral ganglion; **cl**, left secondary columellar muscle; **cm**, columellar muscle; **cn**, cerebro-pedal and cerebro-pleural connectives; **co**, collar vessel; **cr**, right secondary columellar muscle; **cv**, pulmonary (efferent) vein; **da**, digestive gland anterior lobe; **dd**, anterior gastric duct to digestive gland; **df**, dorsal folds of buccal mass; **dg**, digestive gland posterior lobe; **di**, diaphragm or pallial floor; **dp**, posterior gastric duct to digestive gland; **ef,** esophageal fold; **eg**, esophageal glandular portion; **eh**, epiphallus; **ei**, epiphallus inner longitudinal fold; **eo**, spermoviduct; **es**, esophagus; **ey**, eye; **fe**, female right lateral sulcus; **fg**, fecal groove; **fo**, free oviduct; **fp**, genital pore; **ft**, foot; **gl**, glandular portion of penis; **gm**, genital muscle; **go**, gonad; **hd**, hermaphrodite duct; **if**, inner fold of pneumostome; **in**, intestine; **jw**, jaw; **ki**, kidney; **kl**, kidney lobe; **m1–m10**, extrinsic and intrinsic odontophore muscles; **mb**, mantle border (edge); **mc**, circular muscles of oral tube; **me**, ommatophore muscle; **mf**, mantle fold; **mj**, jaw and peribuccal muscles; **mo**, mouth; **nr**, nerve ring; **oc**, odontophore cartilage; **od**, odontophore; **om**, ommatophore; **pc**, pericardium; **pe**, penis; **pg**, pedal gland; **pl**, pleural ganglia bridge; **pm**, penis muscle; **pn**, pneumostome; **pp**, pedal ganglion; **ps**, penis shield; **pt**, prostate; **pu**, pulmonary cavity; **ra**, radula; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sa**, salivary gland aperture; **sc**, subradular cartilage; **sd**, salivary gland duct; **sg**, salivary gland; **sp**, sperm inner longitudinal fold; **sr**, seminal receptacle; **st**, stomach; **sy**, statocyst; **tg**, integument; **to**, tissue on radula at end of radular sac; **ua**, urinary aperture; **un**, union of mantle border with nuchal surface; **up**, primary ureter; **ur**, ureter; **ut**, uterus; **vd**, vas deferens; **ve**, ventricle; **vg**, vagina.

SYSTEMATICS

Drymaeus nigroflavus Simone & Celzard, new species
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(Figures 1-5)

Description.

Shell. (Figures 1, 2A) adult shell around 25 mm, conical-oval; apex bluntly acuminated; greatest width on last whorl; width ~1/2 shell length. Basal color white, with 2 spiral dark brown, narrow stripes in each whorl, one along middle region, another suprasutural, keeping narrow white strip between it and suture; suprasutural band ~double width than middle band. These 2 bands continuing along body whorl up to peristome, disappearing short distance from it (Figures 1B, H, M, J); 2 equidistant and similar characterized bands appearing in inferior half, being inferior band peri-umbilical (Figures 1A, G, I, K, L, 2A). Spire angle ~42°. Protoconch of 2.5 whorls, dark-brown pigmented, width 1.6 mm, ~3% of total shell length, ~13% of shell width (Figure 1D), uniformly sculptured by delicate reticulate pattern (Figures 1E, F); transition to teleoconch clear, slightly

ISSN 0738-9388

prosocline (Figures 1E, F: arrow). Teleoconch smooth, glossy, except for growth lines and extremely delicate spiral striae; of ~5 whorls. Whorls profile slightly convex. Suture well-marked, slightly oblique (diagonal) to columellar axis. Aperture prosocline (~10° from longitudinal general axis) (Figure 1B), oval; ~45% of shell length, ~53% of shell width. Peristome slightly reflected, partially covering umbilicus (Figures 1A, G, I, K, L). Body whorl ~70% shell length. Umbilicus opened, narrow (Figure 2A).

Head-foot. (Figure 4A) of usual shape. Color uniformly clear. Columellar muscle (cm) narrow, flattened, 1.5 whorls in length. Right secondary columellar muscle (cr) slightly narrower than columellar muscle, with 2 anterior insertions in posterior region of haemocoel floor; secondary medial insertion with columellar muscle located more posteriorly; insertions of genital (gm) and ommatophore (me) muscles in its outer edge. Left secondary columellar muscle (cl) ~double width of right muscle, flattened, inserted more anteriorly with 6 branches, successively larger from posterior to anterior, flanking pedal gland (pg); narrow ommatophore muscle inserted in its edge (me).

Mantle Organs. (Figures 2B-E) mantle border thick, lacking pigments (Figure 2E). Pneumostome (pn) protected by outer, right simple flap (mf), with ~1/3 of aperture length. Inner fold (if) about double width of outer flap, ~half its length. Pneumostome (pn) ~1/10 of aperture length, bearing air entrance (Figure 2C: pn), urinary escape (Figure 2C: ua) in left-anterior side, and anus in right-posterior side, separated by transverse fold (Figure 2C: an). Lung of 1.5 whorls in length, ~1.5 longer than wide. Pulmonary vessels conspicuous all along right side (Figure 2B), being more conspicuous in anterior third; mostly bearing transverse, rather perpendicular vessels, clustered; in posterior half more spaced, sometimes bifurcating or anastomosing; in left side of pulmonary vein (cv), visible vessels only in anterior third, occupying right ~half of this area, constituted by oblique, branched vessels, intercalated with branched from collar and from pulmonary vein (Figures 2B, C). Remaining regions of lung almost smooth, with imbricated vessels of difficult visualization. Pulmonary vein (cv) running longitudinally between middle and right thirds of pallial cavity roof, somewhat equidistant from rectum all along its length, but slightly more distant in renal region; anterior end of pulmonary vein curved to right, uniformly branched (Figure 2C: cv), in base of pneumostome (pn). Reno-pericardial area triangular (Figures 2B, C), located posteriorly at middle level of posterior end, occupying ~35% of cavity length and ~50% of its width (details below). Rectum (rt) and ureter (ur) narrow, running along right edge. Urinary aperture very elongated (Figures 2B, C: ua), occupying ~1/8 of ureter length; its posterior end slightly angular, abruptly opening, running as short groove up to left from anus; in region of pneumostome becoming T-shaped, being its left branch longer and anteriorly protected by special fold (Figure 2C).

Visceral Mass. (Figure 4B) ~4 whorls in length. Mantle covering whorls with light spiral band expressing those of shell. Both digestive gland lobes uniformly pale beige in color. Anterior lobe (da) flattened, occupying ~1/6 of visceral volume, located just posteriorly to pallial cavity, continuous with kidney. Posterior lobe (dg) with 2.5 spiral whorls, with ~50% of visceral volume. Stomach (st) with ~1/15 of visceral volume, located between both digestive gland lobes, about 2/3 whorl posterior to pallial cavity. Digestive tubes (described below) surrounding anterior lobe of digestive gland. Gonad clearly multi-lobed, same color as digestive gland, encased between posterior lobe of digestive

gland and columella, occupying ~1/5 of visceral volume.

Circulatory and Excretory Systems. (Figures 2B, D, 4B) Pericardium (pc) ~4 times as long as wide, located obliquely between middle and left thirds of posterior end of pallial roof; occupying ~3% of lung area. Auricle (au) located anteriorly, as continuation from pulmonary vein (cv), same size as ventricle (ve). Kidney (ki) simple, mostly solid, dorso-ventrally flattened; size reported above; somewhat triangular, maximum posterior width ~2/3 of length; inner lobe constituted of longitudinal, tall folds converging anteriorly to middle axis of structure (Figure 2D: kl). Nephropore small, longitudinal slit in anterior-left corner, turned right, inside primary ureter anterior end. Primary and most of secondary ureter closed (tubular); primary ureter (up) lying on right edge of kidney towards posterior and right, after forming strong curve, running afterwards anteriorly, as secondary ureter (ur) along entire left edge of rectum, except for longitudinal urinary aperture of ~1/8 of its length (Figure 2C: ua) (details above).

Digestive System. (Figures 3, 4B, C) Arrangement of foregut essentially same as that described for *Drymaeus castilhensis* (Simone & Amaral, 2018: 171-172, figs. 41-44) except for: m1v, absent; m1l, small pair of lateral jugal muscles, originated in lateral-anterior surface of haemocoel, running short distance, inserting in latero-posterior region of buccal mass, passing through nerve ring (Figure 4B); m2, pair of retractor muscles of buccal mass slightly narrower, with separated insertions in posterior end of odontophore (Figures 4B, C); m3, not detected; m4, thin, wide, with connections in inner surface of cartilages (Figure 4C); m5, thin, narrow, originated on m4 posterior surface; m6, absent; m7, as strong oblique fibers inside tissue inside radular sac (Figure 2I); m10, pair of ventral protractor muscles of buccal mass slightly thinner and narrower; circular muscles of oral tube (mc) not so developed. Cartilages (oc) ~80% fused with each other along median-ventral edge, relatively flattened, rounded. Tissue inside radular sac well developed, solid, with cartilaginous aspect, possessing oblique m7 and exposed anterior surface folded (Figures 2H, I: to). Radular sac short, not extending beyond odontophore. Jaw plate (Figures 2F, G: jw) thin, relatively wide, flexible, yellow; with ~25 pairs of transverse folds of uniform width and length. Radular nucleus (rn) inlaid inside odontophore.

Radula. (Figures 3B-G) as long as odontophore (Figure 4C: rs); with rachidian teeth, and ~130 pairs of lateral/marginal teeth; no clear distinction between lateral and marginal teeth (Figures 3B, F); all teeth with relative long, narrow, flattened base, located closely from neighboring rows; and set of 3 wide, rather triangular cusps in cutting edge preceded by flattened, wide flap curved inwards. **Rachidian** tooth (Figures 3B-E: arrow) small, symmetric, relatively reduced, ~half of neighboring teeth, ~1/150 of radular width; base ~3 times longer than wide, flattened, barely rectangular (Figures 3D, E); central cusp with ~1/4 of base's size, tip blunt; pair of basal cusps with ~1/2 of central cusp's size (Figure 3E). **Lateral teeth** similar to rachidian, except in being two times wider, asymmetric, arched towards lateral region, cutting edge ~2-3 times wider than that of rachidian (Figures 3C, F, G); lateral teeth gradually weakly decreasing towards lateral; set of cusps with ~1/2 of length of base; central cusp as slightly larger, bluntly pointed; other 2 cusps similar shaped, but slightly smaller.

Marginal teeth. Starting with no clear boundary with lateral teeth; shaped similarly to lateral teeth, except for being weakly smaller and with set of 3 cusps with increment of

central cusps and diminishing of both secondary cusps; both secondary cusps very small in marginal teeth (Figure 3C). Each radular row slightly arched disposed from both sides from rachidian (Figure 3B).

Salivary Glands. Appearing as 2 separated, elongated, narrow masses covering lateral sides of esophagus in its region preceding its anterior 1/3 (Figure 4B: sg). Each salivary duct relatively short, differentiable in anterior side of glands, relatively broad, with ~1/20 esophageal width (Figures 3A, 4B: sd). Salivary duct running in both sides of esophageal origin (Figures 3A: sd), penetrating buccal mass wall in region close to buccal ganglia, running immersed in buccal dorsal wall along short distance. Salivary ducts aperture as tight slits, in middle level of dorsal folds, on their middle-posterior level (Figure 3A: sa).

Esophagus. One-whorl long, with relatively firm walls, lacking clear subdivisions (Figure 4B: es), with anterior region with well-developed glandular mucosa (Figure 3A: eg). Stomach (Figure 4B: st) narrow, curved, not bulged; position and size described above (visceral mass); gastric walls thin, flaccid; inner surface smooth. Esophageal insertion on right side, intestinal origin on left side, both close to columella. Duct to anterior lobe of digestive gland located in stomach, highly branched in right side only, covering adjacent right intestinal loop with its first long branch (Figure 4B: dd). Duct to posterior lobe of digestive gland located at short distance from intestinal origin (Figure 4B: dp), elongated, branched after some distance. Intestine as wide as esophageal insertion, relatively narrow all along its length (Fig 4B: in). Rectum and anus position described above (pallial cavity) (Figure 2B: rt, an). Anus sessile, as slit in right end of mantle edge directly turned outside from pneumostome (Figure 2C).

Genital System. (Figures 4D, 5A-C) gonad position described above (visceral mass), composed of 4-5 lobes with minute digitiform acini (Figure 4B: go). Hermaphroditic duct (Figures 5A, C: hd) narrow, weakly coiled in middle region; inserting in left side of receptacle's base (Figure 5C: hd). Seminal receptacle (Figures 5A, C: sr) very small, sac-like, sigmoid, ~3-times longer than wide, with ~1.5 hermaphroditic duct width; tip rounded. Fertilization complex (carrefour) simple, distally triangular, abruptly becoming narrow and elongated (Figure 5C) as duct; ~twice longer than length of receptacle. Fertilization complex partially immersed in albumen gland (Figure 5A), inserting in posterior end of spermoviduct, in base of albumen chamber duct (Figure 5A: ad) relatively wide, simple, ~5-times wider than receptacle's duct. Albumen gland (Figures 5A,C: ag) solid, white, elliptical, 1.5 times larger than gonad (~1/3 whorl). Albumen gland duct terminal, connected to distal end of spermoviduct (Figure 32: ad), in lateral, large, flattened albumen chamber (Figure 32: ac); widely connected to distal end of spermoviduct. Spermoviduct 3 first loops working as secondary albumen chamber (Figures 5A, C: as), as wide, simple loops replete with albumen; after ~1/5 spermoviduct length, usual uterine folds appearing (Figure 5A; ut). Spermoviduct (eo) of ~1 whorl in length, very wide, ~4.5 times longer than wide; uterus (Figures 4D, 4A: ut) wide, walls thin, glandular, externally forming surface with intense convolutions, apparently of chaotic organization. Prostate gland (pt) very narrow, occupying ~1/15 of spermoviduct surface (Figure 4D: pt). Sperm grove simple, along entire spermoviduct (Figure 4D: sp), protected ventrally by small, low fold. Anterior ~1/5 of spermoviduct suddenly narrowing, becoming very narrow duct; in this region sperm grove abruptly becoming tubular, as vas deferens in anterior end of spermoviduct. Free oviduct short and

vagina (Figure 5A: vg) with walls relatively thick; inner surface simple, with 4–5 longitudinal, low, wide folds. Bursa copulatrix (bc) ~1/3 of spermoviduct length; bursa duct as wide as adjacent spermoviduct in its origin, maintaining uniform width along its length (Figure 5A: bd); bursa oval, slightly larger than its duct (bc), not located close to pericardium. Penis ~1/2 of spermoviduct length, as wide as its anterior width (Figure 5A: pe); penis muscle inserting terminally, very short (Figure 5A: pm). Epiphallus ~1/8 penis' length, located as short terminal continuation of penis (Figures 5A, B: eh); inner surface with narrow, irregular longitudinal folds, located close from each other, uniformly sized. Vas deferens inserted subterminally in penis tip (Figures 5A, B: vd). Internal penial surface lacking clear sub-chambers (Figure 5B: pe); proximal half with 3 regions of similar length: 1) basal, with 8-10 low, wide, longitudinal, uniform folds, with relatively ticker muscular walls; 2) middle, initially smooth, gradually pair of wide folds appearing, culminating in pair of strong, tall folds (pf) turned inside and posteriorly, between them narrow, smooth space; 3) distal, with highly glandular mucosa (gl); distal half narrow and relatively uniform, bearing only 3 narrow, low, spaced, equidistant, longitudinal folds, with smooth area in interspaces, these folds appearing suddenly after glandular region in proximal end, continuing along epiphallus (eh) in distal end, with convergency in a side in vas deferens (vd) aperture. Penis shield occupying basal ~1/10 of penis length (Figure 5A: ps); vas deferens piercing its walls close to its base. Genital pore round, simple.

Central Nervous System. (Figures 5D, E) nerve ring surrounding mouth area, anterior to odontophore (Fig4B: nr). Pair of cerebral ganglia (ce) widely fused with each other; cerebral commissure invisible; each ganglion about as wide as adjacent esophageal section; several wide nerves originating in cerebral antero-lateral region. No clear cerebral node or gland. Two pairs of parallel connectives between cerebral ganglia and pedal/pleural ganglia (cn). Pair of pedal ganglia (pp) forming single mass located opposite to cerebral ganglia, slightly larger sized than cerebral ganglia. Pair of pleural ganglion (pl) as small bridge on pedal ganglia, connected with each other. Statocysts (sy) with ~1/10 of pedal ganglia volume, with single statolith, located in lateral-posterior edge of each pedal ganglia. Aorta (aa) wit branch forming strong sponge-like sinus surrounding nerve ring, mainly in region of pleural-pedal ganglia.

Type Material. Holotype: MZSP 159000, shell (Figures 1A-F, 2A). Paratypes: MZSP 159001, 3 shells (Figures 1G-K) from type locality. Brazil. Bahia; Itapebi, near Jequitinhonoa River, 15°57'28.84"S 39°31'04.37"W, MZSP 153113, 7 specimens, 12 specimens lacking shells (Weslley Vailant-Mattos col., xii.2020).

Additional Material Examined. Brazil. Bahia; Itapebi, near Jequitinhonha River, 15°57'08"S 39°30'58"W, MZSP 152693, 4 specimens (Weslley Vailant-Mattos col., 23.xi.2020); Itamaraju, Monte Pescoço, 17°01'07"S 39°32'45.58"W, MZSP 152964, 3 specimens (Weslley Vailant-Mattos col., xii.2020).

Measurements. Holotype MZSP 159000 (Figures 1A-F): 27.6 mm by 12.5 mm; paratype MZSP 159001#1 (Figures 1G-H): 23.3 mm by 11.7 mm; #2 (Figures 1I-J): 25.0 mm by 12.1 mm; #3 (Figure 1K): 26.1 mm by 12.2 mm; MZSP 153113#1 (Fig 1L-M): 26.1 by 12.3 mm.

Type Locality. Brazil. Bahia; Itapebi, Jequitinhonha River Banks, 15°57'09.39"S 39°32'37.1"W [Weslley Vailant-Mattos col., xi.2020].

Distribution. So far known to the Extreme South of Bahia, from Itapebi up to Itamaraju.

Habitat. In forest, ~50 m altitude.

Diagnosis. Shell simple, rather elliptic; aperture ~45% of total length, weakly deflected. Color whitish to whitish-yellow, with 2 spiral dark-brown, narrow stripes in each whorl, 4 equidistant stripes in last whorl. Secondary ureter at some distance preceding pneumostome. Anus external to pneumostome, open directly outside. Aperture of salivary glands as slits, in middle-posterior level of buccal cavity. Intrinsic pair of odontophore muscles relatively thin; m6 absent. Penis slender and short, lacking clear inner chambers but with pair of middle, large folds. Seminal receptacle very small, connected to albumen chamber duct. Albumen chamber flattened; posterior region of spermoviduct working as secondary albumen chamber. Pleural ganglia forming bridge.

Etymology. The epithet *nigroflavus* is a contraction of the Latin words *niger* meaning black, and *flavus*, meaning yellow. It is in reference to its black stripes that stand out against a yellowish-white background.

DISCUSSION

The generic attribution of *Drymaeus nigroflavus* is mainly based on conchological features, such as the reticulated protoconch, with rounded whorls, and a relatively oval shell outline, possessing whorls slightly rounded, with a well-marked suture. While *Leiostracus* Albers, 1850, usually has a more conical shell profile, flat whorls, and a coarser protoconch sculpture; and *Mesembrinus* Albers, 1850, usually has a more elongated shell profile, a more expanded peristome, and a coarser protoconch sculpture (Salvador *et al.*, 2023). The internal ureter aperture is another persuasive factor, as discussed below.

As mentioned above, taxonomic comparison of *Drymaeus nigroflavus* is only necessary with banded congeners. Within the diverse genus, only the banded species present a potential for confusion. Banded species are defined here as those exhibiting a light base color with well-defined, spaced spiral stripes. *D. nigroflavus* displays a relatively low level of variation in shell shape and color, as all examined specimens share similar characteristics (Figure 1, also refer to Femorale, 2004). Its narrow spiral stripes and pale basal color distinguish it from *D. alternans* (Beck, 1837) found in Panama; *D. binominis* (E. A. Smith, 1895) from Caribbean islands; *D. bogotensis* (Pfeiffer, 1855) from Colombia; *D. decoratus* (Lea, 1838) from Colombia; *D. felix* (Pfeiffer, 1862) from Colombia; *D. fidustus* (Reeve, 1849) from Colombia; *D. laetus* (Reeve, 1849) from Colombia; *D. laticinctus* (Guppy, 1868) from Dominica; *D. lividus* (Reeve, 1850) from Venezuela; *D. multifasciatus* (Lamarck, 1822) from Caribbean islands; *D. nigrofasciatus* (Pfeiffer, 1846) from Colombia; *D. poecilus* (d'Orbigny, 1835) from Argentina; *D. rufolineatus* (Drouët, 1859) from French Guyana; *D. semifasciatus* (Mousson, 1869) from Colombia; *D. serperastrum* (Say, 1829) from Mexico; *D. tribalteatus* (Reeve, 1848) from Colombia; *D. tripictus* (Albers, 1857) from Costa Rica; and *D. vexillum* (Wood, 1828) from Peru. In having more elongated shell outline, and narrow spiral stripes, *D. nifroflavus* can be also distinguished from *D. dominicus* (Reeve, 1850) from Florida; *D. eucosmetus* Haas, 1955 from Peru; *D. iris* (Piaget, 1914) from Colombia; *D. mexicanus* (Lamarck, 1822) from Mexico to Peru; *D. m. primularis* (Reeve, 1849) from Peru; *D. m. christopheri* Pilsbry, 1899 from St Kitts-et-Nevis; *D. pervariabilis* (Pfeiffer, 1853); *D. schadei* Quintana &

Magaldi, 1985 from Paraguay; and *D. verecundus* Breure & Mogollón, 2019 from Peru. *D. nigroflavus* differs further from *D. gereti* Ancey, 1901, from central Brazil, in being larger (that species is ~17 mm long), in having a deeper suture, and a proportionally larger aperture (~45 % of shell length, against ~35% of that species). It differs from *D. imperfectus* (Guppy, 1866), from Minas Gerais, Brazil, in being larger (that species is ~14 mm long), in having a deeper suture, a narrower outline and narrower spiral stripes. It differs from *D. fasciarum* Pilsbry, 1939 from Colombia in having more and wider spiral stripes, deeper suture and longer aperture (that species has aperture ~35% of shell length). It differs from *D. murrinus* (Reeve, 1848) from Venezuela and Colombia in having spiral stripes, and in lacking anterior angulation in the peristome. It differs from *D. tropicalis* (Morelet, 1849) from Mexico in not being sinistral, and in lacking a well-developed umbilicus. Finally, it differs from *D. vincentinus* (Pfeiffer, 1846) from St. Vincent and from *D. wintlei* Finch, 1929, from Ecuador, in having fewer spiral stripes, rounded peristome, and lacking anterior angulation.

Some *Drymaeus* species have recently been reclassified in other genera, such as *Mesembrinus*, and *Antidrymaeus* Germain, 1907. However, since they were previously classified within the *Drymaeus*, they are provisionally reported here under that classification to expedite the taxonomic discussion.

In summary, *D. nigroflavus* can only really be confused at first sight with non-Brazilian species, mainly from Colombia. Only two Brazilian species, *D. gereti* and *D. imperfectus* are slightly similar, but possessing the above mentioned distinctions.

In terms of anatomy, *D. nigroflavus* has the usual characters of the known bulimulids, with interesting idiosyncrasies.

Its ureteral aperture (Figures 2B, C: ua) is equivalent to that of *D. castilhensis* (Simone & Amaral, 2018), posterior to the pneumostome, but it is much shorter than that of *D. currais* (Simone *et al*., 2020). While those of so far known *Rhinus* Martens, 1860, *Mesembrinus* (Simone & Salvador, 2016) and *Bulimulus* Leach, 1814 (Simone & Amaral, 2018) the ureteral aperture is directly outside, external to the pneumostome.

The buccal mass of *D. nigroflavus* appears somewhat weak compared with that of its relatives. Its jaw plate (Figures 2F, G) is notably thin and flexible. The odontophore muscles (Figure 4C) are all slender, particularly pairs m2, m4, m5, and m10. The superficial musculature of the buccal mass is nearly absent, with only pair m11 detected (Figure 4B). The radula (Figures 3B-G) is also relatively thin. It is composed of several minute teeth if compared to other congeners, bearing more quantity of smaller sized teeth. The teeth themselves have similar features as those of the other congeners. Although the salivary ducts are relatively broad, their apertures are narrow and inconspicuous (Figure 3A: sa). The salivary glands themselves are small, narrow, and separated into two elongated masses (Figure 4B: sg). The stomach (Figure 4B: st) forms only a simple, narrow curve. These parameters are well developed in known relatives (Simone & Salvador, 2016; Simone & Amaral, 2018; Simone *et al.*, 2020), suggesting an adaptation to a soft diet in this species.

However, the most peculiar feature of the species is its genital system (Figure 5A). The shortness of the penis (pe) and, particularly, of the bursa copulatrix (bc, bd) is intriguing. The

bursa appears relatively atrophied and is situated far from its usual location, near the reno-pericardial region. The spermoviduct also exhibits aberrations, being very narrow at its base (vg) and exceptionally wide distally, with a highly convoluted uterus (ut). Conversely, the prostate (pt) is exceedingly narrow and difficult to discern (Figures 4D, 5A). The typical internal organization of the spermoviduct is absent in its posterior quarter, replaced by loops serving as an additional albumen chamber (Figures 5A, C: as). The true albumen chamber (ac) is flattened in all examined specimens, compressed between the albumen gland (ag) and the first loop of the accessory albumen chamber (as). None of these anatomical peculiarities is observed in known anatomical relatives.

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Cite as:
Simone, L.R.L. & A. Celzard. 2024. A New *Drymaeus* in the Region of Itapebi, Bahia, Brazil (Eupulmonata, Bulimulidae). The Festivus 56(3):187-200. http://doi:10.54173/F563187

ISSN 0738-9388

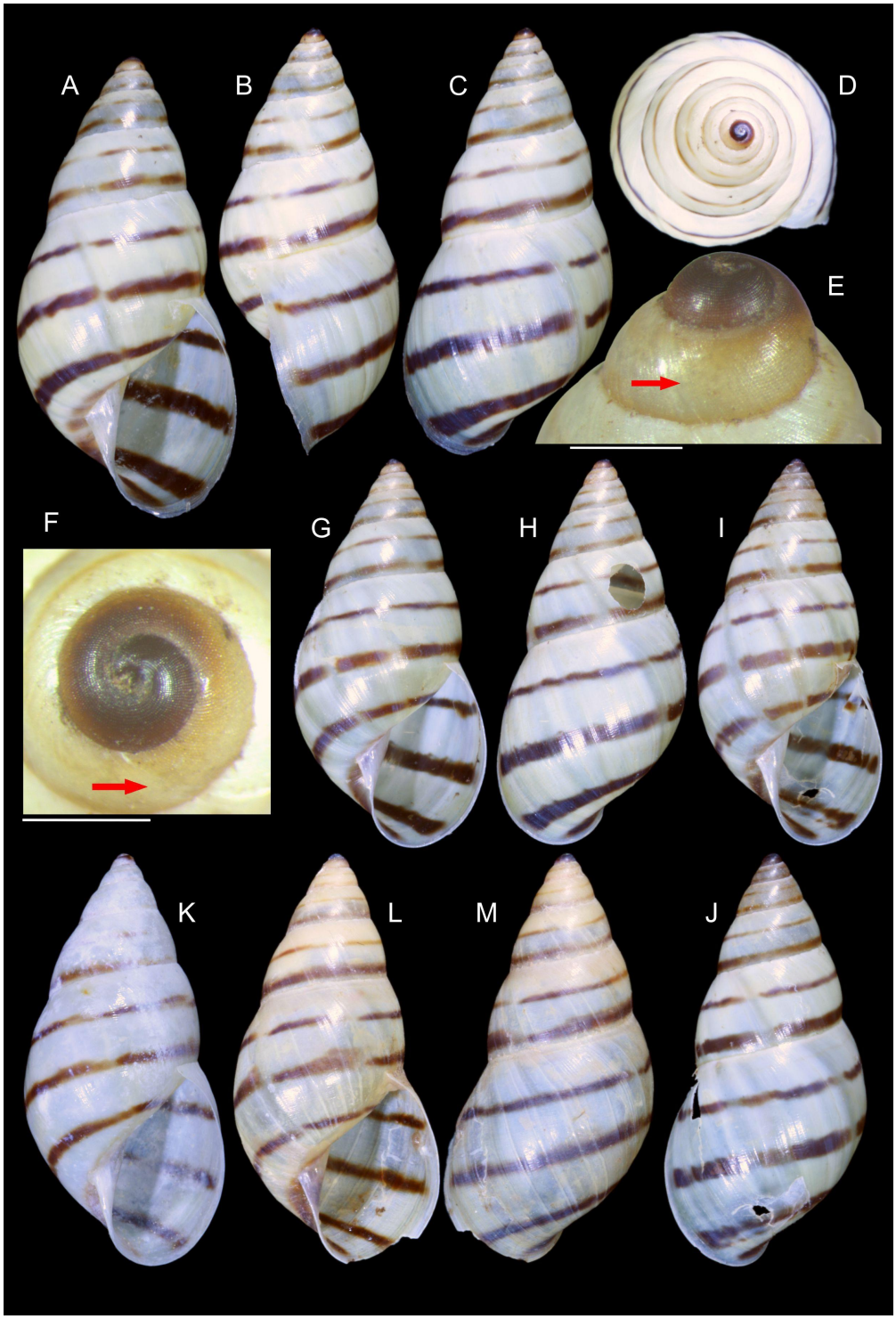

Figure 1. *Drymaeus nigroflavus*, shells of types: **A-F,** holotype MZSP 159000 (L 27.6 mm); **A,** frontal view; **B,** right view; **C,** dorsal view; **D;** apical view; **E-F,** apex, profile and apical views, arrow showing transition protoconch-teleoconch, scales= 1 mm; **G-H,** paratype MZSP 159001#1 (L 23.3 mm), frontal and dorsal views; **I-J,** MZSP 159001#2 (L 25.0 mm), frontal and dorsal views; **K**, MZSP 159001#3 (L 26.1 mm), frontal view; **L-M,** paratype MZSP 153113#1 (L 26.1 mm), frontal and dorsal views.

ISSN 0738-9388

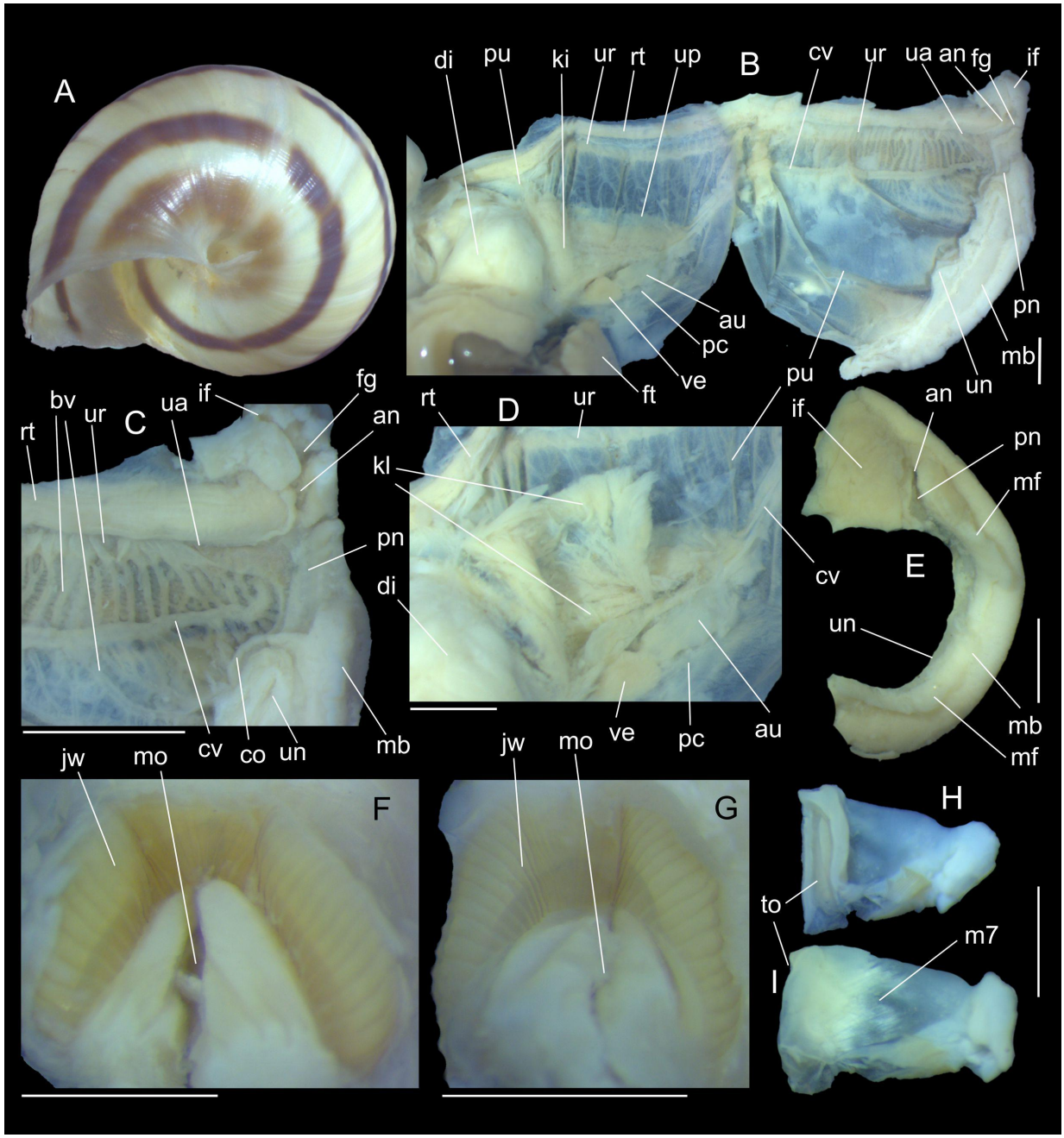

Figure 2. *Drymaeus nigroflavus*, anatomical photos: A. holotype MZSP 159000 shell, anterior view (W 12.5 mm); **B-D, F,** paratype 153113#1; **E, G-I,** paratype 153113#2; **B,** pulmonary cavity, extended, ventral view, portions of visceral mass also shown, scale= 2 mm; **C,** same, detail of region of pneumostome, inner lip of pneumostome sectioned and deflected upwards, scale= 2 mm; **D,** kidney, ventral view, ventral wall sectioned along left edge and deflected upwards to show inner lobe, adjacent structures also shown, scale= 2 mm; **E,** mantle edge, isolated, frontal view, scale= 2 mm; **F,** jaw in situ, ventral view, scale= 1 mm; **G,** same of other specimen, scale= 1 mm; **H-I,** tissue inside radular sac, radular ribbon removed, 2 views, scale= 1 mm.

ISSN 0738-9388

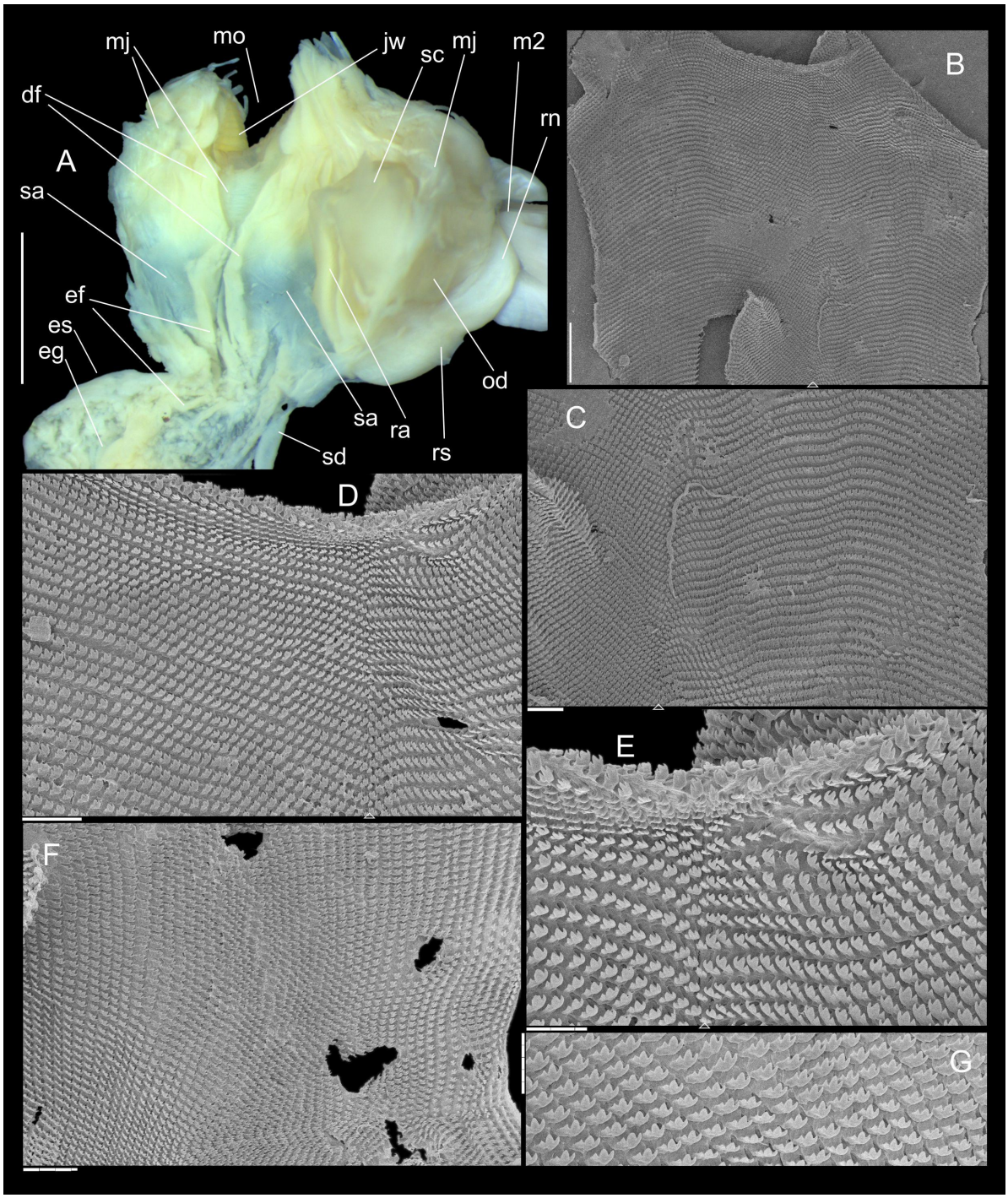

Figure 3. *Drymaeus nigroflavus*, anatomical photo and radulae in SEM: **A,** buccal mass, ventral view, sectioned along right edge (left in Figure), odontophore deflected to right, inner surfaces of buccal cavity and esophagus shown, scale= 1 mm; **B,** radula of holotype, wide view, scale= 200 µm; **C,** same, detail of central region, scale= 100 µm; **D,** same, other region, scale= 100 µm; **E,** same, higher magnification, scale= 50 µm; **F,** radula of paratype MZSP 153113#1, detail of marginal region, scale= 50 µm; G, same, higher magnification, scale= 50 µm. Arrow in Figures B-E indicating rachidian column.

ISSN 0738-9388

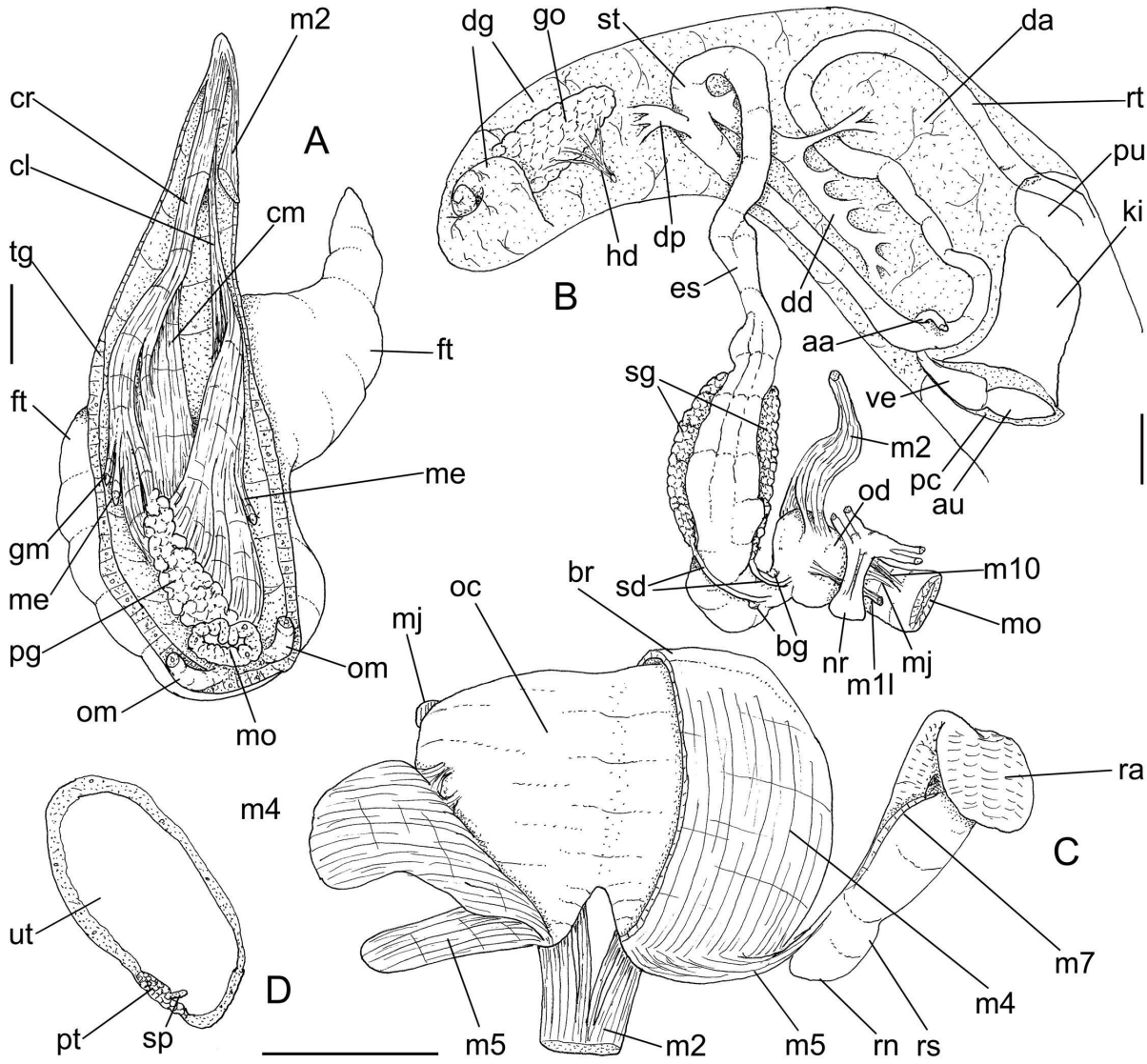

Figure 4. *Drymaeus nigroflavus*, anatomical drawings: **A,** head-foot, dorsal view, head and haemocoel organs removed, columellar muscles uncoiled and partially expanded; **B,** foregut, midgut and uncoiled visceral mass, mostly ventral view, part of digestive gland removed to show internal structures, topology of some pallial organs also shown; **C,** odontophore, dorsal view, superficial layer of membranes and muscles removed, both cartilages deflected, radular ribbon partially removed and deflected to right, left muscles deflected. Scales= 2 mm.

ISSN 0738-9388

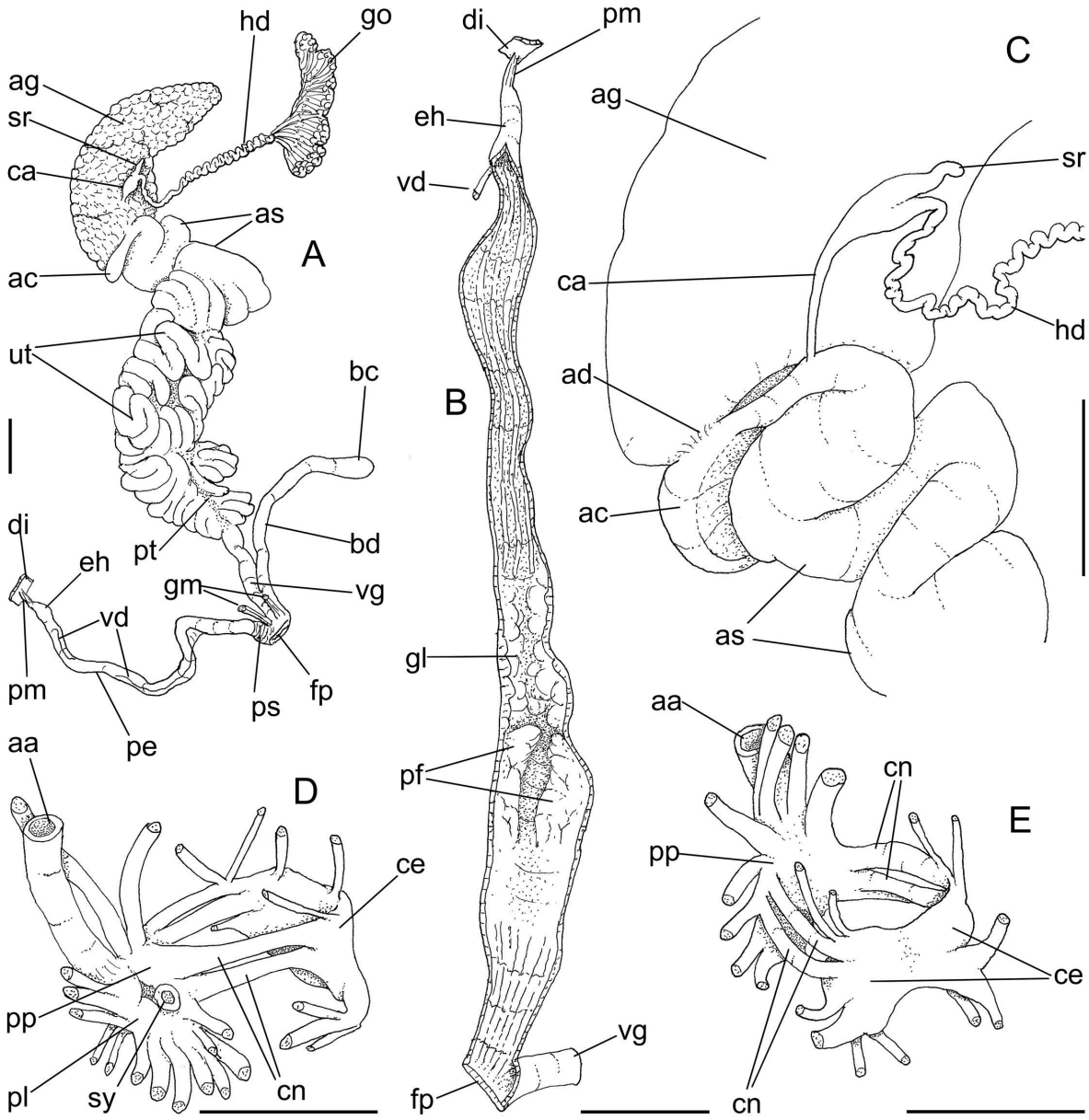

Figure 5. *Drymaeus nigroflavus*, anatomical drawings: **A,** genital system, panoramic ventral view, mostly uncoiled and expanded; **B,** penis opened longitudinally; **C,** region of carrefour, ventral view, seen if albumen gland was transparent, structures uncoiled; **D-E**, central nervous system, ventral-slightly left and dorsal views. Scales= 2 mm.