

Papéis Avulsos de Zoologia

Museu de Zoologia da Universidade de São Paulo

Volume 53(3):47-58, 2013

www.mz.usp.br/publicacoes
http://portal.revistasusp.sibi.usp.br
www.scielo.br/paz

ISSN impresso: 0031-1049

ISSN on-line: 1807-0205

ANATOMY OF PREDATOR SNAIL *HUTTONELLA BICOLOR*, AN INVASIVE SPECIES IN AMAZON RAINFOREST, BRAZIL (PULMONATA, STREPTAXIDAE)

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ABSTRACT

The morpho-anatomy of the micro-predator Huttonella bicolor (Hutton, 1838) is investigated in detail. The species is a micro-predator snail, which is splaying in tropical and sub-tropical areas all over the world, the first report being from the Amazon Rainforest region of northern Brazil. The shell is very long, with complex peristome teeth. The radula bears sharp pointed teeth. The head lacks tentacles, bearing only ommatophores. The pallial cavity lacks well-developed vessels (except for pulmonary vessel); the anus and urinary aperture are on pneumostome. The kidney is solid, with ureter totally closed (tubular); the primary ureter is straight, resembling orthurethran fashion. The buccal mass has an elongated and massive odontophore, of which muscles are described; the odontophore cartilages are totally fused with each other. The salivary ducts start as one single duct, bifurcating only prior to insertion. The mid and hindguts are relatively simple and with smooth inner surfaces; there is practically no intestinal loop. The genital system has a zigzag-fashioned fertilization complex, narrow prostate, no bursa copulatrix, short and broad vas deferens, and simple penis with gland at distal tip. The nerve ring bears three ganglionic masses, and an additional pair of ventral ganglia connected to pedal ganglia, interpreted as odontophore ganglia. These features are discussed in light of the knowledge of other streptaxids and adaptations to carnivory.

KEY-WORDS: Streptaxidae; Carnivorous; Biological invasion; Anatomy; Systematics.

INTRODUCTION

Despite being the largest rainforest in the world, the Amazon Rainforest has only ~5% of South American known species (Simone, 2006). It is not clear if this scarcity is because of an environmental feature, e.g., inadequacy of calcium, or if it is due to a paucity of studies. Possibly both. Anyway, it is common to find new species and genera in every sample collected in that region (e.g., Breure, 2009; Simone, 2010). The present study started like that, investigating what

appeared to be the strangest subulinid ever known. However, during progress of the morphological and bibliographical investigation, we realized that the sample was actually of another invasive species, the micro-predator *Huttonella bicolor* (Hutton, 1834).

Despite being described from India, *Huttonella bicolor* appears to originate from Africa or SW Asia (Dundee, 1974). It has been introduced in several tropical areas worldwide, such as Central America (Pérez *et al.*, 2008; Robinson *et al.*, 2009); Central Asia (Ho, 1995; Ramakrishna & Mitra, 2010); Australia

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and central Pacific (Sanisic, 1981; Gerlach & Bruggen, 1999); and North America (Dundee, 1974; Turgeon *et al.*, 1988, 1998). In South America, the species has been only recently reported in SE Brazil – Rio de Janeiro (Santos *et al.*, 2008). This is the first report from Northern Brazil in the Amazon Rainforest.

The genus *Huttonella* Pfeiffer, 1856 (p. 174), of which *H. bicolor* is the type species, has an original distribution in Africa and SW Asia, and has been considered an artificial, non-monophyletic assemblage of pupiform, elongated streptaxids (Gerlach & Bruggen, 1999). The species has also been referred to as being from the genus *Gulella* Pfeiffer, 1856, with *Huttonella* as subgenus or not, in several papers (*e.g.*, Cowie, 1997; Vermeulen, 2007). These and other taxonomical issues, as well as distribution features of *H. bicolor*, have been discussed elsewhere (*e.g.*, Naggs, 1989). However, the extra-shell biological knowledge on the species is very scanty if compared to its ecological importance as invasive species, and restricted to the radula and genital system (Berry, 1965; Dundee & Baerewald, 1984; Chaijirawong *et al.*, 2008). This paper provides a more holistic anatomical description and a taxonomical treatment, being part of a wider project on phylogeny of the Pulmonata based on the morphology of representatives of all main taxa.

MATERIAL AND METHODS

The samples were sent for identification by Edson Guilherme, from the Universidade Federal do Acre, consisting of preserved animals in 70% ethanol, which were afterwards deposited in the malacological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP). Each specimen was extracted from its shell by means of shell crushing. The animals were dissected by standard techniques, under a stereomicroscope, with the specimen immersed in ethanol. Digital photos of most dissection steps were obtained, as well as drawings with the aid of a camera lucida. The radula was examined by scanning electronic microscopy (SEM) in the Laboratório de Microscopia Eletrônica de MZSP.

In the figures, the following abbreviations are used: **ad**, albumen gland duct; **ag**, albumen gland; **an**, anus; **au**, auricle; **bg**, buccal ganglion; **cc**, cerebral commissure; **ce**, cerebral ganglion; **cv**, pulmonary (efferent) vein; **da**, digestive gland anterior lobe; **dd**, duct to digestive gland; **dg**, digestive gland posterior lobe; **ep**, epiphallus; **es**, esophagus; **ey**, eye; **fc**, fertilization chamber (carrefour), **ft**, foot; **go**, gonad; **gp**, genital pore; **hd**, hermaphrodite duct;

in, intestine; **ka**, kidney aperture to ureter; **ki**, kidney; **m1-m8**, extrinsic and intrinsic odontophore muscles; **m11**, translucent muscular membrane working as ventral tensor muscle of radula; **mb**, mantle border; **mc**, inner layer of circular muscles of odontophore; **mj**, peribuccal muscles; **mn**, mantle connection with nuchal region; **mo**, mouth; **nr**, nerve ring; **oc**, odontophore cartilage; **od**, odontophore; **og**, possible odontophore ganglia; **om**, ommatophore; **ot**, oral tube; **oy**, odontophore cavity; **pc**, pericardium; **pe**, penis; **pm**, penial muscle; **pn**, pneumostome; **pp**, pleuro-pedal ganglion; **pr**, pedal nerves; **pt**, prostate; **pu**, pulmonary (mantle) cavity; **pvr**, pneumostome right flap; **ra**, radula; **rm**, radular muscle; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sc**, subradular cartilage; **sd**, salivary gland duct; **se**, outer layer of circular muscles of odontophore; **sg**, salivary gland; **so**, spermoviduct; **sr**, seminal receptacle; **st**, stomach; **sy**, statocyst with statoconia; **tg**, integument; **tm**, tentacle retractor muscle; **ua**, ureter aperture; **ur**, ureter; **ut**, uterus; **vd**, vas deferens; **ve**, ventricle; **vg**, vagina.

Systematics

Huttonella bicolor (Hutton, 1834)

(Figs. 1-24)

Pupa bicolor Hutton, 1834: 86, 93 [Mirzapore and Agra, India]; Martens, 1867: 384-385 (with complementary ancient synonymy).

Ennea (Huttonella) bicolor: Pfeiffer, 1854(1854-1879): 115 (pl. 32, figs. 15-17), 1856: 120; Nevill, 1868: 6; Tryon, 1885: 104 (pl. 19, figs. 14, 17-18; pl. 20, fig. 24).

Ennea bicolor: Nevill, 1869: 64; Mörch, 1872: 315; Issel, 1874: 51; Fischer, 1891: 18; Fischer & Dautzenberg, 1904: 2; Blanford & Austin, 1908: 19-20 (fig. 12); Barnacle, 1962: 54; Lionnet, 1984: 240; Morgan, 1885: 372; Annandale & Prashad, 1920: 189-190; Laidlaw, 1933: 233; Gerlach, 1987: 10 (2 figs.).

Huttonella bicolor: Stoliczka, 1871: 169; 1873: 11; Jaekel, 1950: 18; Jutting, 1961: 8; Dance, 1970: 153; Sanisic, 1981: 84-86; Turgeon *et al.*, 1988: 277; 1998: 526; Chan, 1995: 4-5; Ho, 1995: 91, 100-101; Vermeulen & Whitten, 1998; Schileyko, 2000: 822 (fig. 1075A); Auffenberg & Stange, 2008: 3 (fig. 8); Santos *et al.*, 2008: 145-148 (figs. 1-3); Pérez *et al.*, 2008: 331; Robinson *et al.*, 2009: 634, 646, (figs. 7C, 8D); Sutcharit *et al.*, 2010: 3, 9, 13; Schileyko, 2011: 27.

Ennea bicolor barkudensis Annandale & Prasad, 1920: 191-194 (figs. 1-3) [Barkuda Is., Chilka Lake, Odisha, India].

Gulella (Huttonella) bicolor: Jutting, 1950: 504-505 (figs. 106-107); Ramakrishna & Mitra, 2010: 39.

Gulella bicolor: Berry, 1963a: 15 (fig. 73); Dundee & Baerewald, 1984: 63-67 (figs. 2-7); Naggs, 1989: 165-168; Cowie, 1997: 31; Gerlach & Bruggen, 1999: 20-21 (figs. 1b; 6a); Vermeulen, 2007: 174-175 (fig. 4); Chaijirawong *et al.*, 2008: 251-254 (figs. 2-3).

Complementary description

Shell (Figs. 1-6, 11): about 6 mm long, turritiform, elongated; width ~30% of length. Walls thin, fragile, translucent (Figs. 5-6) to opaque (Figs. 1-4). Color mostly white, with some reddish or yellowish tones close to apex. Spire elongated, occupying ~70% of shell length. Whorls convex, weakly rounded, suture relatively deep. Protoconch with little more than 1 whorl, smooth, dome-shaped, with ~10% of shell length and ~62% of maximum diameter (Figs. 1-6). Transition protoconch-teleoconch unclear, orthocone (Fig. 4). Teleoconch of three whorls; penultimate whorl about 30% wider than preceding and last whorls (Figs. 2, 5). Sculpture mostly smooth,

with irregular axial, subsutural ribs, ~20 in penultimate whorl, restricted to superior 10% of each whorl (Figs. 1-6); axial sculpture stronger in last half whorl, becoming complete axial ribs (Figs. 3, 1, 6). Umbilicus practically absent (Fig. 2). Aperture with strongly deflected, thick lips, orthocone (Figs. 2, 4); occupying ~30% of shell length and ~85% of shell width. Outline of aperture somewhat rectangular, weakly longer than wide, (Figs. 1, 5). Outer lip rounded, straight in middle; inner lip thick by flattened callus. Apertural teeth (Figs. 1, 5, 11): tall, triangular, wide teeth located in middle of outer lip; palatal teeth located in middle of superior region of callus, with concavity right, forming a canal with tooth of outer lip; parietal tooth elongated, located in middle to inner lip, obliquely placed; inferior tooth small, located in middle level of inferior apertural edge.

Head-foot (Figs. 12, 16): of normal shape. Color uniform pale yellow to cream. Pair of ommatophores well-developed, with strong retractor muscles (tm), normally orange pigmented. Eyes dark. No tentacles found. Columellar muscle thick, 1 whorl in length.

Mantle organs (Fig. 15): mantle border thick, lacking pigments. Pneumostome protected by ventral, right flap (pv), with ~1/4 of aperture length. Pneumostome about 1/8 of aperture length, having on dorsal edge anus right and nephrostome left (Fig. 15: an, ua).



FIGURES 1-6: *Huttonella bicolor* shell: 1) MZSP 98761 (Acre, Brazil), apertural view (H 6.1 mm); 2) same, left view; 3) same, dorsal view; 4) same, right view; 5) MZSP 99734 (Acre, Brazil), specimens with thinner shell, apertural view (H 6.0 mm); 6) same, dorsal view.

Lung almost 2 whorls in length, narrow and elongated. Pulmonary vessels inconspicuous, concentrated in anterior third, surrounded by mucosa strongly pigmented orange (Fig. 6). Pulmonary vein (cv) running longitudinally and weakly oblique, anteriorly between middle and right thirds of pallial cavity, approaching to median line gradually. Middle and posterior thirds of cavity lacking visible vessels except for pulmonary vein. Kidney yellow, located posteriorly, occupying ~20% of cavity length and ~50% of its width (details below). Rectum (rt) and ureter (ur) narrow, running along right edge.

Visceral mass (Figs. 5, 13, 14): about 4 whorls in length. Both digestive gland lobes pale yellow in color. Anterior lobe (Figs. 13, 16: da) flattened, occupying ~1/6 of visceral volume, located just posterior to pallial cavity continuous to kidney. Posterior lobe (dg) with 3 spiral, similar sized whorls, with ~75% of visceral volume. Stomach with about 1/10 of visceral volume, located between both digestive gland lobes, about half whorl posterior to pallial cavity (Fig. 13). Digestive tubes (described below) surrounding anterior lobe of digestive gland. Gonad clearly multi-lobed, cream color, somewhat spherical, encased in middle-right region of posterior lobe of digestive gland, occupying ~1/15 of visceral volume.

Circulatory and excretory systems (Fig. 15): Pericardium about twice as long as wide, located longitudinally between middle and left thirds of posterior end of pallial hoof; occupying ~5% of lung area. Auricle located anteriorly, as continuation from pulmonary vein, with about same ventricle size. Kidney size reported above, simple, entirely solid (Fig. 15: ki), dorso-ventrally flattened. Nephropore small, in anterior-left corner, as tip of small projection of renal tissue, turned right (Fig. 15: ka). Primary and secondary ureter complete and closed (tubular); primary ureter lying on anterior edge of kidney, somewhat perpendicular to pallial cavity longitudinal axis, after running ~half pallial cavity width abruptly turning anteriorly, running as secondary ureter (ur) along right half of posterior end of lung, and along left edge of rectum. Urinary aperture (Fig. 15: ua) simple, turned anteriorly, located on edge of pneumostome.

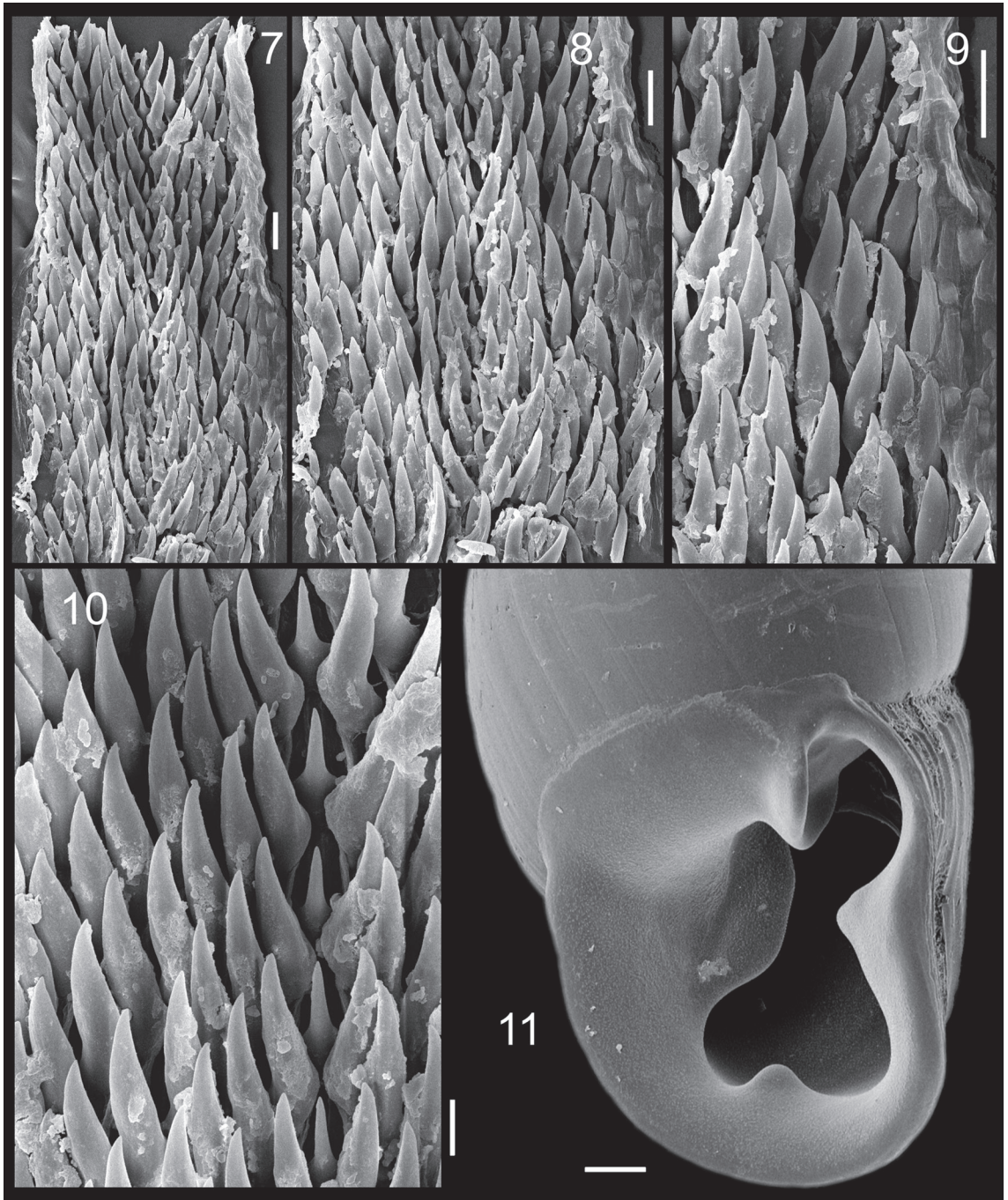
Digestive system (Figs. 12, 16-22): Oral tube relatively long in retracted condition (Fig. 12: ot), passing through nerve ring (nr). Buccal mass elongated, ~4 times longer than wide, with ~1/4 volume of head-foot and ~1/3 whorl in length. Dorsal region of buccal mass totally fulfilled by odontophore;

ventral region mostly hollow, forming oral cavity (Fig. 17: oy; showed opened in Fig. 18). Jaws wanting. Pair of radular muscles, or retractors of buccal mass (Figs. 16-21: rm), very thick, fused with each other, originating in columella, in right side of columellar muscle, running towards ventral side about 1.5 times buccal mass length. Radular muscles inserted in postero-ventral end of odontophore posterior surface. Pair of buccal muscles (Fig. 18: mj) weakly thick, inserted in both sides of odontophore cartilages, extending along entire buccal cavity towards posterior as thin layer of circular fibers (Fig. 18: se). Pair of differentiated jugal muscles (Figs. 17-18: mlv), working as narrow ventral protractors of buccal mass; originating in ventral-anterior region of radular muscles, running towards anterior close to buccal mass ventral surface; inserting in ventral side of mouth. Odontophore with about 90% of buccal mass volume, as long as it, placed ventrally to esophagus but dorsal in a diverticulum forming buccal mass (Fig. 16: od). Odontophore muscles (Figs. 18-21): **m2**, pair of narrow odontophore retractor muscles originating with radular retractors (rm); running close to median line as part of radular muscles (Figs. 20, 21); inserting in posterior end of odontophore cartilages; **mc**, thin muscular layer connecting both outer edge of odontophore cartilages, covering entire odontophore ventral surface along ~85% of odontophore cartilages length (Figs. 20, 21), from posterior end to certain distance from anterior end; **m4**, main pair of dorsal tensor muscles of radula, very thick, originating in central region of radular muscles, apparently lacking connections with odontophore cartilages (Figs. 20, 21), surrounding entire radular sac; inserting in radular sac along its region immediately posterior to buccal cavity (Fig. 21); **m5**, pair of thin auxiliary dorsal tensor muscles; originating in outer edges of odontophore cartilages (Figs. 20, 21), along ~1/5 of their length, ~2/5 of cartilages length posterior to their anterior end; running short distance towards median line; inserting in radular sac just dorsal to m4 insertion; **m6**, horizontal muscle absent (cartilages totally fused with each other); **m8**, pair of narrow muscles running along both sides of subradular cartilage (sc) in its region in buccal cavity, continuing longitudinally through entire odontophore on dorsal side of m4, close to median line, inserting in radular muscles (Figs. 20, 21); **m11**, pair of narrow ventral tensor muscles of radula (Fig. 19), originating in ventro-lateral surface of mc, running close to mc towards anterior and ventral, inserting in ventral end of subradular cartilage. Odontophore non-muscular

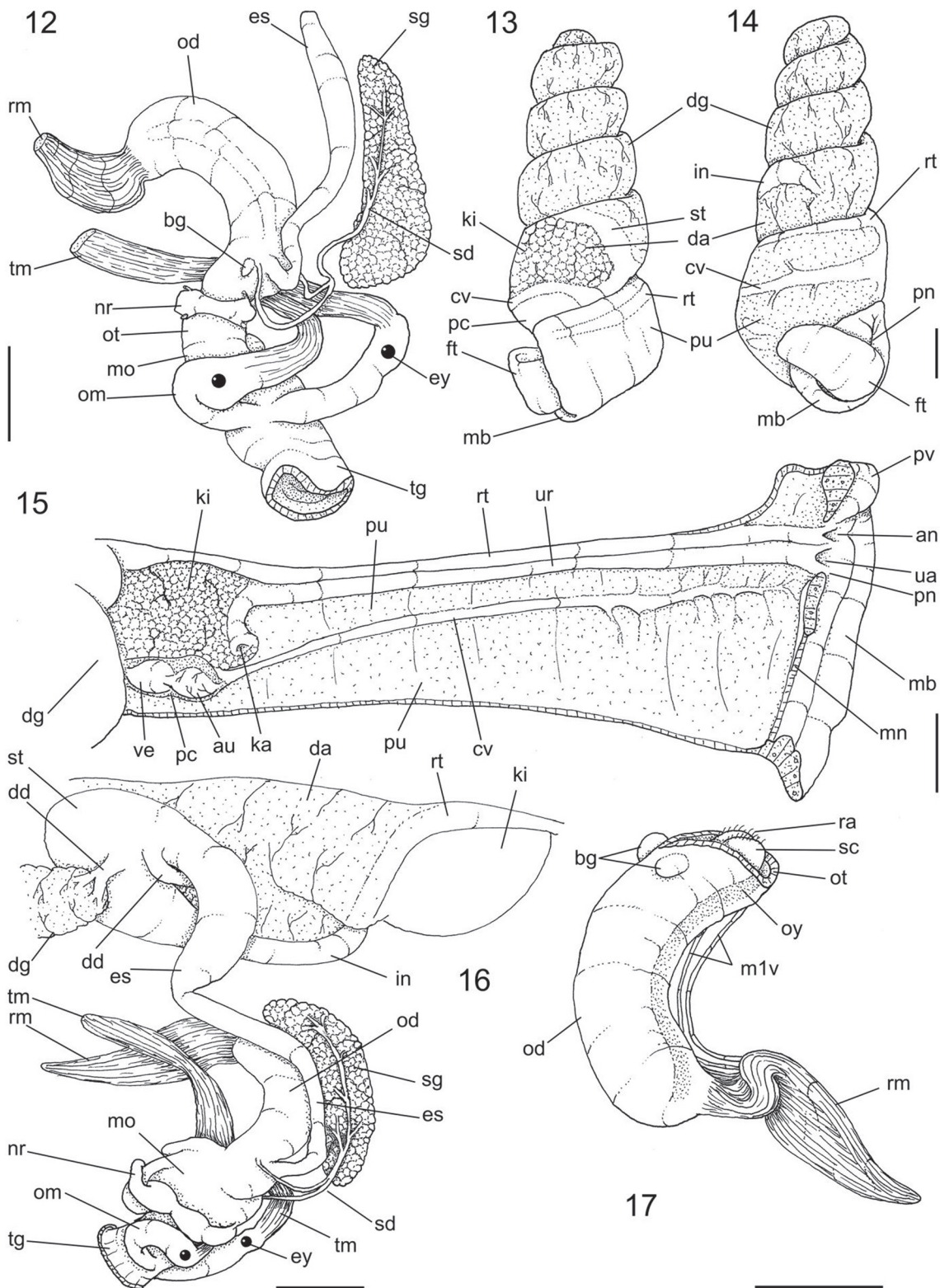
structures (Figs. 19-21): **oc**, odontophore cartilages, flattened, entirely fused with each other forming a wide groove (Fig. 21), anterior end roughly rounded, remaining with uniform width along length, ~5 times longer than wide, posterior end concave, with pair of posterior, thick, short projections, middle

(fusional) region thinner than lateral edges; **sc**, subradular cartilage, with expanding region in buccal cavity protecting subradular membrane (Fig. 21).

Radula about as long as odontophore length. Radula (Figs. 7-10) with rachidian teeth, 9 pairs of lateral teeth; no clear distinction of marginal teeth.



FIGURES 7-11: *Huttonella bicolor* hard parts in SEM: **7)** radula, whole view, scale: 20 μ m; **8)** same, detail of central region, scale: 20 μ m; **9)** same, detail of lateral region, scale: 10 μ m; **10)** same, detail of central region, rachidian close to right side, scale: 10 μ m; **11)** detail of aperture, MZSP 98761, apertural-slightly right view, scale: 300 μ m.

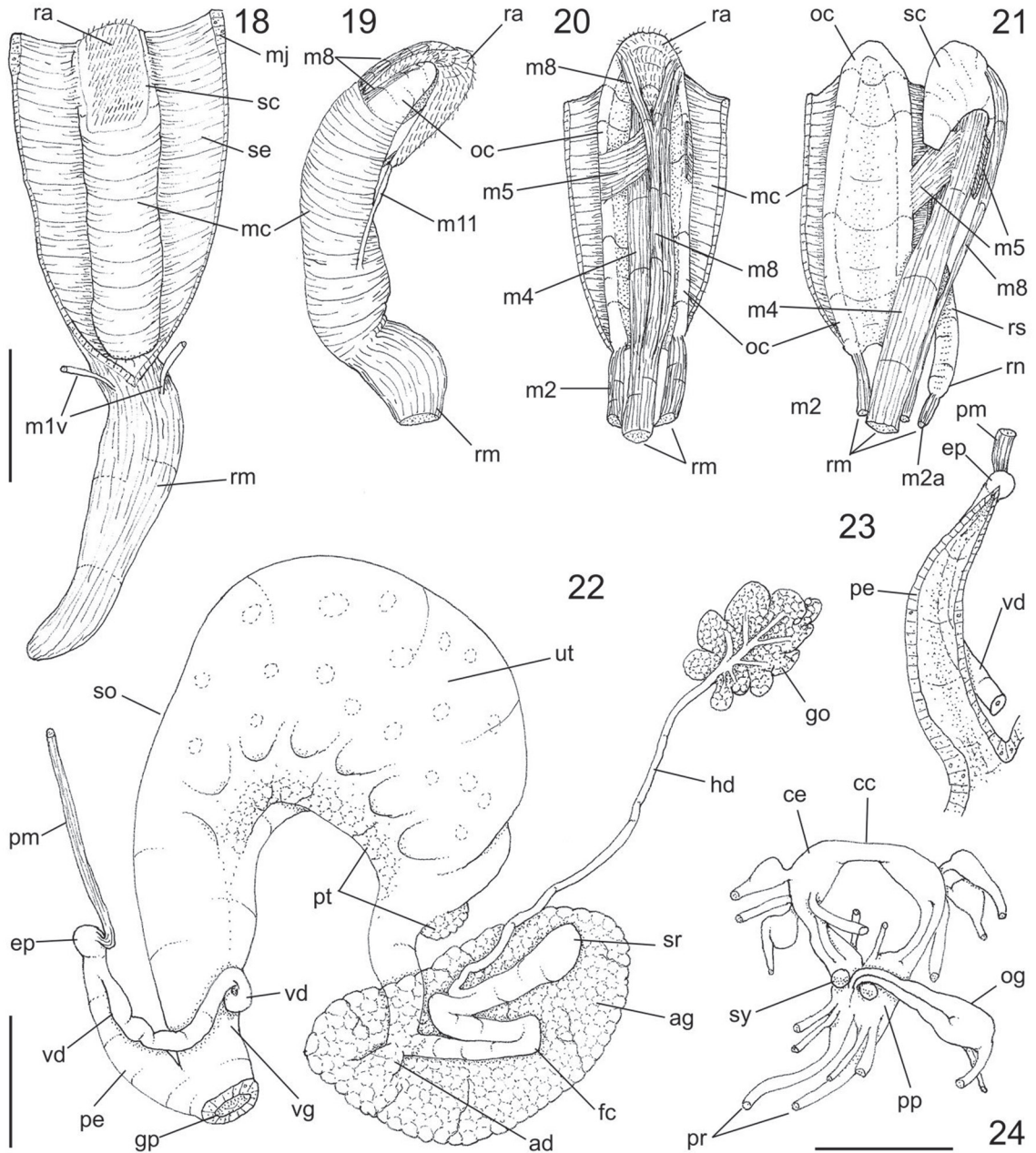


FIGURES 12-17: *Huttonella bicolor* anatomy: 12) foregut and peribuccal region, dorsal-slightly right view; 13) whole specimen just extracted from shell, right view; 14) same, ventral view; 15) pulmonary-pallial cavity, ventral-inner view; 16) digestive tubes as in situ and some adjacent structures, dorsal-slightly right view; 17) buccal mass isolated, right view. Scales = 0.5 mm.

Rachidian tooth (Figs. 8, 10) small, ~5% of radular width and ~5 times longer than wide; base wider and triangular, remaining as rod tapering up to sharp pointed terminal cusp. Lateral teeth similar to rachidian (Figs. 9, 10), except in being slightly asymmetrical, weakly arched, and ~3 times larger; lateral teeth similarly sized, except for marginal teeth, being

~1/2 of remaining teeth. Each radular row disposed as chevrons of ~75°.

Salivary glands covering anterior half of esophagus (Fig. 16: sg), and forming a single, white, thin mass. Single salivary duct differentiable along entire ventral side of glands, with about 1/12 esophageal width. Salivary duct bifurcating only in region



FIGURES 18-24: *Huttonella bicolor* anatomy: **18)** buccal mass, opened longitudinally on median line in its dorsal wall, dorsal view; **19)** same, right view, outer muscular layer removed; **20)** same, inner-dorsal layer of muscles sectioned longitudinally and deflected, dorsal view, left m5 only partially shown; **21)** same, radular sac and adjacent structures partially removed and deflected to right; **22)** genital system, ventral view, base of fertilization complex seen if albumen gland was translucent; **23)** detail of penis, sectioned longitudinally, dorsal view; **24)** nerve ring, ventral view. Scales = 0.5 mm.

anterior to glands (Fig. 16: sd), becoming pair of ducts, running to both sides of esophageal origin. Salivary ducts opening in anterior end of lateral sides of odontophore cavity.

Esophagus as long as about $\frac{3}{4}$ whorl, with thin, flaccid walls lacking clear subdivisions (Figs. 12, 16: es); inner surface of anterior half possessing 4-5 folds. Posterior esophageal half slightly wider, with a smooth inner surface. Stomach position and size described above (visceral mass) (Fig. 13), relatively narrow, curved, somewhat fusiform; gastric walls thin, flaccid; inner surface smooth. Esophageal insertion right, intestinal origin on left side, both close to columella. Duct to anterior lobe of digestive gland encased between esophagus and intestine (Fig. 16: dd). Duct to posterior lobe of digestive gland located a short distance from intestinal origin and posterior do previously described duct (Fig. 16). Intestine initially as wide as esophageal insertion, shortly tapering, flanking left side of anterior lobe of digestive gland, then in region of kidney gradually turning right and anterior, running almost straight forward in pallial cavity (Fig. 16). Rectum and anus described above (pallial cavity) (Figs. 15).

Genital system (Fig. 22): gonad described above (visceral mass). Hermaphroditic duct (hd) narrow and weakly coiled; running for $\sim 1/2$ whorl close to columella. Seminal receptacle (sr) elongated, sac-like, with ~ 5 times hermaphroditic duct width, and $\sim 1/3$ its length. Fertilization complex (fc) as a zigzag, thick muscular, iridescent walled, located as continuation of hermaphroditic duct and duct of seminal receptacle, about as wide as receptacle; length, if straightened, \sim twice receptacle length. Fertilization complex gradually becoming immersed in albumen gland, inserting in posterior end of spermoviduct, just in region of albumen gland duct (ad); all of them with similar width. Albumen gland (ag) solid, white, elliptical, ~ 3 times larger than gonad (about $1/4$ whorl). Albumen gland duct subterminal, connected to distal end of spermoviduct (ad). Spermoviduct as single curve, of about 1 whorl in length and about as wide as albumen gland. Prostate gland occupying $\sim 1/8$ of spermoviduct volume (pt). Uterus occupying about 80% of spermoviduct space, external walls thick-glandular (ut), inner surface smooth, fulfilled by large quantity of iridescent granules. Vas deferens initiating preceding anterior $1/6$ of spermoviduct (vd), $\sim 1/5$ of anterior spermoviduct width, weakly coiled. Vagina with about $1/6$ spermoviduct length, inner surface simple, with 4-5 longitudinal, low folds (vg). Bursa copulatrix wanting. Penis of $\sim 1/5$ spermoviduct length, and

about $2/3$ its anterior width (pe), with penis muscle inserting subterminally. Penial (epiphalic) gland distal, spherical, of about $1/5$ penis width and $1/10$ penis length (ep); internally solid, no duct detectable (Fig. 23). Internal penial surface simple, smooth (Fig. 23), insertion of vas deferens preceded by region running immersed in penis wall along $1/15$ of penis length. Genital pore rounded, simple.

Central nervous system (Fig. 24): located at base of buccal mass (Figs. 12, 16). Paired cerebral ganglia (ce) elliptical, about twice as long as wide; cerebral commissure short, with about half width and length of each ganglion. Each cerebral ganglion of about $1/4$ width of local oral tube. Pair of optical ganglia slightly smaller than cerebral ganglia, located close to these, connected to antero-median side. Tentacular nerves connected more internally than connection of optical ganglia. Pair of pedal-pleural ganglia (pp) forming single mass located opposite cerebral ganglia, and of about the same size as cerebral ganglia. No differentiable ganglion detectable. Several pairs of nerves originate from these ganglia towards anterior. Pair of cerebro-pedal and cerebro-pleural connectives (cn) similar-sized, about as long as cerebral ganglia. Pair of possible odontophore ganglia (of) fused with each other, located a distance equivalent to nerve ring length away from pedal ganglia, connected with them by pair of connectives, inserted in median-ventral side of each ganglion. Pair of buccal ganglia located in antero-dorsal region of buccal mass, close to esophageal origin and salivary insertion (Figs. 12, 17: bg); each ganglion spherical, of about $1/3$ cerebral ganglion size. Pair of statocysts located in ventral region of pedal ganglia, close to median line (sy), containing statoconia. Visceral ganglion located in posterior level of columellar muscle, with $\sim 1/2$ size of cerebral ganglion; connective with nerve ring running towards anterior $\sim 1/3$ whorl, passing just between penis and vagina.

Measurements (in mm): MZSP 98761(1): 6.1 by 1.9; MZSP 99734(1): 6.0 by 1.8.

Distribution: Described from India, but possibly originated from Africa or SW Asia. Presently introduced in Tropical and Temperate regions all over the world (see Introduction). In Brazil so far known from Acre and Rio de Janeiro.

Habitat: Normally in cultivated plains on the ground among fallen leaves, decaying wood, preferably in damp places (Jutting, 1961, Vermeulen, 2007).

Material examined: BRAZIL. Acre (Edson Guilherme col, 2011); Zoobotanic Park of Universidade Federal do Acre, 09°57'20.5"S, 67°52'30.2"W, MZSP 98763, 3 specimens (sta. IA448); Stare Park Chandless, 09°31'31.2"S, 69°55'34.6"W, MZSP 98760, 4 specimens (sta. IA468).

DISCUSSION

The pupiform, elongated outline is not the rule in Streptaxidae, which normally possess discoid forms (Simone, 2006). However, some African and West Asian genera characteristically have a pupiform shell, such as *Huttonella*, *Gulella* and *Sinoennea* Kobelt, 1904 (e.g., Jutting, 1961; Rowson *et al.*, 2010). Even within these, *H. bicolor* appears to have an excessively elongated and narrow shell, almost turriform.

The absence of the pair of lower cephalic tentacles is another noteworthy feature. This is clear in photos of crawling specimens (e.g., Clements, 2006, fig. 1; Chaijirawong *et al.*, 2008, fig. 3; Santos *et al.*, 2008, fig. 1), in such only the ommatophores are visible. It is not clear if this absence is characteristic of the family, but a tentacle is clear at least in *Gulella salpinx* Helbert (2002, fig. 18), as well as other streptaxids (Rowson, *personal communication*). As the examined specimens are all fixed, there is a possibility that the structure can be small and invisible, in inside-out condition of retracted heads. Nevertheless, tentacles are usually clear inside the haemocoel and bear protrusion retractor muscles connecting them to the adjacent region of the haemocoelic surface. None of these structures were found.

The characteristic yellow/orange bicolor, from which certainly has arisen the specific name of *Huttonella bicolor*, is given because of the mantle region surrounding the mantle cavity, seen through shell translucence (Figs. 5, 6). However, it is not clear what produces that effect, or what its function is for the species. The relatively simple pulmonary organization is another interesting feature; no vessels except for the pulmonary vein are visible. On the other hand, the renal and ureteral characters look unlike any other pulmonate. The kidney is entirely solid, lacking any detectable hollow region, it has a short left anterior projection in which the nephrostome is located, turned to the right (Fig. 15: ka); from it a primary ureter arises, running perpendicularly to the longitudinal axis of the pallial cavity a short distance. Normally the primary ureter is turned posteriorly, surrounding the postero-right corner of the pallial cavity; this place is occupied by the kidney

itself in *H. bicolor*, with the ureter flanking anterior margin. If the secondary ureter was away from the rectum, the fashion would be very similar to the Orthurethra.

The radula has been referred as 9+1+9 in formula (Stoliczka, 1871; Annandale & Prasad, 1920, fig. 3; Gerlach & Bruggen, 1999); a feature which has been confirmed herein (Figs. 7-10). The sharp pointed, hook-like teeth are characteristic of carnivore gastropods, a feature widespread amongst the streptaxids (e.g., Abdou *et al.*, 2008: fig. 3). Nevertheless, the radula is not long – being shorter than odontophore length – which indicates that the teeth are not eroded quickly. The very elongated, massive odontophore is a common attribute for streptaxids, certainly used for preying and consuming quickly live food (Steenberg, 1936). However, the odontophore of *H. bicolor* looks more like an enlargement of an ordinary pulmonate odontophore (Figs. 17-21), unlike the structure of other streptaxids, which appears like a proboscis (personal observation). Anyway, the *H. bicolor* buccal mass certainly can be protruded so that the radula directly contacts the prey, as is the case for the remaining known streptaxids. However, in face of the scanty literature regarding buccal and odontophore musculature, it is presently impossible to perform a more complete comparison. The odontophore muscles have some additional singularities, such as the absence of the horizontal muscle (m6), because of an entire fusion of the odontophore cartilages (Fig. 21: oc), the thin pair of auxiliary dorsal tensor muscles of the radula (m5), and the longitudinal position of the main pair of dorsal tensor muscles (m4) (Fig. 21), which strangely lack connections to the cartilages. Another singular feature is the unnamed pair m8 (Figs. 20, 21), which apparently work as another pair of dorsal tensors, with additional anterior branches surrounding the oral cavity. The pair of ventral tensors of the radula (Fig. 19: m11) is very thin and narrow, contrasting with the powerful antagonists (dorsal tensors – m4, m5, m8), indicating that the main force is in putting the food towards esophagus, as intuitive.

The remaining digestive tubes are relatively simple (Fig. 16), with smooth inner surface and absence of intestinal loops. This appears to be a normal feature for carnivores.

Another interesting character of the digestive system is the unique beginning of the salivary duct (Fig. 12: sd). It only bifurcates, becoming a pair, in the region preceding their insertion in odontophore base. As far as I know, this is described for the first time.

Some previous anatomical studies have found narrow and minute bursa copulatrix in *H. bicolor* (Berry, 1965; Dundee & Baerwald, 1984: 67; Chaijirawong *et al.*, 2008, fig. 2). However, no bursa at all was found in the samples herein studied. The absence of a bursa could be explained by the intense coiling of the shell, with scarcity of inner space. However, other highly coiled taxa, such as subulinids, possess well-developed bursas (*e.g.*, Dutra, 1988; Salgado & Coelho, 1999). Besides, the insertion of the vas deferens has been referred to insert remote from the distally inserting penial retractor muscle (Sutcharit *et al.*, 2010: 9); however, as shown in Fig. 23, the vas deferens runs immersed through penis wall up to the distal end. The former discrepancy, related to absence/presence of bursa, can be possibly explained by the presence of a visceral ganglion, and its connective nerve with nerve ring, placed in the same manner as the bursa shown in genital drawings in literature (Berry, 1965, fig. 4). On the other hand, Berry (1965) clearly described spermatozoa and debris in the bursa, and have found penial hooks. This can be indicative that the Brazilian, or Acrean, population can bear some anomaly or has suffered a selfing effect, with reduced bursa and penial hooks (Despite the fact that I have not performed a SEM examination in the penis, the penial hooks are at least undetected in dissecting microscope).

Scanty is the knowledge on the streptaxid anatomy, and relative few papers generally focus on the reproductive system (*e.g.*, Berry, 1963b, 1965; Picoral & Thomé, 1998; Rowson *et al.*, 2009; Verdcourt, 2000). The genital system of *H. bicolor* is somewhat similar, but has some important differences, such as the absence of the bursa copulatrix and the simplicity of the penis (it lacks, *e.g.*, armature – Verdcourt, 2000; Rowson *et al.*, 2009). Among common features are the shortness and the broad vas deferens, and the fashion of the fertilization complex.

The species has been described as feeding on subulinids, pupillids and helixarionids (Mead, 1961; Dundee & Baerwald, 1984; Auffenberg & Stange, 2008), with reports on cannibalism (Ho, 1995). It has even been introduced in order to control other invasive land snails, such as *Achatina fulica* (Bowdich, 1822) and *Subulina octona* (Bruguère, 1792), with feeble success (Mead, 1961; Davis & Butler, 1964; Krauss, 1964; Cowie, 1997). There is no information with respect to the reason for the introduction of *H. bicolor* in the Acre region. It may possibly be accidental, having been introduced with ornamental plants. Due to the scarcity of knowledge on the region's malacofauna, no clue on the impact of this predatory species comes to light.

RESUMO

A morfo-anatomia do micro-predador Huttonella bicolor (Hutton, 1838) é investigada em detalhe. A espécie é um caracol micro-predador que está se espalhando pelas áreas tropicais e subtropicais pelo mundo, sendo este o primeiro registro para a Floresta Amazônica, região Norte do Brasil. A concha é muito longa, com complexos dentes no perístoma. A rádula possui dentes pontiagudos. A cabeça carece de tentáculos, possuindo somente ommatóforos. A cavidade palial carece de vasos bem desenvolvidos (exceto a veia pulmonar); o ânus e a abertura urinária estão sobre o pneumóstoma. O rim é maciço, com ureter totalmente fechado (tubular); o ureter primário é reto, lembrando o modelo orturettra. A massa bucal tem um odontóforo alongado e maciço, cujos músculos estão descritos; as cartilagens do odontóforo são totalmente fundidas uma com a outra. Os ductos das glândulas salivares começam como único ducto, bifurcando somente antes da inserção. Os tubos digestivos médio e posterior são relativamente simples e com superfície interna lisa; praticamente não há alça intestinal. O sistema reprodutor possui um complexo de fertilização em zigzag, próstata estreita, ausência de bursa copulatrix, vaso deferente curto e grosso e pênis simples com glândula no topo. O anel nervoso possui três massas ganglionares e um par adicional ventral conectado aos gânglios pediosos, interpretados como gânglios odontofóricos. Estas características são discutidas sob a luz do conhecimento atual sobre outros Streptaxidae e adaptações à carnívoría.

PALAVRAS-CHAVE: Streptaxidae; Carnívoría; Invasão biológica; Anatomia; Sistemática.

ACKNOWLEDGMENTS

I am grateful to Edson Guilherme, Universidade Federal do Acre, Brazil, for the studied specimens. I also thank Ben Rowson, National Museum of Wales, UK, for comments on the text and streptaxid anatomy.

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Aceito em: 26/10/2012

Publicado em: 31/03/2013

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