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On a new species of *Isomeria* Beck and redescription of species of *Labyrinthus* Beck from South America (Gastropoda: Stylommatophora: Camaenidae)

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ABSTRACT

The Camaenid genera *Labyrinthus* Beck, 1837 and *Isomeria* Beck, 1837 are mainly distributed in northern South America. Current anatomical information available for both genera is scarce, particularly that concerning *Isomeria* species. The morphology of the pallial organs, genital and digestive systems of three species of *Labyrinthus* [*L. subplanatus* (Petit, 1843), *L. dunkeri* (Pfeiffer, 1852), *L. tarapotoensis* Moricand, 1858] and a new species of *Isomeria* are described. The morphology of hooked denticles that topped wall ridges inside penis and vagina in some species of *Labyrinthus* and in *Isomeria* are species-specific characters, differing in shape and size. These structures were not sufficiently studied either in *Isomeria* or in *Labyrinthus* and are absent in all anatomically studied species of *Solaropsis* Beck, 1837, their sister genus. The presence of a bursa copulatrix sac reflexed over its duct is a character shared by all *Labyrinthus* species in which soft anatomy is known, and it was identified as a synapomorphy in a published phylogeny. *Isomeria awa*. n.sp. differs from other species of the genus mainly in shell morphology and characters of the distal genitalia. The presence of a stimulator-like structure in the vagina as well as the presence of a glandular pouch in the vagina are diagnostic characters of this new species, not present in the closely Camaenid related genera.

Key words: Morphology, Taxonomy, Stylommatophora, Helicoidea, Colombia, Neotropical

INTRODUCTION

The genera *Labyrinthus* Beck, 1837 and *Isomeria* Beck, 1837, both components of the Neotropical land snail fauna, are little studied. Both genera share similarities in shell color and size and inhabit similar habitats in South America. Indeed, some authors (Zilch 1959–60) considered *Isomeria* as a subgenus of *Labyrinthus* while others maintained them as independent entities (Solem 1966, Cuezzo 2003). *Labyrinthus* comprises thirty-one nomi-

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nal species, catalogued by Richardson (1985). Anatomical information is available for only eight of them. Of the twenty eight to thirty nominal species of *Isomeria*, there is only some anatomical information available for *Isomeria globosa* (Broderip, 1832) in Solem (1966).

Wurtz (1955), when reviewing the American Camaenidae, made a significant progress on the anatomy of *Labyrinthus*, describing the genitalia of four species: *L. tamsiana* (Dunker, 1847), *L. otis orthorhinus* Pilsbry, 1910, *L. plicatus* (Born, 1780) and *L. clappi* (Pilsbry, 1901). At that time *L. clappi* was considered by Wurtz (1955) to belong within *Isomeria* Section *Ambages* Gude, 1912. Wurtz (1955) proposed a diagnosis for *Labyrinthus* based on three characters: the presence of a long bursa copulatrix duct, reflexed epiphallus and the presence of an internal pilaster running from the flagellum towards the epiphallus. According to Wurtz (1955) *Isomeria* and *Labyrinthus* are distinguished by the morphology of the penial complex. Based on shell characters, Solem (1966) reviewed the genera *Labyrinthus* and *Isomeria*, giving anatomical information on *L. unciger* (Petit, 1838), *L. otis orthorhinus* , *L. diminutus* Gude, 1903, and *I. globosa*. Although this is a major contribution to the knowledge of both genera, Solem expressed his doubts about the validity of both as separate entities due to their similarities in shell morphology. Subsequently, Tillier (1980) described the anatomy of *L. leprieurii* (Petit, 1840) and *L. cf. furcillatus* (Hupé, 1853). A recent cladistic analysis on the Camaenidae based on morphological characters reconfirmed that both genera are separate natural groups with several synapomorphies supporting their monophyly (Cuezzo 2003). *Labyrinthus* and *Isomeria* are sister groups, a relationship supported by two synapomorphies: 1) the presence of denticles in the penis and vagina and 2) the free oviduct branched at an angle with the vagina. In the same phylogenetic hypothesis *Solaropsis* Beck, 1837, is the sister group of the *Isomeria* + *Labyrinthus* clade. *Labyrinthus* and *Isomeria* are classified within Camaenidae, one of the traditional families of the Helicoidea. Information on South American Helicoidean species is scarce and not adequate compared to the level of data available for other Helicoideans from other regions. Bouchet (1997) pointed out this asymmetry in the information, but there are still very few studies describing and reviewing the Neotropical species.

Labyrinthus has a wide geographic distribution, ranging from northern Costa Rica (N 14°) to the south up to Madre de Dios in Peru (S 14°). Eastern limits in South America are in the state of Pará, Brazil, and French Guyana (Solem 1966; Tillier 1980). The distribution of *Isomeria* is more restricted, being known only from Colombia, Ecuador and Peru; however, according to Solem (1966) altitudinal data showed a clear separation of both genera in most areas. *Isomeria* is known to inhabit moderate to higher altitudes (usually above 1900 m) while *Labyrinthus* inhabit low to moderate elevations (usually below 1900 m).

In the present study, a new species of *Isomeria* is described and three species of *Labyrinthus* are fully redescribed, contributing information on their anatomy for a better understanding of these genera.

MATERIAL AND METHODS

Institutional Abbreviations: Instituto Alexander von Humboldt, Bogotá, Colombia (AvH), Fundación Miguel Lillo, Tucumán, Argentina (FML), Field Museum of Natural History, Chicago, USA (FMNH), Museo de la Universidad Católica, Quito, Ecuador (MUC) and Zoologisches Museum Universität Zürich-Irchel, Switzerland (ZMZ). Additional samples of dry shells were also examined at the Academy of Natural Sciences of Philadelphia, Philadelphia, USA (ANSP) and American Museum of Natural History, New York, USA (AMNH). Live specimens from Reserva La Planada, Nariño, Colombia were also used. For anatomical studies, specimens were dissected under a Leica MZ6 stereoscopic microscope and with the help of a camera lucida the different anatomical systems were drawn. The procedure followed for the dissections are detailed in Cuezzo (1997). In order to facilitate the anatomical descriptions, the general body cavity is divided into a visceral cavity and a pedal cavity, separated by a pulmonary cavity as explained by Tillier (1989). Radula and jaw were prepared for scanning electron microscopy (SEM) according to Ploeguer & Breure (1977). Micrographs were obtained using a JEOL Scanning Electron Microscope 35 CF. The terminology used for the descriptions of the reproductive system follows Tompa (1984) and that on pallial and digestive systems follows Tillier (1989). Abbreviations used in the text are: Dmajor: maximum shell diameter; D minimum: smaller shell diameter; H: shell total height; Dap: apertural diameter; Hap: apertural height.

SYSTEMATIC DESCRIPTIONS

Superfamily HELICOIDEA Rafinesque, 1815
Family CAMAENIDAE Pilsbry, 1895
Subfamily CARACOLINAE Cuezzo, 2003
Genus *Labyrinthus* Beck, 1837

Type species: *Helix otis* Lightfoot, 1786 (= *Helix labyrinthus* "Chemnitz" Deshayes, 1838) by subsequent designation by Herrmannsen (1846: 569).

Diagnosis: Shell small to large (10–60 mm) usually uniformly colored; sculpture of wrinkles or granulations, without axial ribs; periphery angulated or keeled; aperture strongly obstructed with denticles and lamellae; shell mark of basal internal tooth always diagonal respect to apertural lip; parietal single lamellae rectangular, merged or not with parietal lip; parietal lip usually raised, lower inner internal palatal lip wall with T-shaped lamellae, or two Y-shaped teeth or conical transverse lamellae; jaw smooth or weakly ribbed; alveoli of ovotestis ovoid to digitiform; bursa copulatrix oval, well differentiated, reflexed over distal portion of duct; penis (in some species also vagina) with hooked denticles of 300 to 400 µm of basal plate maximum length.

Distribution: From Costa Rica south to the Cuzco department in Peru. Easternmost records are in Pará Brazil, although *Labyrinthus* is mainly known from Colombia, Ecuador and Peru.

Discussion: *Labyrinthus* is a monophyletic genus, characterized by the following synapomorphies (Cuezzo 2003): basal internal tooth with diagonal shell mark; internal parietal teeth rectangular or folded merging with the peristome; lower internal palatal wall with two Y-shaped teeth; body whorl shouldered; ovotestis with digitiform alveoli and bursa copulatrix sac reflexed over the duct.

The presence of the reflected penis-epiphallus attached by muscular strands is a character shared with its closest relatives *Isomeria* and *Solaropsis*. Internal hooked denticles are present on top of the ridges in penis and vagina in the two investigated species of *Isomeria* but not in the eight species of *Solaropsis*, in which anatomy was studied (Tillier 1980, Cuezzo 2001). Penial hooked denticles have only been reported in the Scolodontidae (= Systrophiidae), in Streptaxidae as well as in some Zonitidae and Oxychilidae in the Stylommatophora (Hausdorf 2003). Similar hooked denticles were reported in dorid nudibranchs (Valdés 2004), in which they function to reinforce the anchoring of the penis inside the vagina of the partner to prevent premature separation (Valdés 2004). However, in both *Labyrinthus* and *Isomeria* the hooked denticles are present not only in the penis but also in the vagina in most of the species. The function of the penial and vaginal hooked denticles in both genera is probably related to sexual stimulation and to anchoring penis in the vagina. Penial denticles are smaller in *Isomeria* (180–200 μm of basal plate length) than in *Labyrinthus* (300–400 μm of basal plate length).

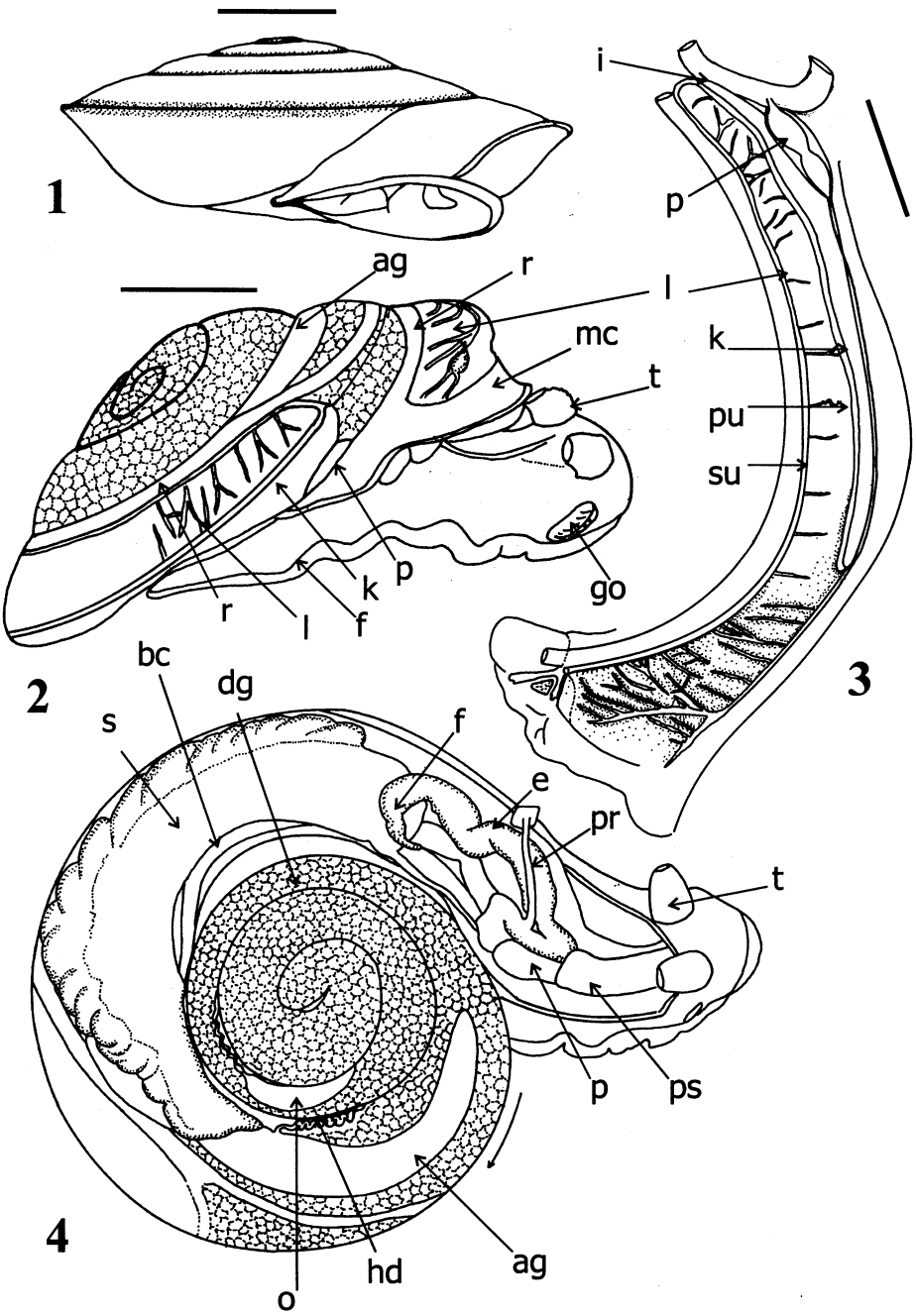
***Labyrinthus dunkeri* (Pfeiffer, 1852)**
Figures 1–14

Helix dunkeri Pfeiffer, 1852: 156.

Description: *Shell*: (Fig. 1) As described by Solem (1966).

Pallial Organs: (Figs 2, 3) Pulmonary roof with few veins becoming more abundant, ramified near mantle collar (Figs 2, 3). Proximal portion of pulmonary roof not extending beyond top of kidney. Dark pigmented spots more abundant in distal portion of pulmonary roof (Fig. 3). Main pulmonary vein splitting into two main branches before reaching mantle collar. Many other minor veins running transversally to main veins. Kidney narrow, long, extending about 60% of pulmonary roof; secondary ureter closed from top of pulmonary roof to mantle collar, running parallel to rectum, ureteric interramus triangular, deeply excavated.

Reproductive system (Figs 4–8; 32–33)**:** Ovotestis consisting of single group of small digitiform acini located between second and third whorls, embedded in digestive gland (Fig. 4); hermaphroditic duct thin, long, convoluted, forming in middle portion, swollen

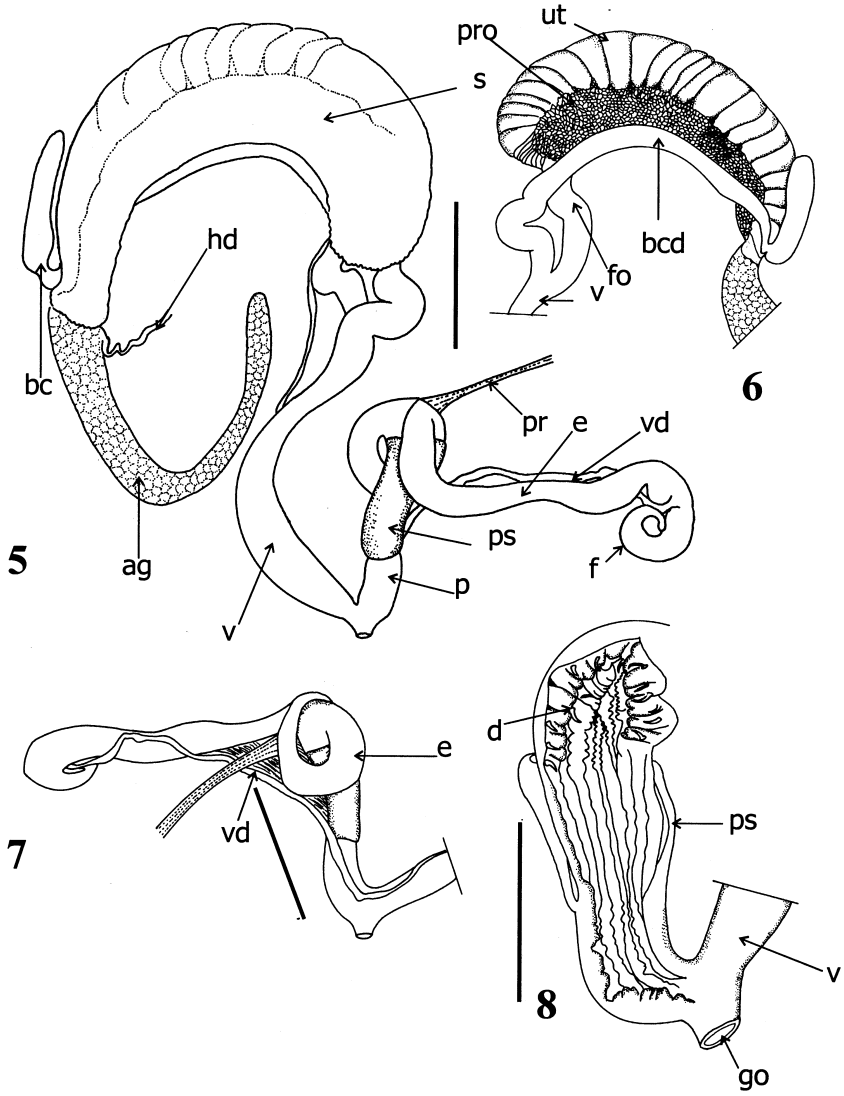


FIGURES 1–4: *Labyrinthus dunkeri*. 1: Diagram of shell morphology, scale bar= 5 mm. 2: Position of pallial organs before dissection, shell excluded, scale bar= 5 mm. Abbreviations: mc: mantle collar; p: pericardium; ag: albumen gland; go: genital orifice; f: foot; l: lung; r: rectum; k: kidney; t: ocular tentacle. 3: Ventral view of the general morphology of dissected out pallial organs, scale bar= 5 mm. Abbreviations: p: pericardium; i: intestine; k: kidney; pu: primary ureter; su: secondary ureter. 4: Position of genital system before dissection, shell excluded, dorsal view. Abbreviations: ag: albumen gland; bc: bursa copulatrix; dg: digestive gland; hd: hermaphroditic duct; e: epiphallus; f: flagellum; ag: albumen gland; dg: digestive gland; o: ovotestis; p: penis; pr: penis retractor muscle; s: spermoviduct; t: ocular tentacle; ps: penis sheath.

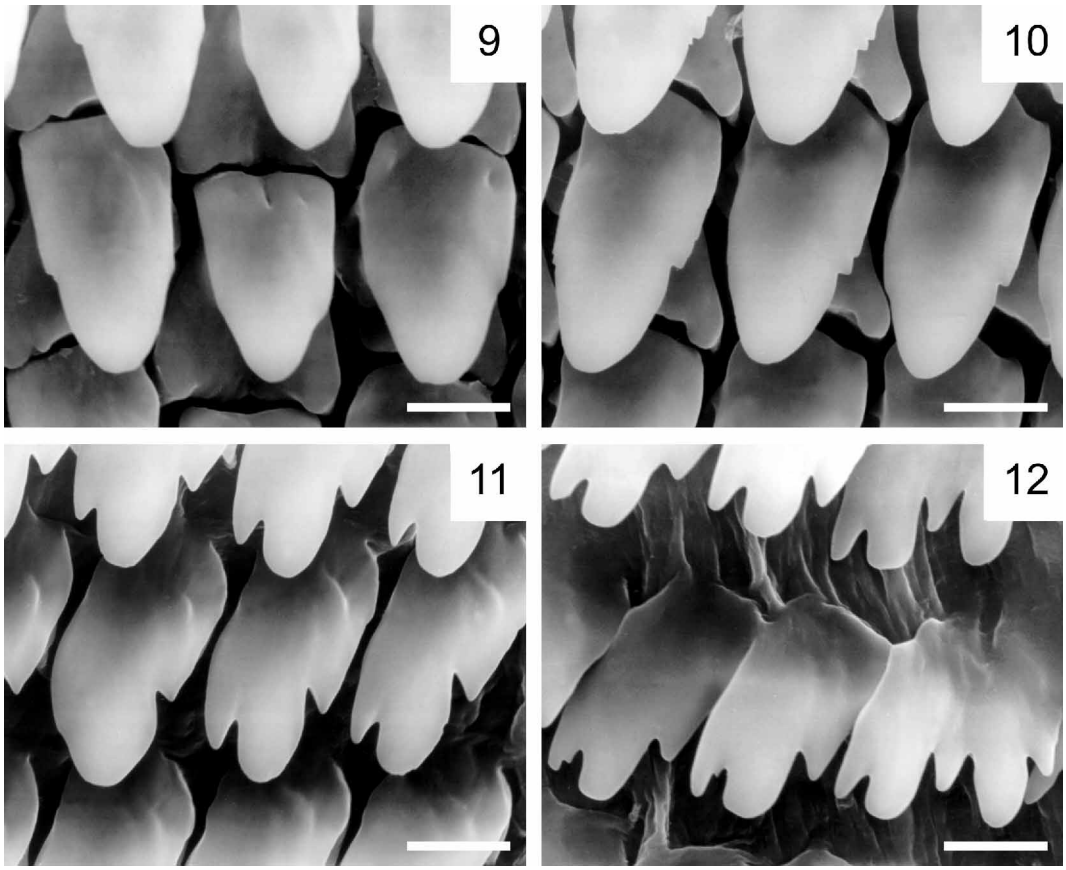
vesicula seminalis. Fertilization pouch-spermathecal complex (FPSC) not evident outside albumen gland, hermaphroditic duct folded over itself, penetrating at distal portion of albumen gland, bean-shaped, continuous with spermoviduct (Figs 4, 5). Oviducal portion of spermoviduct organized into transversal folds over entire length. Prostatic zone continuing distally into long, vas deferens, descending parallel to vagina towards peni-oviducal angle. Vas deferens attached by connective tissue to junction of penis with oviduct. Ascending branch of vas deferens running parallel to penial complex, inserting in proximal epiphallus. Free oviduct a quarter of length of bursa copulatrix duct (Fig. 6). Natural position of free oviduct forming angle with vagina, bursa copulatrix duct continuous with free oviduct. Bursa copulatrix running parallel to spermoviduct until distal portion of albumen gland (Fig. 5). Bursa copulatrix and spermoviduct wrapped together by thin connective tissue. Bursa copulatrix sac elongated, oval, naturally reflexed over duct (Figs 5, 6). Inner structure of vagina consisting of thin parallel longitudinal folds, becoming thicker, deeper, with zigzag pattern. Distal portion of vagina more swollen than proximal part (Fig. 5). Vagina without hooked denticles. Penial complex composed by flagellum, epiphallus, penis (Figs 5, 7). Flagellum short, diameter decreasing towards proximal portion. Internally, flagellar pilaster with dorsal groove ending level where vas deferens enters epiphallus through papilla. Second longitudinal pilaster continuous within epiphallus. Epiphallus cylindrical, elongated with thick muscular walls. Internal structure consisting of thick medial pilaster with wrinkled surface without pustules. Internal pilasters running through entire epiphallus-flagellum length. Vas deferens inserting in proximal epiphallus below flagellum-epiphallus junction. Penis thick, reflexed over epiphallus, tightly packed with muscular fibers (Fig. 7). Penial sheath muscular, cylindrical, with upper proximal, lower distal borders well delimited (Figs 5, 7). Penis retractor becoming thicker before inserting at penis-epiphallus junction. Internal structure of penis consisting of longitudinal, parallel ridges running through entire penis length. Ridges thicker with zigzag pattern at proximal portion, overlapped in part by penial sheath (Fig. 8). White small, fragile denticles with basal oval plate of about 300 μm in length and long hook (Figs 32, 33). Denticles regularly distributed on top of zigzag ridges in proximal penis, absent in distal portion of penis (Fig. 8). Verge absent.

Digestive system (Figs 9–12): Jaw arcuate, apparently smooth without ribs. Thin transversal striae deeper than other perpendicular ones in jaw surface visible in SEM. Central tooth of radula unicuspid, lateral teeth unicuspid (Fig. 9) becoming bicuspids at level of N° 14, mesocone well developed (Fig. 10). First marginal teeth tricuspid (Fig. 11) close to margins of radula, marginal teeth become pluricuspis, wider (Fig. 12). Buccal mass muscular, spherical; esophagus cylindrical, open dorsally. Esophagus wall thick with inner longitudinal, parallel ridges. Two long salivary glands opening through thin ducts into dorsal portion of buccal mass at sides of esophageal opening. Esophageal crop walls thin, transparent without inner special sculpture. Stomach receiving anterior and posterior ducts of digestive gland; anterior opening into concavity between esophageal crop and intestine,

posterior duct opening in parietal portion of stomach. Two internal typhlosoles arising from point of insertion of digestive gland ducts, one, longer, beginning at opening of anterior duct, running into proximal intestine. Intestine running along columelar side of visceral mass, turning down under anterior portion of gastric crop, then forming periaortic loop before finishing in rectum. Rectum closed along its entire length before opening into anus, running parallel to kidney, ending at mantle collar.



FIGURES 5–8: *Labyrinthus dunkeri*. 5: Reproductive system dissected out, ovotestis and part of the hermaphroditic duct excluded, scale bar= 1 cm. Abbreviations: bc: bursa copulatrix; hd: hermaphroditic duct; e: epiphallus; f: flagellum; ag: albumen gland; p: penis; pr: penis retractor muscle; s: spermoviduct; v: vagina; vd: vas deferens; ps: penis sheath. 6: Detail of spermoviduct and bursa copulatrix in ventral view. Abbreviations: bcd: duct of bursa copulatrix; fo: free oviduct; pro: prostate; ut: female portion of spermoviduct; v: vagina. 7: Detail of penis complex in ventral view, scale bar= 1 cm. Abbreviations: e: epiphallus; vd: vas deferens. 8: Inner structure of penis, scale bar= 5 mm. Abbreviations: d: denticles; go: genital orifice; v: vagina; ps: penis sheath.



FIGURES 9–12: *Labyrinthus dunkeri*. 9: Central tooth with two lateral teeth, scale bar= 10 µm. 10: Lateral teeth Nro. 8–10 to the right of central tooth, scale bar= 10 µm. 11: Same row than in fig. 10, showing the change from lateral Nro.14 bicuspid to marginal tricuspid, scale bar= 10 µm. 12: Marginal teeth near radular margin, scale bar= 10 µm.

Material examined: COLOMBIA: FMNH 163709, *Cesar Department*, Sierra Perijá, El Roncon, 10–12 Km East of Becerril, 9°42'N, 73°11'W, 200–300 m.; 16 September, 1969. Borys Malkin Coll. FMNH 173867 *Cesar Department*, Sierra de Perija, El Eocon, 10–12 km east of Becerril, 17 September 1969. B. Malkin Coll. AMNH 39705, Colombia.

Remarks: In species of *Labyrinthus* and *Caracolus* Montfort, 1810, in which the jaw morphology was studied, it was reported as smooth or oxygnath (Wurtz 1955). However, in *L. dunkeri*, the jaw showed incipient vertical ribs, and could not be consider as oxygnath. The morphology of the jaw in the rest of *Labyrinthus* species should be carefully examined to check if it really can be consider smooth and if this character can be used to diagnose the genus. The oxygnath condition is a character that has been used as unique of the American Belogona Euadenia (= Cepoliinae) (Pilsbry 1894). However, this kind of jaw is also present in some Camaenidae and Sphincterochilidae among the Helicoidea (Haus-

dorf 1998, Cuezzo 2003). The rest of the Helicoidean groups have an odontognath jaw (Hausdorf 1998). The length of the hooked penis denticles and the absence of denticles in the vagina clearly separates *L. dunkeri* from the remaining species of *Labyrinthus* in which soft anatomy is known. The hooks on the dorsal portion of the denticles in *L. dunkeri* are more than twice the length than those in other species of *Labyrinthus*.

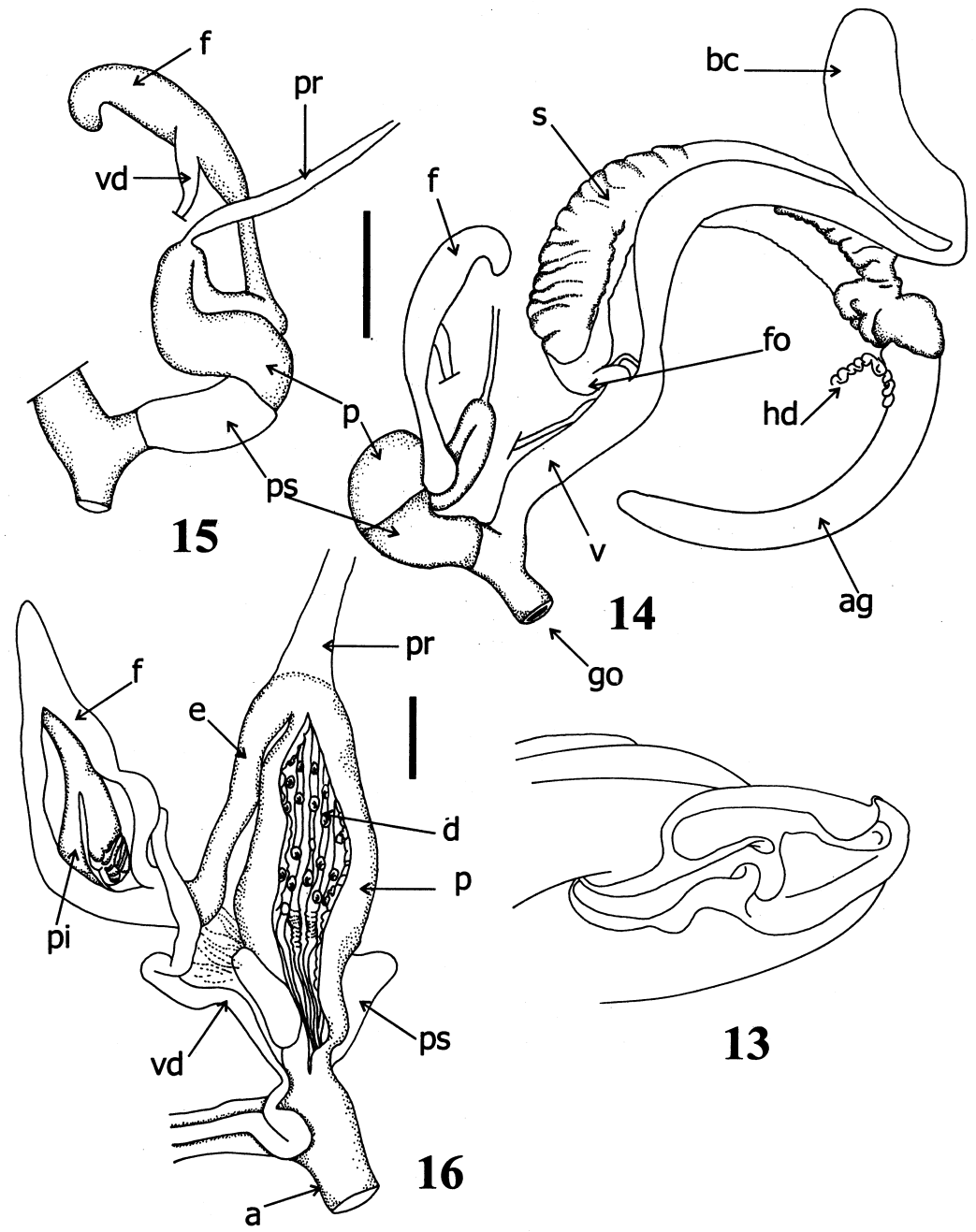
***Labyrinthus subplanatus* (Petit, 1843)**
Figures 13–22

Caracolla subplanatus Petit, 1843, 238.

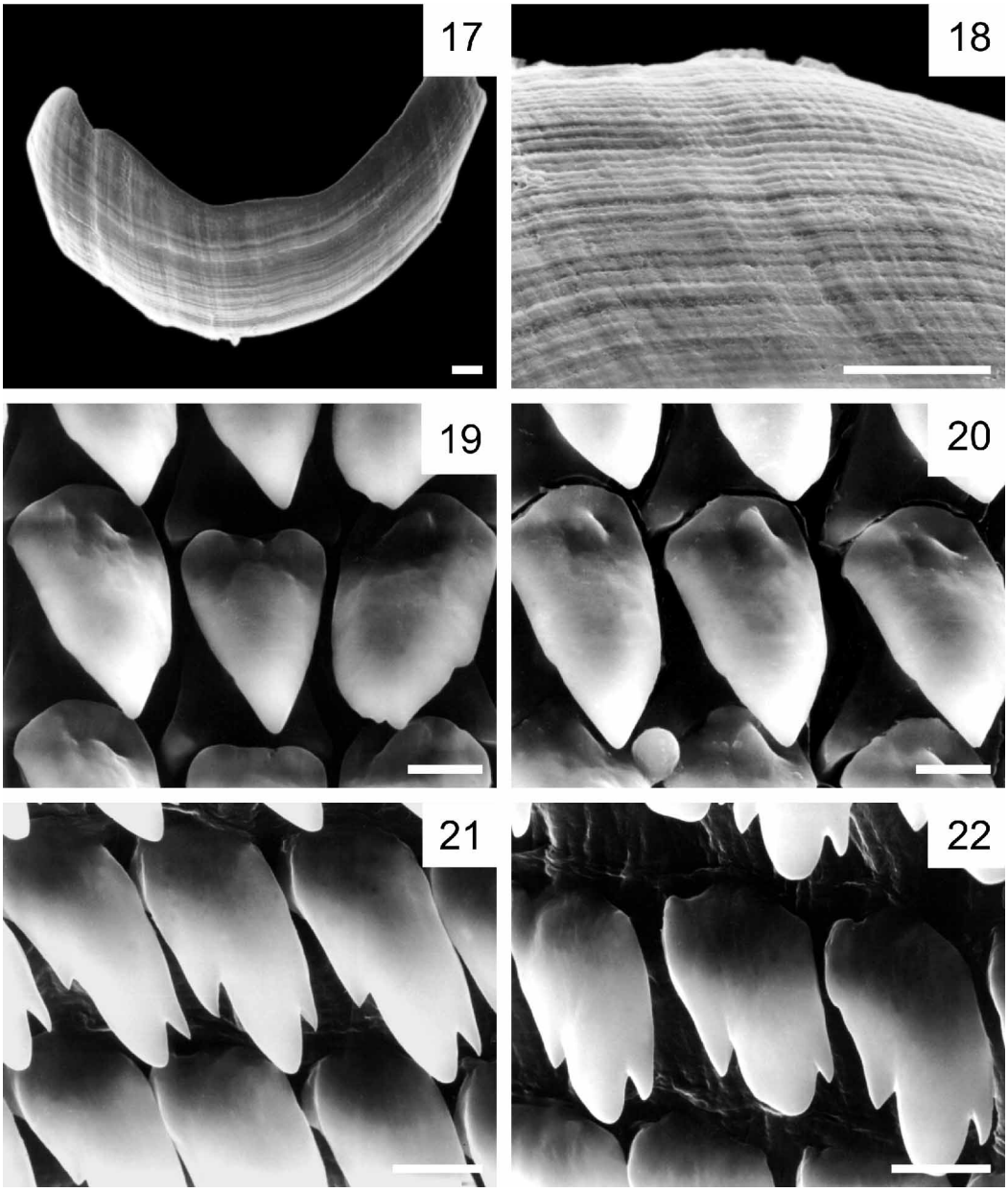
Description: *Shell*: Morphology as described by Solem (1966: 116), (Fig. 13).

Pallial Organs: Kidney long, thin, occupying about 60% of pulmonary roof length. Surface of pulmonary roof densely speckled with dark spots. Thin transversal veins abundant between kidney and rectum. Main pulmonary vein branched before reaching mantle collar. Pulmonary roof not expanded beyond top of kidney. Secondary ureter closed up to mantle collar. Ureteric interramus triangular, deeply excavated. Diaphragm thick, muscular.

Reproductive system (Figs 14–16)**:** Ovotestis formed by elongated digitiform non-ramified acini. Albumen gland yellowish, bean-shaped. FPSC undifferentiated. Hermaphroditic duct reflexed over itself at base of albumen gland. Albumen gland continuous with spermoviduct. Folds of uterine portion transversal with respect to longitudinal axis of spermoviduct (Fig. 14). Free oviduct short, cylindrical, naturally forming angle with vagina. Prostatic duct of spermoviduct extending into proximal portion of free oviduct. Vagina as long as penis. Proximal portion of vagina with inner thick longitudinal ridges in zigzag pattern. Distally, ridges become thinner, straight. Hooked denticles absent in entire length of vagina. Duct of bursa copulatrix long, thick, parallel to spermoviduct up to junction with albumen gland. Bursa copulatrix sac globose, reflexed over duct (Fig. 14). Penial complex formed by flagellum, epiphallus, penis (Fig. 15). Diameter of flagellum progressively decreasing towards tip. Thick internal pilaster extending between flagellum and epiphallus. Pilaster forming papilla-like structure transversally divided at junction between flagellum and epiphallus, point of insertion of vas deferens (Fig. 16). Penis sheath thick, muscular overlapping distal zone of penis. Epiphallus reflexed over penis, wrapped with muscular fibres and connective tissue. Distal zone of penis thicker than proximal. Penis retractor muscle thick, inserting at proximal portion of penis close to junction with epiphallus. Inner penis wall with thick folds, deeper in proximal zone. Dorsal surface of folds with white, oval, hooked pustules, regularly distributed as shown in Fig.16. Verge absent.



FIGURES 13–16: *Labyrinthus subplanatus*. 13: Morphology of shell aperture. 14: General morphology of reproductive system in ventral view, ovotestis not figured, scale bar= 5 mm. Abbreviations: ag: albumen gland; bc: bursa copulatrix; f: flagellum; fo: free oviduct; go: genital opening; hd: hermaphroditic duct; p: penis; s: spermoviduct; v: vagina; ps: penis sheath. 15: Detail of penial complex, dorsal view, scale bar= 5 mm. Abbreviations: f: flagellum; p: penis; pr: penis retractor muscle; vd: vas deferens; ps: penis sheath. 16: Inner structure of penial complex, scale bar= 2 mm. Abbreviations: a: atrium; d: denticles; e: epiphallus; f: flagellum; p: penis; pi: pilaster; pr: penis retractor muscle; vd: vas deferens; ps: penis sheath.



FIGURES 17–22: *Labyrinthus subplanatus*. 17: Dorsal view of jaw, scale bar= 100 µm. 18: Detail of the jaw in dorsal view, scale bar= 100 µm. 19: Central and first lateral tooth, scale bar= 10 µm. 20: Lateral teeth No. 7–9 to the left of central tooth, scale bar= 10 µm. 21: First marginal teeth in the same row of previous view, scale bar= 10 µm. 22: Last marginal teeth close to radular margins, scale bar= 10 µm.

Digestive system: Jaw (Figs 17–18) arched, without vertical ribs (Fig. 17). Surface with thin transverse striation crossed by thin, shallow perpendicular lines giving appearance of reticulated surface (Fig. 18). Lower edge without medial protruded cutting edge.

Central tooth of radula unicuspid, triangular (Fig. 19). Fourteen lateral teeth unicuspid (Figs 19, 20). Marginal teeth tricuspid (Fig. 21). Outermost marginal teeth becoming wider but always tricuspid with more pronounced mesocones (Fig. 22). Buccal mass oval. Rest of digestive tract as in *L. dunkeri.*

Material examined: COLOMBIA: FMNH 163706, *Choco Department*, Choco, Caño Taparral, 20 Km to the north of Palestina, on San Juan River. November 25, 1968. B. Malkin Coll. FMNH 173866, *Choco Department*, San Juan River, Quebrada Docordo. June 5–8, 1969. B. Malkin Coll. FMNH 223561, *Choco Department*, San Juan River, 110 Km to the north of Palestine. January 20,1971. B. Malkin & P. Bouchard Coll.

Remarks: *Labyrinthus subplanatus* belongs to the *L. otis* species complex that was supported as a monophyletic clade within the genus (Cuezzo 2003). The group of *L. otis* is composed by *L. otis* (Lightfoot, 1786), *L. subplanatus*, *L. marmatensis* Pilsbry, 1910, and *L. plicatus*. *Labyrinthus subplanatus* is similar to *L. otis* and both have been confused mostly because their distributional ranges are partly overlapping. However, *L. otis* differs from *L. subplanatus* mainly in having a deep supraperipheral groove and in being much larger (*L. otis* shell diameter up to 58 mm, while *L. subplanatus* diameter up to 45 mm). *Labyrinthus subplanatus* also present a periphery acutely angulated with protruding keel, and the peristome forming a peripheral notch sometimes slightly twisted (see Solem 1966) which is absent in *L. otis*. Differences in the genitalia between these two species are difficult to evaluate because of the poor descriptions presently available of *L. otis.*

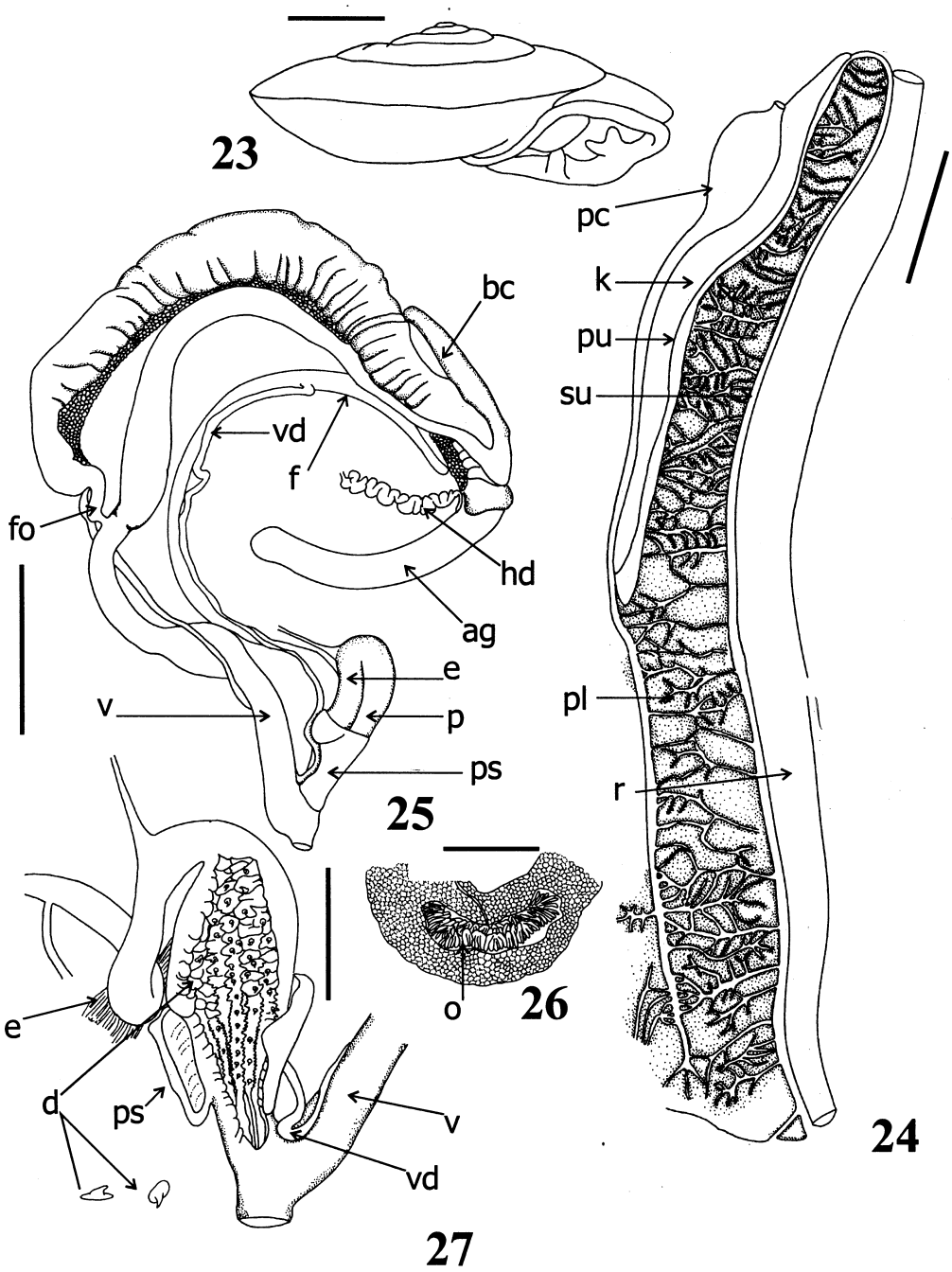
***Labyrinthus tarapotoensis* (Moricand, 1858)**
Figures 23–31; 34–35

Helix tarapotoensis Moricand, 1858: 450, pl.13, fig.2.

Description: *Shell* (Fig. 23)**:** As described by Solem (1966: 80).

Pallial Organs (Fig. 24): Kidney narrow, long, occupying about 50–60% of pulmonary roof length. Both sides of main pulmonary vein with abundant minor veins running transversally respect to longitudinal axis of pulmonary roof. Main pulmonary vein running from pericardic cavity to mantle collar, not bifurcated. Pulmonary roof dark, with abundant black pigmentation bordering pulmonary veins. Secondary ureter closed from top of pulmonary roof to mantle collar. Ureteric interramus triangular, deeply excavated.

Reproductive system (Figs 25–27, 32–33): Ovotestis formed by single group of long non-branched digitiform acini (Fig. 26). Albumen gland bean-shaped, thin, long (Fig. 25). Hermaphroditic duct folded at distal portion inserting in albumen gland. FPSC externally undistinguishable. Proximal portion of spermoviduct voluminous, overlapping distal portion of albumen gland. Uterine portion of spermoviduct transversally folded. Prostatic portion of spermoviduct thin, prolonged into long vas deferens. Vas deferens running towards terminal genitalia surrounding vagina, wrapped by thin connective tissue. Free oviduct



FIGURES 23–27: *Labyrinthus tarapotoensis*. 23: General shell outline, scale bar= 1 cm. 24: Pallial Organs, scale bar= 1 cm: Abbreviations: pc: pericardium; pl: pulmonary roof; k: kidney; r: rectum; pu: primary ureter; su: secondary ureter. 25: Reproductive system dissected out from visceral mass, dorsal view, ovotestis not figured, scale bar= 1 cm. Abbreviations: ag: albumen gland; bc: bursa copulatrix; e: epiphallus; f: flagellum; fo: free oviduct; hd: hermaphroditic duct; p: penis; ps: penis sheath; v: vagina; vd: vas deferens. 26: Detail of the ovotestis (o) embedded in the digestive gland, scale bar= 5 mm. 27: Inner structure of penis, scale bar= 5 mm. Abbreviations: d: denticles; e: epiphallus; ps: penis sheath; v: vagina; vd: vas deferens.

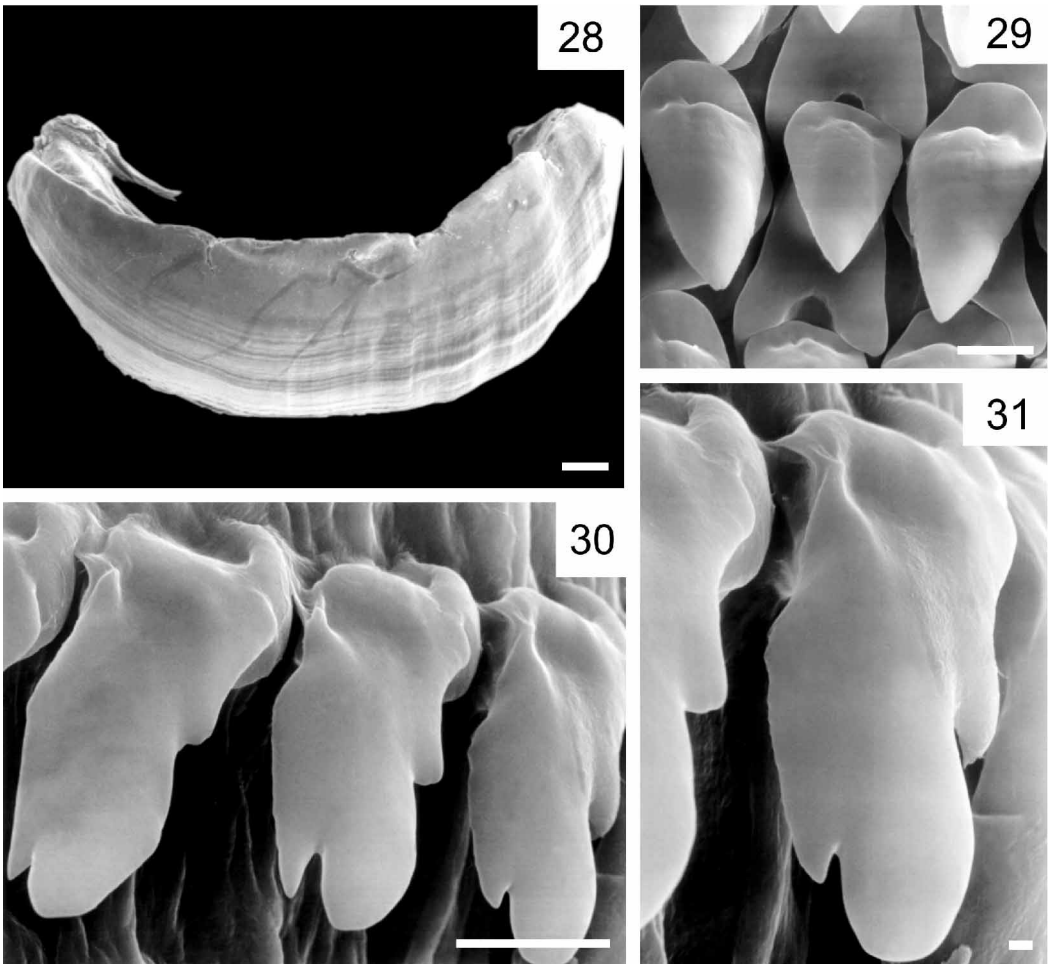
short, in natural position forming angle with vagina while duct of bursa copulatrix continuous with it (Fig. 25). Bursa copulatrix running parallel to spermoviduct up to distal portion of albumen gland. Duct of bursa copulatrix and spermoviduct wrapped together with thin connective tissue. Distal portion of bursa copulatrix sac folded over its duct. Distal portion of bursa copulatrix duct broadened respect to proximal portion. Vagina longer than phallic complex, proximal portion thicker. Inner structure of proximal vagina formed by longitudinal thick, deep cords, divided into rhomboidal portions, regular in shape. Each rhomboidal portion bearing white hooked denticles with oval bases. Denticles densely, regularly distributed in proximal vagina. Distal portion of vagina with longitudinal cords, not divided in rhomboids, lacking hooked denticles. Phallic complex formed by flagellum, epiphallus, penis. Flagellum thin, gradually tapering towards tip. Internally, longitudinal pilaster with dorsal groove ending at point of insertion of vas deferens or slightly lower on proximal epiphallus. Other two internal pilaster continuous within epiphallus. Epiphallus longer, thinner than penis. Penis thick, muscular, with distal portion ensheathed with part of epiphallus by penial sheath (Figs 25, 27). Penial reflexed over distal portion of epiphallus, attached to it by muscular strands. Penis retractor inserted into penial-epiphallus junction. Vas deferens inserted in proximal epiphallus marking limit between epiphallus and flagellum. Epiphallus with internal fine longitudinal folds in zigzag pattern. Penis with thick pilasters folded, densely packed in proximal portion (Fig. 27). Numerous white hooked denticles with oval base of 360 μm stuck to dorsal portion of pilasters (Figs 32–33). Verge absent.

Digestive system: Jaw (Fig. 28) arched, without vertical ribs, only fine transversal grooves on surface. Upper and lower cutting edges even. Central tooth of radula monocuspid, sharp tip (Fig. 29). First lateral teeth unicupid, changing to bicuspidates. Marginal teeth tricuspid (Figs 30, 31) becoming wider, multicuspid close to edges of radula. Rest of digestive system as described for *L. dunkeri.*

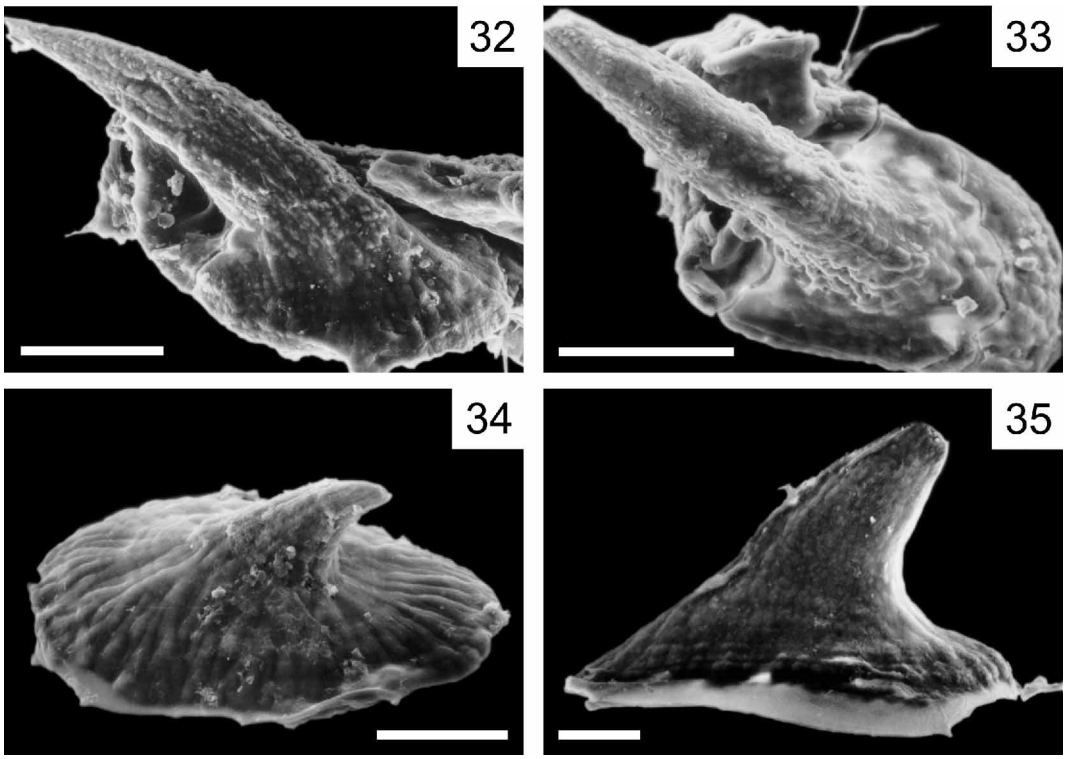
Material examined: ECUADOR: FMNH 173038: *Pastaza Department*, Cusheme River, Cusheme. May 15, 1971. B. Malkin Coll. **COLOMBIA**: FML s/n: *Nariño Department*, Pto. Nariño. E. Dominguez leg.

Remarks: Hooked denticles in *L. tarapotoensis* are more abundant than in other species examined. These denticles are present not only on penis but also in vagina.

Labyrinthus tarapotoensis belongs to the *L. raimondii* species complex (Solem 1966). Among the species included by Solem (1966) into this complex, *L. raimondii* (Philippi, 1867) is the most similar in shell size and morphology to *L. tarapotoensis.* However, *L. tarapotoensis* can be distinguished from *L. raimondii* by its white lip and less angulated periphery. Both species have similar shell diameter (*L. raimondii* shell diameter: 38.6–42.1 mm (Solem 1966), *L. tarapotoensis* shell diameter: 41–42 mm). The anatomy of *L. raimondii* is not known so anatomical comparisons are not currently possible.



FIGURES 28–31: *Labyrinthus tarapotoensis*. 28: General view of the jaw, scale bar= 100 µm. 29: Detail of the central and first lateral teeth of a row, scale bar= 10 µm. 30: Marginal teeth, scale bar= 10 µm. 31: Detail of a marginal tooth, scale bar= 1 µm.



FIGURES 32–35. 32, 33: *Labyrinthus dunkeri*. 32: Lateral view of a denticle from penis wall showing the long hook, scale bar= 100 µm. 33: Dorsal view of a hooked denticle from inner penis wall. Basal plate is partly covered by soft tissue, scale bar= 100 µm. 34, 35: *L. tarapotoensis*. 34: Dorso-lateral view of a hooked denticle from inner penis wall, scale bar= 100 µm. 35: Lateral view of other denticle from penis wall, scale bar= 100 µm.

Isomeria Albers, 1850

Type species: *Helix oreas* Koch, 1844, by monotypy.

Diagnosis: Shell small to large (18–75 mm) generally globose; shell surface sculpture with wrinkles, granulations and/or malleations; periphery convex to obtusely angulated; umbilicus usually closed or very narrow; lip thick, reflected with aperture subquadrate with few teeth and lamellae, toothless in some species; parietal callus usually thin, sometimes raised edge; parietal wall generally toothless or with small triangular teeth or short lamellae; basal lip with 0–2 denticles, palatal lip having small triangular denticle in most species, rarely with large tooth marked by posterior indentation; presence of special structures such as penial appendages, epiphallic flagellum and/or stimulator-like appendage in vagina-atrium; both vagina and penis with internal hooked denticles. Jaw smooth or with weakly developed plaques.

Distribution: distributed from Sierra Nevada de Santa Marta in northern Colombia,

Valle del Cauca, Cordillera Central and Occidental in Colombia south to Cajamarca department in Peru (Solem 1966; Breure 1984). *Isomeria* is more abundant in Ecuador at Esmeraldas and in amazonian localities close to Napo River. Its distributional range seems to be more restricted than that of *Labyrinthus*, further collections will allow to define more precisely the distribution of *Isomeria*.

Remarks: In the phylogenetic hypothesis proposed for Camaenidae by Cuezzo (2003), the synapomorphies supporting the monophyly of *Isomeria* were only shell characters. This is probable a consequence of the scarce anatomical information available for *Isomeria* and the low number of species used in the cladistic analysis. The identified synapomorphies were: 1) aperture shape quadrangular; 2) presence of palatal teeth in the aperture and 3) umbilicus partially or entirely covered by lip. Characters shared with *Labyrinthus* are the presence of hooked denticles in the penis, which are smaller in *Isomeria*; the penis-epiphallus reflection usually wrapped in part by penis sheath. The free oviduct formed an angle with vagina. The jaw in *Isomeria* (as it is the case in some species of *Labyrinthus*) is smooth with transverse striae, not ribbed.

***Isomeria awa* n. sp.**
Figures 36–48

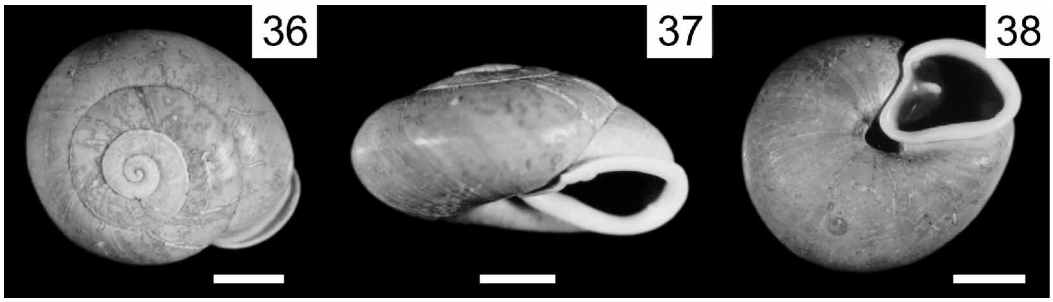
Type material: Holotype: AvH unnumbered. **Paratypes**: FML 14796 A, from type locality.

Type Locality: **COLOMBIA**, *Nariño department*, Reserva Natural La Planada, Nariño, 1730 mts, N 1° 50' W 77° 43' Orejuella, J. E. & Cantillo, G. Coll.

Etymology: the species name refers to the indigenous Inkal Awa community that lives close to the Reserva Natural La Planada in the region of the Cordillera Occidental, Ricaurte County, Nariño Department in Colombia. The name Awa means "people of the mountain". Noun in apposition.

Diagnosis: shell body whorl with axial growth lines, small pustules all over surface. Irregular spots of dark brown coloration on dorsal shell surface. Parietal lamellae small, triangular, not merging with lip, small conical tooth on lower palatal peristomal lip. Umbilicus narrow, open. Vagina long with glandular pouch in distal portion. Presence of inner conical stimulator-like structure in distal vagina.

Description: *Shell* (Figs 36–38): Globose, 4 1/2 whorls, strong, body whorl periphery obtusely angulated; golden yellowish. Axial growth lines with small pustules all over shell surface. Irregular small spots of dark brown color on dorsal side of shell. Body whorl strongly descending behind aperture. Aperture subquadrate, chestnut coloration inside aperture. Peristomal lip white, strongly reflexed, parietal lip with prominent raised edge. Small, triangular parietal lamellae present, not merging with peristomal lip, lower palatal lip with small conical tooth. Suture shallow. Umbilicus narrow, open, with columnar groove noticeable, basal lip extension covering only a small portion.



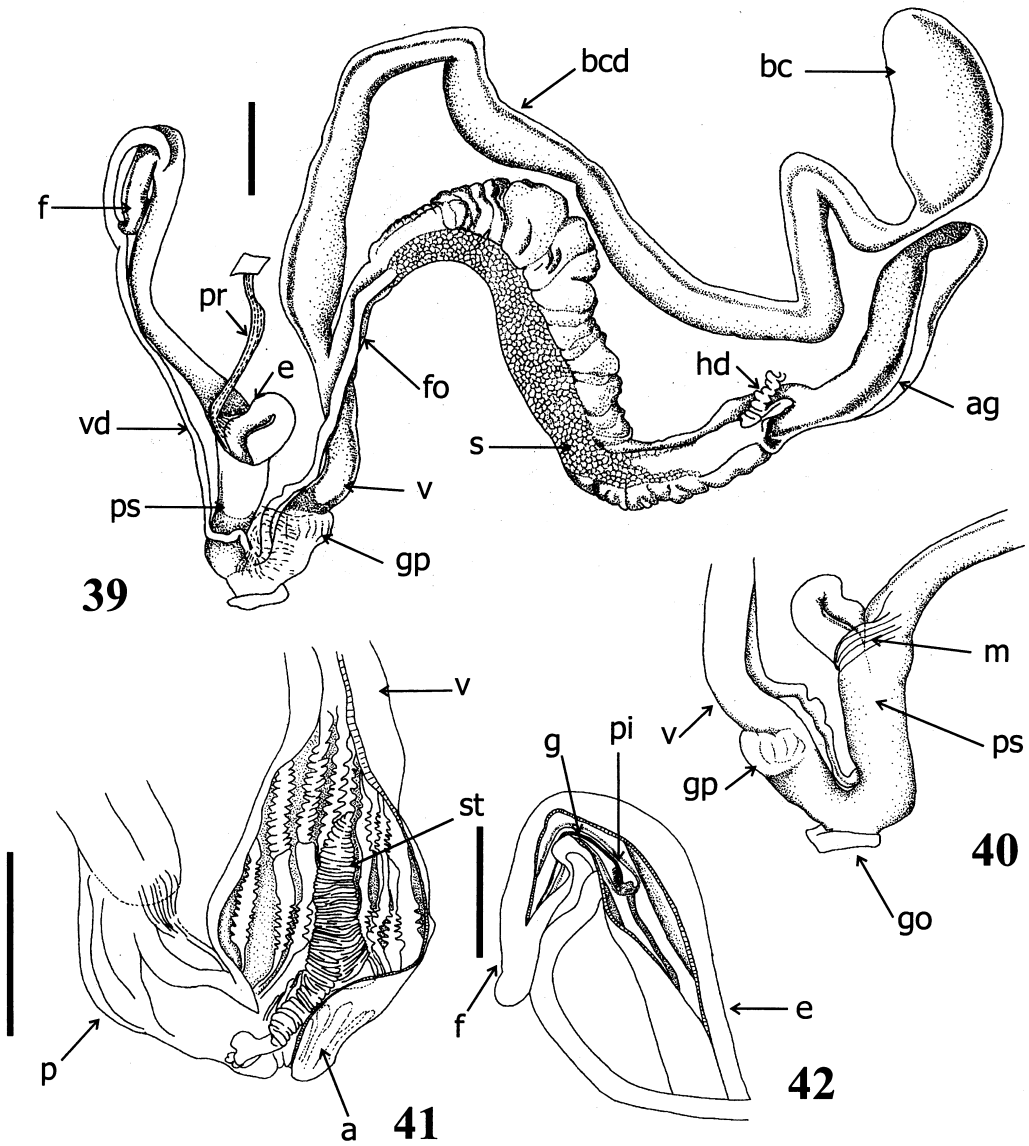
FIGURES 36–38: *Isomeria awa* n. sp. 36: Holotype, dorsal view, scale bar= 1 cm; 37: lateral view, scale bar= 1 cm; 38: ventral view, scale bar= 1cm.

Holotype shell measurements: D major= 39.7; D minor= 34.4; H= 21.5; D ap= 19.7; Hap= 16.3. Paratypes shell measurements (n= 3): D major= 38.8–39.4 (0 = 38.6); D minor= 33.2–34.2 (0 = 33.4); H= 21–21–5 (0 = 21.3); D ap= 19.3–20.1 (0 = 19.6): H ap= 16.2–16.9 (0 = 16.4).

*Pallial Organs***:** Pulmonary roof black due to dense dark pigmentation. Thin grayish minor veins weakly marked, distinguishable mostly between rectum and kidney. Main pulmonary vein running from pericardial cavity to mantle collar, not branched. Kidney narrow, long, occupying about 70% of pulmonary roof length. Secondary ureter closes from top of pulmonary roof to mantle collar. Ureteric interramus triangular, deeply excavated, overlapped by mantle collar.

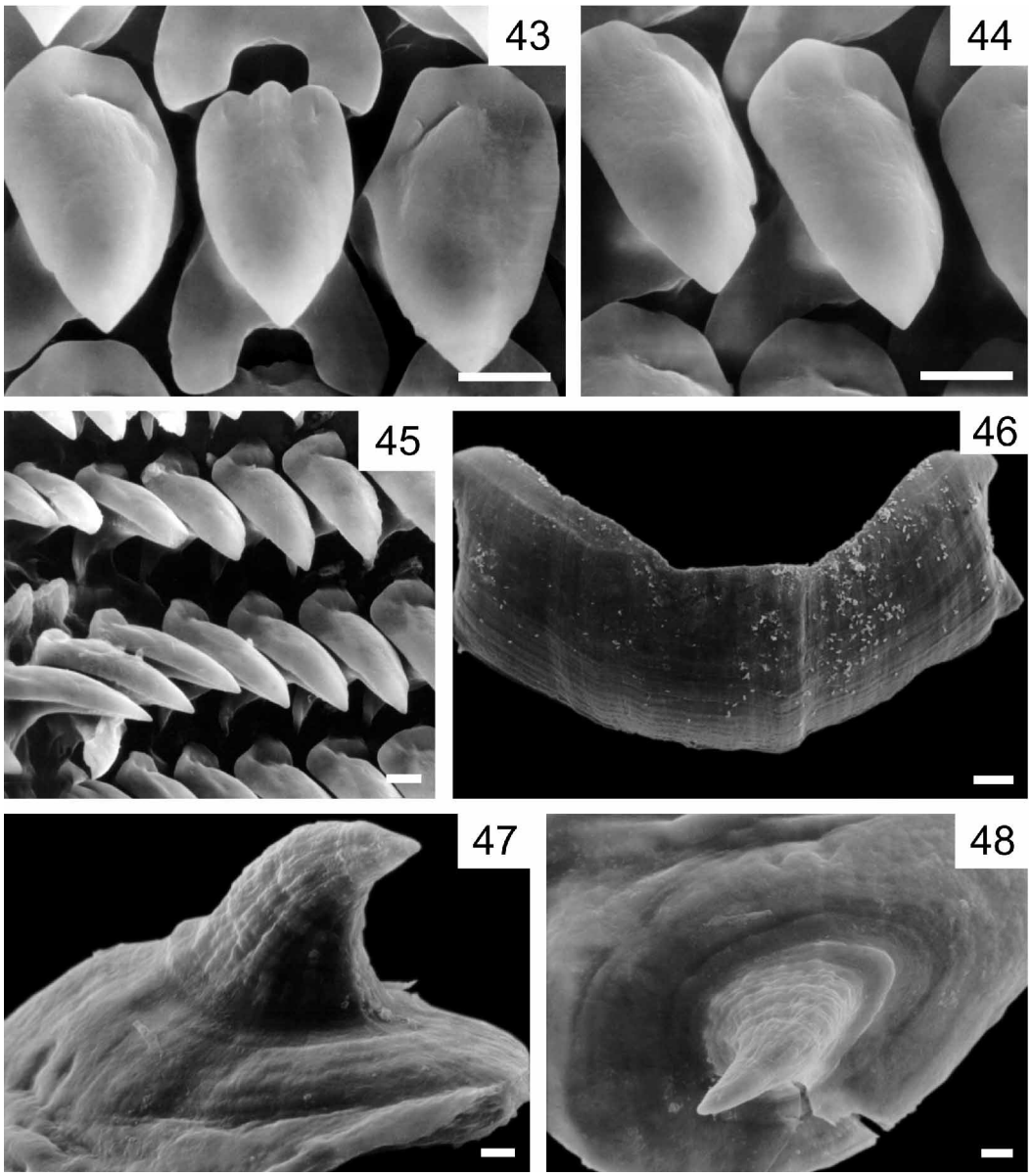
Reproductive system (Figs 39–42, 47, 48): Ovotestis formed by long, apically branched acini embedded in digestive gland. Hermaphroditic duct long, convoluted; distal portion of hermaphroditic duct reflexed over itself before inserting in distal portion of albumen gland. Fertilization pouch-spermathecal complex (FPSC) not distinguishable. Duct of bursa copulatrix thicker than free oviduct, 1 1/2 times as long as spermoviduct length (Fig. 39). Sac oval, voluminous, not reflexed over its duct. Free oviduct short, slightly thinner than vagina. Vagina long, distal glandular pouch close to peni-oviducal angle (Figs 39, 40). Inner structure of proximal portion of vagina consisting of longitudinal, parallel, deep cords with scattered white hooked denticles. Conical stimulator-like structure, present in distal portion of vagina (Fig. 41), attached through base to vagina's wall near vagina-atrium junction, raised free into vagina's lumen. Portion of stimulator-like structure extending into atrium towards distal penis, ending into two finger-like branches (Fig. 41). Penial complex formed by flagellum, epiphallus, penis (Figs 39, 40). Flagellum short, uniform diameter, tip folded. Internally, longitudinal pilaster with open dorsal groove running from top to junction with epiphallus, ending at point of insertion of vas deferens or slightly below (Fig. 42). Pilaster dorsal groove partially overlapped by extension of lateral wall, forming flap. Epiphallus longer, thinner than penis, distally reflexed over penis, overlapped by penis sheath. Penis long. Penial retractor inserting in distal epiphallus. Thick muscular strands attached penis to penis sheath (Fig. 40). Interior wall of proximal penis with thick, deep pilasters bearing hooked denticles regularly dis-

tributed, with oval bases of 180–200 µm of length (Figs 47, 48). Denticles more abundant in penis than in vagina. Verge absent.



FIGURES 39–42: *Isomeria awa* n. sp. 39: Genital system, ventral view, scale bar= 5 mm. Abbreviations: ag: albumen gland; bc: bursa copulatrix; bcd: duct of bursa copulatrix; e: epiphallus; f: flagellum; fo: free oviduct; gp: glandular pouch; hd: hermaphroditic duct; pr: penis retractor muscle; ps: penis sheath; s: spermoviduct; v: vagina; vd: vas deferens; 40: Detail of distal genital system in dorsal view. Abbreviations: go: genital opening; gp: glandular pouch; m; muscular strands; ps: penis sheath; v: vagina; 41: Diagram of the stimulator-like structure extending into atrium towards distal penis, scale bar= 5 mm. Abbreviations: a: atrium; p: penis; st: stimulator-like structure; v: vagina; 42: Pilaster running from top of flagellum to junction with epiphallus showing the dorsal groove, scale bar= 5 mm. Abbreviations: e: epiphallus; f: flagellum; g: groove; pi: pilaster.

Digestive system (Figs 43–46)**:** Jaw arched, incipient plaque in middle of jaw, fine transversal grooves more evident close to one edge (Fig. 46). Upper, lower cutting edges even. Central tooth of radula monocuspid (Fig. 43). First laterals monocuspid, changing into bicuspid (Figs 44, 45). Condition of marginal teeth unknown.



FIGURES 43–48: *Isomeria awa* n. sp. 43: central and first lateral teeth, scale bar= 10 µm. 44: lateral teeth, rows 3 to 5, scale bar= 10 µm; 45: Lateral teeth, rows 20 to 27, scale bar= 10 µm. 46: Dorsal view of the jaw, scale bar= 100 µm. 47: Dorsal view of a hooked denticle from the inner wall of penis, scale bar= 10 µm. 48: Lateral view of a hooked denticle from the penis, scale bar= 10 µm.

Comparative Material examined: COLOMBIA: ZMZ 544602 *Isomeria oreas* (Koch, 1844), G. Schneider, 1912; ZMZ 509673 *Isomeria subelliptica* (Mousson, 1869), Holotype, Bagua, Amazonas, Wallis leg., 1869. **ECUADOR:** MUC s/n, *Isomeria globosa, Pichincha Province*. Puerto Quito, and 5/12/1983.M. Ituwalde. MUC s/n, *Pichincha Prov.*, Puerto Quito, 16/1/1984. Leg. V. Zak.

Remarks: *Isomeria awa* belongs to the *Isomeria oreas* group of species (Solem 1966). *Isomeria awa* is most similar in shell morphology to *I. oreas,* differing in being smaller (adult specimens of *I. oreas,* mean diameter = 57.3 mm; *I. awa* mean diameter= 39 mm); *I. oreas* has fine radial striae and malleations on the surface of the body whorl, while *I. awa* has axial growth lines with small pustules all over shell surface; the shell coloration in *I. oreas* is darker than in *I. awa,* without the characteristics irregular spots present in *I. awa* shells. The number of shell whorls is lower in *I. awa* (41/2 whorls) than in *I. oreas* (5–5 1/2 whorls). Comparison based on anatomical characters is not possible because the anatomy of *I. oreas* is unknown. *Isomeria subelliptica* (Mousson, 1869) is similar to *I. awa* in that they both possess a small parietal tooth and open umbilicus, but *I. awa* has a larger shell [mean diameter of 39 mm, while *I. subelliptica* shell mean diameter is 30.9 mm (Solem 1966)], the umbilicus is narrower than in *I. subelliptica*. Both species also differ in shell color, *I. awa* has a golden yellowish coloration with darker irregular spots while in *I. subelliptica* the shell possess an even dark brown coloration. As in the case of *I. oreas,* anatomical comparisons of *I. awa* with *I. subelliptica* are not possible due to the lack of information on the later. *Isomeria globosa,* whose anatomy was described by Solem (1966), differs from *I. awa* in not having the vagina's stimulator apparatus. Hooked denticles in vagina and penis, and a glandular pouch are present in *I. globosa*. A penial appendix is lacking in *I. awa* but it was described in *I. globosa.*

Two structures in the genitalia of *I. awa* probably represent unique characters within the genus, the presence of a stimulator-like organ within the vagina and a glandular pouch externally visible in the distal portion of the vagina. This kind of stimulator-like organ has never been reported before in any Camaenidae and resembles the ones described in Milacidae (Wiktor 1987). Other stimulator-like appendages have been reported in certain Hygromiidae (Hausdorf 1998). However, several appendages have been called as "stimulators" (Nordsieck 1987; Schileyko 1991; Hausdorf 1998) so that the homology of this kind of structures can only be tested by phylogenetic analyses. The glandular pouch found in *I. awa* is also present in *I. globosa* in which it has been described as a ring of low knobs around the vagina (Solem 1966). A glandular pouch is characteristic of some species of *Polydontes* Montfort, 1810, also member of the Camaenidae, however, this kind of structure appears in the penial complex but not in the vagina. Hooked denticles with oval bases are also present, both in vagina and penis, in some *Labyrinthus,* with similar morphology although they are smaller in *I. awa*. These denticles are usually more abundant in the penis than in the vagina in *Labyrinthus* as well as in *Isomeria*. Another character shared with *Labyrinthus* is the presence of an internal flagellar pilaster, which in *I. awa,* shows a dis-

tinct open dorsal groove. Marginal teeth were not observed in the radulas preparations because they were broken.

***Isomeria tamsiana* (Dunker, 1847) comb. nov.**

Labyrinthus tamsiana (Dunker, 1847), whose anatomy was described by Baker (1926) and Wurtz (1955), shows more anatomical similarities closer to *Isomeria* than to *Labyrinthus.* The presence of a vaginal swelling called ring of vaginal knobs, and the presence of a flagellar pilaster with a terminal papilla through which the vas deferens opens (Wurtz 1955), are characters known to occur in both *I. awa* (this study) and *I. globosa* (Solem 1966), the only species of the genus with described anatomies. Shells of *L. tamsiana* illustrated by Solem (1966) shows that the aperture has a typical subquadrate form with few teeth and lamella, characteristic also of the *Isomeria* species. For these reasons we reclassify *L. tamsiana* within the genus *Isomeria*.

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