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Revaluation of the taxonomic characters and distribution of *Omalonyx geayi* (Gastropoda, Succineidae)

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ABSTRACT. *Omalonyx geayi* Tillier, 1980 was originally described on the basis of specimens from Kaw swamp, French Guiana. This species distinguished from other of *Omalonyx* d'Orbigny, 1837: (i) by hermaphrodite duct twice as long and sacculate, without radial ducts but a funnel-shaped insertion on the ovariotestis, and (ii) by longitudinal wrinkled folds on the phallus inner wall. Two recent collections – from Trinidad and Carauari (Amazonas, Brazil) included specimens with ovariotestis and hermaphrodite duct morphologies similar to that originally described for *O. geayi*, but with phallus morphology not consistent with identification as *O. geayi*. A further eight lots, from Suriname, Ecuador, Brazil (Amazonas and Alagoas States), Bolivia and Cayenne-Kourou Road in French Guiana comprised specimens with phallus morphology analogous to *O. geayi* and ovariotestis and hermaphrodite duct similar to that of other *Omalonyx* species. Based on histological examination, and earlier phylogenetic analyses of morphological characters, we conclude that the ovariotestis and hermaphrodite duct conditions previously described for *O. geayi* were based on parasitized specimens. Accordingly, *O. geayi* is redescribed, and new information presented on the species' wide distribution in South America.

KEYWORDS. Parasitic castration, histology, Neotropical, ovariotestis, hermaphrodite duct.

RESUMO. Reavaliação dos caracteres taxonômicos e da distribuição de *Omalonyx geayi* (Gastropoda, Succineidae). *Omalonyx geayi* Tillier, 1980 foi originalmente descrita com base em exemplares procedentes do pântano Kaw na Guiana Francesa. A espécie se diferencia das demais de *Omalonyx* d'Orbigny, 1837: (i) pelo ducto hermafrodita duas vezes mais longo e convoluto, cuja inserção no ovariotestis é em formato de um funil, ao invés de ductos radiais, e (ii) pelas pregas longitudinais enrugadas na parede interna do falo. Dois lotes – procedentes de Trinidad e Carauari (Amazonas, Brasil) – apresentaram espécimes com ovariotestis e ducto hermafrodita similares aos da descrição original de *O. geayi*, porém com a morfologia do falo distinta. Outros oito lotes procedentes do Suriname, Equador, Brasil (estados do Amazonas e Alagoas), Bolívia e estrada Cayenne-Kourou na Guiana Francesa continham exemplares com morfologia do falo análoga à de *O. geayi*, todavia com ovariotestis e ducto hermafrodita similares aos das demais espécies de *Omalonyx*. Conforme resultados do estudo histológico e da análise filogenética com caracteres morfológicos, concluímos que as condições mencionadas para o ovariotestis e ducto hermafrodita na descrição de *O. geayi* foi baseada em espécimes parasitados. *Omalonyx geayi* é redescrita e novas informações sobre a distribuição na América do Sul são apresentadas.

PALAVRAS-CHAVE. Castração parasitária, histologia, Neotropical, ovariotestis, ducto hermafrodita.

Omalonyx geayi Tillier, 1980 was originally described on the basis of specimens from Kaw swamp, French Guiana (Tillier, 1980). According to the original description, this species' hermaphrodite duct is twice longer and sacculate, with a larger and more constant diameter, compared to the other *Omalonyx* species. The hermaphrodite duct origin from the ovariotestis was described as funnel-shaped, without ductules from the ovariotestis lobes. These characteristics of the gonad and hermaphrodite duct had not been observed in other *Omalonyx* species and thus considered diagnostic of *O. geayi*. The other diagnostic characteristic of *O. geayi* was the longitudinal wrinkled folds on the inner wall of the proximal part of the phallus. The only known material for this species to date has comprised the holotype and 12 paratypes.

Recently, among collections of *Omalonyx*, two series of specimens – Trinidad Island (Caribbean) and Carauari Municipality (state of Amazonas, Brazil) – presented the same ovariotestis and hermaphrodite duct conditions originally described as diagnostic for *O. geayi*. However, the inner phallus wall of both series of specimens were distinct from that described for *O. geayi*, but consistent with that known for *O. matheronii* (Potiez & Michaud, 1835).

Other recent specimens from French Guiana, Suriname, Ecuador, Brazil (states of Amazonas and Alagoas) and Bolivia (Department of Santa Cruz) presented phallus conditions consistent with typical *O. geayi*. In all cases the ovariotestis and hermaphrodite duct differed from that described for *O. geayi*, but similar to other *Omalonyx* species.

A phylogenetic analysis of *Omalonyx* specimens based on morphological characters (J. O. Arruda, unpublished data) yielded a classification that was geographically incoherent. Type specimens of *Omalonyx geayi* were grouped with neither the Trinidad specimens nor the Carauari specimens mentioned above, but with specimens identified as *O. matheronii*. By contrast, the above-mentioned Suriname, Ecuador, Brazil and Bolivia specimens were grouped with *O. geayi* specimens, despite the great dispersion of collection sites in South America and often great distance from the *O. geayi* type locality.

We suspected that lack of phylogenetic signal was related to the aberrant conditions of the ovariotestis and hermaphrodite duct in *O. geayi* type material, due to parasitism. Accordingly a histological examination of the ovariotestes and hermaphrodite ducts were made for the Trinidad and Carauari specimens. Based on detection of parasites in the hermaphrodite ducts and ovariotestes in these histological preparations, and observations of anatomy by dissection of specimens across several *Omalonyx* species, we propose a recharacterization of *Omalonyx geayi* with emphasis on the reproductive system, and redefine the species' geographical distribution.

MATERIAL AND METHODS

Institutions abbreviations mentioned: FMNH, Field Museum Natural History, Chicago, USA; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; MCNZ, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MNHN, Muséum national d'Histoire naturalle, Paris, France; MNKMO, Museo de Historia Natural Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia; FLMNH, Florida Museum of Natural History, Gainesville, USA; USDA, United States Department of Agriculture, Philadelphia, USA; ZMB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany.

Specimens examined: TRINIDAD, **Tunapuna-Piarco**: St. George East (10°41'37.5"N, 61°13'27.9"W), 6 specimens (identified as *O. matheronii* by J. O. Arruda), 15.I.2004, D. G. Robinson col. (USDA 100453). SURINAME, **Paramaribo**: Paramaribo (5°52'N, 55°10'W), 3 specimens (identified as *O. geayi*-like by J. O. Arruda), 15.XII.1978, collected Surinam Agricultural Exp. Sta. (FLMNH 463461). FRENCH GUIANA, Kaw (approx. 4°30'51"N, 52°03'44"W), holotype and 4 paratypes of *O. geayi*, 29.IV.1977, S. Tillier col. (MNHN); Route Cayenne-Kourou (17 km avant le pont de Kourou, on water-cress in small cove, 5°03'37"N, 52°33'44"W), 1 specimen (identified as *O. geayi*-like by J. O. Arruda) (MNHN). EQUADOR, **Sucumbios**: Limnoconcha (0°24'13"S, 76°37'06"W), 2 specimens (identified as *O. geayi*-like by J. O. Arruda) (FMNH 328261). BRAZIL, **Amazonas**: Iranduba (Catalão, 3°09'44"S, 59°54'33"W), 3 specimens (identified as *O. geayi*-like by J. O. Arruda), 22.VII.2006, D. Coscarelli & D. Pimpão col. (INPA 1091); Carauari (Rio Juruá, 4°52'56"S, 66°53'47"W), 4 specimens (identified as *O. matheronii* by J. O. Arruda), L. R. Malabarba col. (MCP 9183); (Bacia do rio Purus, Paraná do Uauaçu, 4°18'57"S, 62°06'15"W), 1 specimen (identified as *O. geayi*-like by J. O. Arruda), 3.XI.2004, M. Rocha col. (INPA 1643); Careiro (ilha Marchantaria, 3°49'41"S, 60°21'36"W), 1 specimen (identified as *O. geayi*-like by J. O. Arruda), 17.XII.1987, M. C. D. Mansur col. (MCNZ 30548); **Alagoas**: Satuba (rio Mandaú, área inundável, 9°34'53"S, 35°49'38"W), 1 specimen (identified as *O. geayi*-like by J. O. Arruda), 25.V.1936, Schubart col. (ZMB 90832); **Rio Grande do Sul**: Santa Maria (Cidade dos Meninos, 29°41'15.3"S, 53°43'10.5"W), 3 specimens [identified as *O. convexus* (Heynemann, 1868) by J. O. Arruda], 8.V.2005, F. Engler, J. O. Arruda & P. Bergonci col. (MCP 8831). BOLIVIA, **Santa Cruz**: Cordillera (Quebrada los Ciros, 18°25'52"S, 60°49'24"W), 1 specimen (identified as *O. geayi*-like by J. O. Arruda), L. Gonzáles col. (MNKMO 7a).

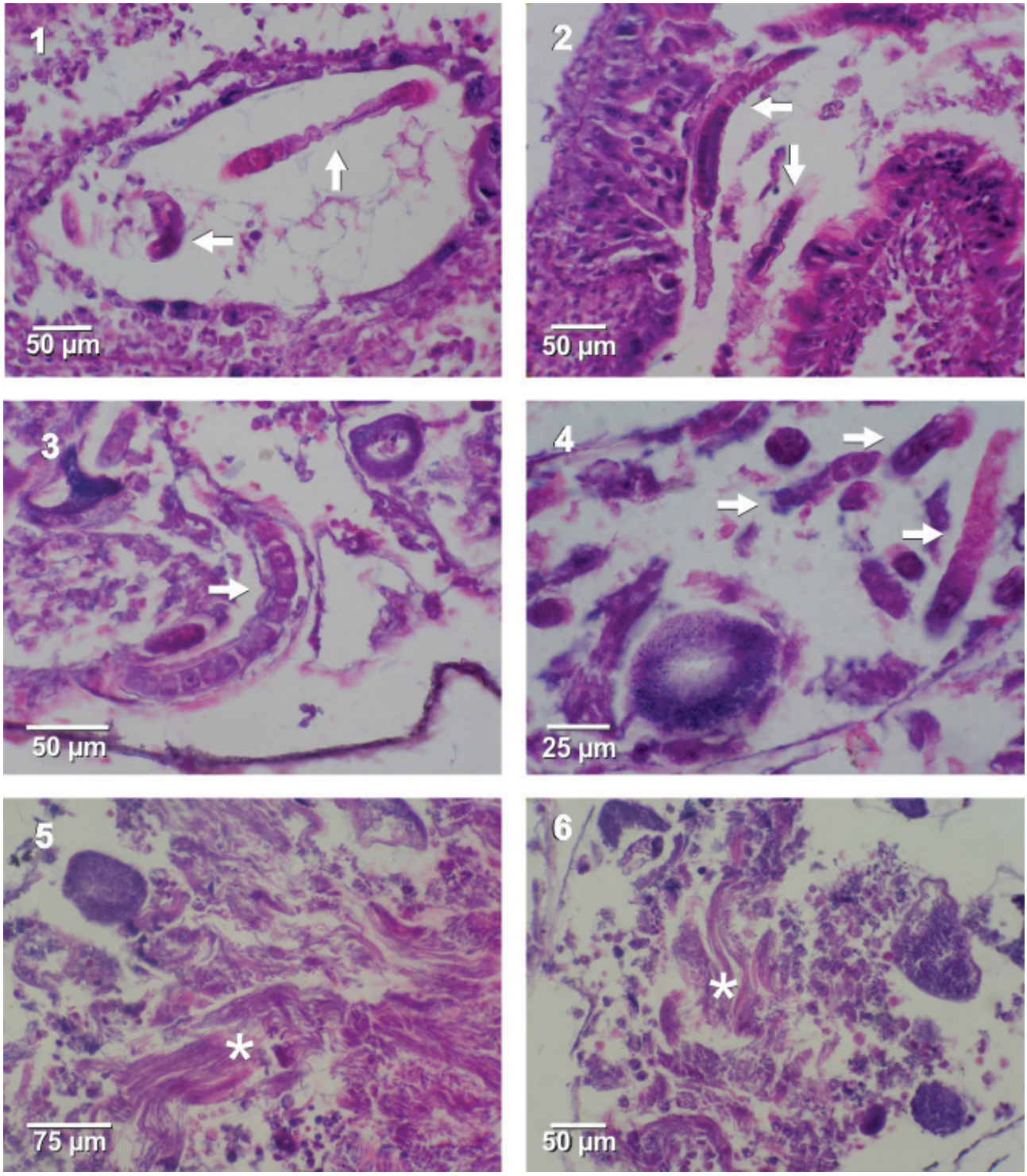
The dissection was done under the stereo microscope. The shell was removed from the body by lifting it from the mantle edge and then it was kept apart. A longitudinal cut was made in the middle of the head, between the tentacles, up to the mantle edge; the next step was to cut both sides of the mantle edge up to its posterior area, which was kept in one piece; this dorsal region was then turned over, being careful to cut muscles and ligaments in order to not break organs or accessory structures, then it was stuck on the dissection plate. With the visceral cavity opened, the reproductive system was seated on its right side and the digestive system on the left side. The ovariotestis is housed under the digestive gland and great care should be taken to release it. The penial sheath was opened with a forceps or iris scissors. The phallus complex (phallus + epiphallus) was stretched and stuck on the dissection plate with a minuten pin in the phallus retractor muscle. The inner phallus wall was opened by a longitudinal cut made with an iris scissors and then its wall was stuck on the dissection plate with minuten pins.

For histological analysis, we examined the ovariotestis and hermaphrodite duct from one specimen from each of Trinidad and Carauari where the organ conditions were similar to that described by TILLIER (1980) for the type specimens of *O. geayi*, and one each from Santa Maria and Carauari where organ conditions were representative of other *Omalonyx* species. From specimens preserved in 70% ethanol, the ovariotestes and hermaphrodite ducts were extracted by dissection, individually dehydrated in an ethanol series, infiltrated and embedded in glycol methacrylate, sectioned at 3.5 µm on a Leica RM2145 microtome, the sections mounted on glass slides and stained with Haematoxylin and Eosin. These histological preparations were photographed under a Nikon E200 compound microscope.

RESULTS AND DISCUSSION

The histological examination of the ovariotestes and hermaphrodite ducts recovered from specimens collected in Carauari and Trinidad demonstrated the presence of parasites,

here interpreted as immature stages of trematodes based on YAMAGUTI (1975) (Figs 1-4). The ovariotestes were found to be saccular, with indistinct acini, thick walled, and opening broadly to the hermaphrodite duct. The acini comprised an enlarged lumen largely deplete of gamete developmental stages but containing parasite stages here considered to be rediae and cercariae. In the remaining Carauari specimens, and those from Santa Maria, no parasites could be detected and ovariotestis acini were packed with male and female gamete stages (Figs 5, 6).



Figs 1-6. Histological micrographs of the ovariotestes of *Omalonyx*. Figs 1-2, parasitised ovariotestis tissues from Carauari (MCP 9183). Figs 3-4, parasitised ovariotestis tissues from Trinidad (USDA 100453). Fig. 5, healthy ovariotestis tissues from Carauari (MCP 9183). Fig. 6, healthy ovariotestis tissues from Santa Maria (MCP 8831). Asterisks indicate spermatozoids, and arrows parasites. Haematoxylin-eosin stain.

The anatomical examination showed specimens from Suriname, Ecuador, Brazil (states of Amazonas and Alagoas), Bolivia and Road Cayenne-Kourou in French Guiana (Fig. 7) to possess male genitalia consistent with description of the type material of *O. geayi* (Tillier, 1980, 1981), but the ovariotestis comprised distinct acini draining to ductules that in turn opened to the hermaphrodite duct, consistent with that usually found in *Omalonyx* species.

Based on these histological and anatomical results, we concluded that the original description for *O. geayi* (Tillier, 1980) was based on parasitized specimens in which the ovariotestis and proximal hermaphrodite duct were deformed. As these components of the reproductive system were considered diagnostic of the species, a redescription based on non-parasitised specimens is warranted. In formulating a redescription of *O. geayi* we also take into account the variation in the anatomy and shell across the geographic range of the species now recognized as occurring more broadly in South America than indicated by Tillier (1980) and subsequent authors.

Omalonyx geayi Tillier, 1980

Omalonyx geayi Tillier, 1980:87, figs 69-71; Pl. 5, Fig. 6; 1981:135, figs 11, 12 (anatomy and distribution).
Omalonyx unguis: Hermann & Dundee 1967:1-5 (in part) [some specimens erroneously determined; not *Omalonyx unguis* (d'Orbigny, 1835)].
Omalonyx matheroni: Tillier, 1981:129 (in part) [synonym list; not *Omalonyx matheronii* (Potiez & Michaud, 1835)].

Type material. Holotype and four paratypes, MNHN unnumbered (examined). Type locality. Kaw swamp, French Guiana.

Diagnosis. Reproductive system (Fig. 7) with phallus complex about 23 mm in length. Phallus slender, about four times length of epiphallus; internally with longitudinal wrinkled folds or longitudinally elongate papillae in the proximal one fourth, followed by an extensive zone of elliptical or polygonal shaped papillae, and distally with discoid papillae; often the entry to the atrium is characterized by lozenge - or rectangular - shaped papillae organized in longitudinal folds. Phallus sheath thick, muscular, to approximately one fifth length of the phallus from its distal extremity, thereafter extending over phallus and epiphallus as a thin, transparent veil. Epiphallus and phallus of the same width. The epiphallus outer wall smooth, with a visible epiphallial sphincter. Free oviduct with longitudinal folds lining the lumen, readily discernable externally.

Shell (Fig. 8) reduced, not capable of housing the animal, sited mid-dorsally and partially covered by mantle; about 13 mm in height, 8 mm width, comprising a nearly obsolete spire (~0.5 whorl) atop of a rapidly expanding, weakly convex body whorl; aperture oval, comprising ~0.96 shell height and entire shell width. Shell relatively larger than in other species.

Distribution. *Omalonyx geayi* had only been previously recorded from the type locality in the Kaw swamp, French Guiana (Tillier, 1980, 1981). Based on the examined material, the species is now recorded for the first time in Suriname, Ecuador, Brazil and Bolivia. In Suriname this species is recorded for Paramaribo, in Ecuador for Limoncocha (Sucumbios), in Brazil for states of Amazonas and Alagoas, and in Bolivia for Department of Santa Cruz. We predict that the species occurs widely in northern and central South America, from latitude 5°N to 18°S.

Remarks. In *O. geayi* the phallus and epiphallus are very similar in width and often it is difficult to distinguish their limits without opening the phallus. According to Tillier (1981), the phallus in *O. geayi* is 30-36 mm when extended. However, in the figure 71 of Tillier (1980), in which the epiphallus and phallus can be easily distinguished, the extended phallus length is depicted at approximately 19 mm. This latter estimate is similar to the phallus lengths measured here for specimens from Suriname, Bolivia and Brazil (Amazonas and Alagoas), which were between 17-19 mm.

We illustrate dorsal, ventral, lateral and protoconch views (Fig. 8) of the shell from an *O. geayi* paratype and this is the same shell depicted the dorsal view by Tillier (1980, Pl. 5, Fig. 6). Although *Omalonyx* shells are not considered very informative in taxonomy, the shell of *O. geayi* is larger, relatively wider, more flattened and ovoid than those of *O. matheronii* and *O. convexus*.

The ovariotestis and hermaphrodite duct described by Tillier (1980) as diagnostic characters for *Omalonyx geayi* were based on parasitized specimens. Despite this systematic misinterpretation, *O. geayi* is a valid species based on the characters of the male genitalia and shell. The first record of parasitism in *Omalonyx* was made by Lutz (1921), who reported a natural infection by a species of *Leuchlocoridium* Carus, 1835 (Trematoda, Leuchlocoriidae). Travassos (1928) subsequently used specimens of *Omalonyx* from Mato Grosso, Brazil as experimental host for this trematode which develops in the slug's visceral cavity, but does not infest host organs. Montresor *et al.* (2008) described an experimental infection of *Omalonyx* sp. by *Angiostrongylus costaricensis* Morera & Céspedes, 1971 (Nematoda, Protostrongylidae), and Mozzer *et al.* (2011) by *Angiostrongylus vasorum* (Baillet, 1866). Although these experiments prove the susceptibility of *Omalonyx* to parasitism by *A. costaricensis* and *A. vasorum*, no natural infections have been recorded. Many other parasites utilize land snails as hosts, but studies of the life cycle in South America are presently limited, but include *Eurytrema coelomaticum* (Giard & Billet, 1892) (Trematoda, Dicrocoeliidae) and *Hasstilesia tricolor* (Stiles & Hassall, 1894) (Trematoda, Brachylaemidae) (Robinson, 1953; Rowan, 1955; Paschoal & Amato, 1995, 1996, 2001). Unfortunately, our *Omalonyx* material was preserved in alcohol and not suitable for determination of the family or specific identity of the parasites infecting the gonad and hermaphrodite duct. No spermatozoids were observed within the parasitized ovariotestes from the Carauari and

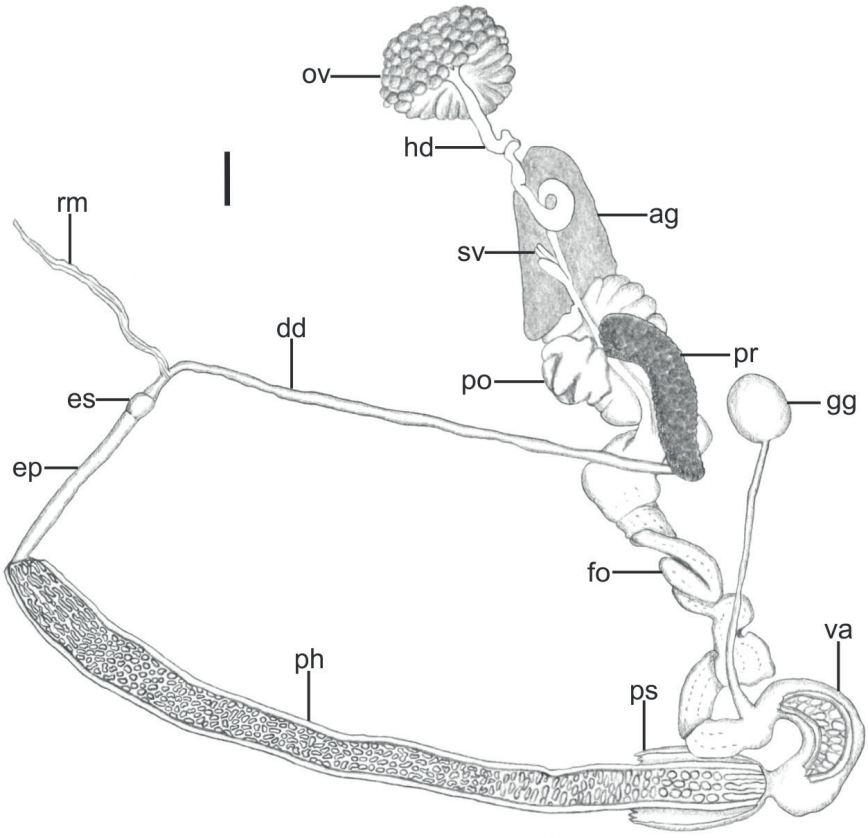


Fig. 7. Reproductive system of *Omalonyx geayi* Tillier, 1980 (Paramaribo, UF 463461), with phallus and vagina opened to show ornamentation of the internal wall (ag, albumen gland; dd, defferent duct; ep, epiphallus; es, epiphallic sphincter; fo, free oviduct; gg, gametolitic gland (*bursa copulatrix*); hd, hermaphrodite duct; ov, ovariotestis; ph, phallus; po, pallial oviduct; pr, prostatic gland; ps, phallus sheath; rm, retractor muscle; sv, seminal vesicles; va, vagina). Scale bar: 1 mm.

Fig. 8. Shell of *Omalonyx geayi* Tillier, 1980 paratype (MNHN unnumbered) in dorsal, ventral, lateral and protoconch views. Height =13 mm (TILLIER, 1980).

Trinidad specimens (Figs 1-4). This absence of male gamete development could indicate parasitic castration. This pathology is well documented for many Gastropoda species (e.g. WILSON & DENILSON 1980; PASCHOAL & AMATO, 1996; JORDAENS *et al.*, 2007; VOUTILAINEN *et al.*, 2009; AVERBUJ & CREMONTE, 2010).

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