

Redefinition of *Thapsia* Albers, 1860, and description of three more helicarionoid genera from western Africa (Gastropoda, Stylommatophora)

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As presently used, the helicarionoid genus *Thapsia* Albers, 1860 embraces a large, heterogeneous assemblage of species. As a first step in the revision of this group of taxa, the genus *Thapsia* (type species *Helix troglodytes* Morelet, 1848) is redefined anatomically and conchologically. In the absence of alcohol-preserved material of *T. troglodytes*, *Thapsia ebimimbangana* spec. nov. from Cameroon and *T. wieringai* spec. nov. from Gabon are described to characterize the soft parts morphology of *Thapsia*. Three new genera are introduced, viz. *Saphtia* gen. nov. (type species *S. granulosa* spec. nov.), *Pseudosaphtia* gen. nov. (type species *P. brunnea* spec. nov.) and *Vanmolia* gen. nov. (type species *Thapsia sjoestedti* d' Ailly, 1896). A second species of *Saphtia*, *S. lamtoensis* spec. nov., is described to illustrate the large conchological variability of the genus. The identity of *Helix calamechroa* Jonas in Philippi, 1843 (now *Saphtia calamechroa* stat. nov.), *Thapsia buchholzi* Bourguignat, 1885, and *Thapsia rosenbergi* Preston, 1909 is briefly discussed.

Introduction

The genus *Thapsia* Albers, 1860 was erected, as subgenus of *Nanina* Gray, 1834, non Risso, 1826, for *Helix troglodytes* Morelet, 1848 from Gabon based only on shell characters. Numerous African species have been attributed to the genus, which, even with the scanty anatomical data available, clearly constitutes a heterogeneous assemblage. Adam (1960) listed about 120 nominal species of *Thapsia*, since then only Verdcourt (1982) has added several species from East Africa. Species attributed to *Thapsia* have a low-spired, thin, yellowish or brownish, rather feature-less shell. These species have at least some fine spiral sculpture on the postembryonic shell, but the sculpture of some large species is decussate or even beaded. The smallest taxa (well under 10 mm) listed by Adam (1960) have since been assigned to genera of other families like the Euconulidae (e.g. De Winter & Van Bruggen, 1992). *Gudeella* Preston, 1913 (type *Thapsia masukuensis* E.A. Smith, 1899) is often used as generic or subgeneric heading for species with shells up to about 14 mm diameter, but is also considered a junior synonym of *Thapsia* (e.g. by Herbert & Kilburn, 2004: 259). The latter opinion is certainly incorrect, preliminary dissections indicate that *Gudeella* is a heterogeneous assemblage of taxa, none of which is closely related to *Thapsia* as defined below (De Winter, unpublished). For the species with shell diameters ranging from about 15 to 30 mm, two supra-specific names are presently available: *Thapsia* [type *Helix troglodytes* Morelet, 1848] and the monotypic taxon *Megathapsia* Raemaekers, 1959 [type *Thapsia (Megathapsia) dartevellei* Raemaekers,

1959, from the DR Congo (former Belgian Congo)]. Adam (1960) severely criticized the introduction of *Megathapsia*, the taxon being based solely on insufficient conchological characters of a single specimen, supposedly differing from *Gudeella* in having a larger shell with a comparatively wide umbilicus, and from *Thapsia* by the sculpture of spiral lines only. However, the taxon name *Megathapsia* was validly introduced and might have to be used once the anatomy of the type species is known.

Due to convergence in shell characters, conchological delimitation of most species attributed to *Thapsia* s.l. is very difficult, and only a handful of papers provide anatomical data, rendering the recognition of nominal species among the numerous undescribed ones virtually impossible.

The present paper is part of a project dealing with the larger-shelled species (about 15-30 mm diameter) from tropical western Africa (Senegal to Gabon) formerly attributed to *Thapsia*. Study of the anatomy of some tens of populations from a geographically wide range in western Africa indicated that at least four genera are needed to accommodate the species studied, some of which are conchologically very similar. As a first step in the revision of this extensive material, the genus *Thapsia* is defined both anatomically and conchologically, and is differentiated from three newly erected genera, in addition to which five new species are described.

Material and methods

The terminology for the soft parts largely follows that employed by Solem (1966, external soft parts, including mantle lobes), Van Mol (1970, genitalia), and Hausdorf (1998, genitalia).

Shell measurements were made by vernier callipers. Methodology for counting whorls follows Kerney & Cameron (1979: 13). Measurements of anatomical structures were made from camera lucida drawings of material preserved in ethanol 70%. Estimates of the extent of the pallial cavity (expressed as the approximate proportion of the last whorl occupied) are crude and likely to be influenced by the degree of contraction of the animal upon fixation. Linear measurements of the pallial organs were obtained from drawings of the pallial roof stretched out after a number of lateral incisions.

In the descriptions, the genital atrium is considered to be distally oriented relative to the proximally positioned ovotestis. Descriptions of internal soft parts focus on the distal genitalia. Organs located in the earlier whorls were studied only occasionally, because of difficulties to extract the proximal soft parts without severely damaging the fragile shell.

Genital organs of some specimens were longitudinally or transversely sectioned at various positions and drawn to provide some understanding of their gross internal organization; denominations of the tissues are to be viewed as tentative, and need confirmation by histological study.

Repositories and their abbreviations

- BMNH The Natural History Museum, formerly British Museum (Natural History), London, U.K.
MRAC Musée Royal d'Afrique Centrale, Tervuren, Belgium.

- RMNH Nationaal Natuurhistorisch Museum Naturalis, formerly Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.
 SMNH Swedish Museum of Natural History, Stockholm, Sweden.

Other abbreviations

a	genital atrium	ls	left shell-lap of mantle
at	axial thread	ld	right shell-lap of mantle
bc	bursa copulatrix (gameolitic gland)	lt	lower tentacle
bd	duct of bursal copulatrix	p	penis
cg	capsular gland	pr	prostate
D	maximum shell diameter	pu	primary ureter
e	epiphallus	pv	pulmonary vein
ec	epiphallic caecum	rm	penis retractor muscle
f	flagellum	s	sole
fo	free oviduct	sod	spermooviduct
go	genital opening	su	secondary ureter
h	heart (pericardium)	ut	upper tentacle
H	shell height	v	vagina
H/D	shell height/shell width ratio	vd	vas deferens
I	intestine	w	head wart
k	kidney	W	number of whorls

Systematic account

Class Gastropoda Cuvier, 1797

Clade Stylommatophora

Superfamily Helicarionoidea Bourguignat, 1877

Thapsia Albers, 1860

Nanina (*Thapsia*) Albers, 1860: 56.

Type species.— *Helix troglodytes* Morelet, 1848 (by original designation).

Diagnosis.— Large-shelled helicarionoid with decussate shell sculpture above the periphery. Foot with long caudal horn. Penis consisting of two morphologically distinct parts, with a papilla-like structure at the transition of distal to proximal penis. Distal penis wider than proximal portion. Vagina greatly swollen at junction with bursa copulatrix and free oviduct. Ampulla of spermatophore elongate-oval, not convoluted. Tail of spermatophore with complex spiny ornamentation comprising a collar of coarse thorns and various longitudinal rows of short and longer spines, those of one row particularly long and asymmetrically branched.

Description.— Shell diameter of adult specimens about 25 mm at 5½-6½ whorls. Shell pale yellowish-brown, thin and fragile, partly translucent. Periphery of adult shell more or less angular except for the rounded last quarter whorl. Embryonic whorls smooth, later whorls with fine decussate sculpture that becomes gradually coarser on

younger whorls; in adult specimens sculpture on last whorl often equally prominent or even less pronounced than on penultimate one. Decussate sculpture not extending below the periphery on the shell base, where only wavy spiral lines are present. Cephalopodium completely retractable into shell. Tail region about as long as anterior portion but less wide, dorsum rounded. Frontal area of head between ommatophores evenly covered by tubercles. Genital opening slightly posterior to right lower tentacle. Furrows between tubercles on tail unite into larger, obliquely oriented grooves, which unite to a more or less straight median furrow along dorsum. Pedal grooves aulacopod. Sole tripartite, central field slightly narrower than outer fields, more strongly so in tail region. Hind end of foot in preserved specimens vertically truncate, with distinct caudal horn above caudal foss; caudal horn length in preserved specimens variable, it may be partly retracted. Male distal genitalia comprise of a bi-partitioned penis, a roundish epiphallic caecum on which penis retractor muscle inserts, and a well-developed epiphallus and flagellum. Flagellum contains axial thread. Vagina strongly swollen at junction with duct of bursa copulatrix and proximal free oviduct. Proximal free oviduct partly enlarged and thick-walled (capsular gland). Spermatophore large, rigid-horny (chitinous), with a large, elongate-oval, not convoluted, sperm-containing head (ampulla), followed by a long convoluted tail with a narrow central canal and complex spiny ornamentation. This ornamentation consists of two longitudinal, parallel rows of long spines, those of one row particularly long and asymmetrically branched, and three longitudinal rows of simple short spinules on last part of tail in addition; a collar of coarse thorns is present directly behind the ampulla, the thorus point towards the tail canal opening, all other spines point in opposite direction towards the ampulla. Tail canal of exchanged (i.e. not self-produced but received from partner) spermatophore with simple terminal opening, through which the sperm is released.

This description of the anatomy is based on characters shared by the two species described in this paper and confirmed by observations on specimens from various other populations from Gabon and Cameroon (De Winter, unpublished), the anatomy of the type species of *Thapsia* being unknown (see below).

Remarks. — *Thapsia* species can strongly resemble large members of *Saphitia* gen. nov. by their shells, but differ, among others, by the possession of a distinct caudal horn, in many aspects of the morphology of the distal genitalia, and by the very different spermatophore morphology. *Pseudosaphitia* gen. nov. and *Vanmolina* gen. nov. have distinctly smaller and differently sculptured shells, as well as different soft parts morphologies.

The shell of *Thapsia* species can continue to grow for at least half a whorl more after the animal has reached sexual maturity. Therefore adult shell size per se is not a very good character for species recognition without taking the number of whorls into account.

Hardly any information of the soft anatomy of true *Thapsia* species has been published. Pfeffer's (1883) brief account of "*Thapsia troglodytes*" from Bonjongo, Cameroon, apparently constitutes the only – rather incomplete – anatomical description of a true *Thapsia* species in the existing literature. Watson's (1934) observations of "*Thapsia troglodytes*" from the Gold Coast (Ghana), Verdcourt's (1982) description and illustration of the genital anatomy of an unnamed species from Togo, and Schileyko's (2002) account of "*Thapsia pellucida* Gould, 1843" from Côte d'Ivoire relate to a genus that is described

below as *Saphtia* gen. nov. Schileyko's (2002) notes were intended as a kind of definition of the genus *Thapsia*, but the anatomical data provided do not refer to the same genus as the depicted shell of "*Thapsia troglodytes*" [sic!] from Fernando Poo, which is a species of true *Thapsia* indeed. Baker's (1941: 212) observations on "*Thapsia troglodytes* (Morelet), approaching *T. pellucida* (Gould), from near Tringa, Lake Nyassa", refer to a different genus not dealt with in the present paper.

Schileyko (2002) incorrectly attributed the authorship of *Thapsia* to Von Martens, who was editor of the second edition of Albers' book. Von Martens (1860: iv) clearly indicated that the authorship of most new taxa in the book is attributable to Albers, these being described in the manuscript he received from Albers' widow. To these new (sub)genera the name of Albers was added as author in the heading, in agreement with article 50.1 of the ICZN (1999).

Thapsia troglodytes (Morelet, 1848)

Helix troglodytes Morelet, 1848: 351 "in Guinea provincia Gabon". Morelet, 1858: 11, pl. 1 fig. 1 (shell). 3 syntypes BMNH Reg. No. 1893.2.4.993-5.

?*Helix troglodytes* [sic!], Petit de la Saussaye, 1852: 67, pl. 1 figs 14-16 (shell). "La côte du Gabon".

Remarks. — The syntype series of *T. troglodytes* in the BMNH consist of three shells, the largest of which is marked as "potential lectotype", probably by Connolly, but a type designation appears not to have been published. The type locality is rather imprecise (Morelet, 1848: "in Guinea provincia Gabon"; Morelet, 1858: "... Gabon, à quelque distance du littoral..."), so that it is not possible to collect fresh specimens at the type locality. This is especially unfortunate since anatomical and conchological variation among the Gabonese populations studied strongly suggests the presence of various species, of which two will be described below. The exact provenance of the type shells is unlikely to be far from the coast, where the French had settlements/fortifications as early as 1846, when M. de Folin collected the type specimens (Morelet, 1858). The type series could even belong to two different species, given differences in shell characters (table 1). The largest of the three syntypes has fewer whorls, a more depressed spire (and consequently a wider aperture), and a more strongly angulate periphery than the other two, which are more similar in these respects. Still, size, outline and sculpture of all three shells fall within the range of variation known for other *Thapsia* populations, and I was unable to match shells of recently collected Gabonese specimens unequivocally with any of the type shells.

The anatomy of the type species of *Thapsia* thus remains unknown. However, there appears to be no urgent need to know the anatomy of the type species for defining the genus. None of the dissected specimens with large shells and decussate sculpture from various localities in northern, central and southern Gabon anatomically resemble species of *Saphtia* gen. nov. (see below) or other helicarionoid *Thapsia*-like genera described from outside the area under study. Species conchologically similar to *Thapsia*, but belonging to *Saphtia* were not found among dozens of such speci-

Table 1. Dimensions of syntypes of *Helix troglodytes* Morelet, 1848 in The Natural History Museum, London (1893.2.4.993-5).

	D	H	W	H/D
Syntype 1	24.9	15.5	6½	0.62
Syntype 2	26.4	14.4	5¾	0.55
Syntype 3	23.1	14.5	6	0.63

mens and populations examined from Cameroon either. In fact, *Saphtia* species with large, *Thapsia*-like shells with decussate sculpture (unlike smaller-shelled *Saphtia* species) have so far not been found east of Togo, whilst specimens anatomically confirming to true *Thapsia* have not yet been found west of Cameroon (De Winter, unpublished observations). It seems therefore most likely that the soft parts of the type specimens of *Thapsia* resembled those described below for two species from Cameroon and Gabon. Should a species conchologically similar to, but anatomically distinct from, *Thapsia* as taken here, be discovered in the coastal regions of Gabon, a neotype for *T. troglodytes* may need to be designated, in which case the ICZN should be requested to invalidate the syntype series. The diversity of *Thapsia* will be further explored in later papers (De Winter, in prep.).

Thapsia ebimimbangana spec. nov.
(figs 1-11)

Material.— **Holotype:** [sta. CAM.132] Cameroon, Sud Province, *Chromolaena odorata*-covered fallow land close to the village of Ebimimbang, 3°02.8'N, 10°26.1' E, alt. ~ 70 m, 30.v.1996, A.J. de Winter & E.-J. Semengue leg. (RMNH.MOL.110333, shell dry, soft parts in alcohol). **Paratypes** (all paratypes were collected less than 2 km to the south of the type locality by A.J. de Winter & E.-J. Semengue): [sta CAM.046] Locus typicus, 12.x.1995 (RMNH.MOL.110334/ 1 adult, shell dry, soft parts in alcohol; MRAC/ 1 specimen in alcohol). [sta. CAM.50a] Undisturbed high forest on slope ~ 1 km WSW of Saa, 3°03'N, 10°26'E, alt. ~ 70 m, 17.x.1995, crawling on tree trunk (RMNH.MOL.110335/ 1 juv. specimen in alcohol). [sta. CAM.130a] Undisturbed swamp forest near Ebimimbang, 3°02.8'N, 10°26.1'E, alt. ~ 70 m, 30.v.1996, in understory vegetation (RMNH.MOL.110336/1 adult, shell dry, soft parts in alcohol). [sta. CAM.113a] Young secondary forest on south bank of the Lokoundjé River, close to Ebimimbang, on palm 1.5 m above forest floor, 3°02.1'N, 10°28.1'E, alt. ~ 70 m, 23.v.1996 (RMNH.MOL.110337/ 1 adult, shell dry, soft parts in alcohol, 1 juv. in alcohol). [sta. CAM.040] Patch of young secondary forest among *Chromolaena odorata*-covered fallow land close to the village of Ebimimbang, 3°02.8'N, 10°26.1'E, alt. ~ 70 m, 10.x.1995 (RMNH.MOL.110338/ 1 adult, shell dry, soft parts in alcohol. [sta CAM.43a] Undisturbed high forest on flat terrain ~ 1 km WSW of Saa, 3°03'N, 10°26'E, alt. ~ 70 m; 11.x.1995, in understory vegetation (RMNH.MOL.110339/ 1 (semi)adult specimen in alcohol). [no station number] *Chromolaena odorata*-covered fallow land close to the village of Ebimimbang, 3°02.8'N, 10°26.1'E, alt. ~ 70 m, 25.v.1996; pair in copula (RMNH.MOL.110340/ 1 specimen, shell dry, soft parts in alcohol; second specimen intact in alcohol).

Diagnosis.— Distal portion of penis rather short, about one fifth of length of proximal penis, with 2 or 3 strong pilasters on inner wall. Spermatophore large, tail with about 13 long, asymmetrically (unilaterally) branched spines, individual spines split in up to 5 minor (second order) spines.

Shell (fig. 1).— Thin and fragile, partly translucent, yellowish-brown, periphery weakly angulate, whorls moderately convex, spire low-conical. Aperture roundish-oval, height/width ratio ~ 0.8. Sculpture as described for genus. Size: D = 24-27 mm, H = 14-17 mm, H/D = 0.55-0.64, W = 6-6½ (n = 14).

Cephalopodium (figs 2-6).— Anterior part of cephalopodium (head to mantle rim) dark-greyish, becoming paler towards tail. Other details as described for genus.

Pallial region (fig. 7).— Both right and left shell laps well developed, left shell lap slender and more elongate than right one. Pallial cavity takes up about 0.8 whorls. Pallial roof well vascularized, densely pigmented by small and larger blackish spots not coalescing into a band. Kidney about 20 mm long, slender, hardly flaring posteriorly, less

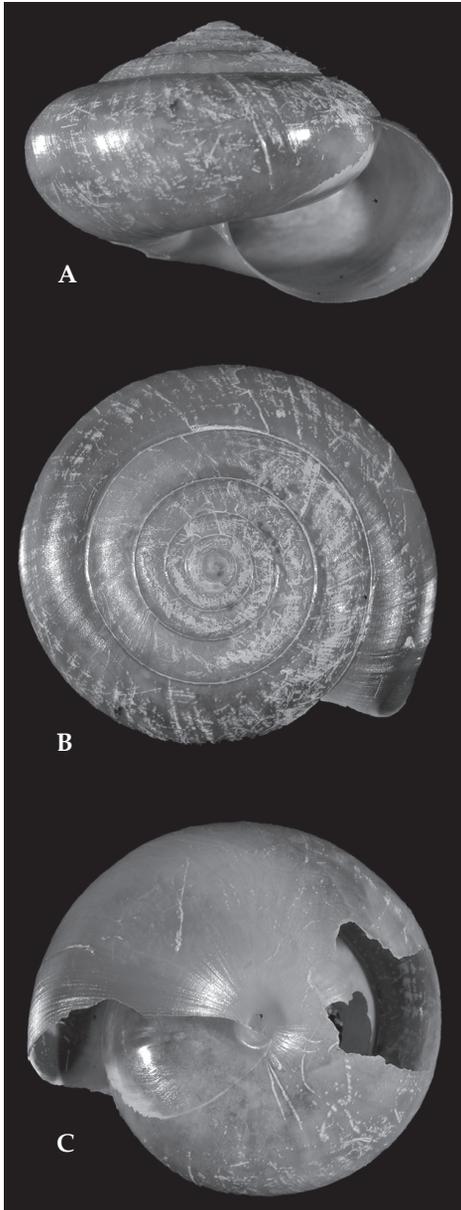


Fig. 1. *Thapsia ebimimbangana* spec. nov.; A-C, different views of holotype shell (RMNH). Actual shell width 24.5 mm.



Fig. 2. *Thapsia ebimimbangana* spec. nov., pair in copula on Araceae leaf. Cameroon, Ebimimbang (paratypes in RMNH).

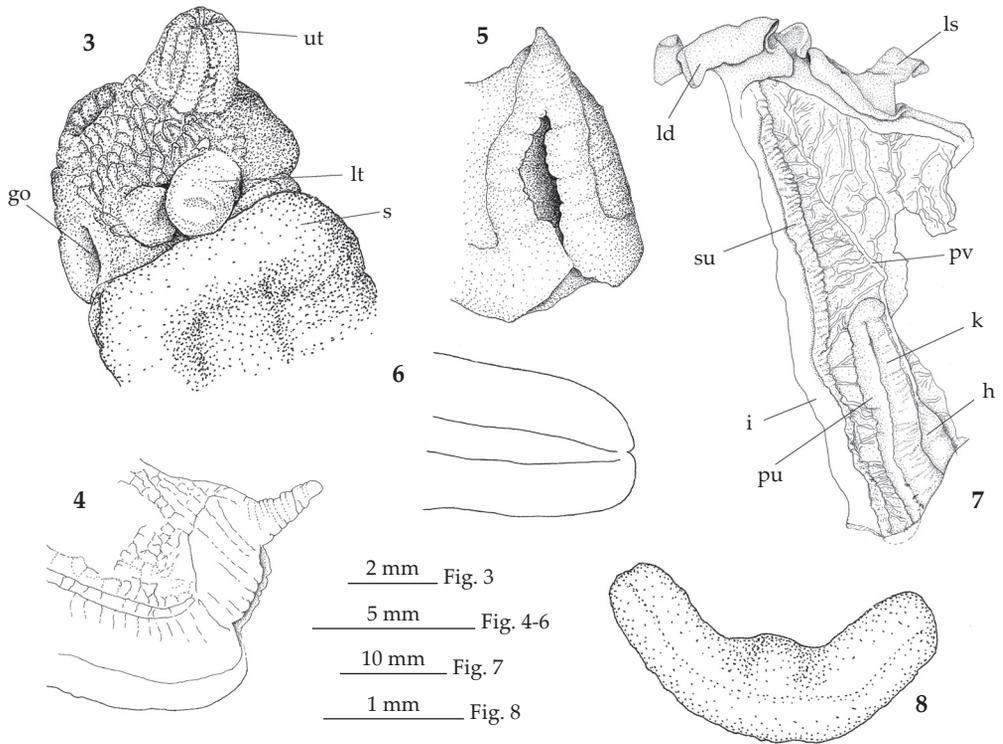
than half the length of pallial cavity. Pericardium about one third of kidney length.

Jaw (fig. 8).— Oxygnathous, pale brown, about 2.5 mm wide, with a short median projection.

Radula (fig. 9).— Teeth rather elongate. Formula (half a row) R ~ 26 - ? Due to folding of radula marginal teeth were not countable, but well exceeding number of laterals. Central tooth little smaller than flanking laterals, mesocone of central tooth moderately elongate, clearly longer than basal plate. Ectocones of marginal teeth much larger than endocones. Transition of laterals into marginals gradual, endocone disappearing at about the 26th lateral.

Reproductive organs (fig. 10).— Atrium longer than wide, internally with 3-4 coarse longitudinal pilasters below the distal penis and many more fine plicae extending from the vagina; this bipartite atrium division is already discernable without further dissection. Upper atrium attached to (internal) body wall by strong, muscular strands of tissue. Penis (between

atrium and epiphallic caecum) about 20 mm long, bipartite, portions very unequal in length. Distal penis rather short, thin-walled, internal lumen spacious, with few and prominent vertical pilasters and a short, papilla-like structure at transition to proximal penis. Proximal penis rather long, about five times longer than distal portion, thick-



Figs 3-8. *Thapsia ebimimbangana* spec. nov. 3, head and anterior sole, frontal view. (paratype, RMNH). 4, tail, lateral view (paratype, RMNH). 5, caudal view of tail (paratype, RMNH). 6, posterior part of sole (paratype, RMNH). 7, ventral (interior) view pallial region (paratype, RMNH). 8, jaw (paratype, RMNH).

walled and muscular, gradually tapering towards the epiphallic caecum, internal wall around narrow lumen with about 6 somewhat irregularly fringed longitudinal ridges. Epiphallic caecum small, ovate, diameter not exceeding width of epiphallus, thin-walled. Penial retractor muscle long and slender, inserting on caecum and originating from columellar muscle complex. Epiphallus much shorter than proximal penis. Flagellum slightly shorter than epiphallus, little convoluted, thick-walled and muscular. Internal glandular wall of flagellum surrounded by thick outer layer of muscular tissue. Vas deferens little convoluted along its entire course, last portion before entering epiphallus somewhat widening. Upper penis connected to epiphallus and part of vas deferens by tissue fibres (not shown in drawing). Vagina close to atrium thin-walled and slender, internal wall with few stronger longitudinal ridges and finer ones in between. More proximally, at junction of bursal duct, vagina strongly swollen, thick-walled and muscular, attached to internal body wall by strong muscles. Lumen of swollen portion of vagina narrow, with deep crypts on one side; the thick inner stratum may be glandular. Free oviduct branches off at about widest portion of vagina, and more proximally becomes wide and seemingly glandular (capsular gland). Duct of bursa

copulatrix thick-walled and muscular close to vagina, wall thickness becoming much less towards bursal sac. Bursal sac very voluminous in specimens containing a spermatophore.

Spermatophore (fig. 11).— Ampulla about 16 mm long and at most 2.0 mm wide. Tail length about 25 mm. Transition of ampulla into tail marked by a sharp curve, a collar of about 10 coarse thorns pointing away from the ampulla and a single small denticle just anterior of thorn collar. A longitudinal row of simple, initially erect, spines follows a short, spineless section posterior of collar. After four spines, there is a second parallel row of 13 much longer spines. First and smallest of these spines with one or two incisions, the following increasing in length to about 2.5 mm, asymmetrically branched into up to 5 minor (second order) spines; last two spines in this row shorter and simpler than preceding ones. One long spine in one spermatophore (out of three spermatophores examined) has an extra, dichotomous split resulting in 7 minor spines; this is probably an aberration. Simple spine row extends farther posterior on tail than branched spines, these spines gradually change in aspect from erect or slightly bent to distinctly curved. Last portion of tail with three parallel longitudinal rows of simple, tiny spinules, arranged spirally around tail axis towards hind tip.

Ecology.— This species occupies a wide range of habitats: from undisturbed high forest to fields (established by slash and burn practices) and fallow land overgrown by the non-native bush *Chromolaena odorata*. In forests, adults and large juveniles were nearly always found rather sparsely on the forest floor or crawling a few meters high on the bark of tree trunks after rain; live small juveniles were collected in larger numbers exclusively on both green and dead leaves in the understory vegetation 1-3 m above the floor.

Etymology.— The name is derived from the village of Ebimimbang, close to the type locality. The epithet *ebimimbangana* is to be used as a noun in apposition.

Remarks.— *Thapsia ebimimbangana* differs from *T. wieringai* spec. nov. by a higher, larger and less strongly angulate shell, a much shorter distal penis, and by a larger spermatophore with more numerous, longer and more strongly branched spines. These

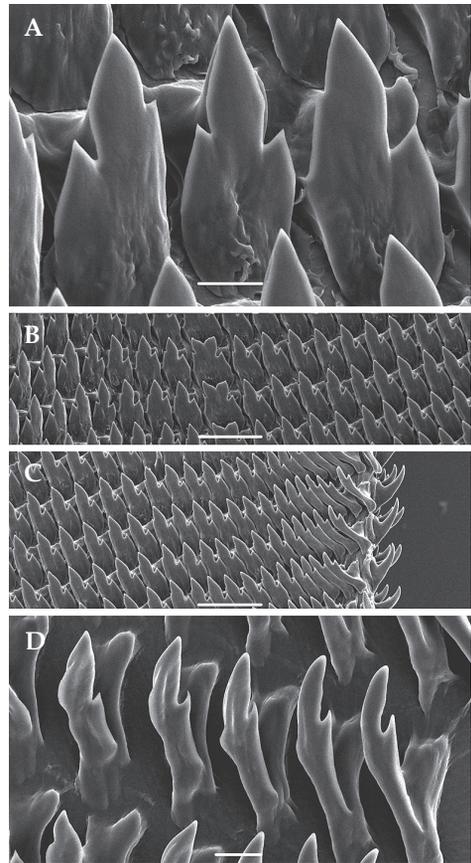


Fig. 9. *Thapsia ebimimbangana* spec. nov., radula (paratype, RMNH); A, central tooth and first laterals; B, early lateral teeth; note aberrant fourth lateral; C, transition of laterals into maginals; D, transitional teeth and first marginals. Scale bars: A, D = 10 μ m; B, C = 50 μ m.

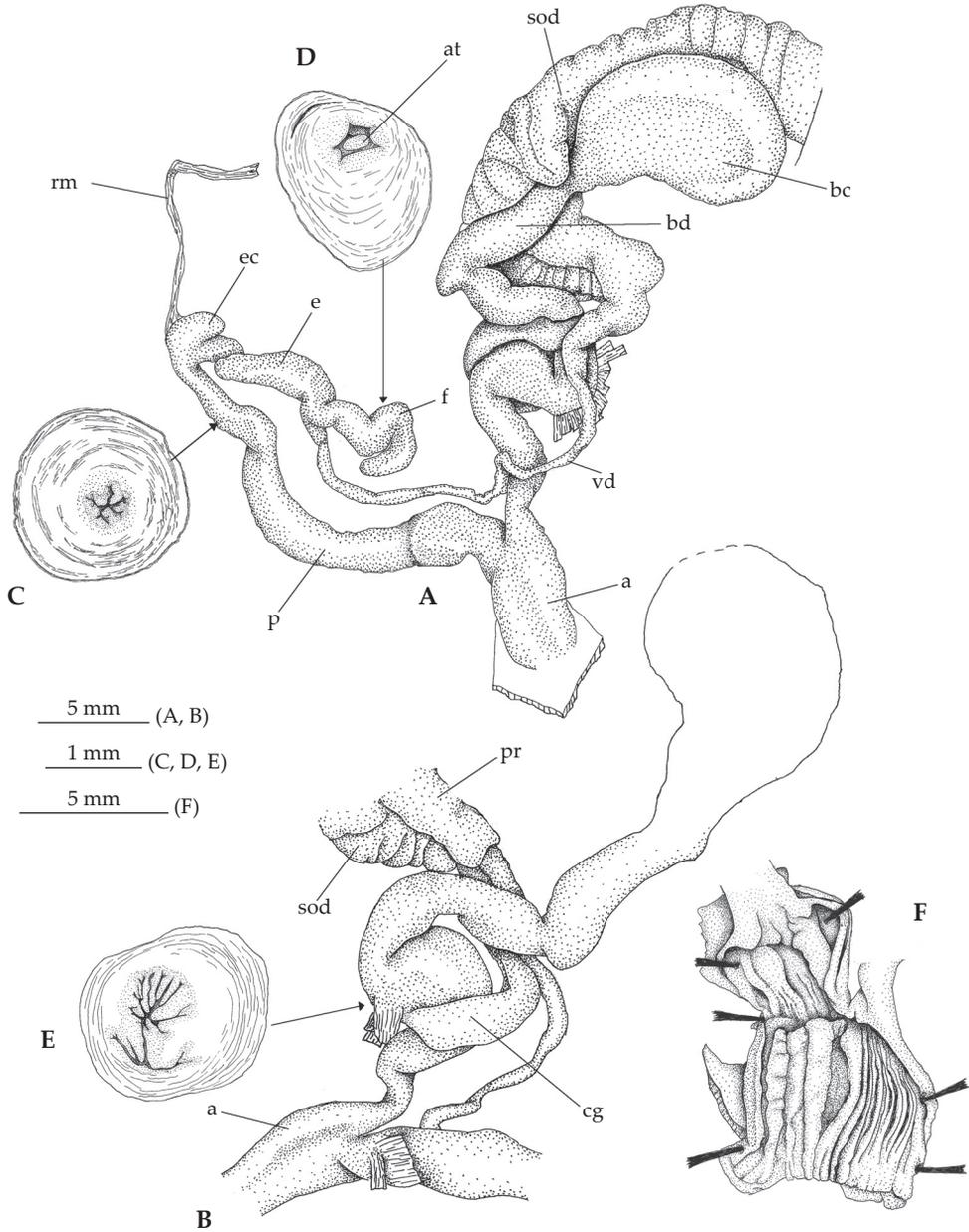


Fig. 10. *Thapsia ebimimbangana* spec. nov., distal genitalia (paratype, RMNH); A, organs approx. in situ, with spermatophore in bursa copulatrix; B, different view of A, organs dislodged, spermatophore removed; C, cross-section proximal penis; D, cross-section flagellum; E, cross-section widened portion of vagina; F, internal morphology of atrium and lower penis. Arrows indicate position where cross-sections are made.

two species are described as new since their provenance is sufficiently far from the surmised coastal Gabonese origin of the type shells of *T. troglodytes* (see above).

The description of the anatomy of "*T. troglodytes*" by Pfeffer (1883) is too imperfect to be of much use. Pfeffer (1883) dissected material from Bonjongo, Cameroon that he had received from the Berlin museum. Von Martens (1876) reported and described as "*Nanina troglodytes* Morelet" material from the same locality, and all this material was probably part of the same lot, collected by Buchholz. Pfeffer possibly dissected the same specimen of which Von Martens (1876) illustrated the tail (von Martens, 1876, pl. 1 figs 9b, 9c). Unfortunately no alcohol-preserved material could be found in Berlin. When distinct, this species should bear the name *Thapsia buchholzi* Bourguignat, 1885, Bourguignat's description being based on the illustration of the shell in Von Martens (1876, pl. 1, fig. 9). Bourguignat (1885) erroneously located the type locality in Mozambique.

No other true *Thapsia* species appear to have been formally described so far.

Thapsia wieringai spec. nov.
(figs 12-15)

Material.— **Holotype**: Gabon, Région Woleu-Ntem, Monts de Cristal, 1 km SE. of Tchimbélé, 0°36.9'N 10°23.8'E, ca. 600 m alt., J.J. Wieringa leg., 17.ix.1994 (RMNH.MOL.110341/ shell dry, soft parts in alcohol). **Paratypes** (all material collected by J.J. Wieringa): same data as holotype (RMNH.MOL.110342/ 1 juv. specimen in alcohol). 0.5 km SW. of Tchimbélé, 0°37'N 10°24'E, primary rainforest, 16.v.1990 (RMNH.MOL.110343/ 1 specimen in alcohol). Tchimbélé, 0°37'N 10°24'E, 18.v.1990 (RMNH.MOL.110344/ 1 dry shell). Tchimbélé, 0°37'N 10°24'E, 28.ii.1990 (RMNH.MOL.110345/ 1 dry shell). Around Tchimbélé, collected between 14.xii.1989 and 26.i.1990 (RMNH.MOL.110346/ 2 subadult specimens in alcohol, 1 shell dry collection, soft parts and specimen with damaged shell in alcohol (ex colln. De Winter 8142); (RMNH.MOL.110347/ 1 adult, shell dry, soft parts in alcohol (ex colln. De Winter 8815). Tchimbélé, primary rainforest, 27.i.1990

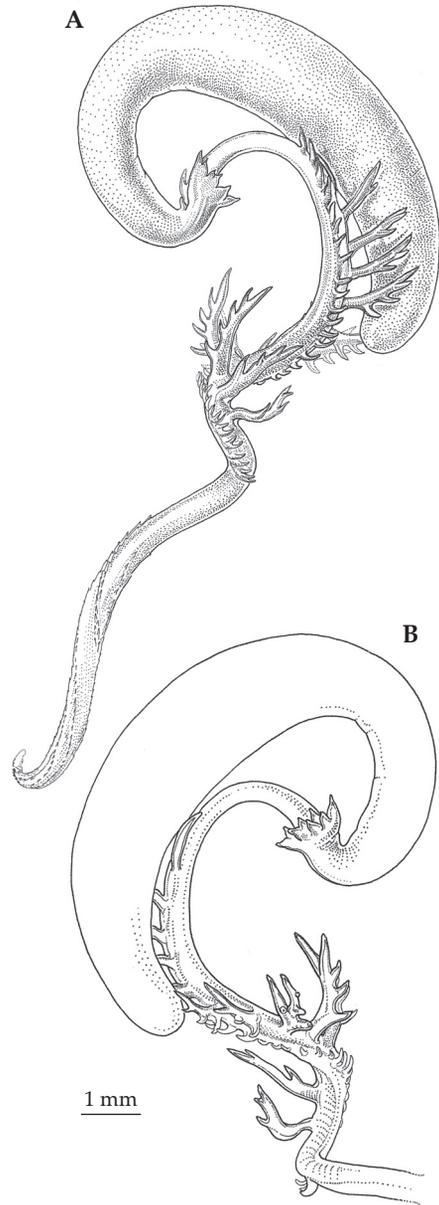


Fig. 11. *Thapsia ebimimbangana* spec. nov., different views of spermatophore from bursa copulatrix of paratype (RMNH).

(RMNH.MOL.110348/ 1 adult, shell dry, soft parts in alcohol (ex colln. De Winter 8140). 1 km ESE. of Tchimbélé, 0°37'N 10°25'E, ca. 600 m alt., primary rainforest, 15.v.1990 (RMNH.MOL.110349/ 1 adult, shell dry, soft parts in alcohol (ex colln. De Winter 8813). Tchimbélé, *Pinus* plantation, 0°37'N 10°24'E, alt. 570 m, 26.iv.1990 (RMNH 97613, 1 adult specimen, shell dry, soft parts in alcohol) (ex colln. De Winter 8141). 0.5 km SW. of Tchimbélé, 0°37'N 10°24'E, alt. 600 m, primary rainforest, 24.iv.1990, pair in copula (RMNH.MOL.97611/ 1 specimen shell dry, soft parts in alcohol, other specimen with damaged shell in alcohol). 2 km SSW. of Tchimbélé, 0°36.5'N 10°23.8'E, alt. 440 m, 26.i.2005 (RMNH.MOL.110350/ 1 adult, shell dry, soft parts in alcohol).

Diagnosis.— Shell periphery more or less angulate in front view. Distal portion of penis about equally long as proximal portion. Spermatophore tail with comparatively few spines, only about 7 of which are long and branched into 2-4 minor (second order) spines.

Shell (fig. 12).— Rather thin and fragile, partly translucent, yellowish-brown but very fresh specimens often with a subtle purplish hue. Periphery of last whorl strongly angulate, except for about the last ¼ whorl which is more rounded (but often still distinctly angular, especially in smaller adult shells). Spire depressed-conical with comparatively flat whorls. Aperture oval-lunate, height/width ~ 0.7. Sculpture as described for genus. Size: D = 21.5-26.0 mm, H = 12.9-15.4, H/D = 0.54-0.62, W = 5.5-6 mm (n = 7).

Cephalopodium.— Anterior part of cephalopodium (head to mantle rim) more or less dark-grey, becoming paler towards tail. Caudal appendage rather long, darker than rest of tail.

Pallial region.— Pigmentation quite variable; either consisting of distinct, small blackish spots not coalescing into a band, or more diffuse brownish pigmentation extending over most of the pallial roof, except for the portion above the strikingly white kidney.

Jaw.— Not examined.

Radula.— Not examined.

Reproductive organs (figs 13-14).— Atrium rather slender, internally with fine, irregular longitudinal ridges. Proximal and distal portion of penis about equally long, entire penis length (between atrium and epiphalliac caecum) about 20 mm. Distal penis almost twice as wide as

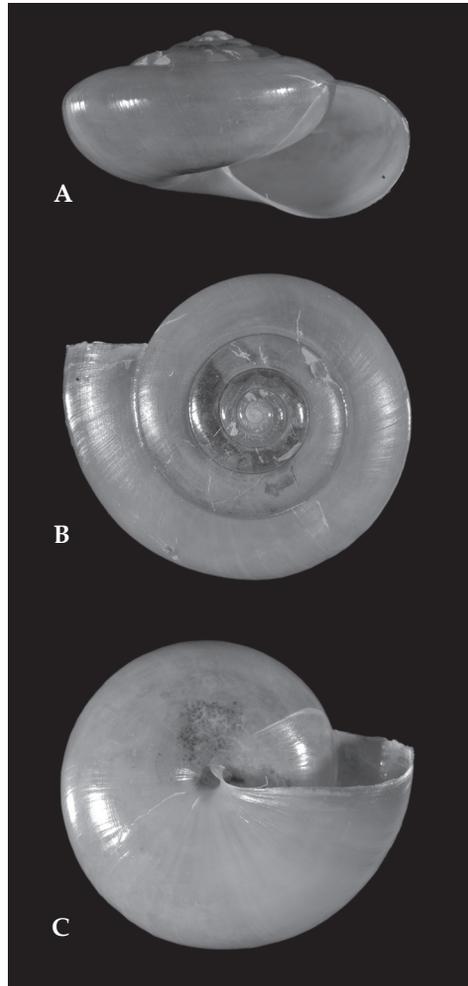


Fig. 12. *Thapsia wieringai* spec. nov.; A-C, different views of holotype shell (RMNH). Actual shell width 23.8 mm.

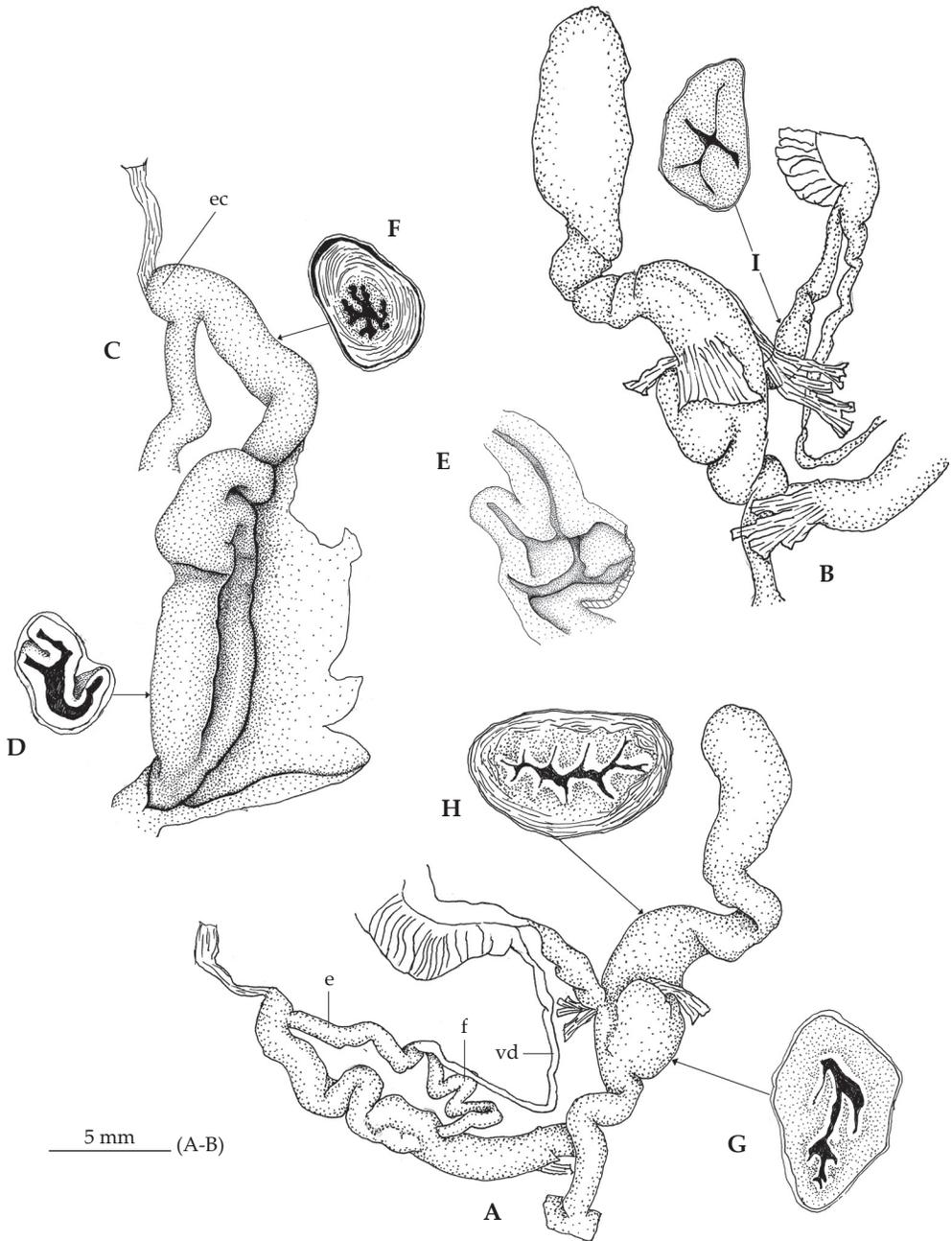


Fig. 13. *Thapsia wieringai* spec. nov., distal genitalia (paratype, RMNH); A-B, different views intact organs; C, penis with penial sheath opened; D, cross-section distal penis; E, longitudinal section transition distal to proximal penis; F, cross-section proximal penis; G, cross-section widened portion of vagina; H, cross-section bursal duct; I, cross-section proximal free oviduct (capsular gland). Arrows indicate position where cross-sections are made.

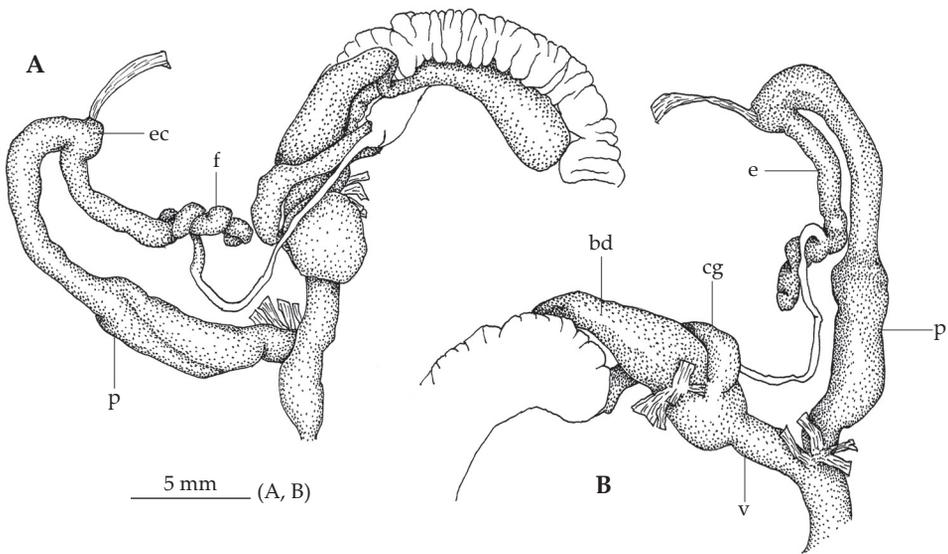


Fig. 14. *Thapsia wieringai* spec. nov., A-B, distal genitalia of paratype (RMNH).

proximal penis, wall of distal penis with deep longitudinal invaginations (externally discernable through the penial sheath), internally resembling strong pilasters. Transition of distal to proximal penis more or less abrupt, with internally a kind of penial papilla. Proximal penis not strongly tapering towards epiphallic caecum, rather muscular and thick-walled, lumen narrowed by fine irregularly fringed longitudinal ridges and tubule-like structures. Epiphallic caecum rather small and inconspicuous. Penial retractor muscle inserts on epiphallic caecum; its point of origin appears to vary between individuals: either the diaphragm, or the columellar muscle complex. Epiphallus somewhat shorter and less wide than proximal penis. Flagellum strongly convoluted, about as long and wide as epiphallus. Vagina distinct, slender distal portion internally with 3-4 rather irregular longitudinal ridges that become more prominent further proximally, with fine irregular plicae in between. Vagina strongly swollen at junction with bursa copulatrix, both externally and on cross-section not appearing muscular, separated from the muscular distal portion of bursal duct by a shallow depression just proximally of where the proximal free oviduct continues; strong strands of muscular tissue from this constriction attach vagina and adjoining bursal duct to the internal body wall. Bursal duct distally rather wide and muscular, somewhat laterally flattened (rather than bulbous) with narrow lumen, internal wall with strong longitudinal ridges; more proximally bursal duct strongly tapering towards the wide bursal sac.

Spermatophore (fig. 15).— Ampulla elongate-oval, about 13 mm long and at most 1.5 mm wide, not convoluted. Tail collar with about 8 coarse, incised thorns, preceded by a single, small inconspicuous denticle. Tail about 24 mm long, ornamented by a row of 4 simple erect spines, followed by 7 long, branched spines, with partly parallel to these a second short longitudinal row of 5 simple, curved spines. Largest, most complex, spine about 1.4 mm long, branched into 4 minor spines. Posterior portion of tail

comparatively straight with three parallel longitudinal rows of simple, tiny spinules. Terminal opening of tail canal simple.

Ecology.— This species was found on the forest floor as well as in the understorey, but the collector did not differentiate between adults and juveniles. The habitat was mostly primary rainforest at around 600 m elevation, but some specimens were also collected in a pine tree (*Pinus* sp.) plantation.

Remarks.— This species differs in various aspects from *T. ebimimbangana*, most conspicuously by the generally smaller, more depressed adult shell with fewer whorls, in proportions and internal morphology of distal and proximal penis, and in the much less elaborate ornamentation of the spermatophore. Many adult specimens, especially the small-shelled ones, have a strongly angulate shell periphery. This may be a paedomorphic character, juvenile *Thapsia* shells are invariably strongly keeled, and sexually mature specimens have not necessarily reached their maximum shell size.

Specimens from the pine tree plantation seemed to possess a shell slightly differently coloured as compared to the ones collected in rainforest (dull brown, without purplish hue), but no significant anatomical peculiarities could be detected, and all are considered to be conspecific.

Etymology.— The species is named after Dr Jan Wieringa, who spent months in the forests around Tchimbélé studying the flora, and collected a considerable number of snails, among others this *Thapsia* species.

Saphtia gen. nov.

Type species.— *Saphtia granulosa* spec. nov.

Diagnosis.— Fully shelled helicarionoid with poorly developed caudal horn, a long verge inside the distal penis and a muscular ring on the distal vagina. Spermatophore ampulla elongate and convoluted, tail with short, unbranched spines; margin of tail canal opening reflected and incised.

Description.— Adult shell diameter between 15 and 25 mm, very thin and fragile,

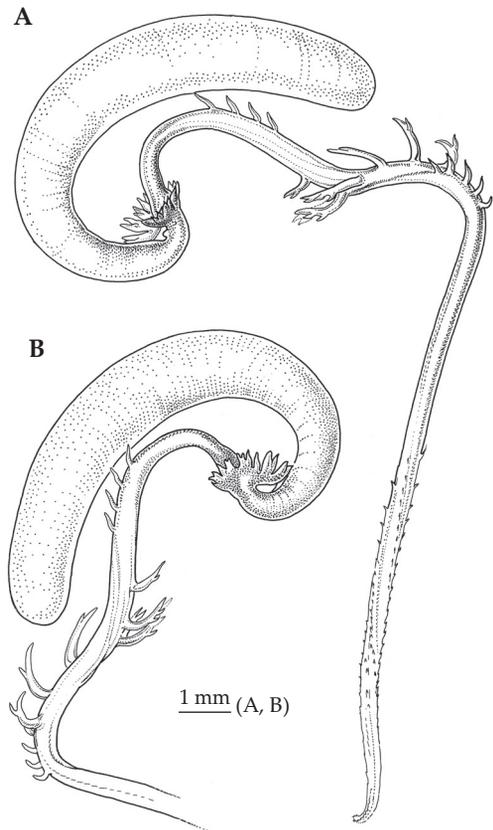


Fig. 15. *Thapsia wieringai* spec. nov., A-B, different views of spermatophore from bursa copulatrix of paratype (RMNH).

wider than high, periphery of adult shell rounded to distinctly keeled. Postembryonic sculpture of shell either decussate-granulose (large species) or consisting of fine spiral lines only. When present, decussate sculpture extends to shell base. Sole tripartite. Caudal horn above caudal foss poorly developed. Distal portion of penis comparatively wide, containing long verge. Epiphallic caecum globular and conspicuous, at least as wide as epiphallus diameter. Epiphallus and flagellum well developed. Flagellum contains axial thread. Penis retractor inserts on epiphallic caecum. Vagina close to atrium partly surrounded by well-demarcated, swollen muscular band. Free oviduct proximally of junction with bursa copulatrix (capsular gland) distinctly widened and thick-walled. Spermatophore rigid, pale-yellowish, with an elongate, convoluted sperm ampulla, followed by a long, narrow, convoluted tail; tail with two spirally arranged rows of simple spines that decrease in size towards posterior tip. Opening of narrow tail canal with disc-like reflected and partly incised margin, resulting in a flower-like appearance.

Remarks. — Large *Saphtia* species can conchologically be very similar to *Thapsia*, but in such coarse-sculptured *Saphtia* shells, the decussate sculpture extends to the shell base, in contrast to the *Thapsia* species examined so far. However, any identification to genus level should preferably be verified by soft part characters. The shell characters of helicarionoids are of such a generalized nature that they are of limited taxonomic value and only apply in a limited geographical area; in view of the poor knowledge of western African helicarionoids, the possibility of additional radiations with similar shells cannot be excluded.

Etymology. — *Saphtia* is an anagram of *Thapsia*, pointing to the conchological resemblance between both genera.

Saphtia granulosa spec. nov.
(figs 16-22)

Material. — **Holotype**: Côte d'Ivoire, Forêt de Banco near Abidjan (no coordinates or other locality information on label), J.J. Van Mol leg., viii.1968 (MRAC 795.167, shell and dissected soft parts). **Paratypes**: same data as holotype (MRAC MRAC 302.305/ ca. 35 undissected paratypes; RMNH.MOL.110351/ 1 specimen, soft parts in alcohol, shell dry; RMNH.MOL.110353/ 4 damaged or juvenile shells. Côte d'Ivoire, Banco National Park, ~ 5°25'N, 4°03'W, alt. 100 m, closed forest, J.J. Wieringa leg., 1.ix.2001 (RMNH.MOL.110352/ 1 juvenile specimen in alcohol).

Other material: Secondary forest near Adiopodoume, 5°12'N, 4°04'W; T. Bongers leg (RMHN.MOL. 110354/ 1 dry shell).

Diagnosis. — Shell diameter about 22-25 mm, low-conical, with strongly angulate periphery. Postembryonic whorls with distinct, comparatively coarse, decussate-granulose sculpture that extends to shell base. Mantle and pallial roof almost without dark pigmentation. Distal penis rather bulbous. Spermatophore large with comparatively coarse spines on tail, reflected margin of tail opening with deep incisions.

Shell (figs 16-17). — Comparatively large, pale yellowish-brown, thin, brittle, low-conical, wider than high. Whorls little convex. Periphery strongly angulate, apart from the rounded last ¼ whorl. Aperture oval-lunate. First half whorl smooth, following two whorls with fine spiral lines, thereafter sculpture finely decussate, gradually becoming coarser towards aperture, giving a somewhat granulose appearance. Decussate sculp-

ture extends over periphery to shell base, becoming finer and less conspicuous towards the umbilicus. Sculpture noticeably finer near upper suture than near lower suture. Umbilicus narrow, but open. Size (adult specimens): D = between 22 and 25 mm, H = 12-14, H/D = 0.54-0.59, W = 5-5¼ (n = 5).

Cephalopodium (fig. 18).— Colour uniformly pale (tentacles and dorsum included), length in fully relaxed preserved specimens about 50 mm. Tail (in preserved specimens) longer than anterior portion, somewhat laterally compressed, dorsum rounded. Genital opening slightly posterior to right lower tentacle. Area between ommatophores covered by close-set tubercles. Caudal horn poorly developed. Caudal foss long vertical slit. Sole tripartite, anteriorly fields about equal in width, posteriorly central field markedly narrower than outer fields.

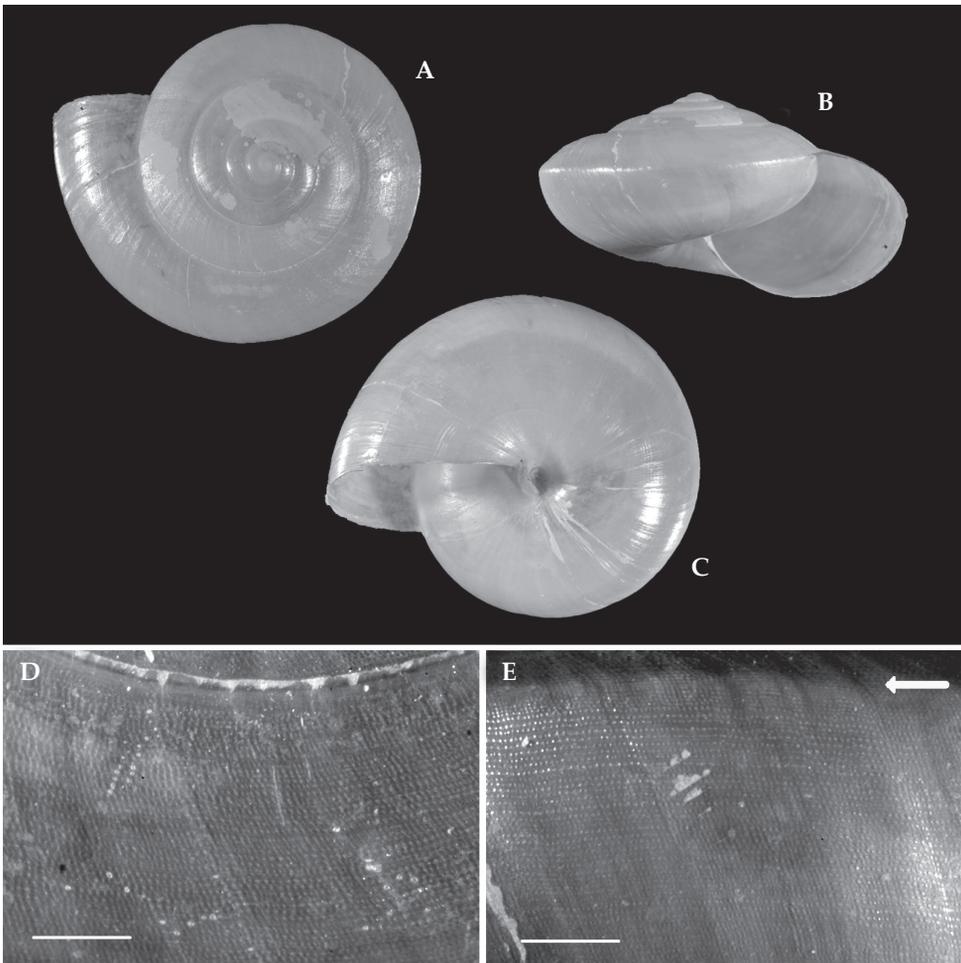


Fig. 16. *Saphtia granulosa* spec. nov., holotype shell (MRAC). A-C, different views of shell (actual shell width 22,4 mm); D, sculpture on penultimate whorl; E, sculpture just below shell periphery (periphery indicated by arrow) (scale bar D, E = 5 mm).

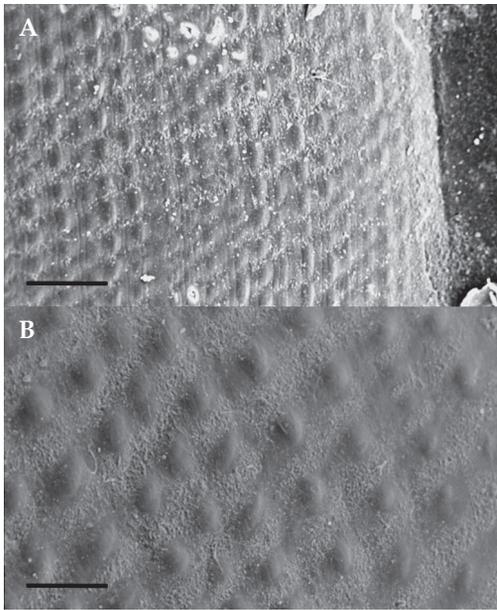
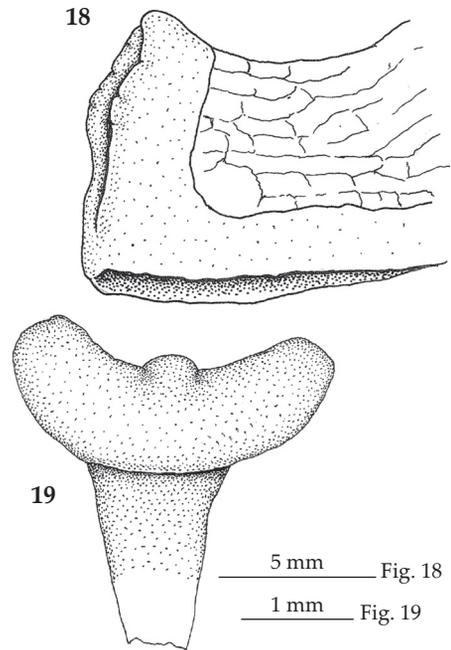


Fig. 17. SEM photographs of shell sculpture (paratype MRAC). A, sculpture on third whorl close to lower suture; B, sculpture central part last (fifth) whorl (scale bar A-B = 100 μ m).



Figs 18-19. *Saphtia granulosa* spec. nov. (paratype, MRAC). 18, lateral view of tail. 19, jaw.

Pallial region.— Both right and left shell laps well developed, left shell lap more elongate than right one. Pallial cavity takes up about half a whorl. Mantle and pallial roof pigmentation limited to some brownish pigment around blood vessels and above kidney. Even in a comparatively fresh alcohol-preserved specimen there are only few, small blackish spots.

Jaw (fig. 19).— Oxygnathous, reddish brown, about 2.7 mm wide, with prominent median projection.

Radula (fig. 20).— Formula (half a row): R - ~ 20 - ~ 57. Mesocone of central tooth moderately elongate, slightly higher than basal plate. Ectocones of laterals much larger than endocones. Transition of laterals into marginals gradual; with one or two transitional teeth. At about the 20th lateral the endocone disappears. Marginal teeth narrower than laterals, bicuspid, with ectocone smaller than mesocone.

Reproductive organs (fig. 21).— Atrium elongate, internal wall with transverse pilasters over entire surface. Penis twisted, consisting of a wide distal portion, gradually passing into a more slender portion towards the epiphallic caecum. Distal portion of penis thick-walled and muscular, lumen with transverse strands of tissue holding tip of long verge. Proximal penis muscular, slender. Penial retractor muscle long and thin, inserting on spherical epiphallic caecum and originating from diaphragm. Epiphallus much shorter than penis. Epithelium of epiphallus lumen surrounded by a thick layer of muscular tissue. Flagellum muscular, stout, about as long and wide as epiphallus, lumen lined with smooth epithelium and containing axial thread attached to apical

end. Vas deferens strongly convoluted between prostate and penoviducal angle, portion between penoviducal angle and epiphallus comparatively straight. Duct of bursa copulatrix with muscular sheath, lumen lined with thick papillose epithelium; lumen narrowing at opening into bursal sac. Free oviduct widening proximally of junction with bursa copulatrix, with thick inner wall (capsular gland), passing into the proximal-most, more slender part of free oviduct through a conical papilla-like structure. Clumps of acini of ovotestis, separated by liver tissue, occupying first 2.5 whorls. Hermaphrodite duct wide and convoluted. Talon hidden within albumen gland.

Spermatophore (fig. 22).— The bursa copulatrix of one paratype contained an about 23 mm long spermatophore comprising an elongate, convoluted sperm-containing sac (ampulla) and a 1.5 times longer convoluted tail. Tail with longitudinal row of comparatively large, simple, spirally arranged spines, joined at about two-thirds down the tail by a second row of spines. Size of spines decreasing towards posterior tip of tail. Tail canal opening disc-like, two-thirds of reflected margin deeply incised.

Ecology.— The type locality is probably in evergreen or wet semi-deciduous lowland forest; one fresh empty shell was collected from a cultivated garden with exotic plants.

Etymology.— The epithet *granulosa* refers to the comparatively coarse beaded shell sculpture.

Remarks.— Shells of both '*Thapsia*' *africana* (L. Pfeiffer, 1850) and '*T.*' *pellucida* (Gould, 1843) conchologically resemble *S. granulosa* and, also in view of their distribution, most probably belong to *Saphtia* (De Winter, unpublished). The type shell of *Helix africana* (in BMNH) has a less sharply angulate periphery, finer sculpture, and more whorls at about the same size. Shells of '*T.*' *pellucida* have coarse granulate sculpture, but are higher and thereby more conical than *S. granulosa*, with a compressed, but less sharply angulate periphery (Johnson, 1964: pl. 37 fig. 7). The specimens reported by Petit de la Saussaye (1852: 69) from Grand Bassam (Côte d'Ivoire) as *Thapsia troglodytes* may be *S. granulosa*.

The original sample of *S. granulosa* (in MRAC) included specimens of a second, much smaller species of the same genus with a shell sculpture of fine spiral lines only.

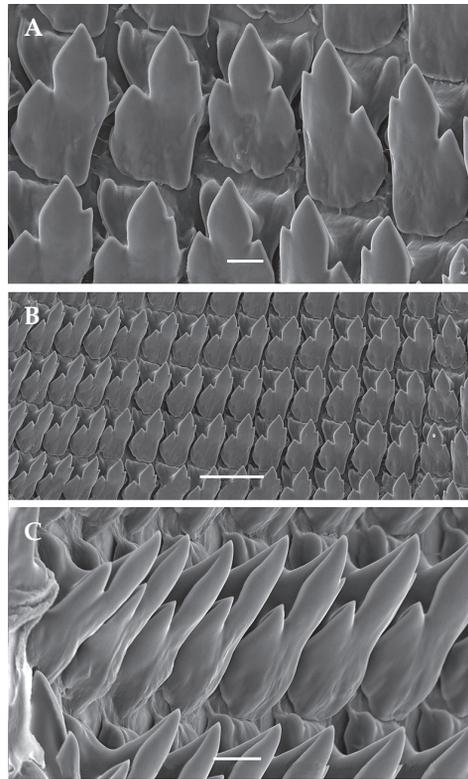


Fig. 20. *Saphtia granulosa* spec. nov., radula (paratype, MRAC). A, central tooth and first laterals (scale bar = 10 µm); B, Central tooth and lateral teeth (scale bar = 50 µm); C, transitional teeth of laterals into marginals (scale bar = 10 µm).

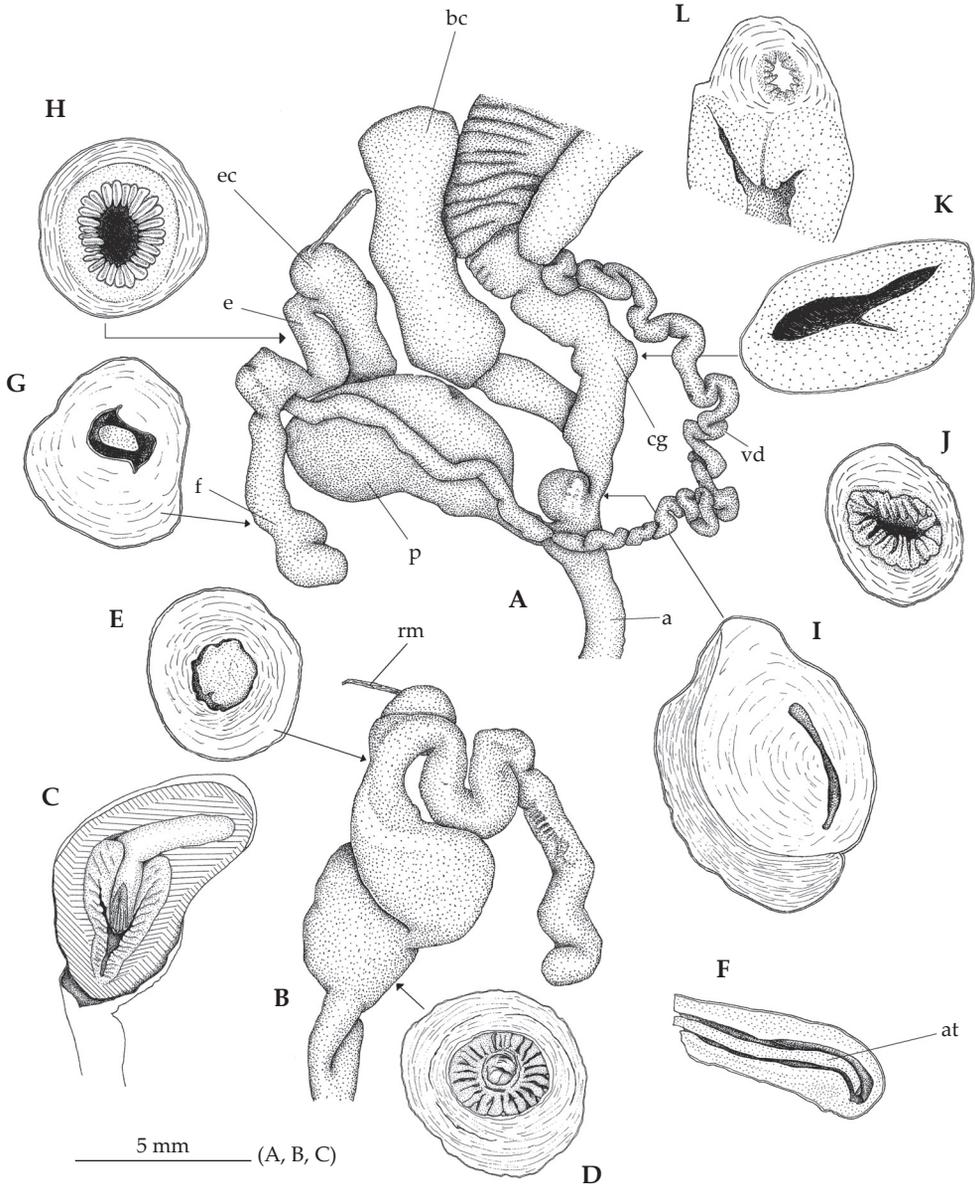


Fig. 21. *Saphtia granulosa* spec. nov., distal genitalia (paratype, MRAC); A, genitalia somewhat dislodged; B, different view of penis; C, longitudinal section distal penis; D, cross-section distal penis; E, cross-section proximal penis; F, longitudinal section flagellum; G, cross-section flagellum; H, cross section epiphallus; I, cross section vagina; J, cross section bursal duct; K, cross section proximal free oviduct (capsular gland); L, longitudinal section capsular gland. Arrows indicate place where cross sections are made.

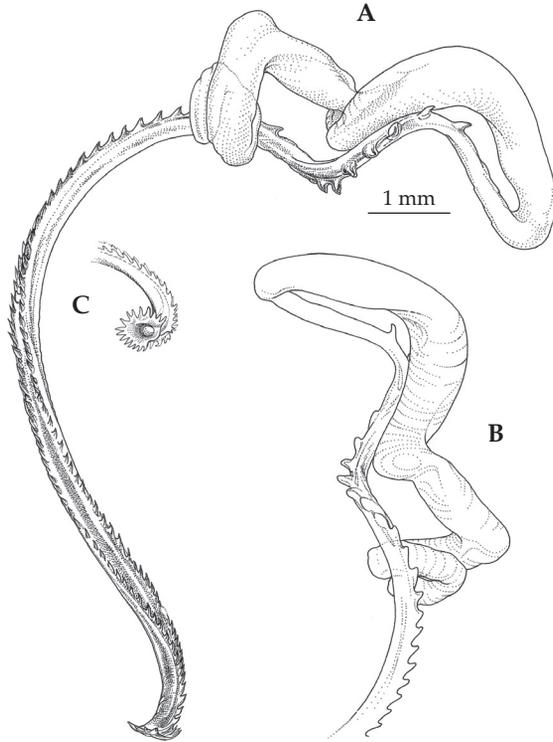


Fig. 22. *Saphtia granulosa* spec. nov., spermatophore from bursa copulatrix of paratype (MRAC). A-B, different views; C, tail canal opening.

These specimens have juvenile genitalia, but they are sufficiently developed to secure their generic attribution, showing that different species of *Saphtia* can occur syntopically.

Saphtia lamtoensis spec. nov.
(figs 23-30)

Material. — **Holotype:** Côte d'Ivoire, Lamto "dans plantation café", J.J. Van Mol leg., 6.viii.1968 (MRAC 795-131). **Paratypes:** same data as holotype (MRAC 795-131/ 35 paratypes in alcohol, shells and shell fragments of dissected specimens dry; RMNH.MOL.110335/ 1 specimen, shell dry, soft parts in alcohol; RMNH.MOL.11035x/ 2 adult and 1 juv. in alcohol). Material almost certainly stems from near the ecological research station of Lamto (about 6°13'N, 5°02'W), situated about 160 km NW. of Abidjan.

Diagnosis. — A pale brownish, comparatively small-sized species of *Saphtia*. Shell periphery rounded, sculpture consisting of fine spiral lines only. Reflected margin of spermatophore tail opening finely incised. Roof of pallial cavity with band of dark pigmentation.

Shell (fig. 23). — Very thin, translucent, pale brownish, low-conical, periphery of last whorl rounded. Whorls moderately convex. Embryonic whorls not demarcated from

later ones, sculpture almost from nucleus onwards consisting of very fine spiral lines that continue on later whorls, thereby becoming gradually coarser; spiral lines more distant near upper suture than further down the whorl. On earliest whorls spiral sculpture visible only in very fresh shells at high magnification. Umbilicus small but open. Size (adult shells): D = 16-18 mm, H = 10-10.5 mm, H/D = 0.57-0.63, W = 4.5-5 (n = 6).

Cephalopodium (figs 24-25).— Basically similar to that of former species. Length of foot about 30 mm in specimens relaxed prior to fixation. After nearly 40 years in alcohol, cephalopodium greyish, without prominent pigment, only somewhat darker behind upper tentacles and on dorsum.

Pallial region (fig. 26).— Pallial lobes unpigmented. Right and left shell lap well developed. Pallial cavity occupying about half a whorl. Roof of pallial cavity with small, elongated dark spots alongside hindgut, coalescing into diffuse band. Roof of cavity above kidney (largely above primary ureter) with a conspicuous dark band.

Jaw (fig. 27).— Reddish brown, about 1.7 mm wide, and comparatively high; median projection not prominent, cutting edge rather irregular in all three specimens examined.

Radula (fig. 28).— Formula (half a row) R - 18 - ~ 33. Mesocone of central tooth lanceolate, markedly longer than basal plate. Endocones of lateral teeth smaller than ectocones. Endocone disappears at about 18th lateral. Marginals narrower than laterals, bicuspid, ectocone smaller than mesocone.

Reproductive organs (fig. 29).— Distal penis wide and twisted, gradually passing into a more slender proximal portion. Distal penis thick-walled, lumen with strands of tissue, surrounding tip of long verge. Penial retractor muscle long and narrow, inserting on spherical epiphallic caecum and originating from diaphragm. At least in some specimens penial retractor seems branched. Epiphallus much shorter than penis. Flagellum comparatively straight, about 1.6-2 times as long as epiphallus and more slender,

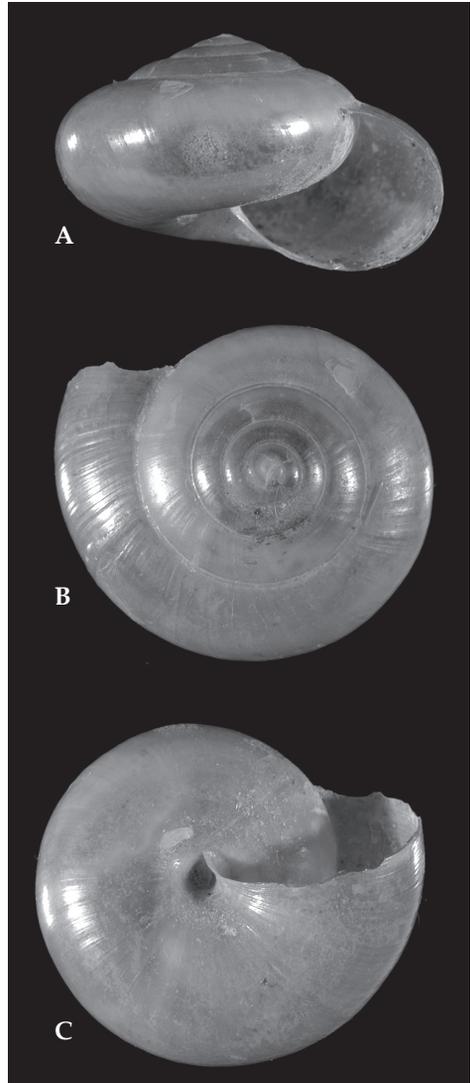
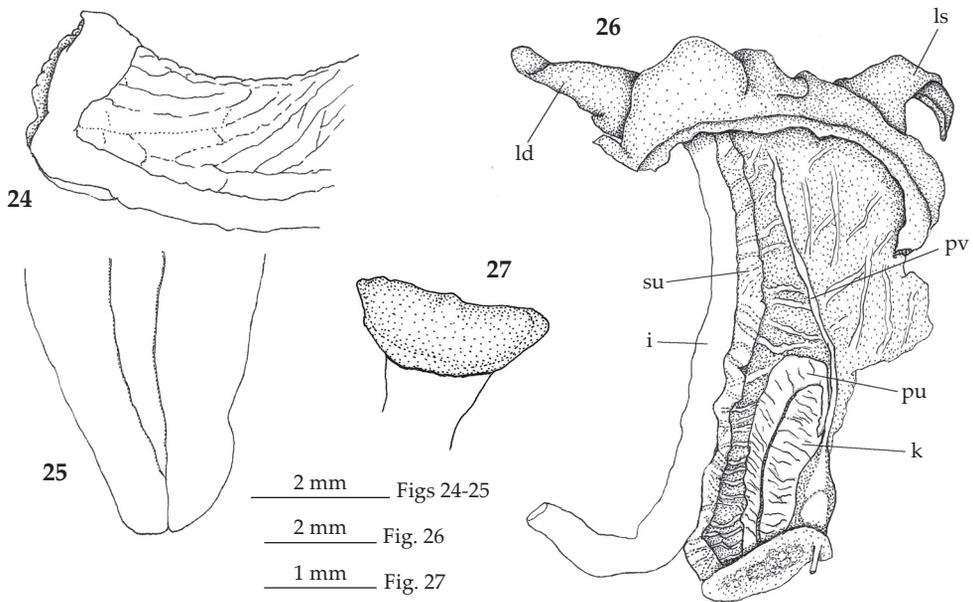


Fig. 23. *Saphtia lamtoensis* spec. nov., A-C, different views of holotype shell (MRAC). (actual shell width 17.8 mm).



Figs 24-27. *Saphtia lamtoensis* spec. nov. paratype (MRAC). 24, tail, lateral view. 25, posterior part of sole. 26, pallial region, ventral (interior) view. 27, jaw.

containing axial thread. Portion of vas deferens between prostate and penoviducal angle strongly convoluted, much less so between penoviducal angle and epiphallus. Duct of bursa copulatrix with muscular outer sheath, lumen lined with a thick papillose stratum, narrowing at opening into bursal sac. Capsular gland twice as wide as bursal duct width, longer than proximalmost portion of free oviduct.

Spermatophore (fig. 30).— In several specimens the bursa copulatrix contained one fresh, intact spermatophore. Entire spermatophore about 18 mm long. Both ampulla and tail convoluted. Tail longer than ampulla, with initially a row of simple, spirally arranged spines, joined about halfway by a second row of spines. First 8 spines conical, comparatively large and prominent, remaining spines becoming flatter and smaller towards tail canal opening. About $\frac{2}{3}$ of disc-shaped margin of tail canal opening delicately incised.

Ecology.— Basically unknown. Specimens were collected at a coffee plantation.

Etymology.— The specific epithet refers to the type locality, Lamto, which is a long-standing research station and nature reserve at the transition of the coastal forest zone into the wooded savannah region of Côte d'Ivoire.

Remarks.— *Saphtia lamtoensis* is conchologically very different from *S. granulosa*, the type species of *Saphtia*, but the two species clearly belong to the same genus, given numerous shared characters of the soft part morphology and spermatophore. The shell of *S. granulosa* strongly resembles species of *Thapsia* in size, shape and sculpture, which illustrates that shells in helicarionoids are poor predictors of the phylogenetic relationships of the animals.

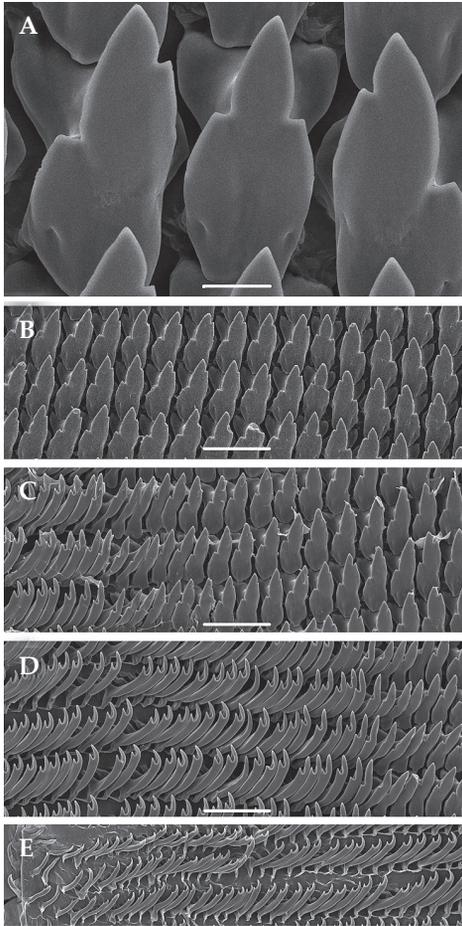


Fig. 28. *Saphtia lamtoensis* spec. nov., radula of paratype (MRAC). A, central tooth and first laterals (scale bar = 10 μ m); B, central tooth and lateral teeth; C, transition of laterals into maginals; D, lateromarginals and early marginals; E, late marginals (scale bars B-D = 50 μ m).

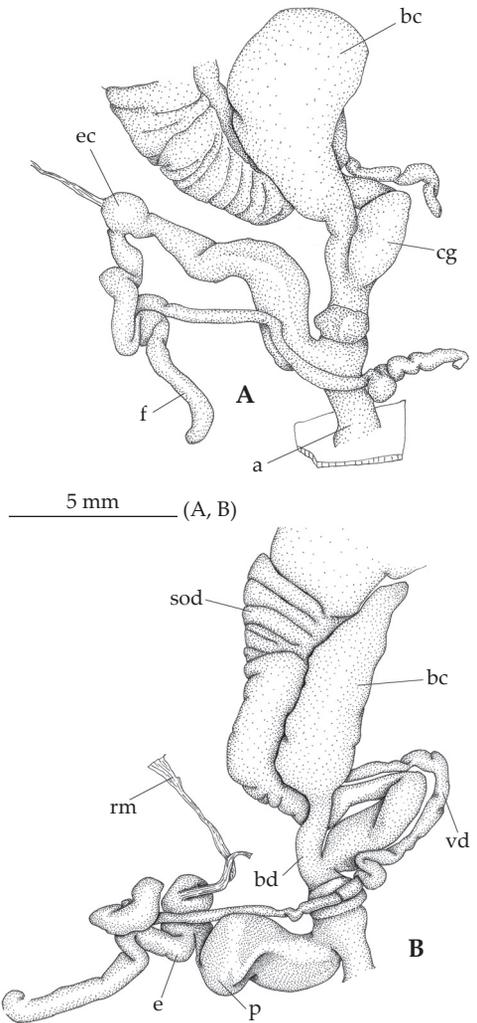


Fig. 29. *Saphtia lamtoensis* spec. nov., distal genitalia of holotype (A, MRAC) and paratype (B, MRAC).

This species could be '*Thapsia*' *calamechroa* (Jonas, 1843), under which name specimens resembling *S. lamtoensis* in shell size and sculpture have been reported from much of western Africa. *Helix calamechroa* was described only after its shell, and the type locality ("Guinea") is very vague. The type material seems to be hidden or lost, but the original description and illustration strongly suggests that the species should be placed in *Saphtia* rather than *Thapsia*, hence *Saphtia calamechroa* stat. nov. Without access to the original specimens, the specific identity of *S. calamechroa* remains obscure.

Pseudosaphtia gen. nov.

Type species.— *Pseudosaphtia brunnea* spec. nov.

Diagnosis.— Fully-shelled helicarioid, diagnostically different from *Thapsia* by the comparatively small shell with fine spiral lines rather than decussate sculpture, and the simple ornamentation of the spermatophore tail, with few branched long spines and no collar of coarse thorns. Differs from smaller-shelled *Saphtia* species by various soft part characters shared with *Thapsia*, notably the distinct caudal horn, the simple posterior opening of the spermatophore tail, and the rather different morphology of the distal penis and vagina. The scattered, swollen, oval-roundish head warts appear to be a unique character for the genus.

Description.— See description of the only attributed species, *P. brunnea* spec. nov.

Etymology.— The name *Pseudosaphtia* refers to the conchological similarity to some (smaller-shelled) *Saphtia* species.

Remarks.— *Pseudosaphtia* is more similar in soft part characters to *Thapsia* than to *Saphtia*, e.g. the strongly swollen vagina at the junction with the bursa copulatrix, overall penis morphology and some aspects of the spermatophore; also the geographic distribution suggests the genus to be related to *Thapsia* rather than *Saphtia*.

The sample of *S. brunnea* (in MRAC) included specimens of two other shelled helicarioid species, one of which is a species of true *Thapsia*.

The scattered, swollen, oval-roundish warts on the head appear to be a unique character for the genus.

Pseudosaphtia brunnea spec. nov.

(figs 31-39)

Material.— **holotype**: Cameroon, Olounou (probably 2°49'N, 12°08'E, see remarks), F. Puylaert leg., 13-19-ix-1971 (MRAC 795.848, shell dry, soft parts in alcohol). **Paratypes**: same data as holotype (MRAC 302.306/ 14 paratypes in alcohol, shells and shell fragments of dissected specimens dry, RMNH. MOL.110356/ 2 shells dry, soft parts in alcohol; 1 entire specimen in alcohol).

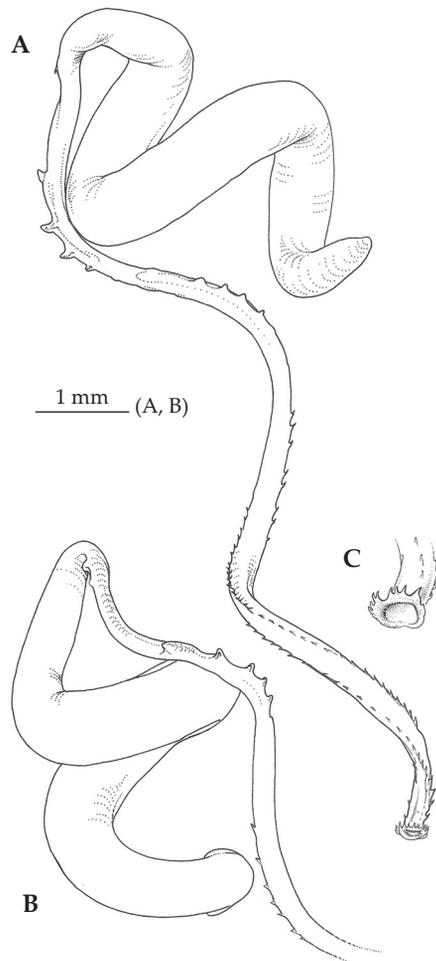


Fig. 30. *Saphtia lamtoensis* spec. nov., spermatophore from bursa copulatrix of paratype (MRAC); A-B, different views; C, tail canal opening.

Diagnosis.— Differs conchologically from the smaller *Saphtia* species described to date by the low-spired shell. Anatomically it is characterized by the generic characters listed above.

Shell (fig. 31).— Shell warm brown, fragile, partly translucent, rather low-spired, periphery rounded. Umbilicus narrow but open. Earliest whorls smooth, not well demarcated from later ones. Postembryonic sculpture consists of fine spiral striae over entire whorl, at some spots sculpture extremely finely decussate where spiral lines are crossed by fine radial lines. Size (adult specimens): D = 18.1-19.1 mm, H = 9.0-11.1 mm, H/D ~ 0.50, W = 5¼-5½ (n = 6).

Cephalopodium (figs 32-33).— Area on head between ommatophores and lower tentacles with scattered, oval-roundish tubercles (warts). Animal rather dark, anterior cephalopodium (apart from contrasting paler ommatophores and head warts) dark grey, followed by a cream-coloured central portion, posterior portion including caudal horn dark grey. Tail with vertical caudal foss and long, distinct caudal horn.

Pallial region (fig. 34).— Occupying about half a whorl. Pallial roof very dark, almost black in the median sector, becoming paler laterally. Mantle lobes dark grey. Right and left shell laps well developed, more or less elongate triangular. Kidney about 8 mm long, less than half the stretched pallial cavity length.

Jaw (fig. 35).— 1.7 mm wide, with prominent median projection.

Radula (figs 36).— Formula (half a row) R - 16 - ~ 64. Mesocone of central tooth elongate, longer than basal plate. Endocone of lateral teeth smaller than ectocone, endocone disappears at about 16th lateral. Marginal teeth very long and narrow, bicuspid, ectocone smaller than mesocone, tip of both ectocone and mesocone very fine.

Reproductive organs (figs 37-38).— Atrium rather long, internally with a strong vertical pilaster in between outlet of male and female tubes. Penis rather long, but length varies among individuals. Distal portion of penis contorted within penial tunica, wider than proximal penis. Inner wall of distal penis with vertical pilasters. Transition of proximal to distal penis marked by presence of small papilla. Proximal penis muscu-

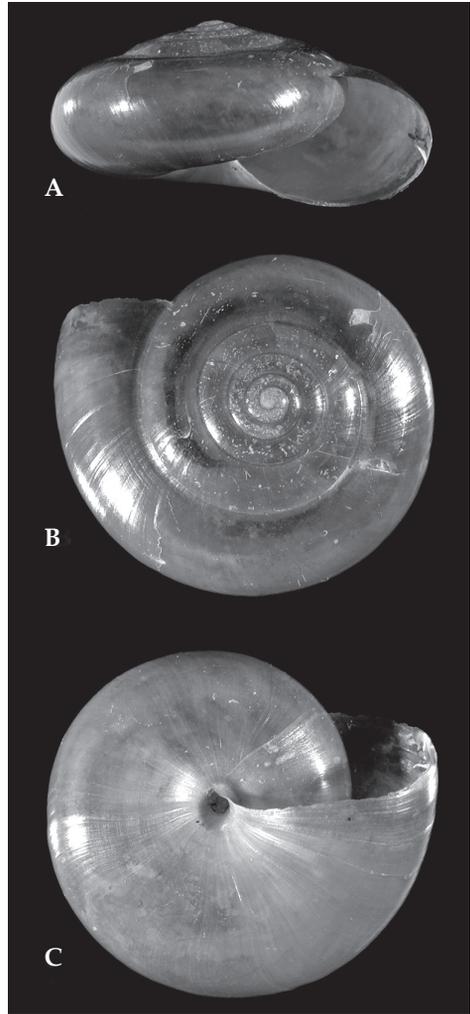
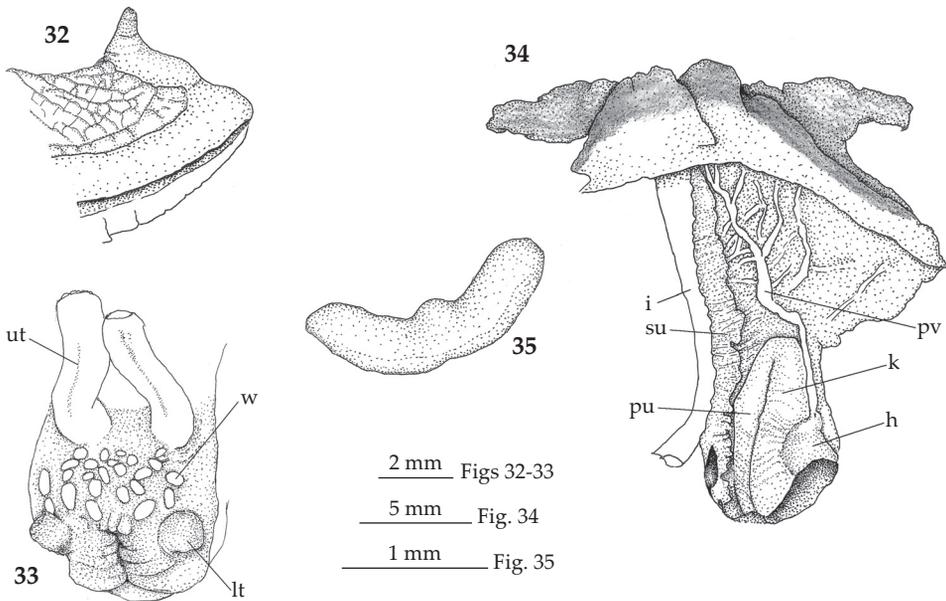


Fig. 31. *Pseudosaphtia brunnea* spec. nov., A-C, different views of holotype shell (MRAC) (actual shell width 18.1 mm).



Figs 32-35. *Pseudosaphitia brunnea* spec. nov., paratype (MRAC). 32, lateral view of tail. 33, head in frontal view. 34, ventral (interior) view pallial region. 35, jaw.

lar, with about 9 longitudinal ridges on inner wall narrowing lumen. Penis retractor muscle narrow, inserting on smallish epiphallic caecum and originating from columellar muscle complex. Epiphallus elongate and little convoluted except at the point of entry of the vas deferens, about as long as flagellum. Epiphallus lumen narrowed by longitudinal ridges, on cross-section appearing as high papillae. Flagellum about half as wide as epiphallus, not strongly convoluted, containing axial thread. Branched spines of spermatophore tail (see below) are moulded in distal, widest portion of flagellum where crypts can be observed either protruding or by transparency. Vagina comparatively stout and muscular, with bulbous widening at junction with proximal free oviduct and bursal duct. Lumen of swollen vaginal portion narrow, at one side strongly branched. Proximal free oviduct with distinct capsular gland. Bursal duct not very long, distal portion wide and muscular with a conspicuous retractor muscle, rapidly narrowing more proximally; inner wall of bursal duct irregular-papillose. Bursal sac not very voluminous, not even when containing a spermatophore.

Spermatophore (fig. 39).— One complete but empty (ampulla flattened) spermatophore and fragments of at least one more were found in the bursa copulatrix of three specimens each. Ampulla elongate-oval. Tail ornamented with comparatively few long spines, 5-6 of which branched, most complex spine divided in four minor spines. Last portion of tail with two rows of sharp, short spinules that disappear shortly before opening of central canal. Opening of tail canal a simple hole.

Etymology.— The specific epithet *brunnea* refers to the dark brown colour of the animal, due to the brown shell colour reinforced by the darkly pigmented soft parts.

Ecology. — Unknown.

Remarks. — There could be some confusion as to the exact location of the type locality. There are at least two, rather distant, localities with the name Olounou in Cameroon, and no coordinates or other details are provided on the label. However, the collector also collected some fish species on the same date at the locality, which are mapped to 2°49'N, 12°08'E (see www.fishbase.com).

Conchologically, *Pseudosaphtia brunnea* somewhat resembles *Thapsia rosenbergi* Preston, 1909, described from "Bitze" (misspelling for Bitey, 3°01'N, 12°22'E) near the Ja River in Cameroon, especially one paratype shell on which Preston (1909) noticed: "one specimen is of a much darker colour than the others..., and the margin of the suture, instead of being whitish, is of even a deeper shade of reddish brown than the rest of the shell...". However, the holotype shell (BMNH) is rather different (shape, smaller size, paler in colour etc.) from *P. brunnea*, so these species are unlikely to be conspecific. In the absence of anatomical data, the generic attribution of *T. rosenbergi* remains unclear, but the species is unlikely to remain in the genus *Thapsia* in view of its shell size and sculpture.

Vanmolia gen. nov.

Type species. — *Thapsia sjoestedti* d'Ailly, 1896.

Diagnosis. — Shell medium-sized, very thin and brittle, capable of covering entire visceral mass and foot, differing from smaller species of *Saphtia* by inconspicuous but regular and close-set growth ridges below the suture and on the shell base. Free oviduct, penis and bursa copulatrix open simultaneously into atrium. Flagellum absent. Spermatophore without spiny ornamentation. Caudal appendage well-developed, overhanging strongly indented caudal foss.

Description. — See the description of the only attributed species, *V. sjoestedti*.

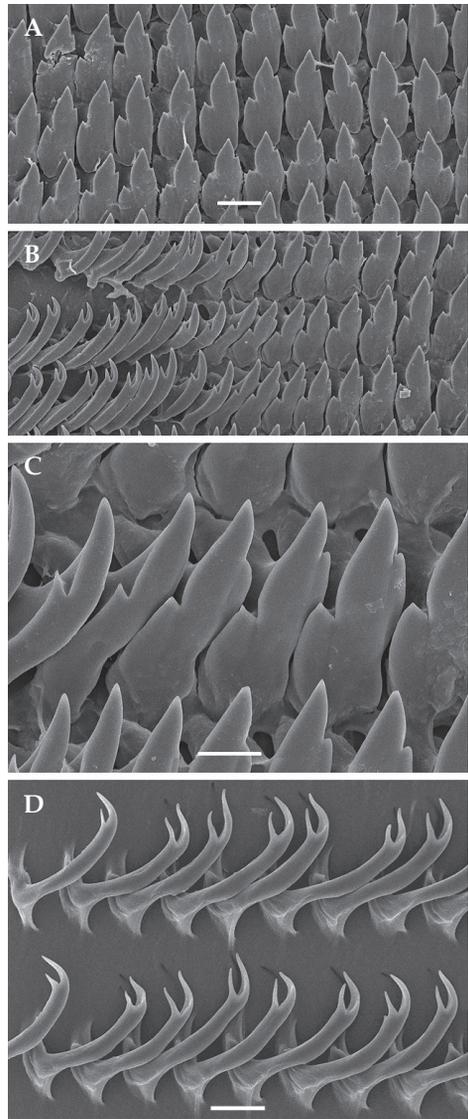


Fig. 36. *Pseudosaphtia brunnea* spec. nov., radula (paratype MRAC). A, central tooth and first laterals (scale bar A-B = 20 μ m); B, transition of laterals into marginals; C, lateromarginals and early marginals; D, late marginals (scale bar C-D = 10 μ m).

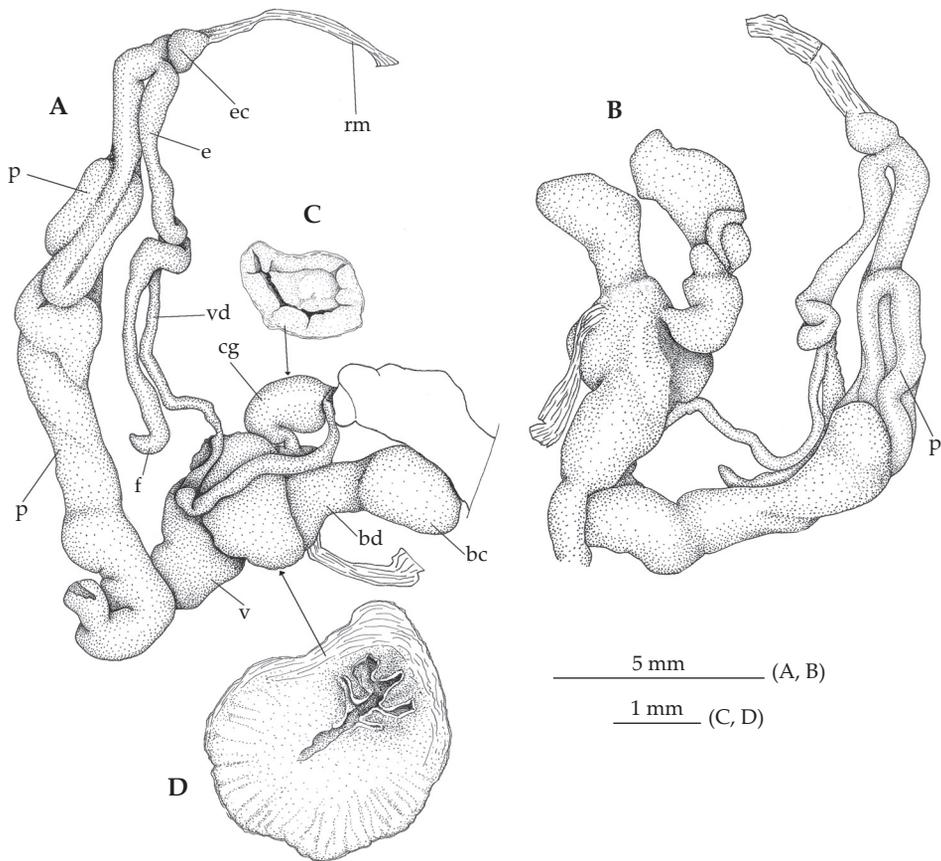


Fig. 37. *Pseudosaphitia brunnea* spec. nov., holotype (MRAC). A-B, different views of distal genitalia; C, cross-section proximal free oviduct (capsular gland); D, cross-section swollen portion vagina. Arrow indicates place where cross section is made.

Etymology. — *Vanmolia* is named after the malacologist Prof. Jean-Jacques Van Mol, whose publications significantly contributed to the knowledge of African helicarioids.

Vanmolia sjoestedti (d'Ailly, 1896)
(figs 40-45)

Thapsia Sjoestedti d'Ailly, 1896: 39, pl. 2 figs 15-20.

Material. — Cameroon, between Mundemba and Mattamani (Mudemba: 4°57'N, 8°52'E), Y. Sjöstedt leg., vi.1891. Various syntypes in alcohol (3 dissected) (SMNH), and 3 dry syntype shells (SMNH 1585A), marked as "type" on label, probably including shell illustrated by d'Ailly, 1896, pl. 2 figs 15-18. Syntype shells also present in MRAC and in Göteborg museum.

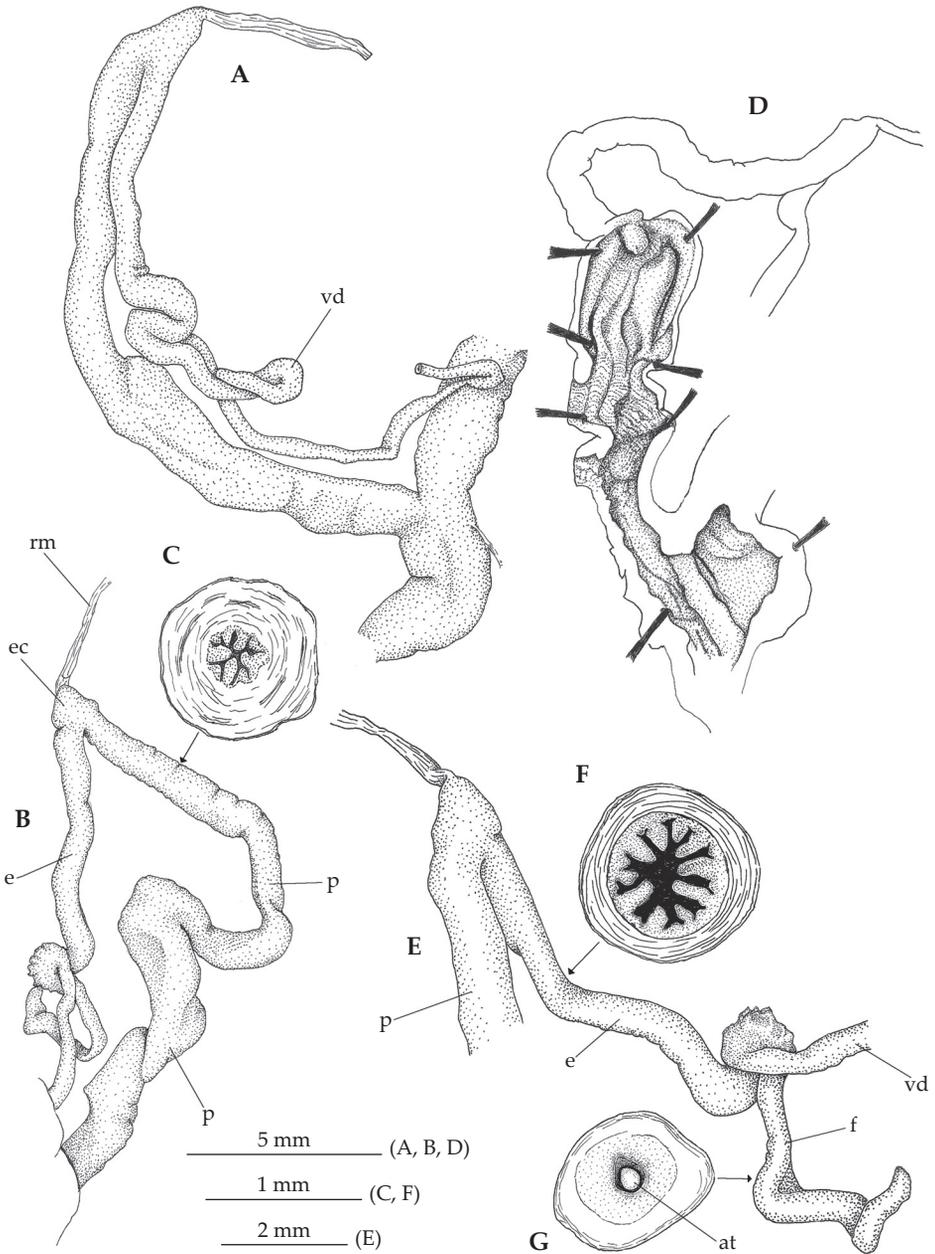


Fig. 38. *Pseudosaphitia brunnea* spec. nov., distal genitalia (paratype MRAC). A, atrium and penis; B, penis, penial sheath removed; C, cross-section proximal penis; D, interior view distal penis; E, epiphallus and flagellum; F, cross-section epiphallus; G, cross-section flagellum. Arrows indicate position where cross sections are made.

Diagnosis.— See genus diagnosis.

Shell (fig. 40).— Very thin, umbilicus narrow, partly covered by the sinuously reflected columella; periphery rounded, colour hyaline-milky, translucent. Earliest whorls smooth, the later ones with very fine, somewhat wavy, spiral striae. The later whorls are finely but regularly plicate, which is particularly visible below the suture and on the shell base. Size: D = 18.1-19.0 mm, H = 10-10.8 mm, H/D = 0.56-0.57, W = $\sim 4 \frac{3}{4}$ (n = 2).

Cephalopodium (fig. 41).— Typically helicarionoid, with tripartite sole. Tail with indented caudal foss and long, prominent caudal horn. Genital opening immediately behind right lower tentacle. All specimens examined are strongly contracted.

Pallial region (fig. 42).— Pallial cavity occupying about half a whorl. Pallial roof well vascularized. Mantle pigmentation of syntypes a pale reddish-brown band above the primary ureter. According to d'Ailly (1896: 40, pl. 2 fig. 19), this pigmentation band is strikingly black and branched in fresh material; the flanking white band in the original description probably represents the kidney. Heart comparatively small, occupying only about 2/7 of the kidney length. Kidney rather narrow, about half as long as stretched-out pallial cavity. Consistency of primary ureter solid, macroscopically similar to that of kidney, secondary ureter thin-walled and transparent, but becomes strongly dilated and much thicker shortly before reaching mantle edge (particularly striking in dorsal view). Pallial lobes well developed; especially right and left shell laps large and wide, rounded.

Jaw (fig. 43).— Oxygnathous, yellowish, about 1.7 mm wide, with prominent median projection.

Radula (fig. 44).— Formula (half a row): R - 18 - >25. Teeth subequal to basal plate. Central tooth distinctly smaller than laterals, with comparatively short, rounded mesocone. Endocone of laterals smaller than ectocone, endocone absent after 18th lateral. Marginals more elongate than laterals, bicuspid with ectocone remaining smaller than mesocone.

Reproductive organs (fig. 45).— Atrium short. Oviduct, penis and bursa copulatrix open together into atrium, a vagina thus being absent or obsolete. Penis consists of three portions: a distal, thin-walled and slender portion with fine longitudinal pilasters on inner wall, abruptly widening into much more voluminous central portion which

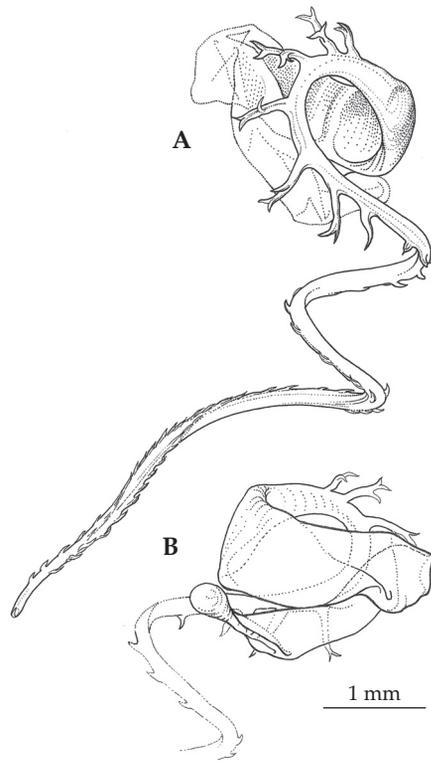


Fig. 39. *Pseudosaphtia brunnea* spec. nov., different views of spermatophore from bursa copulatrix of paratype (MRAC).

contains a long, convoluted verge; most proximal portion globular-spherical, its interior wall covered by coarse, high papillae. Penis retractor inserted on proximal penis. Vas deferens (or epiphallus, see below) opens into proximal penis through an elongate, narrow, tongue-like structure with a slit-like opening. Vas deferens very short, thick-walled, widening at about one third of its length before entering proximal penis. Flagellum or lime sac absent. Bursa copulatrix comprise of a rather wide, thick-walled duct and an elongate, thin-walled sac. Inner wall of bursal duct with coarse ridges on one side and finer papillae on the other, surrounded by layer of muscular tissue. Free oviduct long and slender, attached to inner body wall by muscle tissue.

Spermatophore (fig. 45H).— Bursal sac of the depicted specimen contained a brownish, partly dissolved and possibly incomplete spermatophore, with no indication of a well-defined tail with spines or other ornamentation.

Ecology.— According to field notes by the collector (quoted by d'Ailly, 1896: 40), the species was found in thick, humid, low forest ("Bushwald", probably secondary vegetation), on the forest floor among rotting leaves. The species may locally occur in large numbers: Sjöstedt remarked that at one occasion he could collect a handful at a single spot.

Remarks.— Upon examination of the anatomy of syntypes, the morphology of the genitalia proved to be very different from that of *Thapsia* or any other fully-shelled taxon of Urocyclidae known. The systematic relationships of *Vanmolia* are obscure (see general discussion below).

The terminology of the various parts of the male genitalia of *Vanmolia* is tentative, especially since a well-defined epiphallus and flagellum are absent. The globular-spherical proximal penis externally resembles the epiphallic caecum of *Thapsia*, *Pseudosaphitia* and *Saphitia* species, and, like in these taxa, the penial retractor inserts on it. Its internal morphology strongly differs from the rest of the penis as well as from the wider portion of the vas deferens, and either of these parts, wholly or in part, may represent the epiphallus. The wider portion of the vas deferens on cross-section seems to differ

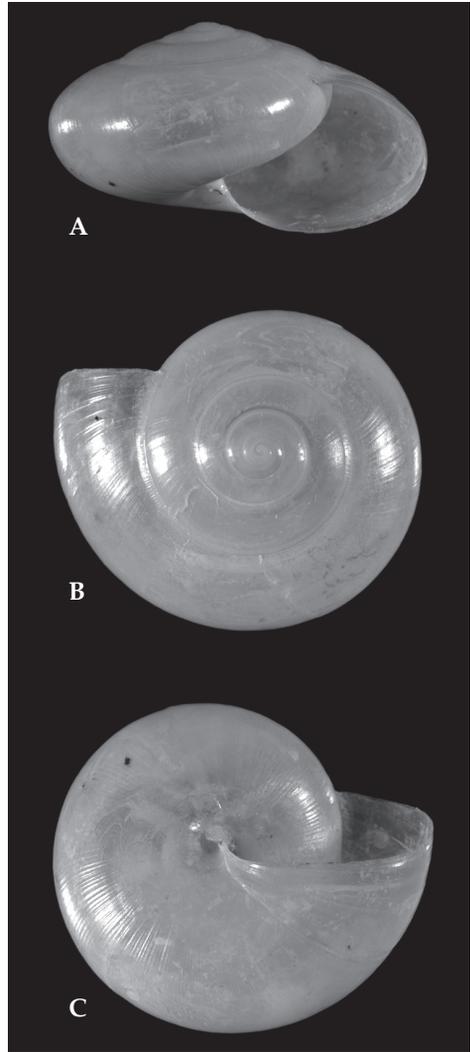
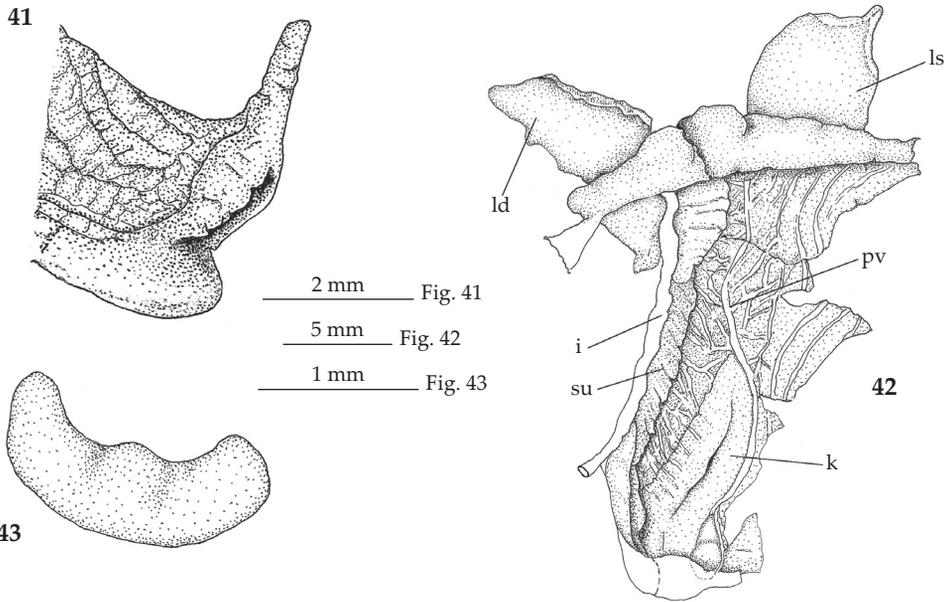


Fig. 40. *Vanmolia sjoestedti* (d'Ailly, 1896), A-C, different views of syntype shell (SMNH) (actual shell width 19.0 mm).



Figs 41-43. *Vanmolia sjoestedti* (d' Ailly, 1896) (syntypes, SMNH). 41, lateral view of tail. 42, pallial region. 43, jaw.

macroscopically only by a thicker outer layer of muscular tissue from the narrower portion. The establishment of the homologies of the various organs require detailed histological studies.

General discussion:

Phylogenetic relationships of *Thapsia*, *Saphtia*, *Pseudosaphtia* and *Vanmolia*

Notwithstanding their conchological similarity, *Thapsia*, *Saphtia*, and *Vanmolia* do not appear to be closely related. Several anatomical features suggest that *Pseudosaphtia* is phylogenetically closer to *Thapsia* than to *Saphtia*. It may be that some genera have closer relationships to certain slug-like taxa than to any shelled helicarionoid in the region under consideration. However, none of the (semi)slug genera dealt with by Van Mol (1970) and Van Goethem (1977) are obvious candidates at this point, though it should be realized that too little comparative data are as yet available; few helicarionoids have been dissected and many taxa probably remain to be discovered in Africa.

Vanmolia is clearly the most deviating taxon dealt with here. It shares several characters with species of the subfamily *Gymnarioninae* Van Mol, 1970, sometimes considered a distinct family of its own (see e.g. Schileyko, 2002), like the absence of a flagellum-like structure and the spermatophore formation taking place in the penis proper (Binder, 1976). However, there are also conspicuous differences between *Gymnarion* and *Vanmolia*: absence in *Vanmolia* of what Pilsbry (1919: 277-278) termed a dart sac or dart gland (glandular atrial diverticulum sensu Van Mol, 1970); a much longer caudal horn in *Vanmolia* than in *Gymnarion*; mantle lobes large and conspicuous in *Vanmolia*,

rather small or absent in *Gymnarion*; distinct verge in penis of *Vanmolia*, penis in *Gymnarion* only with pilasters on inner wall (Pilsbry, 1919; Watson, 1920; Degner, 1934; Binder, 1976). Binder's (1969, 1976) work on the genus *Gymnarion* focused on the frontal organ (not observed in *V. sjoestedti*) and the internal structure of the penis, and a detailed comparison of other parts of the genital organs in a greater number of species is still outstanding.

Another option could be to assign *Vanmolia* to the family Rhysotinidae Schileyko, 2002, recently erected for two species of the genus *Rhysotina*, both endemic to Sao Tomé Island, which, like *Gymnarion* species, lack a flagellum and vagina.

It is even unclear whether the four genera treated in this paper and other shelled African taxa belong the same branch of the Helicarionoidea (sensu Bouchet & Rocroi, 2005). The African shelled and slug-like helicarionoids are often treated as a single family, Urocyclidae, endemic to Africa (including the Arabian peninsula). However, the African taxa seem to be quite heterogeneous and are probably polyphyletic (Bouchet & Rocroi, 2005). Some taxa may be closer to branches of the helicarionoid-ariophantoid radiation recognized outside Africa (south and southeast Asia, Australia, the Pacific islands, and Madagascar). For instance, in several anatomical characters *Vanmolia* superficially resembles the South Asian taxon *Cryptaustenia* (sensu Solem, 1966). True Urocyclidae (e.g. members of the slug genus *Urocyclus* Gray, 1864, see Van Goethem, 1977) have a very different genital morphology from any of the taxa dealt with in this paper. For this reason, the name Urocyclidae for the entire African helicarionoid radiation is avoided here. Clearly, the helicarionoid group (sensu Bouchet & Rocroi, 2005) is in need of a phylogenetic analysis using both morphological and molecular data.

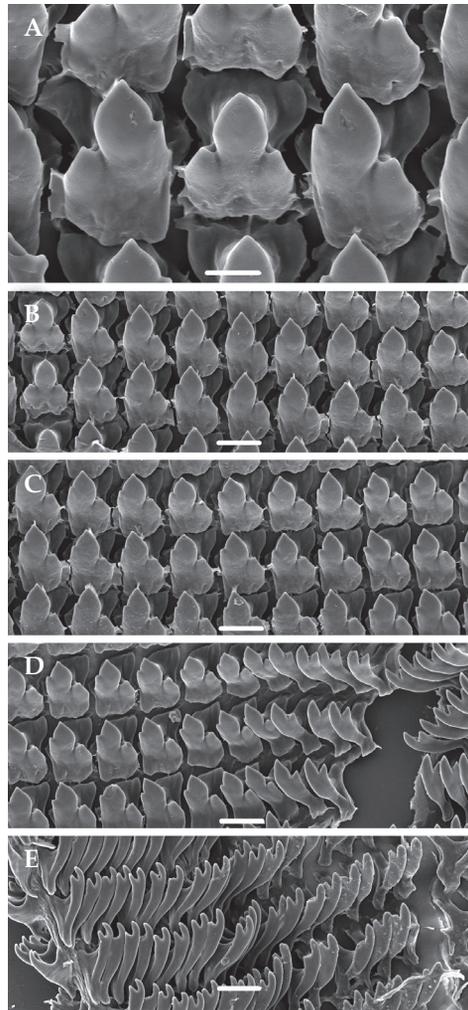


Fig. 44. *Vanmolia sjoestedti* (d'Ailly, 1896), radula (syntype, SMNH). A, central tooth and first laterals (scale bar = 10 µm); B-C, central tooth and lateral teeth); D, transition of laterals into early marginals; E, marginals (scale bars B-E = 20 µm).

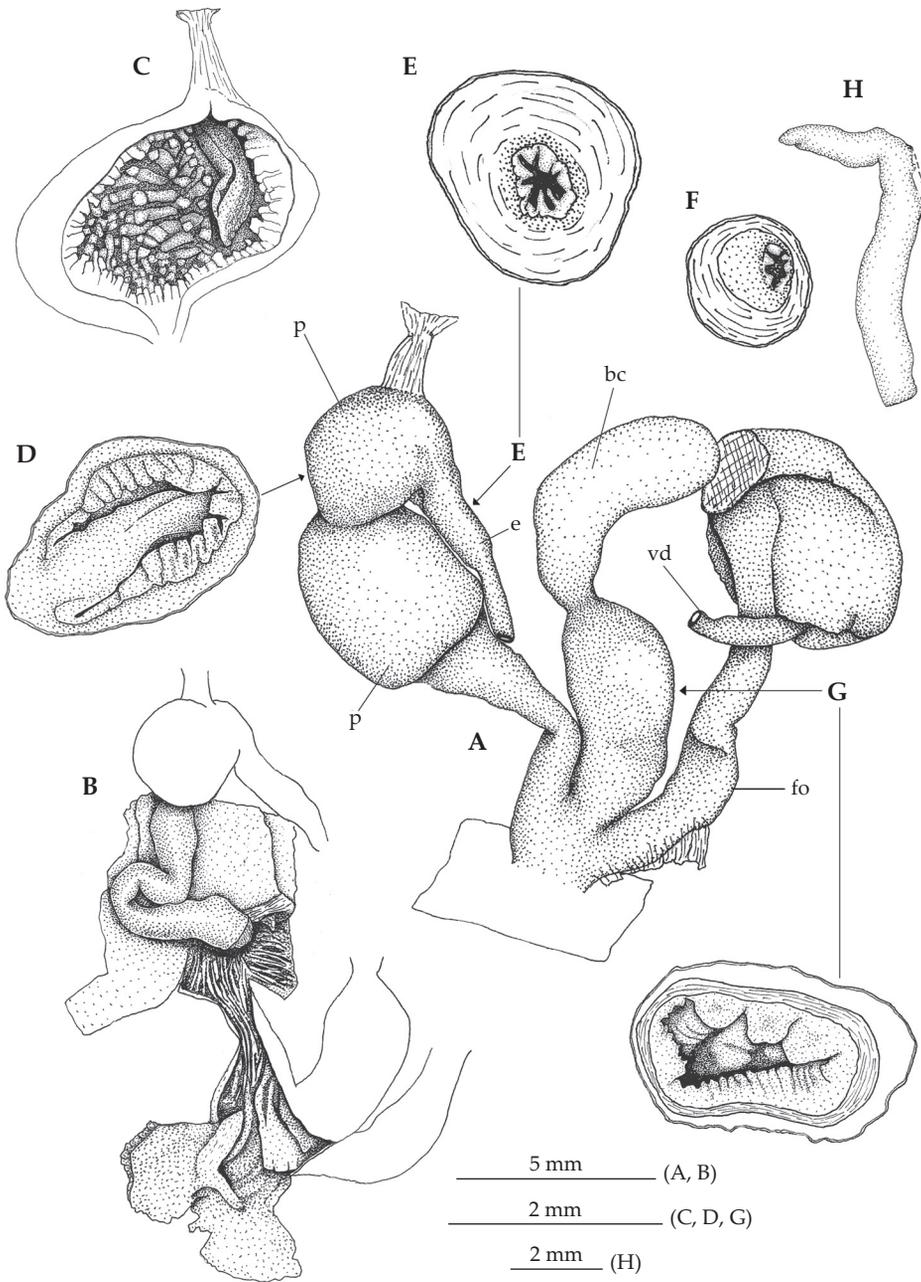


Fig. 45. *Vannmolia sjoestedti* (d'Ailly, 1896), distal genitalia (syntype, SMNH). A, external view, vas deferens cut; B, internal view distal penis; C, proximal penis longitudinally opened; D, cross-section proximal penis (other syntype); E, cross-section 'epiphallus'; F, cross-section vas deferens; G, cross-section duct of bursa copulatrix; H, outline of damaged spermatophore from bursa copulatrix. Arrows indicate position where cross sections are made.

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