

VINUNDU, A NEW GENUS OF GASTROPOD (CERITHIOIDEA: 'THIARIDAE') WITH TWO SPECIES FROM LAKE TANGANYIKA, EAST AFRICA, AND ITS MOLECULAR PHYLOGENETIC RELATIONSHIPS

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(Received 21 May 2002; accepted 22 February 2003)

ABSTRACT

A thiarid gastropod, *Vinundu westae* new genus and new species, is described from Lake Tanganyika, and the species *Nassopsis guillemei* Martel & Dautzenberg, 1899 is transferred to this new genus from *Edgaria* (= *Lavigeria*). The shell of *Vinundu* has equal axial and spiral macrosculpture, producing characteristic regular nodes at the sculptural intersections. Reproduction in *Vinundu* is oviparous, in contrast to the ovoviviparous habit of its sister group, *Lavigeria*. Radular teeth and isotope values indicate that this is a grazer. *Vinundu* species are readily distinguished from their sister clade *Lavigeria* by conchological, anatomical and molecular characters. The two *Vinundu* species are common in deep water, rocky habitats of this clear-water, ancient lake.

INTRODUCTION

Among endemic radiations of freshwater molluscs, the gastropods of Lake Tanganyika are recognized as among the most spectacular. While there are many endemic species [34 currently recognized (Brown, 1994), with approximately 35 more in revision and preparation (West, Michel, Todd, Brown & Clabaugh, 2003; E. Michel & J. A. Todd, in prep.)], it is the evolutionary derivation and morphological disparity of the gastropods that draw attention. The heavy and highly ornamented shells of many of these endemic snails superficially resemble marine prosobranchs more than their close freshwater relatives. This armouring is likely to be the result of co-evolution with the shell-crushing predatory endemic crabs of the lake (West, Cohen & Baron, 1991; West & Cohen, 1996; Hinkley, Michel & Sarikaya, 2001; Phifer, McIntyre & Michel, 2001; Soggi, 2001).

There is a striking degree of evolutionary divergence among Tanganyikan gastropods. Seventeen endemic genera, whose phylogenetic relationships are not, as yet, fully resolved, are currently recognized (Brown, 1994; West *et al.*, 2003). West & Michel (2000) considered the endemic gastropod fauna to be a 'superflock', according to DNA sequence data, with a robust stem to the clade indicating intralacustrine radiation. Internal relationships among the lineages are less robust, suggesting a burst-like radiation for the 17 endemic genera. However, Wilson (2001) counters that a molecular clock suggests that the Tanganyikan lineages originated before the formation of the Tanganyikan basin 9–12 Mya (Cohen, Soreghan & Scholz, 1993) and thus questions the monophyly of the whole group. Nonetheless, both analyses agree on the monophyly of the lineages at the generic level.

In this paper I present the taxonomic description of a new genus, *Vinundu*, and two species (one new, one re-described) of endemic Tanganyikan gastropods. The genus is comprised of one new species, *V. westae*, and one other species, *V. guillemei* (Martel & Dautzenberg, 1899) which is here re-described and removed from synonymy with *Lavigeria spinulosa* (Bourguignat, 1885) (see Leloup, 1953: 173). *Vinundu* is the sister clade to *Lavigeria*, a diverse species-flock (Michel, 2000). This sister-taxon relationship is strongly supported by conchological, anatomical and genetic data.

MATERIAL AND METHODS

Collections were made over many field seasons between 1986 and 2001 using SCUBA to collect only live animals, noting depth and substrate. Collections were made from approximately 75 localities on rocky sites around the shoreline of Lake Tanganyika. The regions of Burundi, northern Tanzania (around Kigoma) and northern Congo (formerly Zaire) have been sampled most intensively, with sites in close proximity, and sometimes visited several times by the author, members of Andrew Cohen's research teams, and Nyanza Project participants. Sites along the southern Tanzanian and Zambian coasts were sampled during several expeditions by Andrew Cohen's research team in 1986 (including Mark Johnston and Kelly West), by Roger Bills in 1991 and by the author in an expedition from the Royal Belgian Institute of Natural Sciences in 1995. Most of the Congo coast remains poorly sampled to date. Museum collections were examined from the BMNH, IRSNB and MNHN for type comparison and for geographic coverage. Site coordinates given in decimal degrees derived from GIS mapping program TANGIS (www.ltbp/TANGIS.HTM).

Shells were prepared by macerating soft tissue and rinsing until clean, or occasionally by extracting body tissue directly. Soft parts were preserved for vouchers by breaking the shell and fixing in 95% ethanol, and in a few cases 70% ethanol for anatomical preparations. Anatomical dissections were done on fresh material, pinning the tissue in a repeatable orientation on a wax dish under a layer of water. Neural tissue was stained with alcian blue. Descriptive anatomical work was done on both *V. westae* and *V. guillemei*, but with a major focus on *V. westae*. Quantitative anatomical work was also done on 18 specimens of *V. westae* from two sites (Michel, 1995; and in prep.). Radulae were prepared by macerating with 5% NaClO (bleach), ultrasonic cleaning, gold coating and images obtained with an ISI scanning electron microscope.

DNA sequence (mitochondrial genes COI, 16S and ND1) and allozymes were collected for many populations (Michel, 1995, 2000) and results are discussed here. Original COI sequence for *Vinundu* is presented in full here. Sites for COI-sequenced specimens were chosen for local replication, sympatric co-occurrence between *V. westae* and *V. guillemei*, and maximum geographic separation within species (i.e. north-south extremes of lake, Figs 10, 14). A minimum of two individuals per site were

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included. Outgroup data were taken from Michel (2000) for four *Lavigeria* species that represent the major branches of that clade, one *Paramelania* and two *Melanoides*, and from West & Michel (2000) for *Cleopatra* and other Tanganyikan endemic thiarids (*Anceya*, *Bathanalia*, *Chytra*, *Limnotrochus*, *Paramelania*, *Reymondia*, *Spekia*, *Stanleya*, *Tanganyicia*, *Tiphobia*). Open nomenclature is used for taxa currently under revision, with reference to West *et al.* (2003). Sequences were generated by amplifying 640 base pairs of COI (Folmer, Black, Hoeh, Lutz & Vrijenhoek, 1994) and sequencing both heavy and light strands with an ABI 373 automated DNA sequencer. Relationships based on unweighted sequences (Clustal W alignment, manual corrections, non-problematic alignment, verified by translation to protein) were determined with parsimony analyses using PAUP 4.0b10 (Swofford, 2002) and bootstrap values for branch support were calculated with 5000 replicates (fast stepwise addition). COI sequences have been deposited with Genbank (Table 1).

Type material and reference specimens have been placed in BMNH, MNHN, USNM, IRSNB, NMK, NMT and ZMAN.

Abbreviations

ANSP, Academy of Natural Sciences, Philadelphia, USA
BMNH, Natural History Museum, London, UK

IRSNB, Institute Royal des Sciences Naturelles de Belgique, Brussels, Belgium

MNHN, Muséum National d'Histoire Naturelle, Paris, France

NMK, National Museums of Kenya, Nairobi, Kenya

NMT, National Museums of Tanzania, Dar es Salaam, Tanzania

USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ZMAN, Zoologisch Museum Amsterdam, The Netherlands

SYSTEMATIC DESCRIPTIONS

Cerithioidea: 'Thiaridae'

Note: It has been tentatively suggested that the Tanganyikan 'thiarids' might be assignable to the sub/family Paludominae/Paludomidae (Glaubrecht, 1999; Strong & Glaubrecht, 2002), but as neither a revised diagnosis of this taxon nor its suggested membership has yet been published, I refer *Vinundu* to the Thiaridae *sensu lato*.

Vinundu new genus

Type species: Vinundu westae new species.

Etymology: The generic name is Swahili for 'possessing many small bumps'. The shell is typified by tuberculate sculpture and

Table 1. Specimen site, sample, and GenBank accession numbers.

Species	Site abbreviation used in this paper; geographic name (collection site name)	Individual codes as listed in Genbank	Genbank accession numbers in order of individual codes
<i>V. westae</i>	CO3; Bemba, Congo (BEM)	Vwest8CO3	AY213155
		Vwest25CO3	AY213156
		Vwest26CO3	AY213157
		Vwest21CO3	AY213165
		Vwest6CO3	AY213169
<i>V. westae</i>	BU1; km 29.8, Burundi (BUkm29.8)	Vwest41BU1	AY213158
		Vwest42BU1	AY213159
		Vwest43BU1	AY213160
<i>V. westae</i> *	BU1; km 32, Gitaza, Burundi (BUkm32)	VwestKWBU2	AY213154
<i>V. westae</i>	BU5; km 114, south of Nyanza Lac, Burundi (BUkm114)	Vwest44BU1	AY213161
		Vwest45BU1	AY213162
<i>V. westae</i>	ZM10; south of Lufubu, Nakaku Village, Zambia (95em7)	Vwest79Zm10	AY213163
		Vwest80Zm10	AY213164
		Vwest1136Zm10	AY213166
		Vwest1135Zm10	AY213167
<i>V. westae</i>	ZM8; Chiluta Cliffs, Kasengo Point, Zambia (95em2)	Vwest1137Zm10	AY213170
		Vwest1005ZM8	AY213171
<i>V. westae</i>	ZM7; Kasanga Bay, Zambia (95em21)	Vwest9ZM7	AY213172
<i>V. guillemei</i>	ZM11; Kachese, Zambia (95em10)	Vguill150ZM11	AY213173
		Vguill147ZM11	AY213174
		Vguill1153ZM11	AY213184
		Vguill1154ZM11	AY213185
<i>V. guillemei</i>	ZM12; Chishiki, Zambia (95em9)	Vguill106ZM12	AY213175
		Vguill105ZM12	AY213176
		Vguill1141ZM12	AY213187
		Vguill1143ZM12	AY213189

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Table 1. (continued)

Species	Site abbreviation used in this paper; geographic name (collection site name)	Individual codes as listed in Genbank	Genbank accession numbers
<i>V. guillemei</i>	ZM6; Chilambo, Tanzania (95em20)	Vguill362ZM6	AY213177
<i>V. guillemei</i>	ZM10; south of Lufubu, Nakaku Village, Zambia (95em7)	Vguill70ZM10 Vguill1134ZM10 Vguill1133ZM10	AY213178 AY213186 AY213188
<i>V. guillemei</i>	ZM9; Muntondwe (Crocodile) Island, Mpulungu, Zambia (95em11)	Vguill186ZM9	AY213179
<i>V. guillemei</i>	CO4; Cape Banza, Congo (CBR)	Vguill50CO4 Vguill48CO4	AY213180 AY213181
<i>V. guillemei</i>	ZM8; Chiluta Cliffs, Kasengo Point, Zambia (95em2)	Vguill1001ZM8 Vguill1002ZM8	AY213182 AY213183
<i>Lavigeria</i> sp. B	CO4; Cape Banza, Congo (CBR)	LspB54CO4	AY213190
<i>Lavigeria</i> sp. N	CO4; Cape Banza, Congo (CBR)	LspN56CO4	AY213191
<i>Lavigeria</i> sp. A	CO4; Cape Banza, Congo (CBR)	LspA60CO4	AY213192
<i>Lavigeria grandis</i>	CO4; Cape Banza, Congo (CBR)	Lgrandis72CO4	AY213193
<i>Anceya giraudi</i> *	Gitaza, Burundi (95kw45)	Anceya1	AY213140
<i>Bathania howesi</i> *	Cameron Bay, Zambia (95kw17)	Bathania	AY213141
<i>Chytra kirki</i> *	Wonzye Point, Zambia (93kw01)	Chytra	AY213142
<i>Limnotrochus thomsoni</i> *	Myiamba, Zambia (95kw12)	Limnotrochus	AY213143
<i>Reymondia horei</i> *	Kasenga Point, Zambia (95kw04)	Reymondia	AY213144
<i>Spekia zonata</i> *	Gitaza, Burundi (93kw04)	Spekia	AY213145
<i>Stanleya neritinooides</i> *	Msamba, Zambia (95kw29)	Stanleya	AY213146
<i>Tanganyicia rufofilosa</i> *	Myiamba, Zambia (95kw13)	Tanganyicia	AY213147
<i>Tiphobia horei</i> *	Nkamba Bay, Zambia (95kw21)	Tiphobia	AY213148
<i>Cleopatra ferruginea</i> *	Kinango Dam, Kenya (93kw57)	Cleopatra	AY213149
<i>Melanoides tuberculata</i> *	Mazeras, Kenya (93kw55)	MsptuberKW	AY213150
<i>Melanoides admirabilis</i>	Malagarasi River Delta region, Rusesa, Tanzania (95em26)	Madmirabilis	AY213151
<i>Paramelania</i> sp. A (damoni-form <i>imperialis</i>)*	Nyanza Lac, Burundi (93kw36)	PdamoniimpKW	AY213152
<i>Paramelania</i> sp. B	Kigoma, Tanzania	ParamelaniaspB	AY213153

*Indicates sequence from West & Michel (2000); however this publication is the first assignment of Genbank numbers. Open nomenclature refers to designations in West *et al.* (2003) and Michel, *et al.* (2003).

Swahili is the common African language spoken all around Lake Tanganyika where this genus is endemic. Gender feminine.

Diagnosis: Oviparous ‘thiarid’ gastropod with broadly conical shell bearing cancellate, tuberculate sculpture; ovipositional gland in right side of head-foot; rachidian and lateral radular teeth weak, with small wings on rachidian tooth.

Description:

Shell (Figs 1–3, 11–13): Medium-sized, squat to elongate, shells (8–23 mm length) with 4–6 rounded whorls and impressed sutures. Distinctive cancellate and tuberculate sculpture (lacking ribbing, axial and spiral elements equal, forming nodules at intersections), often with whitish nodes. Major spiral elements of equal magnitude and colour, 4–5 visible on penultimate whorl, approximately 10 on the last whorl. 15–17 axial elements per adult whorl. Sculpture of basal half of whorl not markedly different from apical half; however, axial register is usually offset, and sometimes spiral sculpture dominates on this part of the shell. Minor spiral cords usually not present, occasionally very weakly developed on final half of adult whorl, or very rarely as thin thread between the two adapical major spiral cords. Microsculpture usually of similar magnitude in axial and spiral directions, often with a cancellate or lattice-like pattern. Imperforate. Aperture broadly ovate, mature specimens often with thickened pearly whitish or purple layers around apertural lip, sometimes flared. Slight modification of external sculpture and change of whorl trajectory at adulthood (usually downturn), marked by onset of determinate growth. Dark brown-purple, brown-black or occasionally white in colour, sometimes with purple-brown banding. Protoconch (Fig. 3) of 1–1.25 whorls with irregularly granulose surface, nucleus large, eccentric, axis of protoconch at angle to teleoconch coiling axis, sharp prosocline boundary with teleoconch.

Operculum (Fig. 4): Paucispiral to subspiral, dark brown when thick, light brown when thin.

Head-foot and internal anatomy: Gonochoristic, oviparous; males aphallate; females with closed pallial oviduct, unpigmented cili-

ated groove on the right side of the head-foot. Eyes at base of tentacles on papillae. Foot shield-shaped. Nerve ring zygoneurous on right side. See detailed description for *V. westae*.

Generic comparison: *Vinundu* can be distinguished from *Lavigeria* Bourguignat, 1888, with which it is often sympatric, by its regular, cancellate, tuberculate sculpture and lack of extensive adult modification in shells (changes in sculpture and orientation at onset of determinate growth). *Vinundu* and *Lavigeria* both have protoconchs with a granulose or wrinkled surface, with an initial coiling axis at a slight but distinct angle from the teleoconch coiling axis (Fig. 3). The protoconch/teleoconch junction is gradual in ovoviparous *Lavigeria*, but sharp in oviparous *Vinundu*. The latter has a light line on the right side of the head-foot, visible most clearly in females, in which it follows the course of a ciliated ovipositional groove ending in a small glandular pit (Fig. 5), whereas *Lavigeria* retains its brood in the pallial oviduct (Fig. 8B), and lacks a groove on the head-foot. Radulae of *Vinundu* and *Lavigeria* can be readily distinguished; *Vinundu* has a relatively long radular ribbon, more widely spaced teeth, and small wing-like projections on the rachidian teeth, which are only weakly angled, whereas *Lavigeria* teeth are more robust and closely spaced. Some species of *Lavigeria* have more cusps especially on the lateral teeth, teeth are more recurved from the radular ribbon, and rachidian central cusps are frequently squared and longer (see Michel, 2000: fig. 5, for five representative species).

***Vinundu westae* new species**
(Figures 1–10)

Lavigeria ‘Small Dark’ Michel, Cohen, West, Johnston & Kat, 1992: figs 1, 11 (l.h.s. figure: mapped distribution), tables 1, 2. *Lavigeria spinulosa*—Nakai *et al.*, 1997: 29 (not *Paramelania spinulosa* Bourguignat, 1885. Specimens not seen). *Lavigeria arenarum*—Bandel, 1998: 260, pl. 3, figs C, D (not *Paramelania arenarum* Bourguignat, 1888). Nov. gen. n. sp. Michel, 2000: figs 3–5. West & Michel, 2000: figs 1R, 3, 4, tables 1, 2. Allison, Paley, Ntakimazi, Cowan & West, 2000: table 3.6.

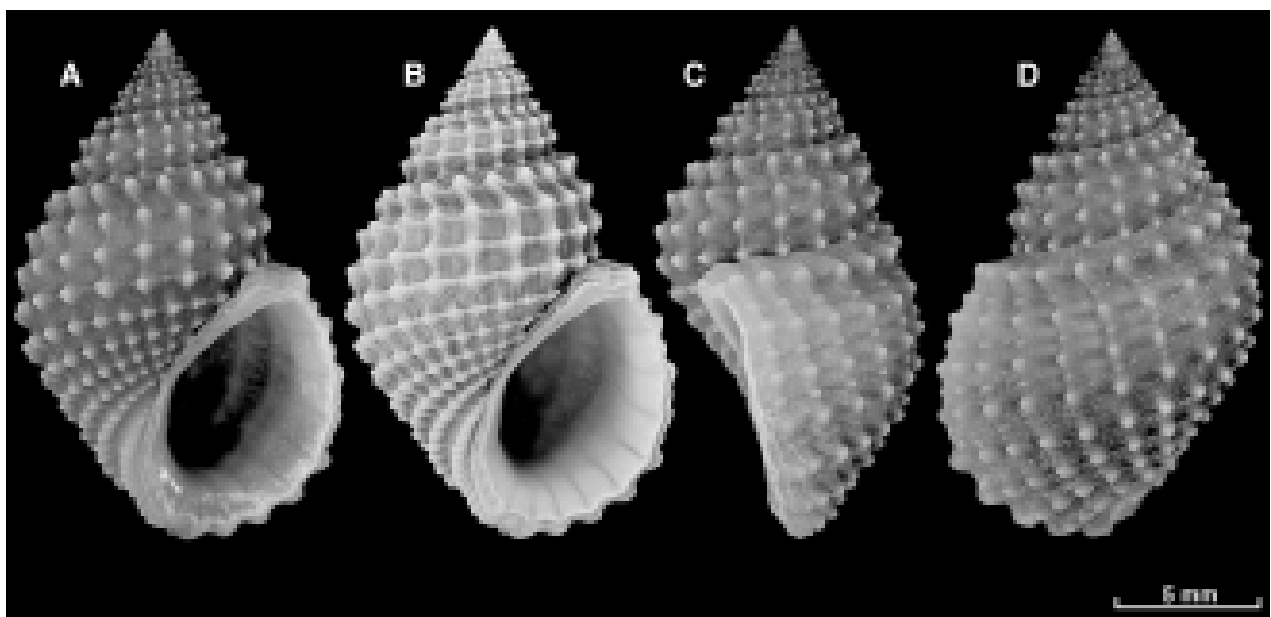


Figure 1. *Vinundu westae* new species, holotype from site BUKm29.8, BMNH 20030010. **A.** Apertural view, note lip thickening and slightly flared aperture. **B.** Apertural view, coated with ammonium chloride to emphasize sculpture. **C.** Side view; note limited adult modification of axial sculpture. **D.** Back view.

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Notes on synonymy: Complete synonymies have been given as far as possible for both *V. westae* and *V. guillemei*. An exception is the material listed under 'formes' of *Lavigeria nassa* (Woodward) in Leloup (1953). Leloup's attempted revision of *Lavigeria* was poor and many of the lots he identified consist of diverse morphologies, even when considered within his framework of 'formes'. Pending detailed examination and re-identification of the material he worked on it is impossible to give accurate synonymies here. Leloup figured details of sculptural patterns for his 'formes' of *Edgaria* (= *Lavigeria*) *nassa* and some of these under 'forme *spinulosa*' clearly represent *Vinundu* (e.g., pl. 8, fig. 3 C left-hand figure, D, E), but the specimens are not identifiable to species level from these alone.

Diagnosis: *Vinundu* with squat shell, round aperture, maximum shell width at midpoint of aperture, aperture greater than half shell height.

Shell (Figs 1, 2, 3A–C, E): Small to medium-sized (adults 8–15 mm), ovately conic with small spire, 4–5 whorls, impressed sutures (Figs 1, 2); cancellate, tuberculate sculpture. Dark

brown-purple, brown-black in colour, often whitish nodes, never spirally striped. Equal spiral and axial microsculpture (Fig. 3E). Imperforate. Aperture broadly ovate, mature specimens often with thickened pearly whitish or purple layers around apertural lip, very little or no flaring on maturity. Microstructure of three crossed-lamellar layers (West & Cohen, 1996). Protoconch of 1.0 whorl, 200–300 µm diameter, with irregularly granulose surface; nucleus large, excentric, with axis of protoconch at angle to teleoconch coiling axis and sharp prosocline boundary with teleoconch (Fig. 3A–C).

Operculum (Fig. 4B, C): Paucispiral, rarely subspiral, dark brown when thick, light brown when thin. Adults may have very thin opercula in some populations.

Head-foot (Fig. 5): Head-foot dark brown to black with mottling of lighter cream-coloured spots or sometimes orange or yellow spots, tentacles frequently banded dark and light. A ciliated groove on right side of head-foot leads from opening of pallial oviduct to small glandular ovipositor in head-foot in females. This groove is unpigmented or less pigmented than surrounding

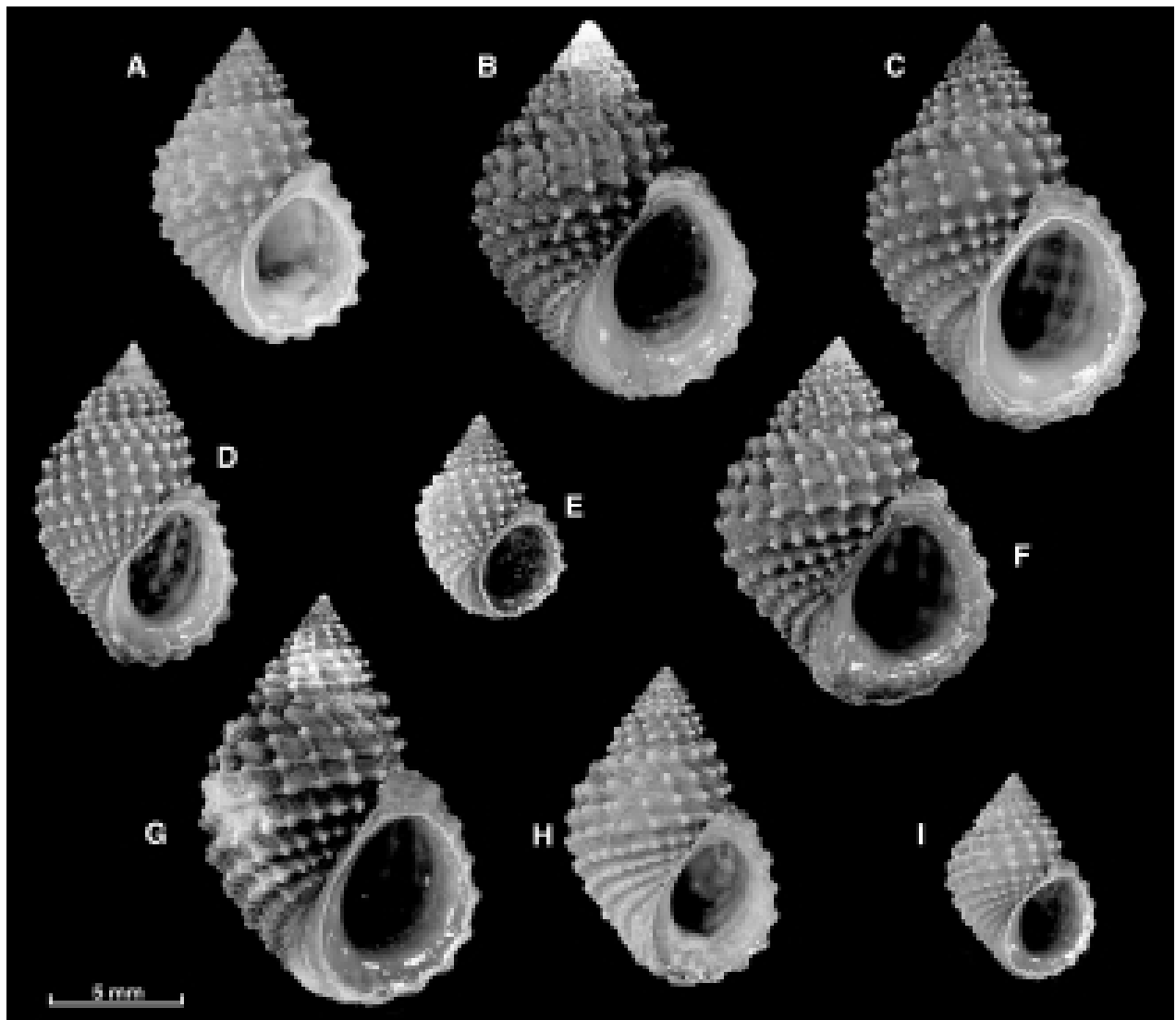


Figure 2. *Vinundu westae* new species, geographic variation. **A.** From site 90em3 Milila Island, Congo, BMNH 20030012. **B.** 89em7 Bemba 60–80', Congo (sequence site CO-3, Fig. 15, Table 1), BMNH 20030013. **C.** 87emBUkm29.8, Burundi (sequence site BU-1), BMNH 20030014. **D.** 90emT1 Kigoma, Tanzania, BMNH 20030015. **E.** 87em1 Kigoma, Tanzania, BMNH 20030016. **F.** 90em16, 60–80' Mahale, Tanzania, BMNH 20030017. **G.** 90em13 Isonga, Tanzania, BMNH 20030018. **H.** 91rb28, Zambia (near sequence site ZM-10) BMNH 20030019. **I.** 86mj25 Ikola, Tanzania, BMNH 20030020.

skin, and more distinct in females. Snout blunt, mouth orientated downward. Foot relatively large, shield-shaped (anterior wide and slightly curved, sides slightly constricted at anterior, posterior rounded to squared); sole unpigmented or pinkish, sometimes with yellow granulations on sole or margin. Anterior pedal gland present. Cephalic tentacles tapering, reaching beyond end of snout at full extension. Eyes at base of tentacles on papillae. Mantle unpigmented, margin moderately papillate, marginal papillae sometimes with dark or bright yellow spots.

Radula and buccal mass (Figs 6, 7): Radula taenioglossate, relatively long, narrow, with 90–110 rows of seven relatively small, widely spaced teeth. Rachidian and lateral teeth with little curvature, perpendicular to the radular ribbon. Rachidian tooth with wide, rounded central cusp flanked by two rounded lateral cusps characterized by small, wing-like lateral projections pointing towards marginal teeth (Fig. 6). Clavate inner marginal teeth mitten-shaped with large rounded central cusp, very small medial cusps and rudimentary outer cusp. Clavate outer marginal teeth scoop-shaped and ringed with 5–10 equal-sized

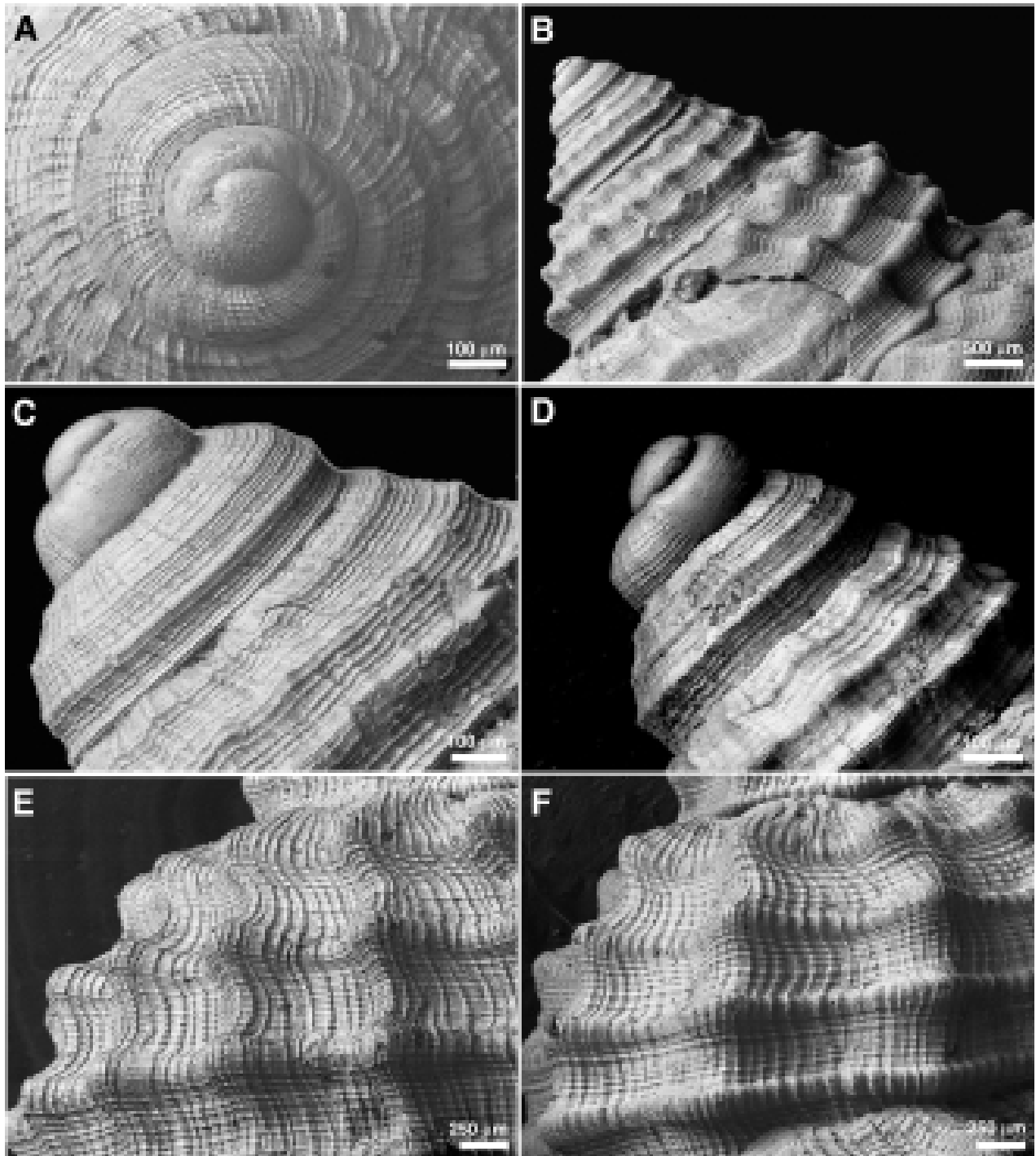


Figure 3. Protoconchs of *Vinundu*. **A–C.** *V. westae* from type locality, BUkm29.8. Note predation scar on juvenile shell. **D.** *V. guillemei* from site 86mj24 Kibwesa, southern Mahale, Tanzania. Note sharp discontinuity between protoconch and teleoconch. **E.** Microsculpture of *V. westae* from type locality, BUkm29.8. **F.** Microsculpture of *V. guillemei* from 86mj24. Note regularity of axial and spiral microsculpture.

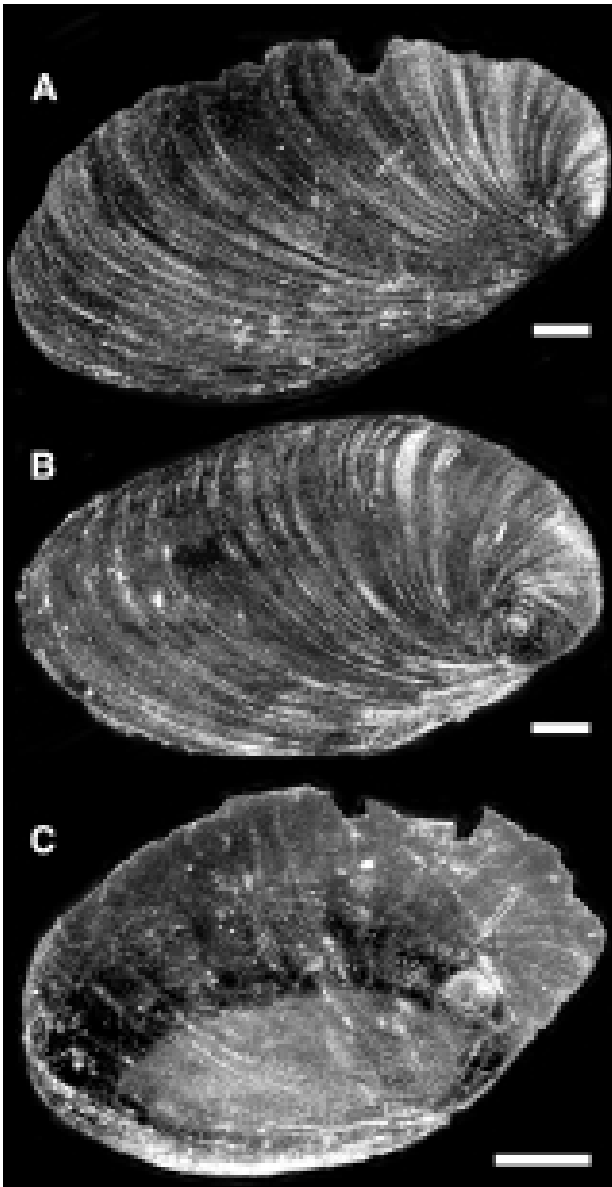


Figure 4. Opercula of *Vinundu*. **A.** *V. guillemei* from 95em11 Mutondwe Island, Zambia. **B.** *V. westae* from type locality, Bu29.8, Burundi. **C.** *V. westae* from 89em9 Luhanga, Congo. Scale bars = 0.5 mm.

rounded cusps. Alary processes relatively wide (Fig. 7). Oesophageal pouches posterior to nerve ring (Fig. 7), coiled tubes of salivary ducts above and anterior to nerve ring, but ramose glands may also be found posterior to buccal ganglia (Fig. 7).

Mantle cavity organs (Fig. 5): Gill filament triangular (deltoid) and slightly more acute (fin-shaped) at anterior end, approximately equilateral with flexible folds along the middle and major part of ctenidium, and acutely peaked with an extension of the lateral ridge (fin-shaped) at posterior end (Fig. 5). Osphradium a thin, unbranched cord with pigmented sidelines lying in a groove extending three-quarters the length of ctenidium. Hypobranchial gland with moderate glandular development.

Reproductive organs (Fig. 8): Gonochoristic, oviparous; males aphyllate; females with closed pallial oviduct (Fig. 8A) containing a spermatophore bursa. Oviduct floor folded, rugose, thickened, with deep oviducal groove, opening via single, relatively

small, slit facing away from rectum. Sperm gutter just inside pallial oviduct against lateral wall (next to rectum, right side), opening to spermatophore bursa. Spermatophore bursa (sb) extends half to two-thirds length of pallial oviduct, with folded and rugose interior surface, occasionally containing white or bright green spermatophores; ends in a blind tube, without opening to proximal end of oviducal groove. An infolding into brood chamber from oviduct wall continues along lateral wall and around proximal end of pallial oviduct, terminating in small seminal receptacle. Seminal receptacle is a blind tube often filled with sperm, with its opening directed proximally towards opening of oviduct. Male pallial gonoduct simple, its proximal end an expanded cavity with longitudinally or laterally folded floor (Fig. 8C). In distal third, gonoduct constricted, folds are transverse, floor somewhat thickened. The textures and occasionally colours of the upper and lower parts of the male gonoduct differ, but both regions appear to be glandular. The lower chamber may contain the glandular tissue that secretes the casing for the spermatophore.

Visceral organs: Stomach with two chambers: posterior or main chamber, and anterior chamber or style sac with pear-shaped to round crystalline style (Fig. 9). Kidney large, extending into pallial roof, sometimes purple or indigo blue (Fig. 5). Heart with thin-walled auricle, and thick-walled ventricle with short aortic trunk. Gonad impressed over digestive gland in uppermost whorls of body. Female gonadal tissue with lumpy, sometimes green and blue, ovarian tissue. Male gonadal tissue fine-grained, cream coloured.

Nervous system (Fig. 7): Nerve ring well developed, zygoneurous on right side.

Parasitism: Digenean trematode parasites commonly found in gonad tissue, in heavy infections cercaria may also be found in pallial oviduct.

Habitat and distribution: Found on hard substrates such as cobbles, boulders, stromatolites and shell lags, moderate to deep, 10–50 m, but occasionally as shallow as 1 m at some sites. Generally rugophilic, cryptic when shallow. Endemic to Lake Tanganyika, present in all sampled regions, though may be locally patchy, of Burundi, Zambia and Congo, with small gap in southern Tanzania (Fig. 10).

Etymology: Named for colleague and friend Dr Kelly West who shared her knowledge and provided much practical support over our coeval years of study of the gastropods of Tanganyika and who is continuing work on conservation of East African freshwaters.

Type locality: Burundi, kilometre marker 29.8 south of Bujumbura, first major rocky shoreline, coordinates $-3.640, 29.361$ or $3^{\circ}38'25''$ S, $29^{\circ}21'40''$ E, 20 m water depth. Stromatolite-covered rocks and boulders.

Type material: Holotype: BMNH 20030010 (dry shell from type locality; Fig. 10). Paratypes (all from type locality): BMNH 20030011 (5 dry shells); BMNH 20030014 (figured specimen, dry shell, Fig. 2C); BMNH 20030025 (1 broken shell and body in ethanol); MNHN (5 dry shells, 1 unbroken shell in ethanol, registered by name); USNM 1006828 (1 dry shell); IRSNB 29.709 (1 dry shell); NMK (2 dry shells); NMT FWM 19 (1 dry paratype shell); ZMAN 4.02.016 (1 dry shell).

Other material examined: Deposited voucher material: site coordinates given on first mention only. BMNH: 2 soft parts and broken shells in 70% ethanol (BMNH 20030026) and 2 dry shells

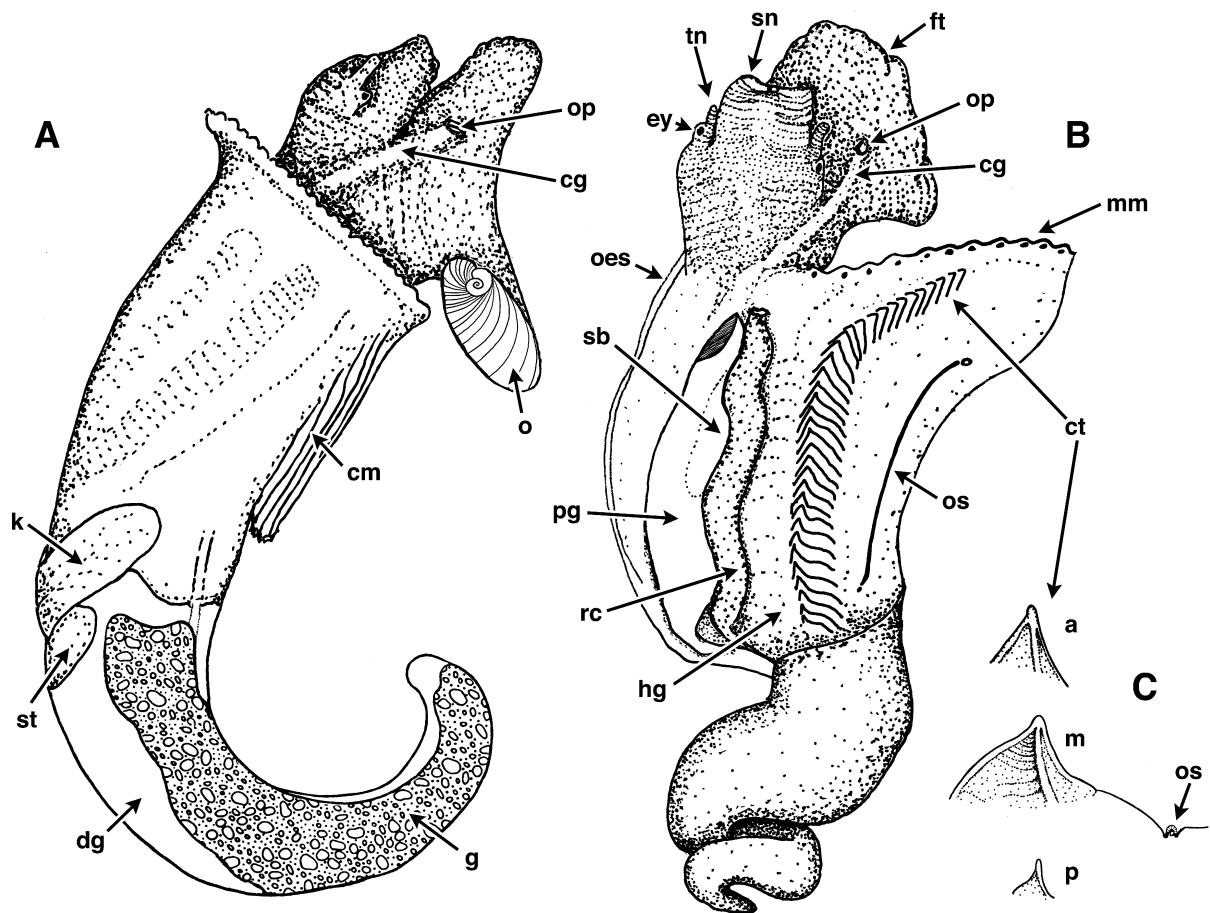


Figure 5. Gross anatomy of *Vinundu westae*. **A.** Right side of animal extracted from shell. Note unpigmented ciliated groove for oviposition. **B.** Mantle cavity dissected open, cut on animal's left side under osphradium, mantle reflected to the right. Abbreviations: cg, ciliated groove; cm, columellar muscle; dg, digestive gland; oes, oesophagus; ey, eye; ft, foot; g, gonad; hg, hypobranchial gland; k, kidney; mm, mantle margin; o, operculum. op, ovipositor; os, osphradium; pg, pallial gonoduct; rc, rectum; sb, spermatophore bursa; sn, snout; st, stomach; tn, tentacle.

(BMNH 20030023) from Luhanga, south of Uvira, Congo (89em9, -3.600, 29.150); 1 shell from Mlila Island, north of Kalemie, Congo (90em3, -5.617, 29.417) (BMNH 20030012, Fig. 2A); 1 shell from Bemba, Congo (89em7, -3.600, 29.350) (BMNH 20030013, Fig. 2B); 1 shell from south side of Kigoma Bay, Tanzania (90emT2-HTP, -4.890, 29.6101) (BMNH 20030015, Fig. 2D); 1 shell from Kigoma Bay, Tanzania (87em1, -4.880, 29.620) (BMNH 20030016, Fig. 2E); 1 shell from Mahale Park, Tanzania (90em16, -6.250, 29.733) (BMNH 20030017, Fig. 2F); 1 shell from Kisonga, Tanzania (90em13, -6.467, 30.150) (BMNH 20030018, Fig. 2G); 1 shell from Kombe, Zambia (91rb28, -8.783, 31.017) (BMNH 20030019, Fig. 2H); 1 shell from near Ikola, Tanzania (86mj25, -6.767, 30.400) (BMNH 20030020, Fig. 2I); 3 shells from south of Malagarasi Delta, Tanzania (90em24, -5.300, 29.783) (BMNH 20030021); 3 shells from km32.6, Burundi (86mj12, -3.650, 29.333) (BMNH 20030022); 3 shells from km39.5, Burundi (87emkm39.5, -3.700, 29.340) (BMNH 20030024). MNHN: 2 soft parts and broken shells in 70% ethanol from Luhanga, Congo (89em9); 1 shell from Mlila Island, north of Kalemie, Congo (90em3); 2 shells from Luhanga, Congo (89em9); 1 shell from Kigoma Bay, Tanzania (87em1); 1 shell from Mahale Park, Tanzania (90em16); 1 shell from Kisonga, south of Mahale Park, Tanzania (90em13); 1 shell from Bemba, Congo (89em7); 1 shell from Kombe, Zambia (91rb28); 3 shells from south of Malagarasi Delta, Tanzania (90em24); 3 shells from Burundi km32.6 (Bukm32.6); 3 shells from Burundi km39.5 (87emkm39.5)

(vouchers registered by name). Additional material: 67 lots from 38 sites, 842 shell specimens in author's collection, descriptive anatomy from multiple specimens from type locality, as well as Uvira, Congo and Kigoma, Tanzania.

Remarks: For comparison of the two species, see Remarks under *V. guillemei*. Nakai, Kusuoka & Yamasaki (1997) misidentified this species as *L. spinulosa* (Bourguignat), a distinctive species of *Lavigeria*, with unusually regular nodulose ornament and a very thin white wash to the adult aperture (Fig. 11G, H). Bandel (1998) identified *V. westae* as *L. arenarum* (Bourguignat), presumably based on Bourguignat's inaccurate figures. The latter species is known from only two very worn syntype specimens that are clearly assignable to *Lavigeria*. These shells have whorls dominated by axial sculpture and are almost flat-sided in their upper parts giving a very different, more conical shape. Both specimens show adult apertural modifications (Papadopoulos, Todd & Michel, 2004), such as downward deviation of the aperture and crowded, irregular, axial sculpture that are lacking in *Vinundu*. Additionally, both specimens have prominent brown/purple and grey spiral colour patterns and lack a purple coloration to the inside of the aperture. Bandel (1998: 259) supposed that specimens of *V. westae* lose their purple apertural coloration rapidly after death so substantiating his identification of this species with *L. arenarum*. Generally, however, dead shells retain their dark colour until they become completely taphonomically bleached.

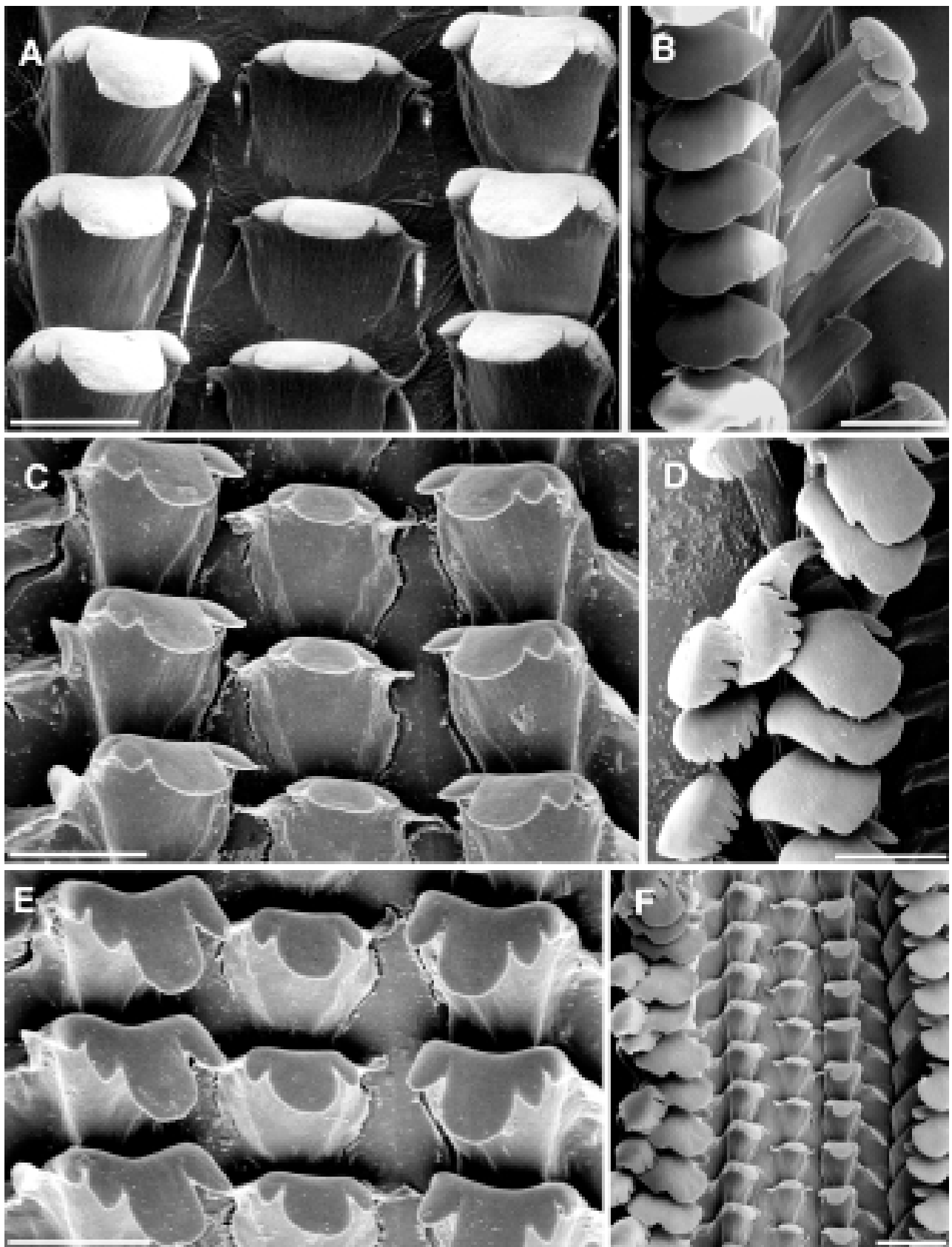


Figure 6. Radulae of *Vinundu*. **A, B.** *V. guillemei*, rachidian and two lateral teeth (**A**), and right side marginal teeth (**B**) from site 95em13 Kipili, Tanzania. **C, D.** *V. westae* rachidian and two lateral teeth (**C**), and left side marginal teeth (**D**) from type locality, BUkm29.8. **E.** Same *V. westae* rachidian and lateral teeth tilted 20° to allow more complete view of the surface of the rachidian teeth, as the teeth are short and orientated perpendicular to the horizontal plane. **F.** Complete view across radular ribbon for *V. westae* from type locality. Scale bars: **A, C, E** = 50 µm; **B, D, F** = 100 µm.

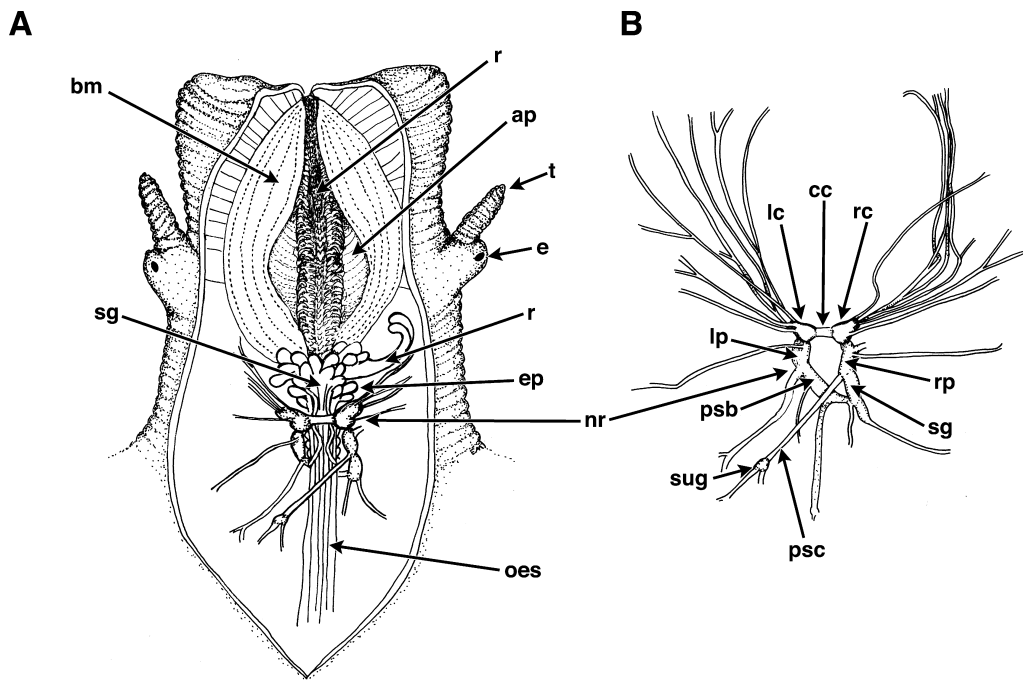


Figure 7. *Vinundu westae*. **A.** Dissection of head-foot. Abbreviations: ap, allary process; bm, buccal mass; e, eye; ep, oesophageal pouch; oes, oesophagus. nr, nerve ring; r, radula; sg, salivary glands; t, tentacle. **B.** Nervous system. Abbreviations: cc, cerebral commissure; lc, left cerebral ganglion; rc, right cerebral ganglion; lp, left pleural ganglion; rp, right pleural ganglion; sg, subesophageal ganglion; psc, pleuro-superesophageal connective; sug, supra esophageal ganglion; psb, pleuro-subesophageal connective. Not shown: pedal ganglia and statocysts below nerve ring.

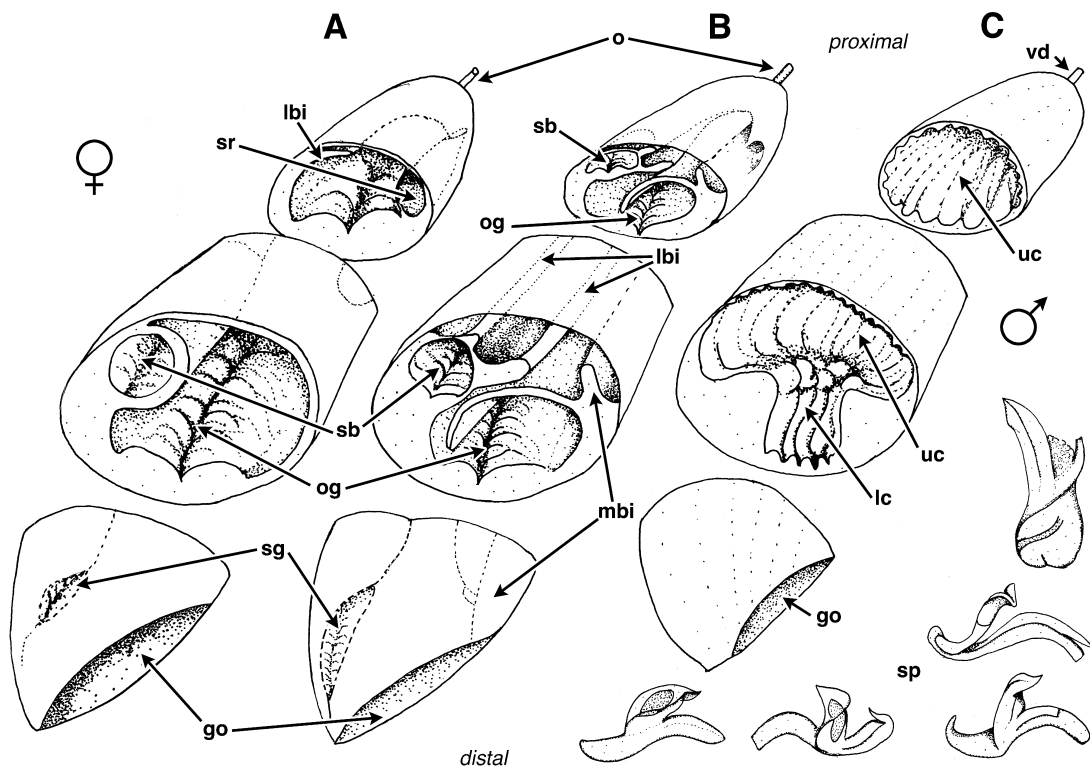


Figure 8. Gonoducts of *Vinundu westae* and *Lavigeria* sp. **A.** Three-dimensional reconstruction of pallial oviduct of *V. westae*. Note the limited infoldings of the oviduct wall and well-developed seminal receptacle. **B.** Pallial oviduct of *Lavigeria* sp. B for comparison. Note extensive development of infoldings of the oviduct wall that function to hold in brood of young snails. **C.** Male *V. westae* gonoduct. Abbreviations: go, gonoduct opening; lc, lower chamber of male gonoduct; lbi, lateral broodchamber (or oviduct) infolding; o, oviduct; og, oviducal groove; mbi, medial broodchamber infolding; sr, seminal receptacle; sb, spermatophore bursa; sg, sperm gutter; sp, spermatophores (drawn from material dissected from female gonoduct of *V. westae*); uc, upper chamber of male gonoduct; vd, vas deferens.

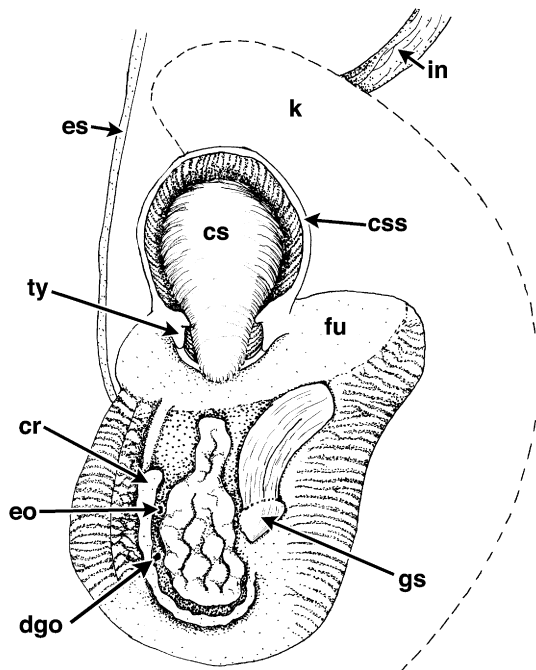


Figure 9. Stomach of *Vinundu westae*. Abbreviations: k, kidney; fu, fundus; gs, gastric shield; dgo, digestive gland opening; eo, esophageal opening; cr, crescent ridge; ty, edge of typhsole; cs, crystalline style; css, crystalline style sac; es, oesophagus.

***Vinundu guillemei* (Martel & Dautzenberg, 1899)**
(Figures 3D, F, 4A, 6A, B, 11–14)

Nassopsis guillemei Martel & Dautzenberg, 1899: 172–173, pl. 8, figs 12, 13 (Mpala, Democratic Republic of Congo; lectotype and paralectotype designated herein, see below, MNHN).

Edgaria guillemei—Ancey, 1907: 252 (listed).

Nov. gen. [*Nassopsis*] *guillemei*—Michel, 2000: figs 3, 5, table 1.

Nov. gen. *guillemei*—West & Michel, 2000: fig. 1T (copy of fig. 1 of West & Cohen, 1994).

New genus n. sp. 'guillemei'—Alin, Cohen, Bills, Gashagaza, Michel, Tiercelin, Martens, Coeveliers, Mboko, West, Soreghan, Kimbadi & Ntakimazi, 2000: appendix 1 (listed).

Nassopsis crassilabris—Martel & Dautzenberg, 1899: 171–172, pl. 8, figs 10, 11 (Original material examined, MNHN. Not *Paramelania crassilabris* Bourguignat, 1885).

Edgaria crassilabris—Smith, 1904: 91 (BMNH 93.5.17.14, examined). Pilsbry & Bequaert, 1927: 329 (original material examined, ANSP 117876, 132256). Darteville & Schwetz, 1948: 43, 76–77 (in part for each; listed in synonymies of this species. Not *Paramelania crassilabris* Bourguignat, 1885).

Edgaria nassa forme *spinulosa*—Leloup, 1953: 173–174 (in part, not pl. 8, fig. 3A–C nor pl. 13, fig. 9A–E. Listed in synonymy. Not *Paramelania spinulosa* Bourguignat, 1885).

Lavigeria spinulosa 'long' Nakai, Kusuoka & Namasaki, 1997: 29 (identification uncertain, not *Paramelania spinulosa* Bourguignat, 1885).

Lavigeria 'Tall Dark' (LTDA TAN) Michel, Cohen, West, Johnston & Kat, 1992: figs 1, 11 (l.h.s. figure: mapped distribution), tables 1, 2.

Lavigeria nassa form *giraudi*—West & Cohen, 1994: fig. 1T (not *Paramelania giraudi* Bourguignat, 1885).

Lavigeria sp. West & Cohen, 1996: fig. 1F (examined).

Diagnosis: *Vinundu* with high-spired shell, aperture slightly elongated and expanded at base, maximum shell width at base of aperture, aperture less than half shell height.

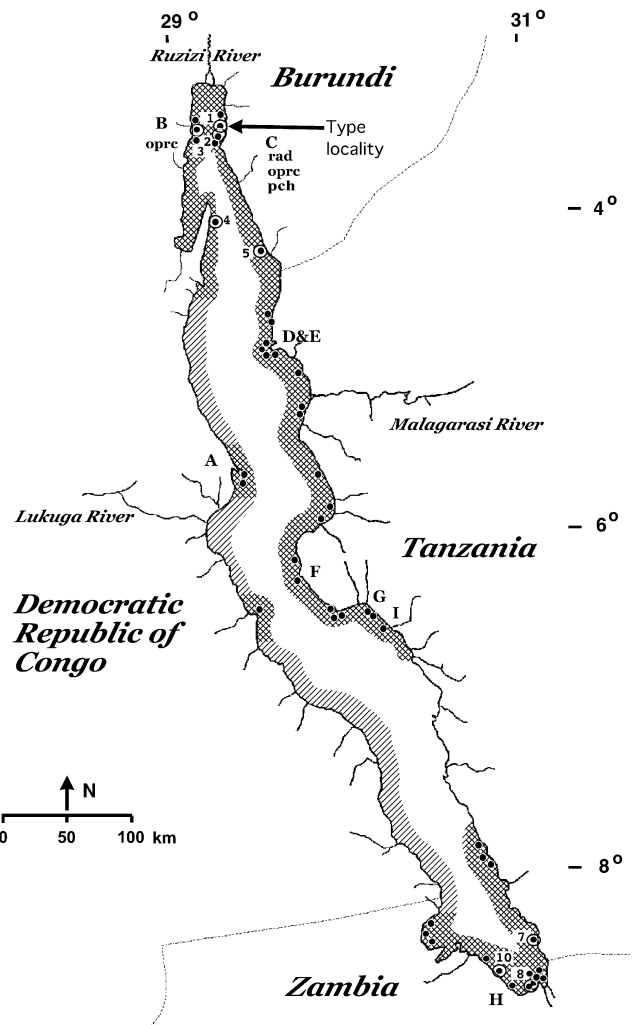


Figure 10. Distribution of *Vinundu westae*. Sites for figured specimens (Fig. 2) indicated with corresponding letters. Sites for sequenced specimens circled and numbered. Individual sites not specified in areas of dense sampling around Uvira Congo, Kigoma, Tanzania and Mpulungu, Zambia. Inferred total distribution indicated with shading; darker shading indicates areas broadly sampled by the author where *V. westae* occurs on suitable substrates; lighter shading in Congo indicates presumed distribution as this area has suitable substrates, *V. westae* occurs on the few places sampled; however, it has not been sampled with SCUBA. Figured radula, operculum and protoconch from type locality (Burundi km29.8).

Shell (Figs 3D, F, 11–13): Medium-sized (adults 15–23 mm), high-spired, ovately conic with 4–5 whorls, impressed sutures (Figs 11–13), cancellate tuberculate sculpture. Purple to dark brown; some populations white or cream with fine brown to orange stripes on spiral cords; occasional individuals all white. Equal spiral and axial microsculpture (Fig. 3F). Imperforate. Aperture broadly ovate; mature specimens often with thickened pearly whitish or purple layers around apertural lip; aperture somewhat to notably flared. Protoconch of 1.25 whorls, 180–250 µm diameter, with irregularly granulose surface, nucleus large, excentric; axis of protoconch at angle to teleoconch coiling axis; sharp prosocline boundary with teleoconch (Fig. 3D).

Operculum (Fig. 4A): Subspiral, dark brown.

Head foot and internal anatomy: Without discernible differences from *V. westae* described above.

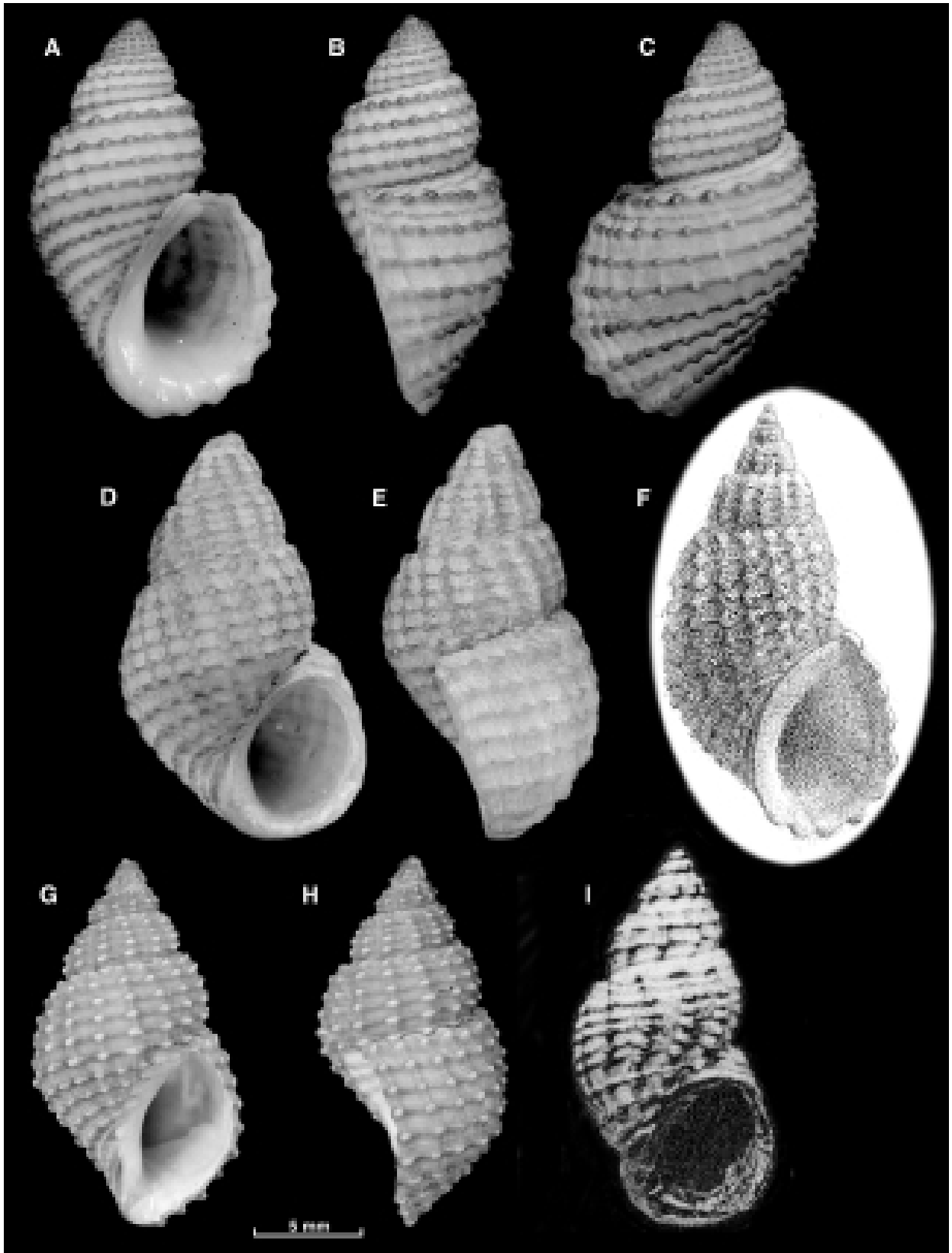


Figure 11. A-C. *Vinundu guillemei* (Martel & Dautzenberg) lectotype MNHN. D-I. Specimens of gastropods that are not *Vinundu*, but whose names have been misapplied to specimens currently recognized to be *Vinundu guillemei*. D, E. *Lavigeria crassilabris* (Bourguignat 1885) syntype (MNHN) figured in Bourguignat, 1888: pl. 16, figs 15, 16, locality Mlilo? F. Drawing reproduced from Bourguignat, 1888: pl. 16, fig. 16, which should be the shell shown in D and E (based on label and individualistic marks), but showing artistic license in changed proportions, added spire tip, added apertural margin and exaggerated tuberculate sculpture. This is common in Bourguignat's illustrations of his specimens. G, H. *Lavigeria spinulosa* (Bourguignat, 1885) syntype (MNHN), locality Mlilo. I. Undescribed species of *Lavigeria* reproduced from Leloup, 1953: pl. 8, fig. 9D (right-hand specimen) as '*nassa forme spinulosa*'.

VINUNDU, NEW GENUS FROM LAKE TANGANYIKA

Habitat and distribution: Restricted to hard substrates including cobbles, boulders and stromatolites, at moderate depths, 10–50 m. Endemic to Lake Tanganyika, common along the Congolese, Tanzanian and Zambian coastlines, but not known from Burundian or northern Congolese (Uvira region) coast (Fig. 14).

Type material: Fischer-Piette (1950: 167) recorded the illustrated syntype (Martel & Dautzenberg, 1899: pl. 8, figs 12, 13) as the

‘holotype’ and another unfigured syntype as ‘paratype’ (both in MNHN collections) but it is debatable whether this constitutes a valid lectotype designation under Art. 74.5 of the ICZN code (ICZN, 1999). Both specimens were collected from Mpala, D.R. Congo by Guillemé. Additional probable syntypes are present in the Martel collection in IRSNB (Leloup, 1953: 173 lists additional specimens collected by Guillemé). To eliminate all ambiguity, and to stabilize the confused systematics and nomenclature of this group, I here formally designate the figured syntype of

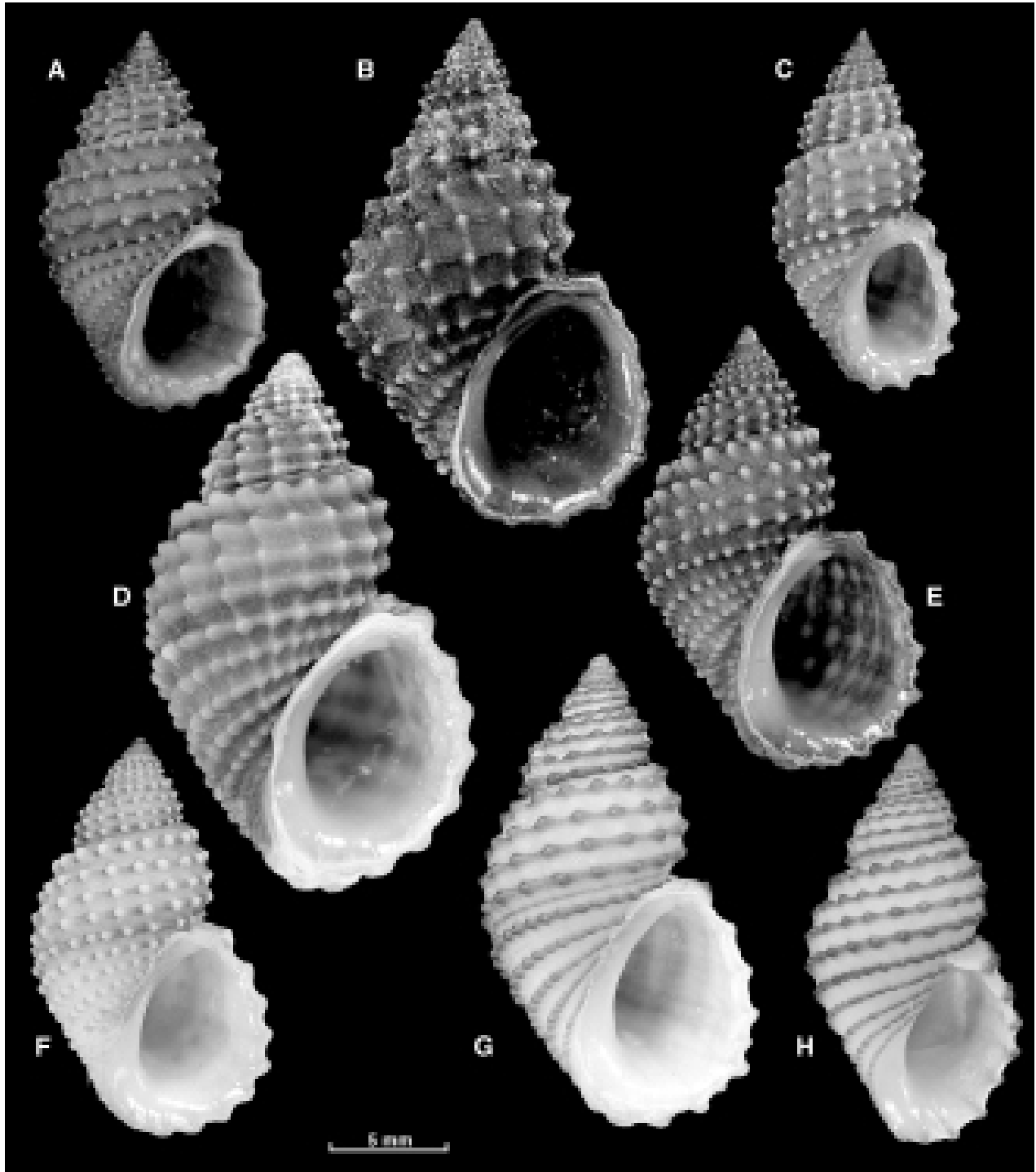


Figure 12. *Vinundu guillemei*, geographic variation. **A.** 90emT1 Kigoma, Tanzania, BMNH 20030027. **B.** 90em15 Mahale, Tanzania, BMNH 20030028. **C.** 86mj24 105' Kibwesa S. Mahale, Tanzania. **D.** 91rb26 Mutondwe Island, Zambia (sequence site ZM-9, Fig. 15, Table 1), BMNH 20030030. **E.** 86mj32 Kizumbi, Tanzania, BMNH 20030031. **F.** 91rb24 Chiluta Cliffs, Zambia (sequence site ZM-8), BMNH 20030032. **G, H.** adult and juvenile, 91rb11 south of Lufubu, Zambia (near sequence site ZM-10), BMNH 20030033.

Martel & Dautzenberg (height 19 mm, listed by Fischer-Piette as holotype), refigured herein (Fig. 11A–C), as lectotype of *Nassopsis guillemei*. The unfigured syntype in MNHN becomes a paralectotype.

Other material examined: Deposited voucher material: Site coordinates given on first mention only. BMNH: 2 dry shells and 3 pre-

served soft parts in ethanol from Jakobsen's Beach, south of Kigoma, Tanzania (JKB, -4.910, 29.590) (BMNH 20030040 and BMNH 20030041 respectively); 1 shell from Kigoma Bay, Tanzania (90emT2-HTP, -4.890, 29.6101) (BMNH 20030027, Fig. 12A); 1 shell from Salambulu, Tanzania (90em15, -6.433, 29.900) (BMNH 20030028, Fig. 12B); 1 shell from Kalya, Tanzania (86mj24, -6.550, 30.200) (BMNH 20030029); 1 shell



Figure 13. *Vinundu guillemei*, geographic variation, continued. **I, J.** Adult and juvenile. 86mj36 Inangu Peninsula, Zambia, BMNH 20030034. **K.** 91rb3 Kombe, Zambia, BMNH 20030035. **L.** 91pv1 Kamambwa, Congo, BMNH 20030036. **M.** 86mj37 Chishiki, Zambia, BMNH 20030037. **N.** 91pv1 Kamambwa, Congo, note colour and shape variation compared with **L.**, BMNH 20030036. **O.** 90em1 Kibige Island, Congo, BMNH 20030038. **P, Q.** Colour variants. 90em3 Mlila Island, Congo, BMNH 20030039.

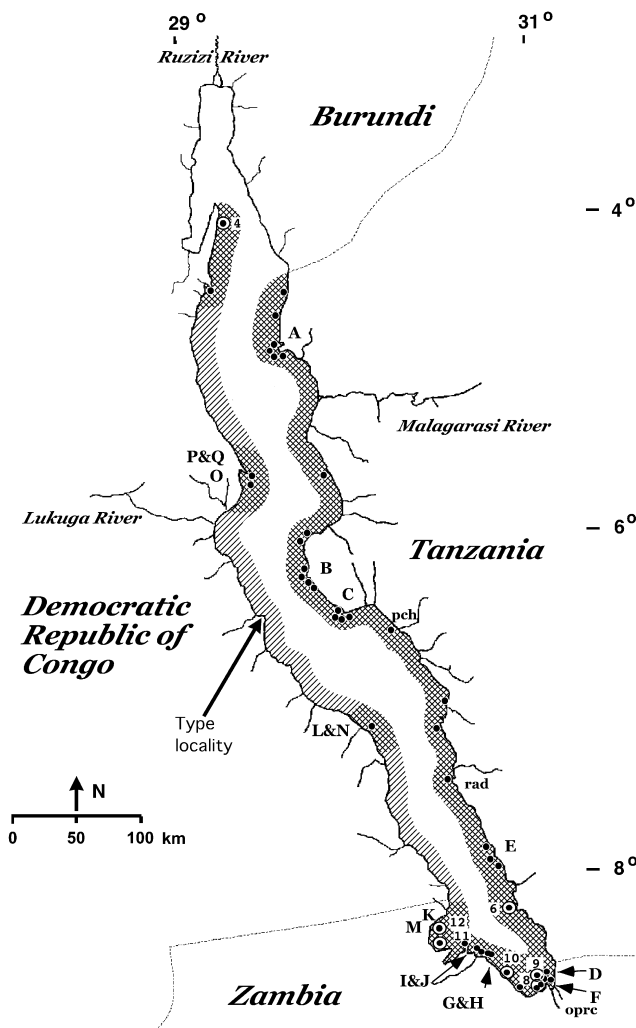


Figure 14. Distribution of *Vinundu guillemei*. Sites for figured specimens (Figs 12, 13) indicated with corresponding letters. Sites for sequenced specimens circled and numbered (southernmost Tanzanian site given ZM-prefix for regional clarity on tree). Individual sites not specified in areas of dense sampling around Uvira (Congo), Kigoma (Tanzania) and Mpulungu (Zambia). Inferred total distribution indicated with shading – darker shading indicates areas broadly sampled by the author where *V. guillemei* occurs on suitable substrates, lighter shading in Congo indicates presumed distribution as this area has suitable substrates; *V. guillemei* occurs in the few places sampled; however, it has not been sampled with SCUBA. Site for figured radula indicated 'rad', for figured operculum indicated 'oprc', for figured protoconch indicated 'pch'.

from Muntondwe (Crocodile) Island, north of Mpulungu, Zambia (91rb26, –8.700, 31.117) (BMNH 20030030, Fig. 12D); 1 shell from southern Tanzania (86mj32, –7.870, 30.790) (BMNH 20030031, Fig. 12E); 1 shell from Chiluta Cliffs, Zambia (91rb24, –8.733, 31.167) (BMNH 20030032, Fig. 12F); 2 shells from south of Lufubu River, Zambia (91rb11, –8.567, 30.783) (BMNH 20030033, Fig. 12G, H); 2 shells from Inangu, Zambia (86mj36, –8.490, 30.670) (BMNH 20030034, Fig. 13I, J); 1 shell from Katete, Zambia (91rb3) (BMNH 20030035, Fig. 13K); 2 shells from Kigambwa, Congo (91pv1, –7.217, 29.488) (BMNH 20030036, Fig. 13L, N); 1 shell from southern Tanzania (86mj37, –8.360, 30.470) (BMNH 20030037, Fig. 13M); 1 shell from Kibige Island north of Kalemie, Congo (90em1, –5.667, 29.417) (BMNH 20030038, Fig. 13O); 2 shells from Mlila Island north of Kalemie, Congo (90em3, –5.617, 29.417) (BMNH 20030039,

Fig. 13P, Q). MNHN: 3 preserved soft parts and broken shells in ethanol and 2 dry shells from Jakobsen's Beach south of Kigoma, Tanzania (JKB); 1 dried shell from Kigoma Bay (90emT2); 1 shell from Salambulu north of Kibwesa, Tanzania (90em15); 1 shell from Kalya, Tanzania (86mj24); 1 shell from Muntondwe (Crocodile) Island, north of Mpulungu, Zambia (91rb26); 1 shell from southern Tanzania (86mj32); 1 shell from Chiluta Cliffs, Zambia (91rb24); 1 shell from south of Lufubu River, Zambia (91rb11); 1 shell from southern Tanzania (86mj37); 1 shell from Kibige Island north of Kalemie, Congo (90em17); 1 shell from Mlila Island north of Kalemie, Congo (90em3); 1 shell from Tembwe, Congo (91pv2, –6.533, 29.483); 1 shell from Cape Banza (CBR, –5.667, 29.417) (all registered by name and location). USNM: 2 preserved soft parts in ethanol and 1 dried shell from Jakobsen's Beach south of Kigoma, Tanzania (JKB) (USNM 1006832, USNM 1006829); 1 shell from southern Tanzania (86mj33, –7.910, 30.830) (USNM 1006830); 1 shell from Mlila Island, north of Kalemie, Congo (90em3) (USNM 1006831). IRSNB: 2 preserved soft parts in ethanol and 1 shell from Jakobsen's Beach, Kigoma, Tanzania (JKB); 1 shell from southern Tanzania (86mj33); 1 shell from Mlila Island, north of Kalemie, Congo site (90em3) (all under registration IRSNB I.G. n° 29.709). ZMAN: 1 shell from Jakobsen's Beach, Kigoma, Tanzania (JKB); 1 shell from southern Tanzania (86mj33); 1 shell from Mlila Island, north of Kalemie, Congo (90em3). NMK: 1 shell from Jakobsen's Beach, Kigoma, Tanzania (JKB); 1 shell from southern Tanzania (86mj33); 1 shell from Mlila Island, north of Kalemie, Congo (90em3); NMT – 1 shell from Jakobsen's Beach, Kigoma, Tanzania (JKB) (NMT FWM17); 1 shell from southern Tanzania (86mj33) (NMT FWM18); 1 shell from Mlila Island, north of Kalemie, Congo (90em3) (NMT FWM16). Additional material: 75 lots containing 830 specimens from 50 sites for shell specimens from the author's collections, anatomical material from Kigoma, Tanzania and Mpulungu, Zambia.

Remarks: The two species in this new genus can be distinguished by their relative spire heights, *V. guillemei* is relatively high spired, whereas *V. westae* is comparatively squat with a smaller spire. Generally, *V. westae* has four spiral elements above the suture on the penultimate whorl, whereas *V. guillemei* has five. Some individuals or populations of *V. guillemei* are white or light coloured with fine purple and brown spiral colour bands coinciding with the spiral ornament, whereas *V. westae* never shows banding, is generally darker in overall colour and frequently has a purple apertural lining. In addition, *V. guillemei* generally has a heavier operculum than *V. westae*. In many places these two species are sympatric; when both are present *V. westae* is generally the smaller.

Martel & Dautzenberg (1899) illustrated a dark coloured, unbanded, specimen of *V. guillemei* (pl. 8, figs 10, 11) under the name *Nassopsis crassilabris* Bourguignat, in the same paper in which they described and figured *N. guillemei*. This misidentification of Bourguignat's species has been followed by other authors (e.g. Smith, 1904; Pilsbry & Bequaert, 1927), undoubtedly due to the very inaccurate and misleading illustration of *crassilabris* given in Bourguignat (1888: pl. 16, figs 15, 16; reproduced here as Fig. 11F). The figure exaggerates the relative height of the last whorl and the scalloping of the outer lip and has a remarkable coincidental resemblance to *V. guillemei*, a species that had yet to be collected when Bourguignat made his studies, as no specimens are found in his collections. Bourguignat's *Paramelania crassilabris*, which Martel & Dautzenberg referred to as *N. crassilabris*, is actually a distinct species of *Lavigeria*, type specimens of which are very different from that illustrated (E. Michel & J. A. Todd, unpublished observations). An abraded specimen [inferred to be from the type locality, Mlilo (now Moliro), Congo, see Bourguignat, 1885] is illustrated here (Fig. 11D, E) for comparison.

This species, *L. crassilabris*, shows an increase in number of major spirals through growth as intercalated spirals increase in prominence until they attain the size of primary spirals; this pattern is typical of *Lavigeria*, but not of *Vinundu*. The adult shell has a downward-deflected aperture which is internally thickened and reduced in size, compared with the upward and outward-flaring lip developed in *V. guillemei* (see Fig. 11B).

Leloup (1953) synonymized *Nassopsis guillemei* under his *Edgaria nassa* forme *spinulosa* Bourguignat, 1885, a taxon otherwise consisting of a heterogeneous assemblage of *Lavigeria* species, including an undescribed species with elongate whorls and a superficially similar gross morphology (Fig. 11I). A sub-adult specimen referable to *L. spinulosa* (Bourguignat) is illustrated (Fig. 11G, H) for comparison with *guillemei*. This species is known from very few shells but has a primary spiral ontogeny typical of *Lavigeria*, and further differs from *V. guillemei* in its less pronounced cancellate sculpture and thin, white apertural lining. In both *L. crassilabris* and *L. spinulosa*, spiral microsculpture is more irregular in spacing and prominence than in *Vinundu* species and axial microsculpture is much weaker.

The type locality for *V. guillemei*, Mpala, Congo, has not been re-sampled, thus the radulae of conchologically very similar shells from Kipili Islands, Tanzania, are illustrated here (Fig. 6A, B). Some specimens that conchologically fall within the diagnosis of *V. guillemei* presented here show some radular differences, but more sampling, in concert with molecular analyses, is needed to determine whether these differences are taxonomically significant.

MOLECULAR PHYLOGENETIC RELATIONSHIPS

The strict consensus of 188 parsimony trees (tree length 1451 steps, CI = 0.87) based on nucleotide sequences of the mitochondrial COI gene for 54 samples indicates robust clade structure for each species, *V. westae* and *V. guillemei* (bootstraps 91% and 100%, respectively, Fig. 15, Genbank accession numbers and site information in Table 1). Specimens that are geographically widely separated, but have similar morphology, form monophyletic groups. Branch length on the phylogram (Fig. 15) indicates relative number of base-pair changes. Within each clade there is some substructuring, as indicated by strong bootstrap branch support at the base of clades generally uniting specimens from a site. The relationship of *V. westae* and *V. guillemei* as sister taxa is also strongly supported (bootstrap 75%). *Vinundu* and *Lavigeria* form a robust clade based on this COI sequence (bootstrap 99%) (see also Michel, 2000; West & Michel, 2000).

DISCUSSION

Although the Tanganyikan mollusc fauna has generated considerable evolutionary discussion over the years (Boss, 1978; Brown, 1980, 1994; Brown & Mandelbarth, 1987; Coulter, 1991; Michel, 1994; West & Cohen, 1996; Bandel, 1998; Fryer, 2000; Strong & Glaubrecht, 2002), it has remained difficult to work throughout the region due to challenges in transportation and political unrest, leaving the molluscan fauna relatively poorly studied. The two species described herein are typical of deep water and rocky substrata, thus not easily collected by dredging, and are generally not found as beach-washed shells. Consequently their distinctness from *Lavigeria* species has remained unrecognized until recently. *Vinundu* specimens are very common in the deep-water habitats and the two species are sometimes found living sympatrically at sites throughout their ranges. They are easily distinguished from *Lavigeria*, even underwater, and by relatively inexperienced observers.

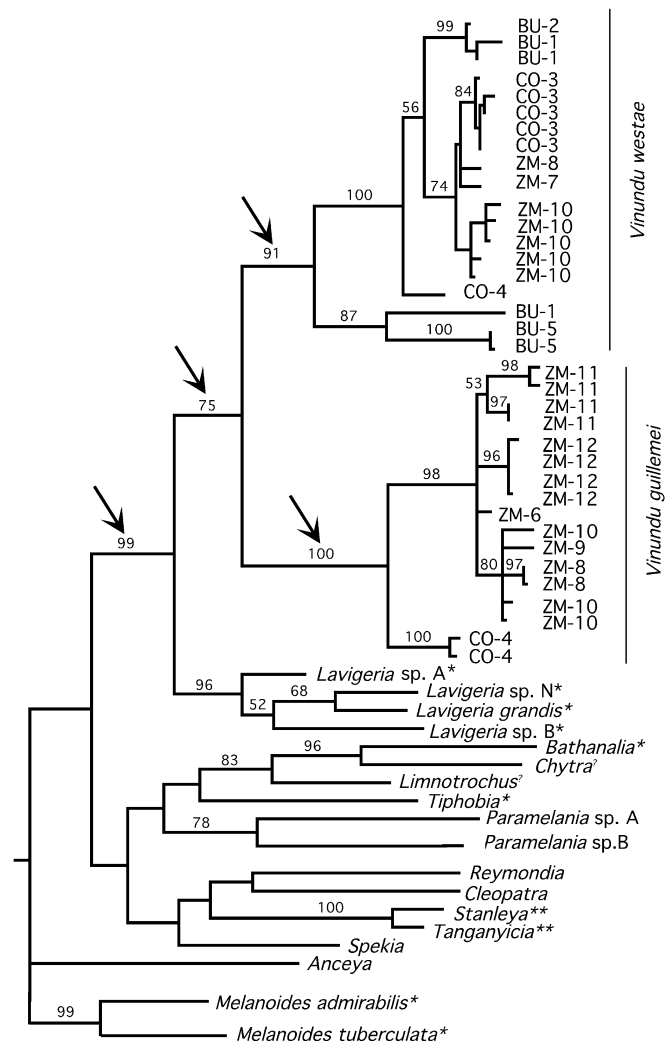


Figure 15. Molecular phylogenetic relationships based on COI DNA sequence for *Vinundu westae*, *V. guillemei* and outgroups from other Tanganyikan endemics and *Melanoides*. Individuals indicated by country and site number as indicated in distribution maps (Figs 10, 14, Table 1). Bootstrap values greater than 50% indicated above branches. Note *V. westae* and *V. guillemei* each form robust clades, and form a clade together, and are sister to the *Lavigeria* clade, as indicated by the arrows at the node of each clade. Reproductive mode indicated by: *, pallial oviduct brooder; **, head-foot brooder; ?, uncertain; no indication, egg layer (including *Vinundu*, *Paramelania*, *Reymondia*, *Cleopatra*, *Spekia*, *Anceya*); sources: Brown (1994), West et al. (2003).

Ecological information on the Tanganyikan gastropods, and *Vinundu* in particular, has been weak in many historical past studies. Until A. Cohen and P. Kat began collecting by SCUBA in 1985, the major malacological collections were made by dredging, which biases against hard substrate specialists and mixes specimens from different habitats (e.g. Leloup, 1953). Furthermore, some workers have substituted careful fieldwork with facile generalizations that do not hold up under scrutiny. For example, Bandel (1998: 254) suggests that '*L. arenarum* [*V. westae* based on his figures, but possibly including *V. guillemei* based on our sampling of his collection sites] lives below 3 m on the undersides of stones', whereas it is not common until 10 m and may be found on the surface of stromatolites, embedded in the crevices. It is likely that Bandel's collections were made only at the surface with snorkel, and from a few sites around heavily

populated Kigoma Bay, thus his comment that this is a microcosm of the whole lake should be treated with caution.

Reproduction: Sexual dimorphism is not evident in *Vinundu*. Sex ratios usually average 1:1, thus these snails are likely to be obligately gonochoristic. The ciliated groove along the right side of the head that leads from the opening of the pallial oviduct to a glandular pit in the foot comprises what is probably an ovipositor (R. S. Houbriek, personal communication). The ciliated groove is less pigmented than the skin around it, making it possible to distinguish *Vinundu* females from males without extracting the animal from the shell. This cannot be done for *Lavigeria*. *Vinundu* males sometimes have a corresponding unpigmented strip where the ciliated groove would be for females, but it is less distinct than the groove and lacks the glandular pit at the base. The pallial oviduct lacks the lateral and medial laminae found in brooding *Lavigeria*, therefore the pallial oviducal cavity is undivided (Fig. 8A, B). Presumably this allows eggs to pass unimpeded to the ovipositor. The floor of the pallial oviducal cavity is thickened, and may be a capsule or albumen gland. The spermatophore bursa is slightly shorter than in *Lavigeria* and the sperm gutter is also shorter. At the terminus of the spermatophore bursa a lamina continues along the medial wall and around the proximal end of the pallial oviduct, terminating in a small sac. This sac appears to be a blind tube with its opening directed proximally towards the opening of the oviduct. As I have often found this sac filled with sperm, it is clearly involved in fertilizing eggs as they are delivered into the pallial oviduct. In most animals examined the medial spermatophore bursa was closed, but in a few cases it seemed that it was open at the proximal end. In some populations of *V. westae* the incidence of parasites is very high, up to 26% (e.g. type locality, Bukm29.8). Because of the ciliated groove it is possible to sex animals even after destruction of reproductive tissue by trematodes, and it appears that females are more heavily parasitized than males.

Reproduction, however, remains cryptic. I have not seen eggs in my dissections of live animals or collections of shells, and thus cannot comment on rates of reproduction or modes of juvenile dispersal. I have not found eggs adherent on shells of adults [as has been noted for *Spekia zonata* by K. West (personal communication), for example], thus it is likely that the eggs are deposited in the local environment. Freshwater gastropods do not in general have a planktonic veliger stage. Very early stage, juvenile *Vinundu* are present under rocks and in cracks in the same rocky and stromatolite habitats where adults occur and genetic results all suggest strong population substructuring, thus dispersal is unlikely to be over significant distances.

Phylogenetic context: *Lavigeria* is the clear sister clade to *Vinundu* based on the COI sequence presented here (see also West & Michel, 2000), on a 1400 base-pair sequence from the 16S-ND1 mitochondrial gene (Michel, 2000), and 17 allozyme loci (Michel, 1995). The same clear distinction between *V. westae* and *V. guillemei* is indicated in allozyme data (Michel, 1995), as is the clade substructuring, suggesting lineage divergence and potential cryptic species, which warrant further investigation. However, allozyme comparisons of colour morphs of *V. guillemei* show no divergence between sympatric dark brown and cream individuals with brown spirals.

Sister clade comparisons: The sister relationship between *Vinundu*, an egg-layer and *Lavigeria*, a brooder, is an indication that reproductive mode can undergo major character state changes within endemic lineages in the lake. West alluded to this in her work on the other Tanganyikan endemic genera (West, 1997; West & Michel, 2000). However, in these other cases the molecular relationships remain unresolved between taxa with contrasting reproductive modes (Fig. 15). *Vinundu* and *Lavigeria* species

appear to fill a similar distributional niche in that adults are commonly found on many kinds of rock surfaces, although *Lavigeria* species dominate in shallower waters whereas *Vinundu* are most plentiful in waters deeper than 15 m.

Stable isotope signatures indicate trophic distinction between *Lavigeria* and *Vinundu* (Michel, 2000; McIntyre & Michel, 2001). Consistent, significant differences in δC^{14} and δN^{15} are evident among sympatric individuals, collected from the same depth and substratum. *Vinundu* have higher δN^{15} which is likely to be linked with a diet of non-nitrogen fixers such as benthic diatoms, whereas *Lavigeria* tissues have a very low δN^{15} , thus the animals are likely to be grazing on nitrogen fixers such as cyanophytes (P. B. McIntyre, personal communication). The specific source of relatively lower δC^{14} in *Vinundu* tissue requires detailed sampling of the aufwuchs. Nonetheless, this appears to be a lineage-specific trophic difference. The radular differences between *Vinundu* and *Lavigeria* are a likely to have functional importance in the gathering of what appear to be different food sources. Further testing should include faecal, gut content and fatty acid analysis.

Because the protoconch–teleoconch boundary in *Vinundu* is clearly demarcated, *Vinundu* species have two clear ontogenetic transitions that can be used for homologizing shell characters within the group: the protoconch–teleoconch boundary early in ontogeny, and adult modifications of determinate growth. Furthermore, this provides a useful homologue for understanding the ontogeny of shell ornament in *Lavigeria*, for which this transition is less distinct (Papadopoulos & Todd, 2001; Papadopoulos *et al.*, 2001, 2004). This is extremely useful, as homology determination in organisms showing accretionary growth is plagued by problems when the ontogenetic transitions are not indicated independently from the characters, e.g. ornament, under study.

A striking clade-level difference between *Vinundu* and *Lavigeria* is the apparent difference in number of species. Although further research may reveal a few additional species within *Vinundu*, the amount of morphological divergence is relatively limited within this clade, though the two species described in this paper are consistently separable. In addition, they occur in sympatry and remain distinct, thus are not simply allopecies. In contrast, the lineage divergence in *Lavigeria* is very high, with many sympatric species and local endemics (Brown, 1994; Michel, 1995, 2000; Todd, Michel, Cohen, McIntyre, Kingma, Grill & Cleary, 2001; Michel, Todd, Cleary, Kingma, Cohen & Genner, 2003; West *et al.*, 2003). A systematic revision of the approximately 35 currently recognized species of *Lavigeria* is in preparation (E. Michel & J. A. Todd, unpublished observations) and extrapolations from current sampling suggest that lake-wide species diversity is around 43 species (Michel *et al.*, 2003). Within this genus shell sculpture and size variation is much greater than in *Vinundu*. This is likely to be linked to more limited dispersal in *Lavigeria* due to its brooding habit (Cohen & Johnston, 1987; Michel, 1995). Tests of dispersal and population structure of *Vinundu* and *Lavigeria* will shed light on the causes of these differences in species-richness.

ACKNOWLEDGEMENTS

Jonathan Todd (BMNH) provided stalwart support in discussions of taxonomy and biology. Taxonomy was greatly assisted by Koen Martens (IRSNB), Virginie Héros and Philippe Bouchet (MNHN). Field collections were made possible by Andy Cohen, Erik Verheyen and the IRSNB expedition, Roger Bills, Pierre Verhoyen, Kelly West and the Brichards, Alain Gillot, the Vaithas (Aqua Products Kigoma). Logistics and collections permits were supported by TAFIRI-Kigoma and COSTECH (Tanzania), CRH-Uvira (Congo), University of Burundi, and Zambian Fisheries

Station at Mpulungu. Sequence data benefited from interaction with members of the Brown Lab, University of Michigan, especially Tim Collins. Assistance in graphics and SEM imaging was provided by Jan van Arkel, David Bentley, BMNH photography unit, Dirk Platvoet and Irene Kingma. The manuscript benefited from comments by David Brown and two anonymous referees. Financial support for collections was provided by University of Arizona, NSF RTG in Biological Diversification #BIR 9113362, NSF Postdoctoral fellowship #DEB 9303281, Nyanza Project NSF #ATM-9619458, Western Society of Malacologists student grant, Fulbright Fellowships, National Underwater Research Council ROV # UCAP-92-04, and NSF research grant # BSR 8415289. Special thanks to D. Chitamwebwa, Tijs Goldschmidt, and Anna Samwel-Terry for discussions on an appropriate Swahili name for a bumpy little snail.

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