



The morphology and independent origin of ovoviviparity in *Tiphobia* and *Lavigeria* (Caenogastropoda: Cerithioidea: Paludomidae) from Lake Tanganyika

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Abstract

To better understand the diversification of the endemic thalassoid (i.e. marine-like) cerithioidean gastropods of Lake Tanganyika, as well as the origin and significance of brooding among lake species, we here redescribe the anatomy and ontogeny of the ovoviviparous *Tiphobia horei* from Lake Tanganyika and compare it to that of *Lavigeria* sp. A, representing another ovoviviparous lake clade that has acquired a uterine brood pouch independently. Within the phylogenetic framework provided by recent molecular analyses, the distant relation of these two taxa is corroborated by many external and internal anatomical differences. Comparison of the brood pouches demonstrates that they each bear unique features consistent with their independent modification for brooding. Despite representing functionally analogous structures, they also share several similarities in organization likely representing symplesiomorphies of the Lake Tanganyika species flock. The ontogeny is characterized by the presence of a velum and by delayed calcification producing a characteristically wrinkled embryonic cap. Comparison with other brooding cerithioideans reveals that *T. horei* and *Lavigeria* sp. A retain many more embryos than other freshwater cerithioideans of comparable size with a uterine brood pouch, possibly facilitated by the presence of longitudinal lamellae. Compartmentalization of the oviduct and delayed calcification is strongly linked to the brooding of embryos.

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Introduction

Lake Tanganyika is not only the largest and the oldest of the East African Rift Lakes, but is also a hotspot of biodiversity and well known for its unique, endemic species assemblage (Coulter 1991; Martens et al. 1994; Rossiter 1995; Fryer 1996; Rossiter and Kawanabe 2000). Like other ancient lakes, Lake Tanganyika

represents an ideal laboratory for evaluating models of diversification and adaptation and the roles of intrinsic vs. extrinsic speciation mechanisms (e.g. Michel et al. 1992; Michel 1994; Martens 1997; Glaubrecht 1996, 1998, 2001). The large radiation of cichlid fishes in Lake Tanganyika has become well established as a model system and their morphological, molecular, and behavioural evolution rather thoroughly documented (e.g. Sturmbauer et al. 2001; Salzburger et al. 2002; Kocher 2004, 2005; Salzburger and Meyer 2004). Less well known are the ~70 species (Michel 2004) of

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phenotypically diverse cerithioidean gastropods. These species have long captured the imagination of scientists who have sought to understand the origins and evolution of this unique species flock. Although several recent studies have produced phylogenies of these species based on mitochondrial DNA (West and Michel 2000; Michel 2004; Wilson et al. 2004), much of their basic biology remains poorly documented or completely unknown. This prohibits the critical evaluation of speciation mechanisms that may have been influential in promoting the diversification of these species, as has been done for other species flocks of related riverine and lacustrine cerithioidean gastropods (e.g. Glaubrecht and Köhler 2004; Rintelen et al. 2004).

Tiphobia horei Smith, 1880, with prominent curving spines and pronounced siphonal canal, is one of the most distinctive and well-recognized taxa from the lake. At the time of its description, Smith (1880) remarked that *T. horei* was one of the most remarkable freshwater Mollusca yet discovered. Indeed, the conchological resemblance of *Tiphobia* to marine Muricidae (Bourguignat 1886; Moore 1903) or Ficidae (Bourguignat 1886), in addition to the appearance of other “halolimnic” (Moore 1898a) species in the lake, prompted Bourguignat (1885) to call the Lake Tanganyika “prosobranch” gastropods “thalassoid”, i.e. marine-like in appearance. This resemblance, as well as their alleged morphological affinity with various marine families, particularly in features of the alimentary and nervous systems, formed the basis for Moore’s (1898c, 1903) hypothesis that Lake Tanganyika represents a relictual Jurassic sea. Although that notion has long been dismissed, the origin and evolution of Lake Tanganyika’s distinctive thalassoid fauna have been the focus of intense debate (see Glaubrecht 1996, 2001; Strong and Glaubrecht 2002; and the references cited in those works).

As noted by Yonge (1938, p. 465), “The controversy which once raged over Moore’s theories has long ago died down, but it has unfortunately been succeeded by a complete neglect of the really significant side of his work, his descriptions...of the anatomy of many of these thalassoid Prosobranchia.” This statement is equally true today as it was nearly 70 years ago, as little new information has been brought to light on the internal anatomy of these forms in the intervening years (see Bouillon 1955, for a rare exception). As part of an ongoing effort to understand the evolutionary dynamics of the cerithioidean species flock in Lake Tanganyika and the evolution of viviparity in limnic gastropods (e.g. Strong and Glaubrecht 2002, 2003), we here provide a redescription of the internal anatomy of *T. horei*, and for the first time document the ontogeny of a limnic cerithioidean from embryos preserved within the brood pouch. This is compared to the anatomy and ontogeny

of a member from the *Lavigeria* clade. The anatomical features of *Tiphobia* and *Lavigeria*, and especially of their brood pouches, are interpreted within the phylogenetic framework provided by recent molecular analyses which support the independent origin of uterine brooding in these two taxa within Lake Tanganyika (West and Michel 2000; Glaubrecht 2001; Strong and Glaubrecht 2001; Wilson et al. 2004; Michel 2004).

Material and methods

Alcohol-preserved material (70% ethanol) of two female specimens of *T. horei* Smith, 1880, provided by the Museum of Comparative Zoology, Harvard University, was supplemented by collections made at the lake by A. Wilson (University of Zurich). Unfortunately, material of *Lavigeria* species available to us had been inadequately preserved for detailed morphological and histological study, with the exception of one lot of alcohol-preserved material of *Lavigeria* sp. that was provided by the Musée Royal L’Afrique Central, Tervuren. Identity of this material was subsequently confirmed as *Lavigeria* sp. A (J. Todd, E. Michel, pers. comm.). It should be noted that this designation does not imply uncertainty about the species identification; pending a thorough systematic revision of the *Lavigeria* species flock including the description and formal application of specific epithets, the nomenclature of constituent taxa remains in flux (West et al. 2003).

Codens for institutions from which additional shell material was borrowed: AMS = Australian Museum, Sydney; BMNH = The Natural History Museum, London; DBL = Danish Bilharziasis Laboratory, Charlottenlund; MCZ = Museum of Comparative Zoology, Cambridge, MA; MRAC = Musée Royal L’Afrique Central, Tervuren; NMNH = National Museum of Natural History, Washington, D.C.; ZMB = Museum für Naturkunde, Humboldt Universität, Berlin (formerly Zoologisches Museum Berlin).

Terminology referring to early shelled stages in the brood pouch (= embryonic shells) follows Strong and Glaubrecht (2002, 2003). Measurements of the embryonic shell follow the methods and terminology described in Glaubrecht (1996, pp. 28, 298). Measurements of developing embryos and young juveniles were taken from scanning electron micrographs.

Embryos were treated with hexamethyldisilazane following the procedure described in Nation (1983), and photographed with a JEOL 6300F scanning electron microscope at ZMB. Histological sections of the gonoducts were prepared for one female (MCZ 30.1576) and one male (ZMB 220.095) of *T. horei*, and for one female (MRAC 621282–288) of *Lavigeria* sp. A; tissues were embedded in paraplast, sectioned at 6 µm, and stained with hematoxylin and eosin-phloxine.

Results

Family Paludomidae

Tiphobia horei Smith, 1880

Material examined: TANZANIA, Lake Tanganyika 2 km off Magambo (5°58'S, 29°50'E), 70–90 m, trawl on soft mud, October 1986, leg. P. Kat, $n = 2$ (MCZ 30.1576; Fig. 1A and B); ZAMBIA, Chipata Bay (8°41.70S, 31°08.95E), 80 m, $n = 2$ (ZMB 220.095; Fig. 1C and D).

Shell microstructure: Shell thin, translucent, comprising two layers of crossed lamellar structure, bounded by thin outer irregular, prismatic and inner regular, simple

prismatic layers (Fig. 1G). Thickness of layers variable during ontogeny and between individuals.

Operculum: Concentric with small, central paucispiral nucleus of approx. 3 whorls; dark amber brown in colour (Fig. 2A, op).

External anatomy: Large, elongate, dorso-ventrally flattened, extensible snout. Retracted cephalic tentacles (Fig. 2A, t) long, tapering, slightly longer than snout. Small eyes located approximately one fourth of tentacle length from base. Foot very broad and fleshy (f). Anterior pedal gland present along margin of narrow propodium, opening to shallow groove.

Mantle edge (me) smooth. Ctenidium (Fig. 2B, ct) with large, elongate triangular filaments, extending from

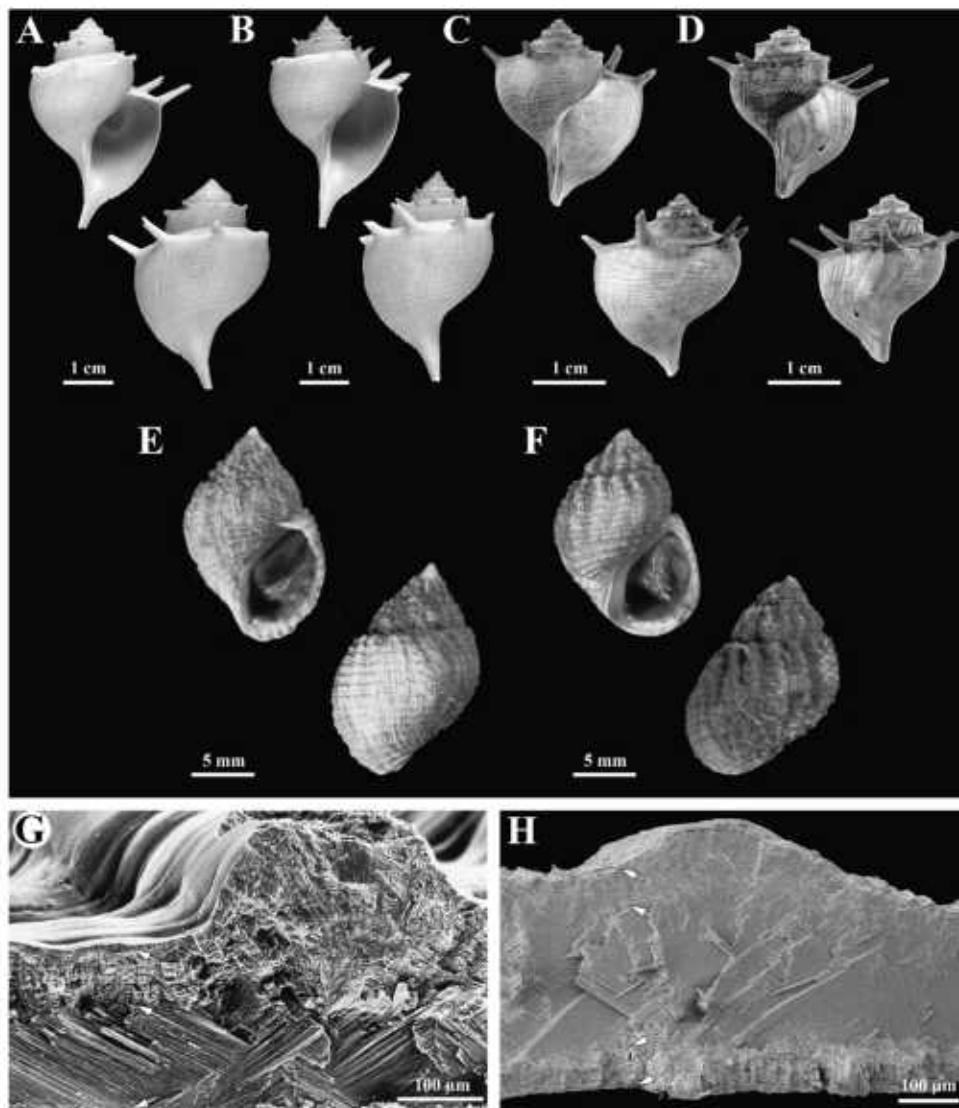


Fig. 1. (A–F) Shell specimens used in anatomical reconstructions; (A–D) *T. horei* (A, B Tanzania, MCZ 30.1576; C, D Zambia, ZMB 220.095); (E, F) *Lavigeria* sp. A (DR Congo, MRAC 621282–288). (G, H) Shell microstructure; external surface at top; note layers of crossed lamellar structure bounded by thin outer irregular, prismatic and inner regular, simple prismatic layers; arrows indicate transitions between layers; (G) *T. horei* (MCZ 30.1576), two layers; (H) *Lavigeria* sp. A (MRAC 621282–288), three layers.

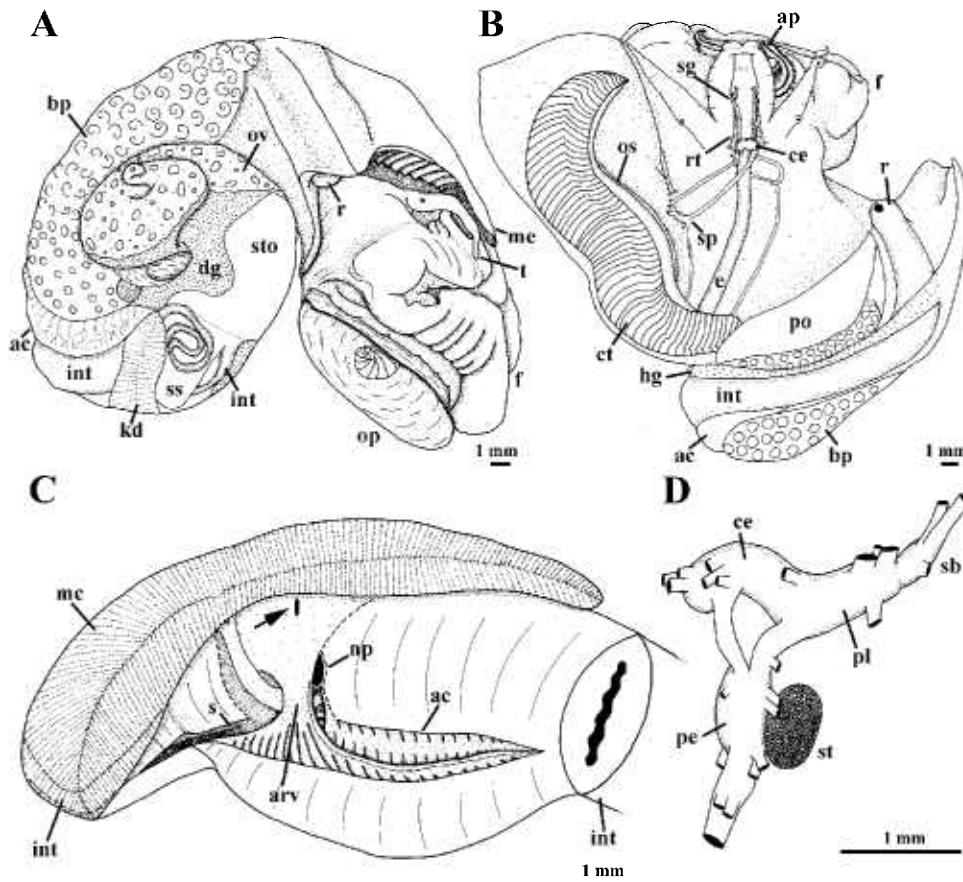


Fig. 2. Anatomy of *T. horei*. (A) External anatomy (MCZ 30.1576); stippling within kidney and anterior kidney chamber indicates excretory tubules. (B) Anatomy of mantle cavity and cephalic haemocoel (MCZ 30.1576), dorsal view, anterior at top; stippling within buccal cavity indicates jaws. (C) Kidney morphology (ZMB 220.095), right lateral view, anterior at right; internal features of bladder and anterior kidney chambers revealed by removing intestine (int) and portion of kidney wall (dashed line) between nephropore (np) and septum (s); arrow indicates communication between main kidney chamber (mc) and bladder; dot-dashed line indicates extent of cavity under excretory tubules. (D) Circum-oesophageal nerve ring (MCZ 30.1576), left lateral view. Abbreviations: ac = anterior kidney chamber; ap = anterior pedal gland; arv = afferent renal vessel; bp = brood pouch within pallial oviduct; ce = cerebral ganglion; ct = ctenidium; dg = digestive gland; e = oesophagus; f = foot; hg = hypobranchial gland; int = intestine; kd = kidney; mc = main kidney chamber; me = mantle edge; np = nephropore; op = operculum; os = osphradium; ov = ovary; pe = pedal ganglion; pl = pleural ganglion; po = pallial oviduct; r = rectum; rt = buccal mass retractor muscle; s = septum; sb = sub-oesophageal ganglion; sg = salivary gland; sp = supra-oesophageal ganglion; ss = style sac; st = statocyst; sto = stomach; t = cephalic tentacle.

base of pallial cavity to mantle margin, curving towards the left along anterior fourth. Apices of gill filaments aligned along midline. Osphradium (os) approximately one third length of gill, forming simple, narrow ridge along efferent branchial vein. Hypobranchial gland (hg) weakly developed.

Radula: Long, with approximately 72–76 rows ($n = 2$); denticle patterns variable within and between individuals (Fig. 3). Rachidian rectangular, taller than wide, tapering to v-shaped lower margin (E–F). Upper margin slightly concave, with cutting edge bearing 8–15 finely fringed denticles bounding a single, prominent, sharply pointed cusp. Lateral teeth (A–D) with extremely long lateral extensions. Single, sharp, prominent cusp flanked by 3–6 inner and 5–16 outer finely serrated,

pointed denticles. Inner edge of lateral straight, tapering at base to a prominent basal, pointed projection (D). Marginal teeth (G–I) long, slender and delicate. Inner marginal teeth tapering slightly to rounded tip, with 5–8 fine, sharp denticles along lower margin; outer marginal teeth tapering to pointed tip, with 1–3 finely serrated denticles on lower margin.

Foregut: Mouth opening at anterior end of highly folded, extensible snout (Fig. 2B). Buccal mass narrow, elongate, with small odontophore occupying posterior half of buccal cavity. Narrow, glandular, sub-radular organ lying along floor of buccal cavity at anterior end of odontophore. Paired jaw dorsally flanking mouth. Shallow, non-glandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear

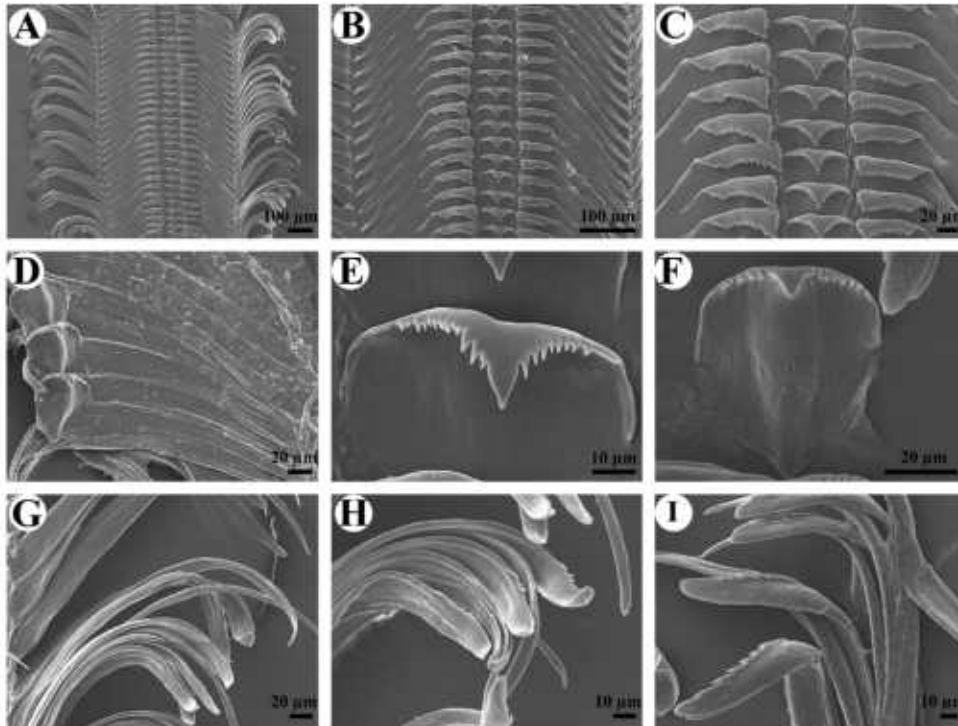


Fig. 3. Radula of *T. horei*. (A) Section of radular ribbon near anterior one-third (ZMB 220.095); note long extensions on lateral teeth. (B) Lateral and rachidian teeth (ZMB 220.095). (C) Detail of cusps of rachidian and lateral teeth (ZMB 220.095). (D) Detail of lateral teeth of second specimen at slightly different angle (MCZ 30.1576); note variation in laterals between specimens, and prominent pointed projection at inner edge of tooth base. (E) Detail of rachidian tooth (ZMB 220.095). (F) Detail of rachidian tooth of second specimen (MCZ 30.1576); note v-shaped base of rachidian, and variation between individuals in number of denticles. (G) Detail of marginal teeth (ZMB 220.095); note unequal numbers of fine denticles on inner and outer marginal teeth; also note rounded tip of inner tooth and pointed tip of outer tooth. (H) Detail of inner and outer marginal teeth (ZMB 220.095). (I) Detail of inner and outer marginal teeth of second specimen (MCZ 30.1576); note variation in number of denticles between individuals.

of buccal cavity. Salivary glands (sg) forming long, unbranched tubules, opening dorso-laterally alongside odontophore, with posterior tips lying within circum-oesophageal nerve ring (cg). Nerve ring lying at base of cephalic tentacles, well back from buccal mass. Paired buccal retractors (rt) extending from back wall of buccal mass, inserting on lateral walls of cephalic haemocoel just in front of nerve ring. Radular sac short, projecting slightly past end of buccal mass. Tall mid-ventral fold lying in deep depression just behind odontophore in anterior oesophagus, surrounded laterally and posteriorly by v-shaped fold, with base of v projecting posteriorly into oesophagus. Anterior oesophagus long, with walls bearing paired, longitudinal ventral and dorsal folds. Mid-oesophagus bearing numerous folds of equal size, lacking oesophageal gland.

Midgut: Oesophagus opening to gastric chamber floor on left side (Fig. 4, e). Marginal fold (mf), passing anteriorly from oesophageal aperture to opening of intestine (int), then turning posteriorly bordering edge of large sorting area (sa). Marginal fold bearing median longitudinal groove. Sorting area rectangular, with rounded posterior margin. Marginal fold elaborated

into small pad at left, posterior tip of sorting area (sap). Accessory marginal fold (amf) emerging from left side of oesophageal aperture, paralleling marginal fold around posterior tip of sorting area; accessory marginal fold bifurcate posteriorly. Epithelium finely grooved on surface of major typhlosole and midgut floor to right of marginal fold. Midgut roof to left of sorting area lined with cuticularized epithelium, irregularly folded anteriorly, rather smooth posteriorly (cu). Gastric shield (gs) large, continuous with cuticle of midgut roof and crystalline style pocket (p). Weakly developed fold bounding u-shaped depression (u) present below lip of style sac (ss). Glandular pad (gp) large, broadly rounded with small, smooth accessory pad (ap) present at anterior end. Crescentic ridge (cr) extending back from near oesophageal aperture and fusing to right side of glandular pad, bounding deep crescentic groove. Proximal tip of crescentic ridge curving into deep pouch bearing two digestive gland ducts (dd). Shallow caecum (c) extending ventrally under glandular pad behind gastric shield. Single, weak, longitudinal fold with several finer folds (cf) along floor behind gastric shield, opposite caecum. Proximal tip of major typhlosole

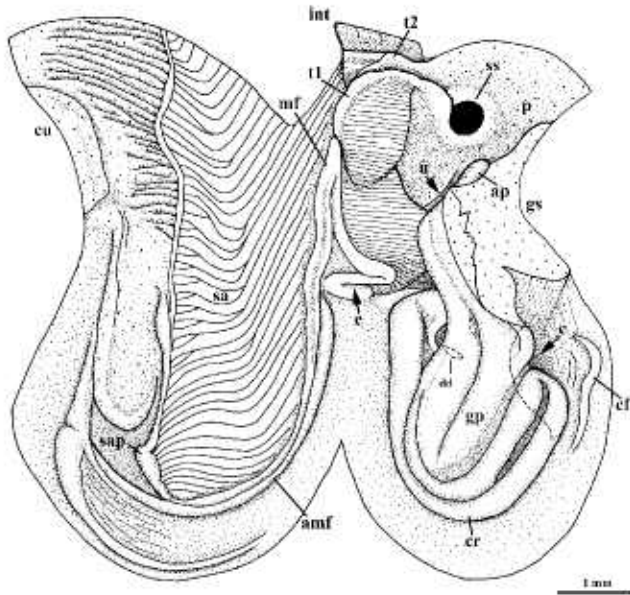


Fig. 4. Midgut morphology of *T. horei* (MCZ 30.1576), midgut opened along dorso-lateral incision on right, flap reflected to left, anterior at top; coarse stippling indicates extent of cuticularization of stomach roof (cu); dotted line indicates extent of shallow caecum (c) under glandular pad (gp). Abbreviations: amf = accessory marginal fold; ap = accessory pad; c = caecum; cf = caecal folds; cr = crescentic ridge; cu = cuticularized region of stomach roof; dd = duct of digestive gland; e = oesophageal aperture; gp = glandular pad; gs = gastric shield; int = intestine; mf = marginal fold; p = crystalline style pocket; sa = sorting area; sap = sorting area pad; ss = lip of style sac; t1 = major typhlosole; t2 = minor typhlosole; u = u-shaped fold.

forming prominent flap within gastric chamber (t1), bearing fine, parallel grooves across surface; minor typhlosole simple (t2). Style sac (ss) communicating proximally with intestine (int). Crystalline style present.

Hindgut: Intestine emerging from gastric chamber (Fig. 2A, int), passing ventrally under distal end of style sac (ss), then turning posteriorly and completing two loops over dorsal style sac wall near anterior end of gastric chamber; intestine then turning anteriorly and traversing right kidney wall (kd), exiting through papillate anus near mantle margin (r).

Reno-pericardial system: Voluminous kidney (Fig. 2A–C, kd, ac) partially subdivided internally into several chambers. Main kidney chamber (Fig. 2C, mc) anteriorly overhanging base of mantle cavity; small anterior chamber (ac) extending into pallial roof between intestine (int) and pallial gonoduct approximately half length of pallial gonoduct. Right kidney chamber (exposed chamber in Fig. 2C) forming narrow bladder, weakly lined along floor and walls by excretory tissue. Bladder separated dorsally and laterally on the left from main chamber containing large mass of excretory

lamellae in kidney roof (mc); bladder communicating to main chamber via small aperture (arrow) just behind afferent renal vessel (arv). Bladder partially subdivided by incomplete horizontal septum (s). Large mass of excretory tubules branching from afferent renal vessel along kidney floor in bladder and extending into anterior pallial chamber (ac), partially separating large dorsal and shallow ventral chambers (dotted line). Nephridial gland absent.

Narrow, deep pericardium extending underneath kidney alongside style sac (Fig. 2A, ss) to intestinal loops.

Nervous system: Circum-oesophageal nerve ring (Fig. 2D) lying near base of cephalic tentacles, well behind buccal mass. Cerebral ganglia (ce) connected by short, stout commissure. Six nerves emerging from each cerebral ganglion. Buccal connectives long, innervating buccal ganglia lying ventro-laterally at base of buccal cavity. Pleural ganglia (pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (pe) with one prominent anterior nerve and seven smaller accessory nerves. Large statocysts (sc) with numerous statoconia present dorso-laterally alongside pedal ganglia. Sub-oesophageal ganglion (sb) closely connected to left pleural ganglion. Right dialyneury present between nerves from sub-oesophageal and right pleural ganglia within wall of cephalic haemocoel (Fig. 2B). Long connective uniting right pleural and supra-oesophageal ganglia (sp). Left dialyneury formed between pallial nerve of left pleural ganglion and nerve from supra-oesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present below pericardium on the right.

Reproductive system: Gonad (Fig. 2A, ov) dorsally overlying digestive gland (dg) from tip of visceral mass to posterior end of gastric chamber (sto). Oviduct emerging ventrally from ovary. Renal oviduct (Fig. 5A, ovi) deflected dorsally in short loop behind mantle cavity before entering base of glandular oviduct. Pallial oviduct, with proximal albumen (ag) and distal capsule glands (cg). Narrow aperture (black arrows) along anterior one-third to one-half of oviduct opening to sperm gutter (sg) in medial lamina. Gutter leading posteriorly to elongate spermatophore bursa (spb); aperture larger (greater than half length of oviduct) in mature specimens containing large numbers of embryos. Inner wall of medial lamina fusing to ventral channel (Fig. 5A and B, vc), leaving only small aperture (white arrows) opening to capsule gland along anterior one-fourth to one-fifth of oviduct. Albumen gland (Fig. 5C, ag) forming c-shaped tube with flattened lumen. Albumen gland lumen continuous with gonoductal groove of capsule gland. Capsule gland (Fig. 5A and B, cg) with weakly glandular laminae bounding deep gonoductal groove dorsally (gg), forming voluminous brood pouch (Fig. 2A and B, bp). Lateral lamina bearing single,

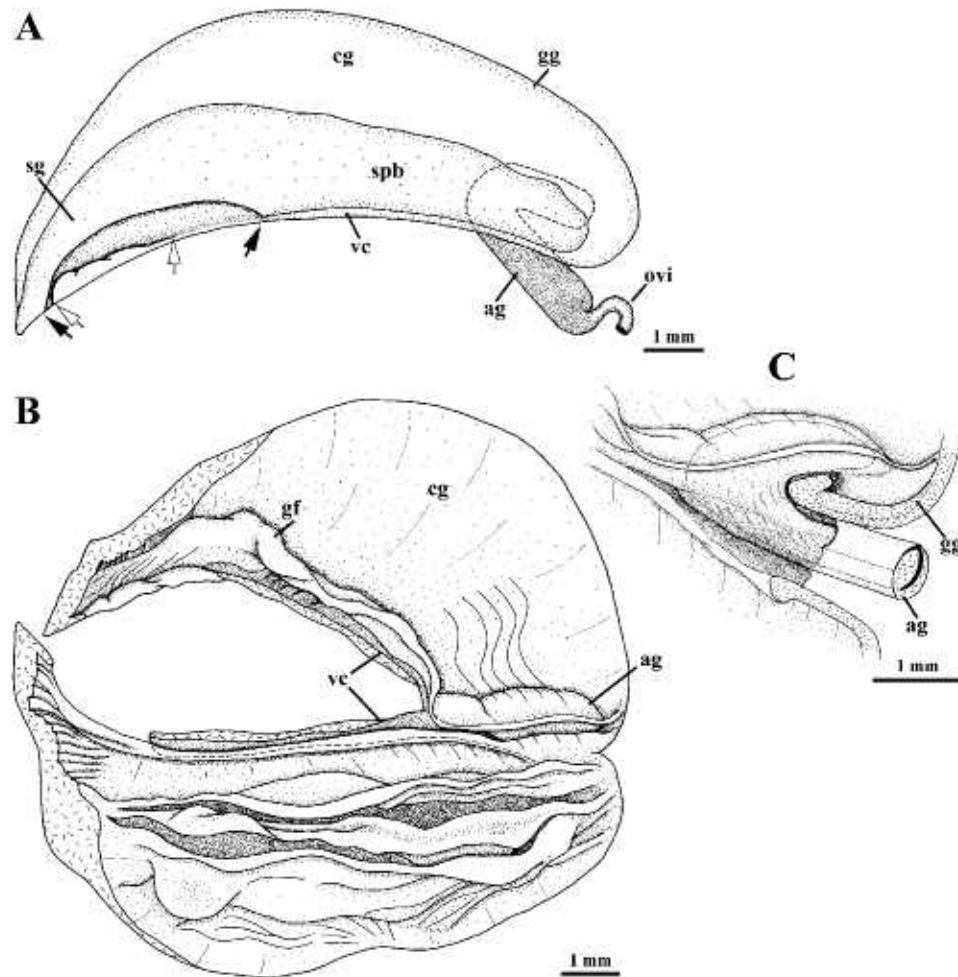


Fig. 5. Pallial oviduct of *T. horei* (ZMB 220.095). (A) External, left lateral view, anterior at left; note ‘c-shaped’ albumen gland (ag); arrows indicate extent of openings to mantle cavity. (B) Internal view, oviduct opened ventrally along ventral channel and dorsally along oviductal groove with medial lamina deflected to left; note anastomosing lamellae in medial lamina and weakly developed glandular fold (gf) along floor of lateral lamina bounding ventral channel. (C) Detail of proximal pallial oviduct, showing connection between albumen and capsule glands. Abbreviations: ag = albumen gland; cg = capsule gland; gf = glandular fold; gg = gonoductal groove; ovi = renal oviduct; sg = sperm gutter; spb = spermatophore bursa; vc = ventral channel.

glandular longitudinal fold (Fig. 5B, gf) overhanging ventral channel (vc). Medial lamina bearing numerous branching and anastomosing longitudinal lamellae (Fig. 6A, l) that separate rows of embryos; number of folds variable and apparently increasing with maturity. Folds composed of simple cuboidal, non-glandular epithelium. Seminal receptacle absent.

Brood pouch containing fertilized eggs, immature embryos posteriorly (Fig. 7A–L) and shelled juveniles anteriorly (Fig. 8A–N). Two females examined containing $n = 488$ and 18 embryos at various stages of development, respectively. Fertilized eggs approximately 520 μm in diameter. Embryos surrounded by membranous egg capsule (e.g. Fig. 7C and G). Capsule remaining intact throughout duration of development within brood pouch; no evidence of adelphophagy (Fig. 9).

Two spermatophores found within mantle cavity of one female (MCZ 30.1576), approx. 12 mm (broken) and 17 mm in length (Fig. 10A). Spermatophores translucent, pale yellow in colour. Spermatophores bifurcate, with two long, narrow shafts projecting from common base. Longer shaft approximately 4–5 \times length of shorter shaft. Longer shaft narrowing and flattening to pointed tip, with convex suture along one edge; tip of shorter shaft bluntly rounded. Base tapering to pointed or slightly rounded tip. Base approximately equal in length to shorter shaft. Spines lacking. See Fig. 10B for inferred position during formation within male pallial gonoduct.

Narrow vas deferens emerging ventrally from testes. Short distal portion of vas deferens thickened and forming straight seminal vesicle. Vas deferens narrowing and curving dorsally to enter posterior end of prostate

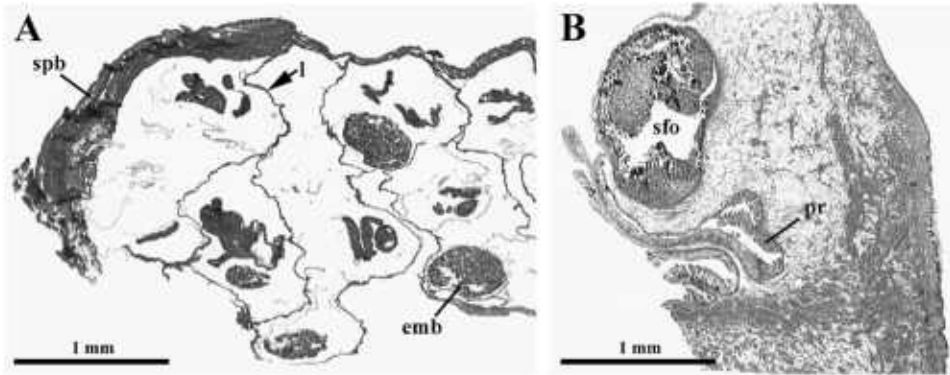


Fig. 6. Histology of the pallial gonoduct of *T. horei*. (A) Oblique cross-section through anterior pallial oviduct (MCZ 30.1576); note thin, non-glandular lamellae of medial lamina. (B) Cross-section through anterior prostate and spermatophore-forming organ (ZMB 220.095); note w-shaped lumen of spermatophore-forming organ. Abbreviations: emb = embryo; l = lamellae; pr = prostate; sfo = spermatophore-forming organ; spb = spermatophore bursa.

(Fig. 10B, pr) at base of mantle cavity. Prostate glandular, forming flattened tube, opening to mantle cavity through narrow slit along anterior one-fourth to one-third (arrow). Posterior half of lateral lamina irregularly, longitudinally folded; posterior half of medial lamina rather smooth and separated from anterior half by vertical fold. Dorsal, anterior portion of prostate forming separate, glandular, tube-like spermatophore-forming organ (Figs. 6B and 10B; sfo). Organ terminating blindly anteriorly and communicating posteriorly via narrow aperture with gonoductal groove. Lumen of organ w-shaped (Fig. 6B, sfo).

Ontogeny: Earliest stages of egg cleavage (Fig. 7A–C) evident in proximal brood pouch. Gastrulation by epiboly (D–E). Following gastrulation, embryo elongating, foot and mantle beginning to differentiate, resulting in distinct asymmetry of embryo (F). During early veliger stage, coiling of visceral mass beginning, with velum, mantle edge and developing foot becoming discernible and formation of calcium carbonate plates across surface of apex beginning (G–H). Subsequently, effects of torsion evident as head–foot rotated counter-clockwise relative to viscera and mantle (I–J), resulting in anterior position of mantle cavity over head and velum (K–L). Accretionary growth of shell margin beginning after torsion (Fig. 8). Operculum first becoming visible as accretionary growth of teleoconch commencing (Fig. 8A); onset of operculum formation unclear. Shrinking of underlying yolk mass bringing calcium carbonate plates into contact and allowing them to completely fuse.

Mature shelled stages within brood pouch comprising about 2 whorls (Fig. 8K–N). First whorl coarsely textured and rugose, indicating late calcification (O). Short transition zone at about 1–1.25 whorls yielding to even growth lines and 2–4 spiral cords. Most prominent cord at shoulder appearing first, with less prominent

threads appearing slightly later in ontogeny lower on whorl. Two mature juveniles from anterior brood pouch with width \times height = 1.14 \times 1.23 mm and 1.21 \times 1.47 mm, respectively (measured from SEM; Fig. 8K–N). First spine appearing after hatching at about 3.25 whorls (Fig. 9) along prominent spiral cord at shoulder; cord continuous through spine (Fig. 9A). Whorl profile gradually becoming more angulate above shoulder with gradual development of keel. Early spines produced at regular intervals (D–E). Umbilicus open in pre-hatching and early post-hatching shelled juveniles; umbilicus gradually closing after three whorls (A, D).

Lavigeria sp. A

Given the taxonomic confusion surrounding identification of *Lavigeria* species, we here refrain from placing a name on the specimens examined. However, the specimens have been provisionally assigned to *Lavigeria* sp. A, pending revision of all *Lavigeria* species (E. Michel and J. Todd, pers. comm.).

Material examined: DR CONGO, Kasekesi (MRAC 621282–621288; Fig. 1E–F).

Shell microstructure: Shell microstructure in mature specimens comprising three layers of crossed lamellar structure, with crystals of layers offset by 90°, bounded by thin outer irregular, prismatic and inner regular, simple prismatic layers (Fig. 1H).

External anatomy: Large, broad, dorso-ventrally flattened, extensible snout (Fig. 11A, sn). Retracted cephalic tentacles (t) short, thick and tapering, slightly longer than half of snout length. Small eyes located on prominent protuberances approximately half of tentacle length from base. Foot (f) broad, squarish in outline. Anterior pedal gland (ap) present along margin of propodium, opening to shallow groove along anterior edge of foot and curving around sides along anterior quarter of foot. Operculum paucispiral, with spiral,

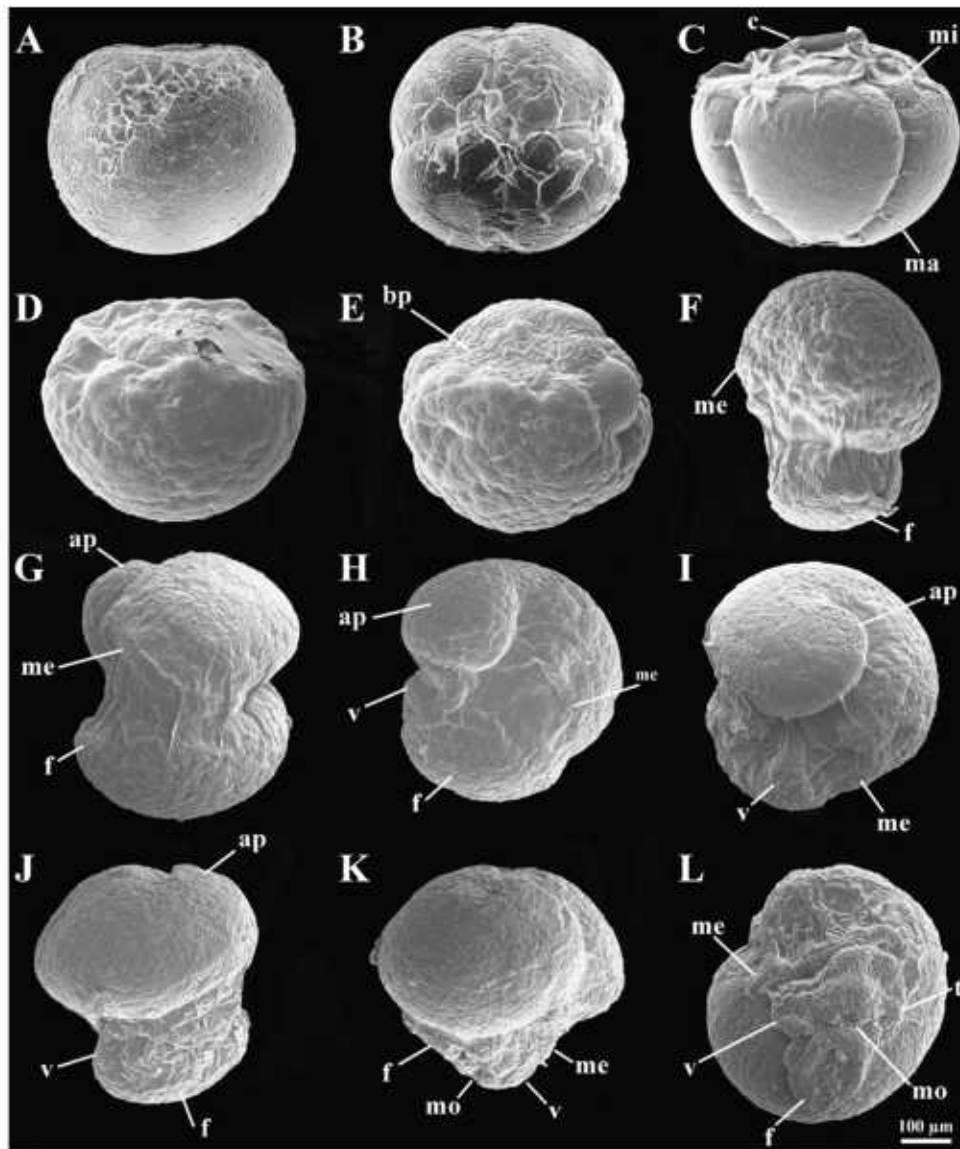


Fig. 7. Early development of *T. horei* (MCZ 30.1576). (A) Fertilized egg from proximal brood pouch; animal pole at top. (B) 4-cell stage; cross furrow visible through capsule; note approx. equally sized cells. (C) 12-cell stage. (D) Early gastrula, vegetal pole at top; note several large macromeres surrounding incipient blastopore. (E) Young gastrula at beginning of epiboly. (F) Late trochophore showing elongation of embryo. (G–H) Early pre-torsional veligers showing initiation of coiling, and progressive differentiation of mantle edge and velum. (H) First stages of calcification of apical cap just becoming evident. (I–J) Torsional veligers showing rotation of velum, and developing foot relative to mantle edge; both embryos have completed approximately 90° of rotation. (K–L) Two views of post-torsional veligers. All embryos to scale. Abbreviations: ap = apex; bp = blastopore; c = capsule; f = foot; ma = macromere; me = mantle edge; mi = micromere; mo = mouth; t = cephalic tentacle; v = velum.

subcentral nucleus of about 3 whorls; dark amber brown in colour (Fig. 11B).

Mantle edge lobate but lacking papillae (Fig. 11C). Ctenidium (ct) with large, broadly triangular filaments, extending from base of pallial cavity to mantle margin, curving towards left at anterior tip. Narrow, projecting apices of gill filaments aligned slightly off centre. Osphradium (os) approximately half length of gill, forming simple, narrow ridge in shallow trough along

thick efferent branchial vein. Hypobranchial gland (hg) weakly developed.

Radula: Radular ribbon narrow with short, robust teeth (Fig. 12A). Rachidian rectangular, taller than wide, tapering to v-shaped lower margin (C). Upper margin slightly concave, with cutting edge bearing single, rectangular central cusp bounded by 1 tiny outer denticle and 1 large, triangular inner denticle on each side. Lateral teeth similar to rachidian (A–B), with short

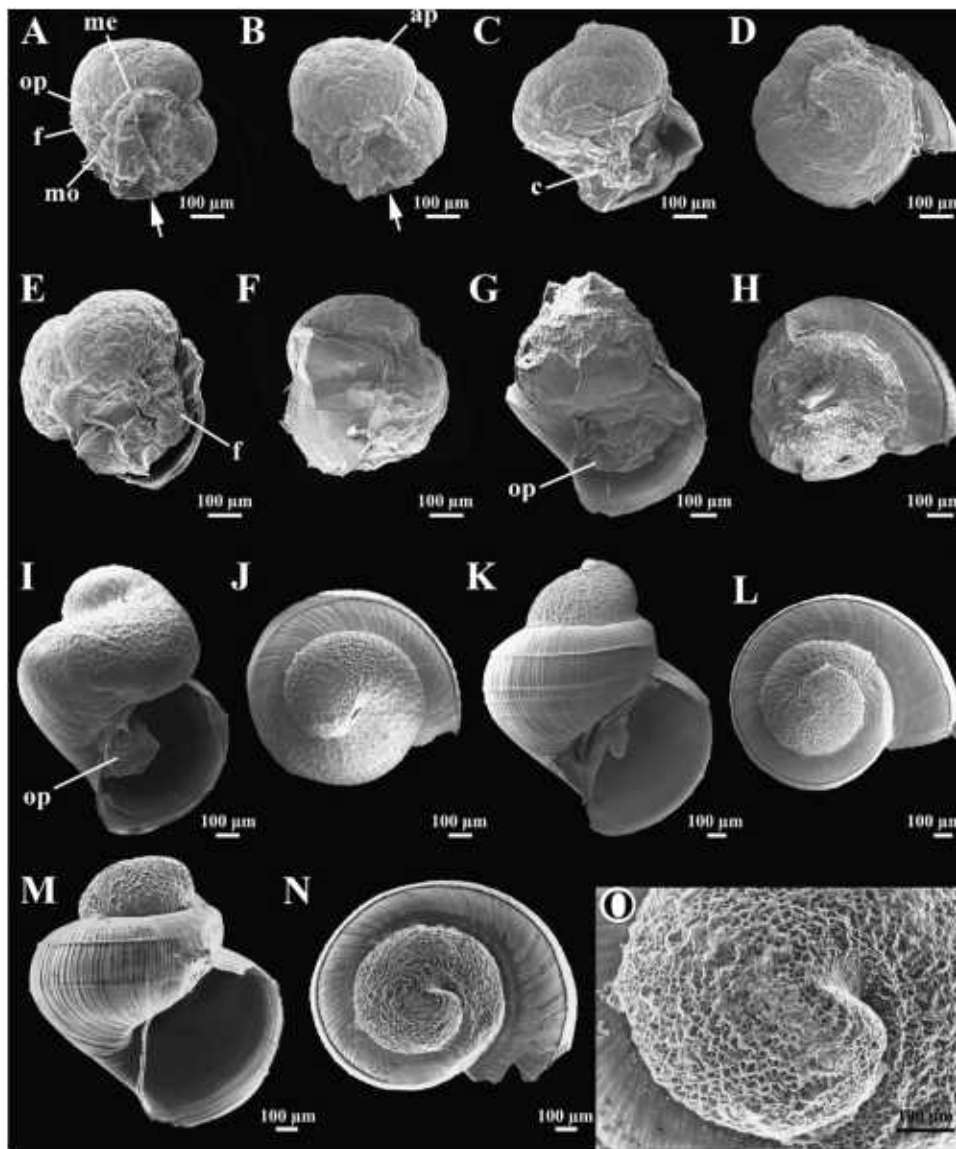


Fig. 8. Pre-hatching shelled juveniles of *T. horei* (MCZ 30.1576). (A–B) Young juvenile showing initiation of accretionary growth. (C–D) Young juvenile with one-eighth whorl of accretionary growth. (E–F) Young juvenile with one-fourth whorl of accretionary growth. (G–H) Young juvenile with one-third whorl of accretionary growth. (I–J) Young juvenile with solid apical cap and one-half whorl of accretionary growth. (K–N) Two mature shelled juveniles from distal brood pouch. (O) Detail of complete apical cap. Abbreviations: ap = apex; c = capsule; f = foot; me = mantle edge; mo = mouth; op = operculum.

lateral extensions. Single, prominent spatulate cusp flanked on either side by 1 tiny outer and 1 large, triangular inner denticle; the latter may be bi- or multi-lobed (B). Marginal teeth (D) short and robust, with unequal numbers of broad, smooth cusps. Inner marginal teeth with single prominent spatulate cusp, bounded by two inner and at least 1 outer smaller triangular cusp. Outer marginal teeth with 5 large, rounded cusps; outer cusp typically notched at outer base.

Foregut: Mouth opening ventrally at anterior end of folded, extensible snout (Fig. 11C, sn). Buccal mass

rounded and robust, with large odontophore (dotted line) occupying posterior half of buccal cavity. Narrow, glandular sub-radular organ lying along floor of buccal cavity at anterior end of odontophore. Weakly developed jaw present, dorsally flanking mouth. Deep, folded, glandular buccal pouches (bu) extending underneath dorsal folds behind buccal ganglia at rear of buccal cavity and into anterior oesophagus. Rather prominent horizontal folds bound inner edges of blind posterior ends of pouches. Right pouch larger than left. Salivary gland ducts (sg) opening dorso-laterally alongside odontophore, expanding into lobate glands

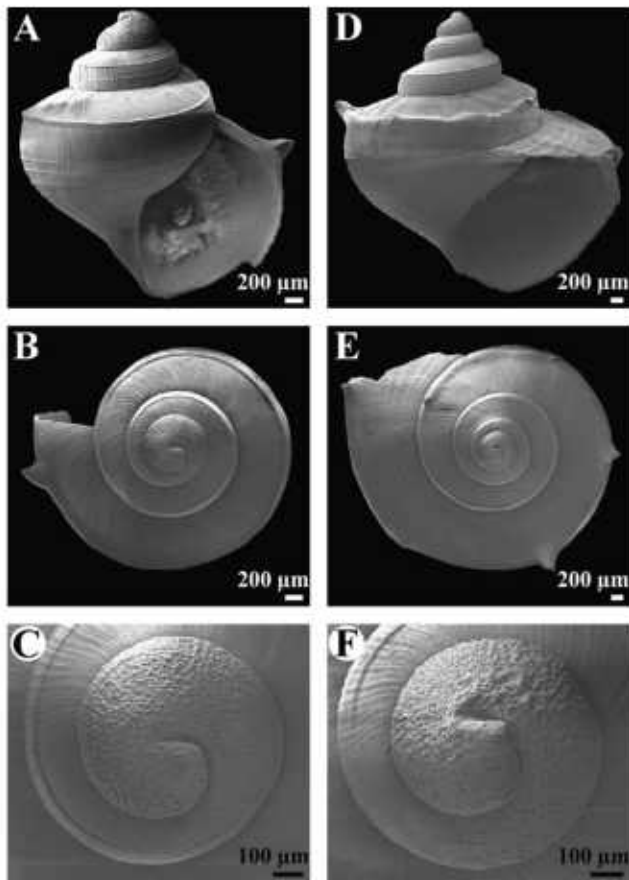


Fig. 9. Post-hatching shelled juveniles of *T. horei* (DBL). (A–C) Early post-hatching shelled juvenile with single spine; note partial closure of umbilicus. (D–E) Advanced juvenile showing regular spine formation along keel; note cord along keel continuous through spine; umbilicus completely closed.

upon passing through circum-oesophageal nerve ring. Nerve ring lying immediately behind buccal mass, well back from base of cephalic tentacles. Thick, robust buccal retractors (rt) extending from back wall of buccal mass, inserting on lateral walls of cephalic haemocoel just in front of nerve ring. Radular sac (rad) long, curving dorsally behind buccal mass on the right. Between buccal pouches, floor of anterior oesophagus elaborated into tall mid-ventral fold lying in deep depression just behind odontophore, surrounded laterally and posteriorly by u-shaped fold, with base of u projecting posteriorly into oesophagus. Anterior oesophagus long, with walls bearing paired longitudinal ventral and dorsal folds. Mid-oesophagus bearing numerous folds of equal size, lacking oesophageal gland.

Midgut: Midgut somewhat poorly preserved. Oesophagus opening to gastric chamber floor on left side (Fig. 13, e). Marginal fold (mf) passing anteriorly from oesophageal aperture to opening of intestine (int) beside

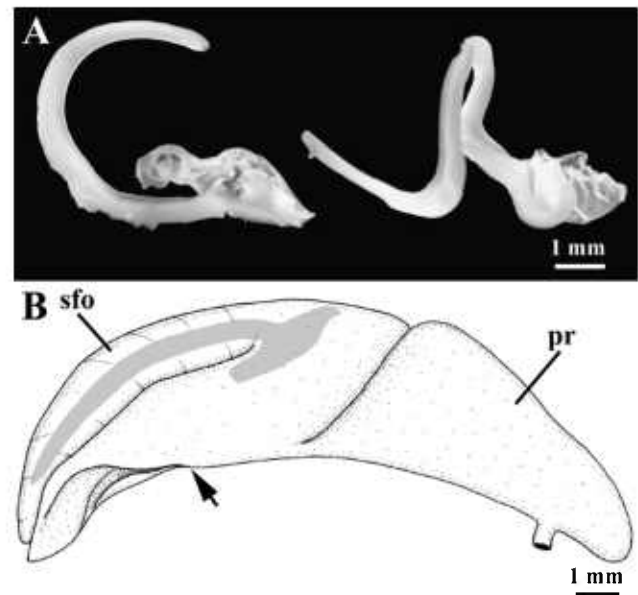


Fig. 10. Spermatophores and male pallial gonoduct of *T. horei*. (A) Spermatophores found in mantle cavity of mature female (MCZ 30.1576). (B) Pallial gonoduct of male (ZMB 220.095); arrow indicates posterior extent of opening to mantle cavity; presumptive position of spermatophore formation shown in grey. Abbreviations: pr = prostate; sfo = spermatophore-forming organ.

expanded proximal tip of major typhlosole (t1), then turning posteriorly bordering edge of large sorting area (sa). Sorting area elongate triangular, with straight left margin and tapering to pointed posterior tip. Accessory marginal fold (amf) emerging from below oesophageal aperture, paralleling marginal fold and extending past posterior tip of sorting area; accessory marginal fold bifurcate posteriorly. Epithelium finely grooved on midgut floor to right of marginal fold. Midgut roof bounding sorting area lined with cuticularized epithelium, coarsely folded anteriorly and rather smooth posteriorly (cu). Gastric shield (gs) robust, continuous with cuticle of midgut roof and style sac pocket (p). Glandular pad (gp) large, broadly rounded posteriorly, with accessory pad (ap) present at anterior end. Crescentic ridge (cr) extending back from oesophageal aperture and fusing to right side of glandular pad, bounding deep crescentic groove. Proximal tip of crescentic ridge bounding deep pouch bearing two digestive gland ducts (dd). Shallow caecum (c) extending ventrally under glandular pad behind gastric shield. Single, weak, longitudinal fold (cf) bifurcating anteriorly along floor behind gastric shield, opposite caecum. Style sac (ss) communicating proximally with intestine (int). Crystalline style present.

Hindgut: Intestine emerging from gastric chamber (Fig. 11A, int), passing ventrally under distal end of style sac (ss), and extending along right wall of style

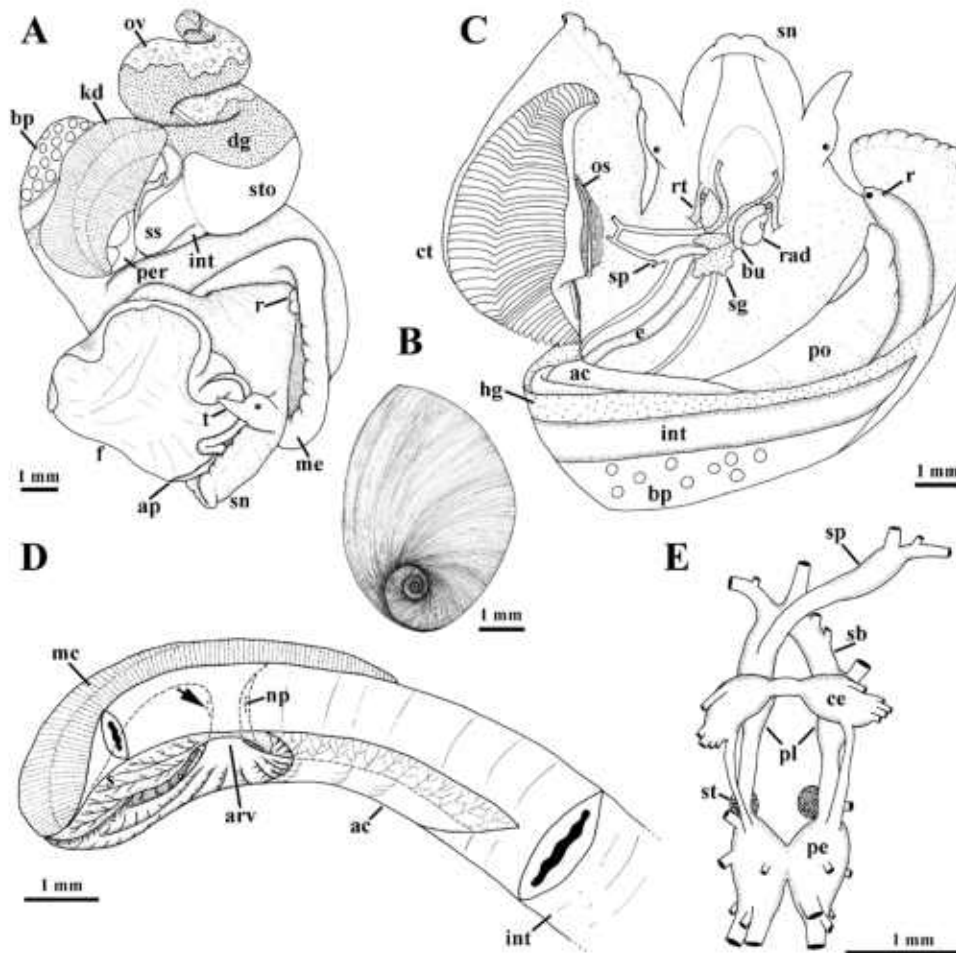


Fig. 11. Anatomy of *Lavigeria* sp. A (MRAC 621282–288). (A) External anatomy; stippling within kidney indicates excretory tubules. (B) Operculum. (C) Anatomy of mantle cavity and cephalic haemocoel, dorsal view, anterior at top; stippling within buccal cavity indicates odontophore; note small buccal ganglia visible between buccal mass retractor muscles (rt) and buccal pouches (bu). (D) Kidney morphology, right lateral view, anterior at right; internal features of bladder and anterior kidney chambers revealed by removing intestine (int); kidney wall incised posteriorly along right ventral edge and floor deflected downward; arrow indicates communication between main kidney chamber (mc) and bladder; features within anterior kidney chamber viewed by transparency. (E) Circum-oesophageal nerve ring, frontal view. Abbreviations: ac = anterior kidney chamber; ap = anterior pedal gland; arv = afferent renal vessel; bp = brood pouch within pallial oviduct; bu = buccal pouches; ce = cerebral ganglion; ct = ctenidium; dg = digestive gland; e = oesophagus; f = foot; hg = hypobranchial gland; int = intestine; kd = kidney; mc = main kidney chamber; me = mantle edge; np = nephropore; os = osphradium; ov = ovary; pe = pedal ganglion; per = pericardium; pl = pleural ganglion; po = pallial oviduct; r = rectum; rad = radular sac; rt = buccal mass retractor muscle; s = septum; sb = sub-oesophageal ganglion; sg = salivary gland; sn = snout; sp = supra-oesophageal ganglion; ss = style sac; st = statocyst; sto = stomach; t = cephalic tentacle.

sac to anterior end of gastric chamber (sto); intestine then turning anteriorly and traversing right kidney wall (kd), exiting through papillate anus near mantle margin (r).

Reno-pericardial system: Voluminous kidney anteriorly overhanging base of mantle cavity (Fig. 11A, kd) and extending into pallial roof (Fig. 11C, ac) between intestine and pallial gonoduct, slightly less than half length of pallial gonoduct. Kidney lumen partially subdivided internally into several chambers (Fig. 11D). Right kidney chamber (exposed chamber) forming

bladder, lined along floor and walls by excretory tissue. Bladder separated dorsally from main chamber containing large mass of excretory lamellae in kidney roof (mc); bladder communicating dorsally to main chamber via small aperture (arrow) just behind afferent renal vessel (arv). Bladder partially subdivided by incomplete horizontal septum (s) formed by excretory tubules. Large mass of excretory tubules branching from afferent renal vessel along kidney floor in bladder and largely occluding lumen of pallial chamber (ac). Nephridial gland absent.

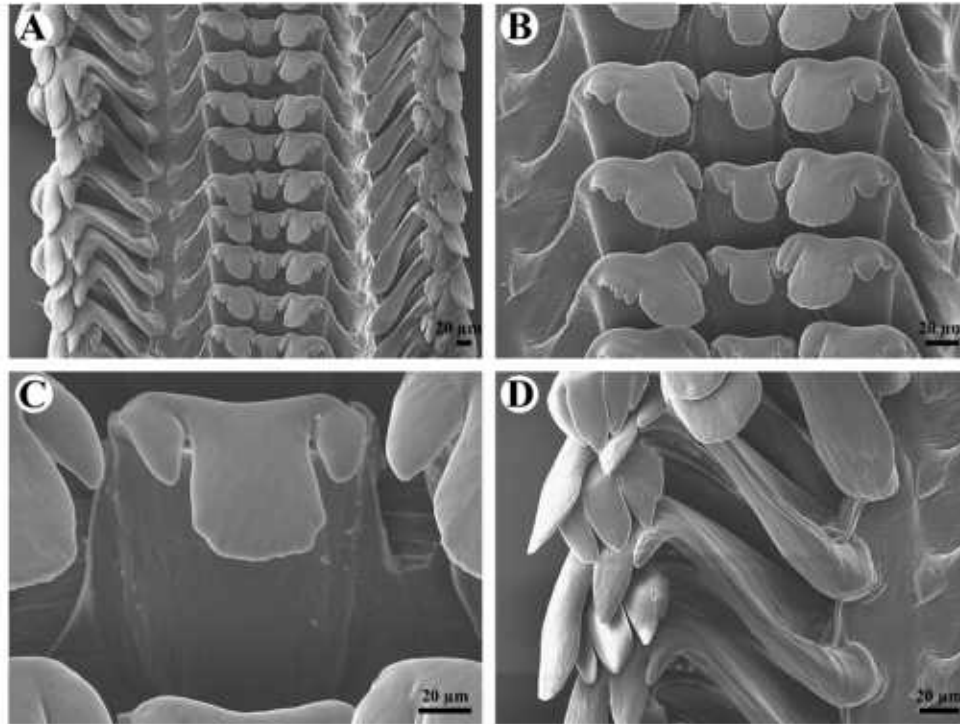


Fig. 12. Radula of *Lavigeria* sp. A (MRAC 621282–288). (A) Section of radular ribbon near anterior one-third. (B) Rachidian and lateral teeth. (C) Detail of rachidian tooth. (D) Marginal teeth; note unequal numbers of cusps on inner and outer teeth.

Narrow, deep pericardial cavity (Fig. 11A, per) extending underneath kidney (dotted line) to posterior intestinal loop.

Nervous system: Circum-oesophageal nerve ring (Fig. 11E) lying immediately behind buccal mass, well behind base of cephalic tentacles. Cerebral ganglia (ce) connected by short, stout commissure, each producing five prominent nerves. Buccal connectives short, innervating buccal ganglia lying ventro-laterally at base of buccal cavity immediately behind buccal retractor muscles. Pleural ganglia (pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (pe) with two prominent anterior nerves and five smaller accessory nerves. Small statocysts (st) with numerous statoconia present dorsally alongside pedal ganglia behind pedal connectives. Sub-oesophageal ganglion (sb) closely connected to left pleural ganglion. Zygoneury formed between sub-oesophageal and right pleural ganglia. Long connective uniting right pleural and supra-oesophageal ganglia (sp). Left dialyneury formed between pallial nerve of left pleural ganglion and nerve from supra-oesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present between pericardium and kidney at base of mantle cavity, above posterior oesophagus on the right. Ganglion producing three prominent nerves.

Reproductive system: Only two females available for examination; male reproductive anatomy unknown.

Ovary (Fig. 11A, ov) dorsally overlying digestive gland (dg) from tip of visceral mass to near posterior end of gastric chamber (sto). Oviduct emerging ventrally from ovary. Renal oviduct (Fig. 14A, ovi) deflected dorsally at base of mantle cavity around seminal receptacle before entering base of glandular pallial oviduct. Pallial oviduct, with proximal albumen (Fig. 14A and B, ag) and distal capsule glands (cg). Albumen gland (ag) forming c-shaped tube with flattened lumen opening laterally to lumen of capsule gland (see Fig. 14C). Capsule gland (cg) weakly glandular, bounding deep gonoductal groove, forming voluminous brood pouch (Fig. 11A and C, bp). Brood pouch containing fertilized eggs, immature embryos posteriorly (Fig. 15A) and shelled juveniles anteriorly, each contained within fluid-filled egg capsules (Fig. 15B, c). Lateral lamina bearing prominent glandular fold (Figs. 14C and 15B; gf) overhanging ventral channel. Fold with deep medial gutter along much of its length and forming many ridges and grooves that separate clusters of embryos. Inner wall of medial lamina smooth. Oviduct communicating along anterior one-fifth to mantle cavity (Fig. 14A, arrows). Deep sperm gutter (sg) above aperture leading posteriorly to long, narrow spermatophore bursa (spb) in medial lamina;

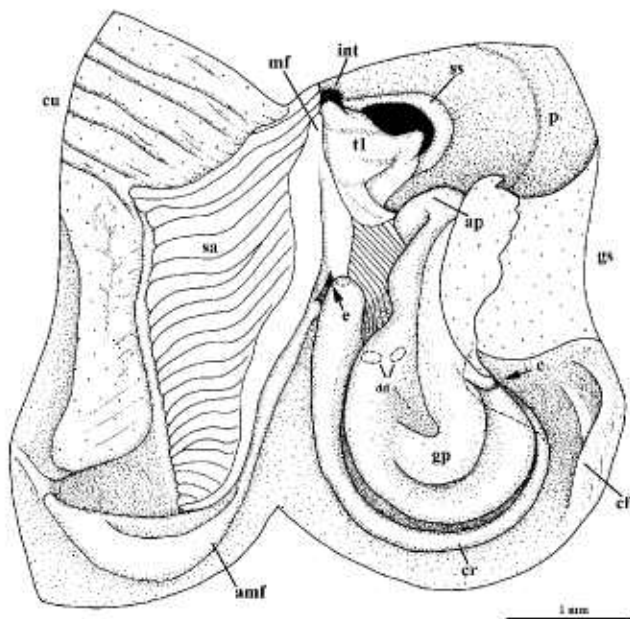


Fig. 13. Midgut of *Lavigeria* sp. A (MRAC 621282–288), opened along dorso-lateral incision on right, flap reflected to left, anterior at top; coarse stippling indicates extent of cuticularization of stomach roof (cu); dotted line indicates extent of shallow caecum (c) under glandular pad (gp). Abbreviations: amf = accessory marginal fold; ap = accessory pad; c = caecum; cf = caecal folds; cr = crescentic ridge; cu = cuticularized region of stomach roof; dd = duct of digestive gland; e = oesophageal aperture; gp = glandular pad; gs = gastric shield; int = intestine; mf = marginal fold; p = crystalline style pocket; sa = sorting area; ss = lip of style sac; t1 = major typhlosole.

shallow groove arising near posterior tip of bursa within sperm gutter leading posteriorly to seminal receptacle (rcs). Ventral edge of sperm gutter inner wall remaining free (Fig. 14A, dashed line), not fused to ventral channel.

Two adult females examined; one mature female processed for histological sectioning, the second, young female containing $n = 154$ fertilized eggs (Fig. 16A), uncalcified embryos (B–E), and 5 pre-torsional juveniles undergoing preliminary stages of shell calcification (F). Fertilized eggs about $217\ \mu\text{m}$ in diameter. Maximum height of embryos within brood pouch about $288\ \mu\text{m}$.

Discussion

Evaluation of morphological characters

The current findings largely agree with the anatomical organization of *T. horei* presented by Moore (1898b), as far as such details were provided. There are, however, several discrepancies between the two accounts. (1)

Moore found jaws to be lacking and the salivary glands to be branched. (2) The presence of a pallial kidney extension was neglected by Moore. (3) The nervous system was found to be dialyneurous on the right and left sides here, but only on the left by Moore. (4) Numerous minute statoconia were found within the statocysts, rather than the few somewhat large statoconia found by Moore. (5) The anterior pedal nerves were described by Moore to be connected by ladder-like cross-connections of nerves, whereas no cross-connections were found in the present study. (6) The statocysts were found to be closely appressed to the posterior dorsal surface of the pedal ganglia, but Moore described an “anomalous” position above and separated from the pedal nerve centres. (7) Moore assumed presence of a muscular introvertible penis, based on the presence of an outgrowth from the male pallial gonoduct. The structure, function and homologies of this structure have been discussed by Strong and Glaubrecht (2002) and Glaubrecht and Strong (2004); it is here confirmed to represent a glandular spermatophore-forming organ.

Although no complete anatomical description is available for any species of the *Lavigeria* clade, Moore (1899) provided information on the alimentary, nervous and female reproductive systems for specimens that were clearly misidentified as *Nassopsis nassa* (= *Lavigeria nassa*). Michel (2004) provided data on features of the midgut, nervous system, and reproductive system for *Vinundu*, the oviparous sister group to *Lavigeria*, as well as comparative data on the pallial oviduct for *Lavigeria* sp. B.

Those previously published results are compatible with ours, and indicate that *Lavigeria* and *Vinundu* share the presence of a paucispiral operculum, buccal pouches, a long radular sac, midgut with a broadly rounded glandular pad, crystalline style, and a highly condensed nerve ring with a short, stout zygonis between the right pleural and sub-oesophageal ganglia. Similar to *Lavigeria* sp. A, *L. sp. B* also possesses a large glandular fold within the medial lamina – a structure lacking in *Vinundu* (Michel 2004). Moore (1899) again noted the presence of cross-connections between the pedal cords; as for *Tiphobia*, we found pedal cross-connections to be lacking in *Lavigeria* sp. A.

Ontogeny

Many scattered observations are available on the developing larvae of marine and freshwater cerithioideans, particularly on their shells. Yet no detailed description of the complete ontogenetic sequence, from egg to juvenile, of any freshwater cerithioidean has been published. Although it is difficult to reconstruct the continuous process of embryonic development from the ‘snapshots’ preserved within the brood pouch, brooding

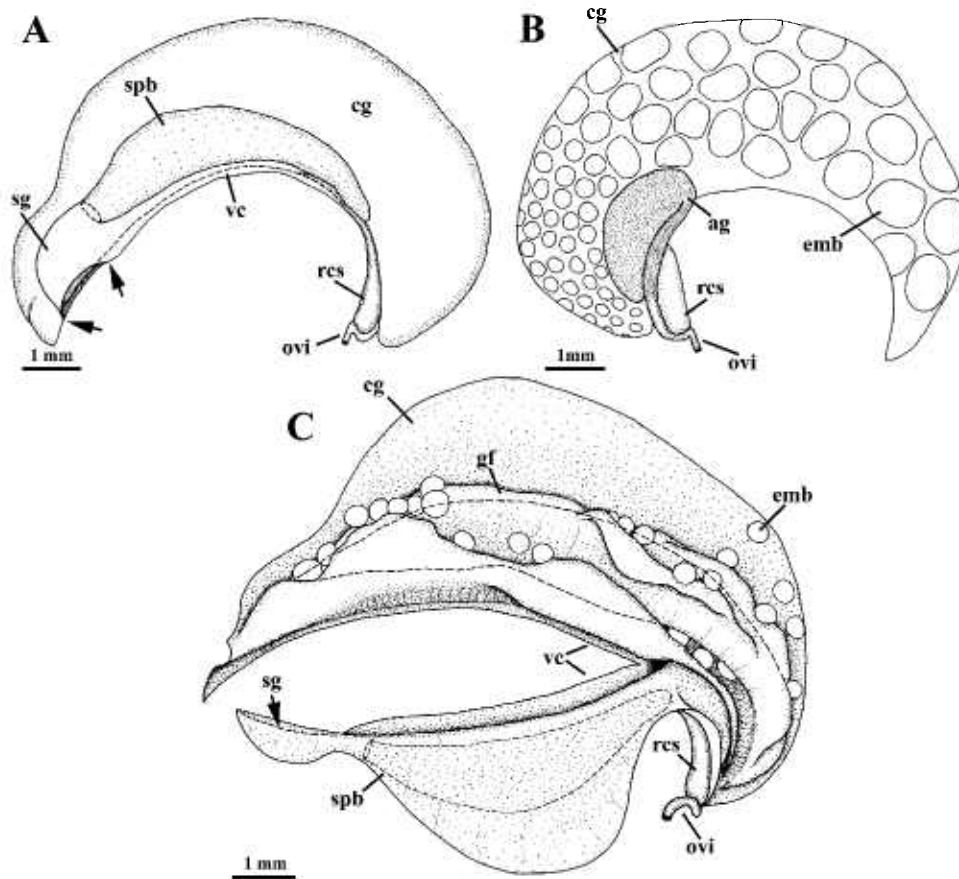


Fig. 14. Pallial oviduct of *Lavigeria* sp. A (MRAC 621282–288). (A) External, left lateral view, anterior at right; arrows indicate extent of opening to mantle cavity; dashed line indicates free edge of sperm gutter inner wall. (B) External, right lateral view, anterior at right; note ‘c-shaped’ albumen gland (ag). (C) Internal view, oviduct opened ventrally along ventral channel and dorsally along oviductal groove with medial lamina deflected to left; note prominent glandular fold along floor of lateral lamina bounding ventral channel; this specimen less mature than that figured in A and B, with relatively few, immature embryos. Abbreviations: ag = albumen gland; cg = capsule gland; emb = developing embryo; gf = glandular fold; ovi = renal oviduct; res = seminal receptacle; sg = sperm gutter; spb = spermatophore bursa; vc = ventral channel.

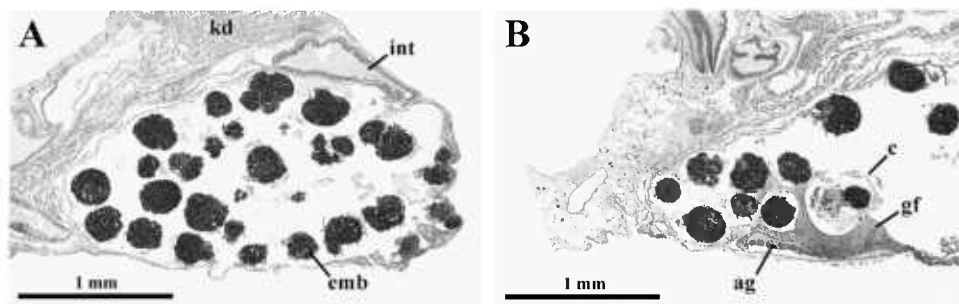


Fig. 15. Histology of the pallial oviduct of *Lavigeria* sp. A (MRAC 621282–288). (A) Cross-section through posteriormost pallial oviduct with fertilized eggs. (B) Cross-section through albumen gland and overlying glandular fold. Abbreviations: ag = albumen gland; c = egg capsule; emb = embryo; gf = glandular fold; int = intestine; kd = kidney.

cerithioideans provide a unique opportunity to study the ontogenetic sequence of embryonic morphological differentiation. The present analysis of *T. horei* confirmed that gastrulation appears to take place by epiboly

(Fig. 7D–E), consistent with observations on other caenogastropods (Raven 1958; Verdonk and van den Biggelaar 1983). Following gastrulation, the embryo elongates, the foot and mantle begin to differentiate,

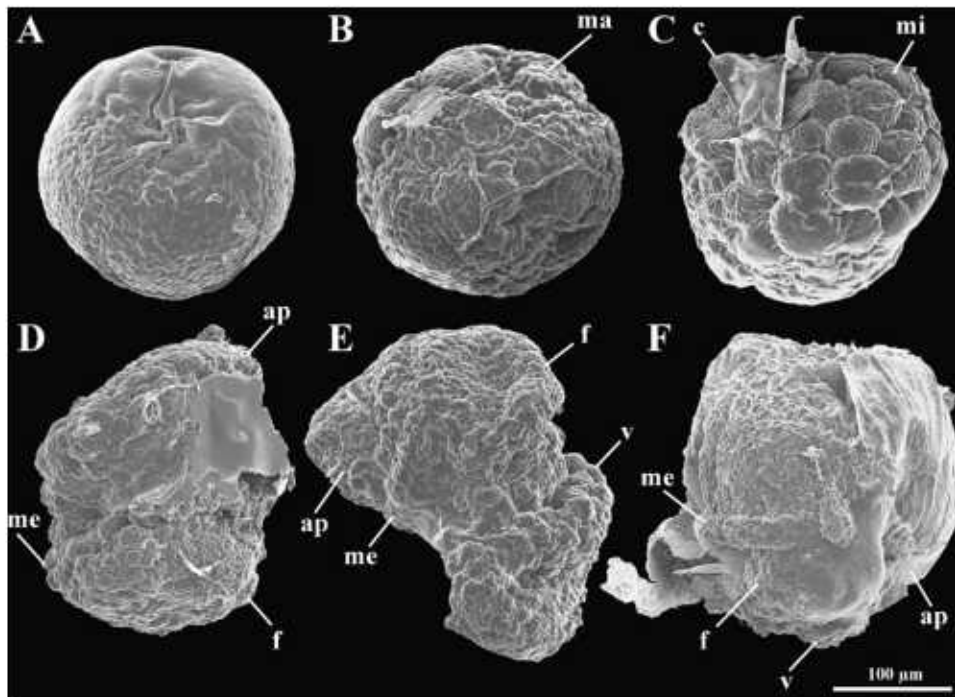


Fig. 16. Early development in *Lavigeria* sp. A (MRAC 621282–288); early, not well preserved embryos from young female. (A) Fertilized egg from proximal brood pouch; animal pole at top. (B) Vegetal pole of early embryo showing macromeres. (C) Animal pole of early embryo showing micromeres. (D) Late trochophore showing elongation of embryo and differentiation of mantle edge. (E–F) Early veligers showing differentiation of foot and velum, and initiation of calcification. All embryos to scale. Abbreviations: ap = apex; c = egg capsule; f = foot; ma = macromere; me = mantle edge; mi = micromere; v = velum.

and a distinct asymmetry becomes apparent (Fig. 7F). As demonstrated in other gastropods, the primary source of this pre-torsional asymmetry is differential growth (Verdonk 1979). The tiny plates of calcium carbonate forming over the embryonic cap are brought into contact and allowed to completely fuse apparently through the shrinking of the underlying yolk mass; this occurs after approximately one-half whorl of accretionary growth is complete. This process produces a characteristically wrinkled apical whorl of the embryonic shell which has been observed in many other brooding freshwater Cerithioidea (Riedel 1993; Glaubrecht 1996).

Although cerithioideans emerge as crawling juveniles, the hallmarks of planktonic larval gastropod development are nonetheless evident, the most striking being the presence of a velum. This structure becomes apparent first during the earliest stages of elongation of the embryo (Fig. 7F, v) and continues to develop and become more prominent during the pre-torsional stages. The presence of a velum in other gastropods that undergo intracapsular development to emerge as crawling juveniles has been noted in caenogastropods and heterobranchs (e.g. Raven 1958; Moran 1999), including some cerithioids in the Thiaridae s.s. (e.g. Hubendick 1952; Glaubrecht 1996; Bandel and Kowalke 1997),

Pleuroceridae (e.g. Dazo 1965) and Potamididae (Houbrick 1984). The retention of a velum in gastropods with nonplanktonic development may be the consequence of developmental constraints, may indicate an evolutionarily recent shift to intracapsular development, or may reflect specific feeding and/or respiratory functions within the egg capsule (see review in Moran 1999). However, Hubendick (1952) speculated that the velum in *Fijidoma maculata* may function as a sort of placenta – a role that was confirmed for the first time by Moran (1999), who established that the velum has been co-opted for endocytotic protein uptake within the egg capsule in several *Littorina* species. The precise role, if there is any, of the velum in *Tiphobia* and *Lavigeria* embryos remains to be established, but it may function in nutrient uptake within the large, fluid-filled capsules.

Due to rarity of appropriately preserved specimens, only a single, young female was available for examination of embryonic stages in the brood pouch of *Lavigeria* sp. A (a second female had to be used for histological sectioning). This female (Fig. 14C) contained only fertilized eggs and pre-torsional embryos within the brood pouch. In addition, the embryos were not exceptionally well preserved. Thus, it is not possible to describe the sequence of embryonic development in

detail comparable to that for *T. horei*. However, it is clear that a similar sequence and timing of events occurs in *Lavigeria* sp. A, with cleavage and elongation of the embryo, followed by progressive differentiation of the head-foot, velum and mantle edge (Fig. 16A–E) and delayed calcification of the embryonic cap (Fig. 16F). Similar to *T. horei*, embryos develop within individual egg capsules with no evidence of adelphophagy. The limited comparison possible between the two species nonetheless reveals that shells of the females from which the embryos were taken differ in size by a factor of approximately 1.8 (excluding the long siphonal canal of *Tiphobia*), while fertilized eggs differ in size by a factor of about 2.4. This, in addition to values available for other thalassoid species (Table 2), suggests that the eggs and hence the hatchlings are disproportionately small in *Lavigeria* sp. A given the size of the adult female. This is true of several other *Lavigeria* species as well, but significant variability is evident in the clade (Kingma and Michel 2000).

Systematic affinity of *Tiphobia* and *Lavigeria*

Features of the shell of *Tiphobia*, particularly the spines, as well as aspects of internal anatomy, led several authors to presuming affinity with *Bathanalia* (Moore 1898b; Pelseneer 1906; Darteville and Schwetz 1948), sometimes also including *Limnotrochus* in the family Tiphobiidae Bourguignat, 1886 (Germain 1908). Other workers more or less maintained the cohesion of this grouping, for example by recognizing the Tiphobiidae as a family closely related to the “Melaniidae” (Pelseneer 1906), or as a grouping within the “thalassoid ‘Melaniidae’ of Lake Tanganyika” (Pilsbry and Bequaert 1927).

As with all members of the Lake Tanganyika species flock, the systematic placement of *Lavigeria* has been highly unstable, with suggested affinities ranging from the Purpuridae (Germain 1908) and “Melaniidae” (Pelseneer 1906; Pilsbry and Bequaert 1927) to Pleuroceridae (Morrison 1954). Indeed, as late as the 1930s *Lavigeria* was allied to the Architaenioglossa (e.g. Thiele 1925, 1929; Wenz 1939). Only since the treatments of Darteville and Schwetz (1948) and Leloup (1953) has their affinity to other Lake Tanganyika cerithioideans gained widespread acceptance.

Recent molecular analyses of the Lake Tanganyika thalassoid gastropods (West and Michel 2000; Michel 2004; Wilson et al. 2004) have not supported monophyly of the lacustrine species, with *Cleopatra* – a widespread African genus of the family Paludomidae – falling within the ingroup. One molecular analysis (Wilson et al. 2004) placed *Tiphobia* in a clade with *Paramelania* and *Limnotrochus* (Fig. 17), substantiating earlier views to some extent, whereas a second analysis placed

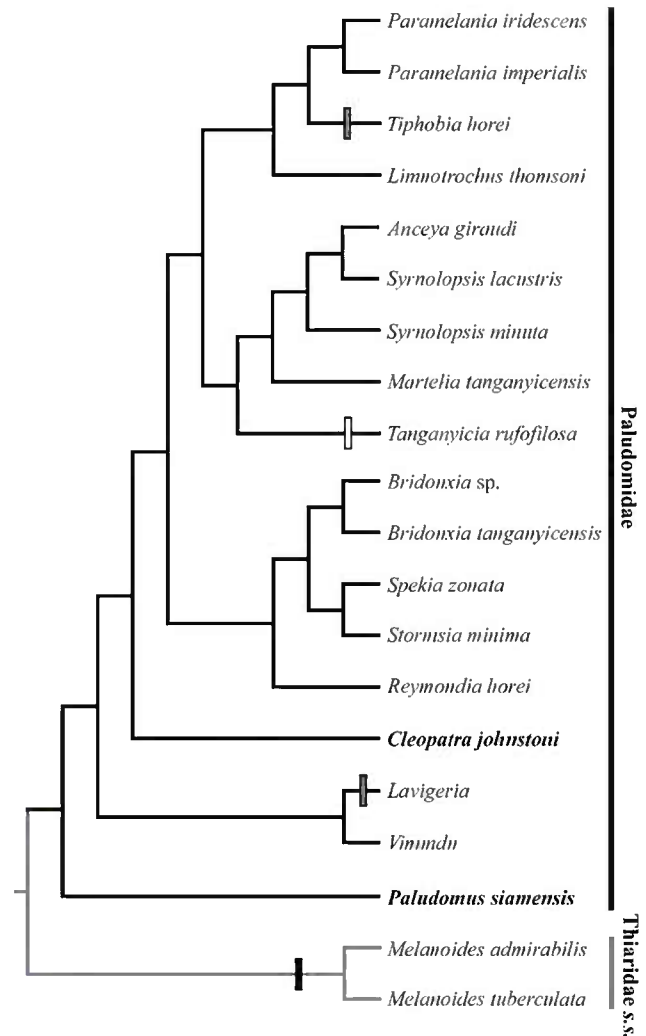


Fig. 17. Evolution of brooding among thalassoid gastropods mapped onto cladogram resulting from analysis of combined 16S and COI sequences; adapted from Wilson et al. (2004, fig. 1). Two species of Thiaridae s.s. as outgroups; non-lacustrine Paludomidae in boldface. Grey hash marks indicate independent origin of a uterine brood pouch in *T. horei* and the *Lavigeria* clade in Lake Tanganyika; white hash mark indicates unique origin of mesopodial brood pouch in *Tanganyicia rufofilosa*; black hash mark indicates presence of a subhaemocoelic brood pouch in outgroup.

Tiphobia in a clade with *Paramelania* and *Anceya* (West and Michel 2000). The former analysis did not include *Bathanalia*, but the latter found support for a clade including *Bathanalia*, *Chytra*, and *Limnotrochus*. Both studies supported a derived position for *Tiphobia*. In contrast, both of these analyses placed the *Lavigeria* clade in a basal position, as the first offshoot, or perhaps even an independent lineage, of the species flock.

The distant relationship between *Tiphobia* and *Lavigeria*, as supported in these molecular analyses and in ongoing morphological studies (Strong and Glaubrecht

Table 1. Comparison of morphological differences between *Tiphobia horei* and *Lavigeria* sp. A

	<i>Tiphobia horei</i>	<i>Lavigeria</i> sp. A
<i>Shell microstructure</i>		
Number of crossed lamellar layers	Two	Three
<i>External anatomy</i>		
Operculum	Concentric with spiral nucleus	Paucispiral
Mantle edge	Thin, simple	Scalloped
<i>Alimentary system</i>		
Radular sac	Short	Long
Buccal pouches	Absent	Present
Sorting area	Rectangular	Tapering
Sorting area pad	Present	Absent
Cleft in accessory marginal fold	Broad	Narrow
Glandular pad	Elongate, narrow	Broadly rounded
Hindgut	Several loops	One loop
<i>Reno-pericardial system</i>		
Incomplete horizontal septum in kidney	Weakly developed	Large and well developed
<i>Nervous system</i>		
Connection between right pleural and sub-oesophageal ganglia	Dialyneury	Zygoneury
<i>Reproductive system</i>		
Lamellae in medial lamina	Present	Absent
Glandular fold	Present, small	Present, hypertrophied
Seminal receptacle	Absent	Present
Inner wall of medial lamina	Fused to ventral channel	Free

2001, 2002, 2003; Strong unpubl. data), is corroborated by the marked morphological differences between these two taxa in all organ systems (Table 1), not just in reproductive anatomy as detailed below.

Origin of brooding in Lake Tanganyika

Consistent with their distant relationship, plotting the origin of brooding on cladograms produced in recent studies (West and Michel 2000; Strong and Glaubrecht 2001; Michel 2004; Wilson et al. 2004) supports the independent acquisition of uterine brooding in *Lavigeria* and *Tiphobia* (Fig. 17). Consequently, despite being formed by homologous structures – the pallial oviduct – the uterine brood pouches of these two taxa are functionally analogous. Thus, from the point of view of homology assessment, it is useful to compare the structural features of the brood pouches in these two genera in detail.

Comparison of the pallial oviducts in *Tiphobia* and *Lavigeria* indicates that each presents unique features consistent with their independent modification for brooding (Table 1). The most significant difference between the two is that the inner wall of the medial lamina in *Tiphobia* bears glandular lamellae that branch and anastomose, likely creating increased surface area

where developing embryos can be protected, while at the same time directing embryos anteriorly towards the genital aperture as they develop; such lamellae are absent in *Lavigeria*. In contrast, *Lavigeria* has developed a similar system through hypertrophy of the longitudinal glandular fold in the lateral lamina.

In addition to these differences, the pallial oviducts of *Tiphobia* and *Lavigeria* share many similarities with each other and other thalassoid species (Strong and Glaubrecht 2002, 2003; Strong unpubl. data). All species investigated thus far possess a closed pallial oviduct, a spermatophore bursa in the medial lamina, a coiled albumen gland, and some modification of the glandular fold overhanging the ventral channel. The ubiquitous presence of these features in lake species, as well as in non-thalassoid African (*Cleopatra*) and Asian (*Paludomus*) members of the Paludomidae, indicates that they likely represent symplesiomorphies of the species flock.

An additional species, *Tanganyicia rufofilosa* possesses a brood pouch within the foot – a so-called mesopodial brood pouch (Strong and Glaubrecht 2002). This represents a third independent origin of this life history strategy in the lake, as well as a unique brooding structure in the Cerithioidea (Strong and Glaubrecht 2002) (see Fig. 17).

Thus, there are at least three independent origins of brooding within the lake: in *Lavigeria*, *Tiphobia*

and *Tanganyicia*. In addition, species in the riverine *Potadomoides* inhabiting the Malagarasi and Congo River systems are also uterine brooders, but these have yet to be included in any molecular analyses of the species flock. However, morphological data (anatomy, radula, operculum) support the close affinity of *Potadomoides* to the *Lavigeria* clade (Glaubrecht 1996; Strong and Glaubrecht 2001; Glaubrecht and Strong, 2007), but placement relative to the oviparous *Vinundu* from Lake Tanganyika requires further investigation. One possibility is that the uterine brood pouch of *Potadomoides* is homologous to that of *Lavigeria*, but it may also represent a fourth independent origin. The details of this case will be discussed elsewhere (Glaubrecht and Strong, 2007).

The significance of brooding in Lake Tanganyika is still unclear (for reviews and discussion, see Glaubrecht 1996, 1999, 2001, 2006). There is no apparent correlation between the origin of this life history strategy and any obvious morphological, ecological or biogeographical attribute. Instead, brooding is widely distributed across taxa highly divergent in morphology and varying in habitat from the splash zone on rocks to quiet, deeper-water, muddy habitats. For example, this reproductive strategy occurs across considerable ranges in body size (10.6–51.8 mm), fecundity (68–488 embryos), egg diameter (217–520 µm), and hatchling size (558 µm–1.47 mm) (Table 2).

Brooding does not appear to be strictly correlated with species richness either. Cohen and Johnston (1987) speculated that gene flow between populations of lacustrine brooders may be greatly inhibited by extreme localization (i.e. diminished dispersal), thereby facilitating speciation. Several workers have advocated the general validity of this correlation, apparently by extrapolating from the species-rich *Lavigeria* clade (e.g. Cohen and Johnston 1987; Coulter 1991; Brown 1994; Michel 1994, 2004). However, as acknowledged by some (e.g. Cohen and Johnston 1987; Michel 1994), the occurrence of brooding in the species-poor *Tiphobia* and *Tanganyicia* argues against high interdependence between viviparity and formation of speciose clades. Indeed, *Lavigeria* seems to be an exception rather than the rule. A viviparous reproductive strategy may be significant in some cases, as is assumed for other species-rich lacustrine gastropods, such as *Tylomelania* in the central lakes on Sulawesi (Rintelen et al. 2004). However, additional aspects of reproductive biology, such as gestation period and other as yet unrecognized factors, may be at least equally influential and should be investigated (e.g. Köhler et al. 2004). Thus, the propensity to speciate is more likely a complex combination of factors, including physiology, behaviour, trophic specificity, and ecological stenotopy (Michel 1994).

Brooding in Cerithioidea

Numerous freshwater cerithioideans have independently evolved differing incubatory strategies, including brooding in the mantle cavity (e.g. *Jagora*, Pachychilidae), in the glandular pallial oviduct or uterus (e.g. *Tylomelania* and *Pseudopotamis*, Pachychilidae; *Lavigeria*, *Potadomoides* and *Tiphobia*, Paludomidae; *Semisulcospira*, Pleuroceridae), in the foot (*Tanganyicia*, Paludomidae) and within the body cavity, or in a subhaemocoelic brood pouch (e.g. Thiaridae s.s.). Subhaemocoelic brood pouches are also found in the marine Planaxidae and one species of Siliquariidae, with isolated reports of brooding in the mantle cavity from the marine Turritellidae and Siliquariidae (see Table 2 and references therein).

Table 2 represents a compilation of comparative reproductive strategies for a sampling of brooding cerithioideans, including maximum shell dimensions for adults, condition of the oviduct, position and condition (e.g. compartmentalization) of the brood pouch, type and location of embryonic development, fecundity, and size of the eggs and hatchlings. It is important to note that number of juveniles in the brood pouch, size at maturity and size of adult females vary both geographically and seasonally (the table gives the maximum values reported for the respective species). Often fertilized eggs are not found within the brood pouch, especially in species that brood only a few, large juveniles. In these cases, the width of the apical whorl is given as a proxy and will provide a minimum estimate for egg diameter, as elongation and shrinkage of the embryo at the time of calcification will produce an apical whorl that is narrower than the maximum egg diameter.

A range of strategies is apparent in these lineages, from strongly r-selected (e.g. release of thousands of free-swimming veligers in Thiaridae s.s.), to strongly K-selected strategies (release of a few large juveniles in Pachychilidae) (reviews in Glaubrecht 1996, 1999, 2006; Köhler and Glaubrecht 2003; Köhler et al. 2004). The diversity of these varied brooding strategies makes it difficult to formulate generalities concerning the origin of this reproductive mode, but several patterns are evident:

- (1) The origin of brooding is not clearly linked to the condition of the oviduct (open vs. closed). Uterine brooding has arisen independently a comparable number of times among those taxa with closed pallial oviducts (two to three times among *Lavigeria*, *Tiphobia* and *Potadomoides* in Paludomidae; see text for discussion) as among those with open pallial oviducts (twice among *Semisulcospira* in Pleuroceridae and *Pseudopotamis*, *Tylomelania* in Pachychilidae) (Glaubrecht and Rintelen 2003; Rintelen and Glaubrecht 2003, 2005; Prozorova and Rasshepkina 2005).

Table 2. Comparison of reproductive strategies for a selection of brooding cerithioideans

	Max. shell height	Oviduct	Egg diameter (µm)	Max. embryo number	Max. hatchling height	Post-metamorphic development	Brood pouch	Compartments or lamellae	Brooding/feeding mode
<i>Freshwater</i>									
Paludomidae									
<i>Lavigeria</i> sp. A	16.1 mm	Closed	217	154+ (n = 1)	288 + µm	Intracapsular	Uterine	Glandular fold	Ovoviviparous lecithotrophic
<i>Lavigeria grandis</i>	31.2 mm	Closed	~250-1000	100	2.5 mm	Intracapsular	Uterine	Glandular fold	Ovoviviparous lecithotrophic
<i>Lavigeria nassa</i>	23.4 mm	Closed	~250-750	~290	750 µm	Intracapsular	Uterine	Glandular fold	Ovoviviparous lecithotrophic
<i>Potadomoides pelseneeri</i>	10.6 mm	Closed	250	195 (n = 1)	558 µm	Intracapsular	Uterine	Compartments	Ovoviviparous lecithotrophic
<i>Tanganyicia rufiflora</i>	17.3 mm	Closed	250 ± 23 ^a	68 (n = 1)	928 µm	Intracapsular	Mesopodial	Long. Lamellae	Ovoviviparous lecithotrophic
<i>Tiphobia horei</i>	51.8 mm	Closed	520	488 (n = 2)	1.47 mm	Intracapsular	Uterine		Ovoviviparous lecithotrophic
Paechyhelidae									
<i>Adamietta housei</i>	28.9 ± 7.2 mm	Open	1000	<1000	2.5 mm	Intracapsular	Subhaemocoelic	No compartments	Ovoviviparous lecithotrophic
<i>Brotia costula</i>	39.5 ± 9.1 mm	Open	1000	120 (n = 2)	2.5 mm	Intracapsular	Subhaemocoelic	No compartments	Ovoviviparous lecithotrophic
<i>Brotia hainanensis</i>	34.6 ± 8.9 mm	Open	1000	248 (n = 3)	1.5 mm	Intracapsular	Subhaemocoelic	No compartments	Ovoviviparous lecithotrophic
<i>Brotia pageli</i>	46.0 ± 11.4 mm	Open	1000	320 (n = 3)	2.8 mm	Intracapsular	Subhaemocoelic	No compartments	Ovoviviparous lecithotrophic
<i>Brotia pagodula</i>	29.2 ± 5.7 mm	Open	1000	1 (n = 1)	5.6 mm	Intracapsular	Subhaemocoelic	No compartments	Ovoviviparous lecithotrophic
<i>Brotia testudinaria</i>	29.8 ± 3.4 mm	Open	1000	120 (n = 3)	1.3 mm	Intracapsular	Subhaemocoelic	No compartments	Ovoviviparous lecithotrophic
<i>Jagora asperata</i>	48.5 ± 6.0 mm	Open	1100	275 (n = 1)	1.7 mm	Intracapsular	Mantle cavity	n/a	Ovoviviparous lecithotrophic
<i>Jagora dactylus</i>	47.0 ± 5.4 mm	Open	1100	90 (n = 4)	1.7 mm	Intracapsular	Mantle cavity	n/a	Ovoviviparous lecithotrophic
<i>Pseudopotamius supralirata</i>	23.7 mm	Open	110 ^a	3 (n = 4)	6.5 mm	Intracapsular	Uterine	Transverse septae	Ovoviviparous lecithotrophic
<i>Pseudopotamius semoni</i>	21.4 mm	Open	100 ^a	1 (n = 2)	4.1 mm	Intracapsular	Uterine	Transverse septae	Ovoviviparous lecithotrophic
<i>Tylomelania bakara</i>	63.5 mm	Open	83.3 ± 5.7 ^a	17 (n = 21)	10 mm	Intracapsular	Uterine	Transverse septae	Ovoviviparous lecithotrophic
<i>Tylomelania helmuti</i>	34.6 mm	Open	88.3 ± 5.9 ^a	15 (n = 24)	6.5 mm	Intracapsular	Uterine	Transverse septae	Ovoviviparous lecithotrophic
<i>Tylomelania kraumeli</i>	69.3 mm	Open	97.3 ± 5.7 ^a	14 (n = 17)	11 mm	Intracapsular	Uterine	Transverse septae	Ovoviviparous lecithotrophic
Pleuroceridae									
<i>Semisulcospira libertina</i>	?	Open	~413	?	?	Intracapsular	Uterine	Compartments	Ovoviviparous lecithotrophic
Thiaridae s.s.									
<i>Fijidoma maculata</i>	~14 mm	Closed	?	79	~1.6 mm	Intracapsular	Subhaemocoelic	Compartments	Viviparous? lecithotrophic
<i>Hemisimus brasiliensis</i>	~39 mm	Closed	96.4 ± 6.1 ^a	5	3.0 mm	Extracapsular	Subhaemocoelic	Compartments	Viviparous lecithotrophic

<i>Melanoides tuberculata</i>	~50 mm	Closed	83.9 ± 8.64 ^a	265	4.3 mm	Extracapsular	Subhaemocoelic	Compartments	Viviparous lecitotrophic
<i>Stenomelania plicaria</i>	~70 mm	Closed	~80 ^a	?	?	?	Subhaemocoelic	No compartments	Ovoviviparous lecitotrophic
<i>Stenomelania punctata</i>	~50 mm	Closed	~78 ^a	?	~150 µm	Planktonic	Subhaemocoelic	No compartments	Ovoviviparous planktotrophic
<i>Tarebia granifera</i>	~40 mm	Closed	76 ± 7.3 ^a	74	10.0 mm	Extracapsular	Subhaemocoelic	Compartments	Viviparous lecitotrophic
<i>Thiara amarula</i>	~50 mm	Closed	100	"Several thousand"	~770 µm	Planktonic	Subhaemocoelic	Compartments	Ovoviviparous planktotrophic
<i>Thiara scabra</i>	~29 mm	Closed	82 ^a	110	3.0 mm	Extracapsular	Subhaemocoelic	Compartments	Viviparous adelphophagy
MARINE									
Planaxidae									
<i>Angiola lineata</i>	10 mm	Open	?	30	100 µm	Planktonic	Subhaemocoelic	Compartments	Ovoviviparous planktotrophic
<i>Fissilabia decollata</i>	30 mm	Open	~111 ^a	436	400 µm	Planktonic (-)	Subhaemocoelic	Compartments	Ovoviviparous lecitotrophic
<i>Fossarus ambiguus</i>	4 mm	Open	~55	2000	77 µm	Planktonic	Subhaemocoelic	No compartments	Ovoviviparous planktotrophic
<i>Hinea brasiliana</i>	20 mm	Open	?	?	300 µm	Planktonic (-)	Subhaemocoelic	Compartments	Ovoviviparous lecitotrophic
<i>Planaxis sulcatus</i>	35 mm	Open	?	2000	150 µm	Planktonic	Subhaemocoelic	Compartments	Ovoviviparous planktotrophic
<i>Supplanaxis nucleus</i>	20 mm	Open	?	12,886	150 µm	Planktonic	Subhaemocoelic	Compartments	Ovoviviparous planktotrophic
Siliquariidae									
<i>Siliquaria weldtii</i>	?	Open	?	150	?	Intracapsular?	Subhaemocoelic	n/a	Ovoviviparous lecitotrophic
<i>Stephopoma roseum</i>	?	Open	?	15	?	Intracapsular	Mantle cavity	n/a	Ovoviviparous lecitotrophic
Turritellidae									
<i>Gazameda gunni</i>	?	Open	1000	?	3.0 mm	Intracapsular	Mantle cavity	n/a	Ovoviviparous lecitotrophic
<i>Vermicularia spirata</i>	13.0 cm	Open	300	Mean of 11 (48 capsules)	630 µm	Planktonic (-)	Mantle cavity	n/a	Ovoviviparous lecitotrophic

Sources: Morton (1951), Carriek (1980), Houbrecht (1987, 1990), Nakano and Nishiwaki (1989), Bieler and Hadfield (1990), Glaubrecht (1996), Bandel et al. (1997), Schütt and Glaubrecht (1999), Kingma and Michel (2000), Köhler and Glaubrecht (2001), Strong and Glaubrecht (2002), Köhler (2003), Bieler (2004), Köhler et al. (2004), Prozorova and Rasshepkina (2005), Glaubrecht and Strong (2007), present study, Strong (unpubl. data).

^aWidth of apical whorl (egg diameter unknown). For *Lavigeria* sp. A, estimates of embryo number hatching size from one immature female are considered low. (-) In *Fissilabia*, *Hinea* and *Vermicularia* there may be only a short lecitotrophic phase. *Planaxis sulcatus* displays a variety of developmental modes in different geographic localities; see Houbrecht (1987), Bouchet (1989) and Glaubrecht (1996) for discussion on poecilogony and a possible cryptic species in the northwestern Indian Ocean. Juveniles in viviparous species spend time within the brood pouch after hatching from the egg capsule, feeding on nutritive secretions from the brood pouch epithelium. See text for additional discussion.

- (2) The presence of lamellae within the pallial oviduct is strongly linked, or perhaps even strictly correlated, with brooding in the oviduct. For example, the brood pouch of *Tylomelania* contains up to 23 embryos, separated by transverse folds; maximum embryo size varies with size of the mature female, and ranges from 2.5 to 20 mm (Rintelen and Glaubrecht 2003, 2005). The brood pouch of *Pseudopotamis* contains 1–3 large, shelled embryos also separated by thin transverse folds of tissue from the floor of the genital groove (Glaubrecht and Rintelen 2003). In *Semisulcospira*, many small brood chambers are formed by thin sheets of non-glandular epithelium (Nakano and Nishiwaki 1989). Although the precise number of embryos was not specified, the diagrammatic representation suggests far fewer than are found in mature *Tiphobia* or *Lavigeria*. Thus, the fecundity of Lake Tanganyika thalassoid gastropods surpasses that of other cerithioideans with uterine brood pouches and is uniquely correlated with the longitudinal arrangement of folds in the brood pouch which may facilitate such high productivity.
- (3) Delayed calcification in conjunction with shrinking of the large yolk mass, producing a characteristically wrinkled embryonic cap, is evident in many brooding cerithioideans, including members of the Paludomidae, Pachychilidae, Planaxidae, and Thiaridae s.s. (e.g. Houbriek 1990; Riedel 1993; Glaubrecht 1996; Bandel et al. 1997; Rintelen and Glaubrecht 1999; Köhler and Glaubrecht 2001, 2003; Strong and Glaubrecht 2002; Glaubrecht and Rintelen 2003; current study). As noted by Riedel (1993), the precise mode of calcification varies, producing distinct shell textures in various taxa. Consequently, the texture of embryonic shells ranges from exceptionally rugose (e.g. *T. horei*) to only slightly wrinkled (e.g. *Tanganyicia rufofilosa*; Strong and Glaubrecht 2002). A notable exception is the smooth embryonic shell of *Vermicularia spirata* (Bieler and Hadfield 1990). The resemblance of this protoconch to non-brooding turritellids with planktonic lecithotrophic development (e.g. *Turritella communis*; Lebour 1933) suggests that development in *V. spirata* has been little modified from its non-brooding relatives. However, consistent with other species exhibiting increased parental care, egg diameter is significantly larger: 300 µm compared to an average diameter of 139 µm in *Turritella communis* (Kennedy and Keegan 1992).
- (4) As is evident from a comparison of such taxa as the oviparous, species-rich freshwater Pleuroceridae and Melanopsidae versus the viviparous, species-poor marine Planaxidae (see Table 2), the evolution of brooding is generally but not strictly associated with life in freshwater, suggesting that there is likely a strong selective pressure for increased parental care

in freshwater. However, it is neither a prerequisite for the colonization of this biotope nor does it necessarily promote speciation (see also Glaubrecht 1996, 2006; Köhler et al. 2004).

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