A morphological reanalysis of *Pleurocera acuta* Rafinesque, 1831, and *Elimia livescens* (Menke, 1830) (Gastropoda: Cerithioidea: Pleuroceridae)

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ABSTRACT

Pleurocera acuta and *Elimia livescens* have been the subject of several anatomical and ecological studies and are two of the most thoroughly documented species of North American Pleuroceridae. Yet significant gaps still remain in our understanding of their structure. Consequently, the anatomy of these two species is re-described, allowing a re-interpretation of pallial oviduct homologies; features not previously portrayed in the literature (midgut and kidney) are newly described. These taxa are characterized by the presence of an ovipositor, a kidney with a subdivided internal lumen that invades the pallial roof, a prostate with a highly folded anterior spermatophore-forming region, and a pallial oviduct with spermatophore bursa but lacking a seminal receptacle. This analysis verifies the degree of similarity between the two species, but a number of differences were identified including features of the ovipositor, pallial oviduct, prostate, anterior esophagus, midgut, kidney, pericardium and nervous system. Comparison to other pleurocerids confirms that species distributed in Western North America (*Juga*) and Asia (*Hua, Semisulcospira*) share the presence of a seminal receptacle—a feature that is lacking in all described Eastern North American species.

INTRODUCTION

The freshwater Pleuroceridae Fischer, 1885, comprises one of the most species-rich assemblages of limnic mollusks occurring in North America and Eastern Asia. In North America, they are represented by eight genera (*Athearnia* Morrison, 1971, *Elimia* H. and A. Adams, 1854, *Io* Lea, 1831, *Juga* H. and A. Adams, 1854, *Leptoxis* Rafinesque, 1819, *Lithasia* Haldeman, 1840, *Pleurocera* Rafinesque, 1818, and the extinct *Gyrotoma* Shuttleworth, 1845) and estimates of 159 species currently considered valid; of these, 34 are extinct and 59 are listed as critically imperiled (G1) or imperiled (G2) (Johnson et al., 2005).

The current concept of the family Pleuroceridae (e.g. Bouchet and Rocroi, 2005) can be traced to the works of Thiele (1928, 1929) who recognized 6 subfamilies within the heterogeneous "Melaniidae" (an invalid name for Thiaridae Gill, 1871), including the Pleurocerinae. An alternative, highly polyphyletic view promoted by Morrison (1954) caused great confusion for more than four decades concerning the extension and independence of the Pleuroceridae and Pachychilidae P. Fischer and Crosse, 1892 (e.g. Ponder and Warén, 1988). Recent work on the systematics of limnic lineages within the Cerithioidea Fleming, 1822 (e.g. Glaubrecht, 1996, 1999; Köhler et al., 2004) has resolved some of this confusion and supports the distinctiveness of these families on both morphological and molecular grounds. However, molecular data (Lydeard et al., 2002) do not support monophyly of the Pleuroceridae as currently defined, but suggest that a clade of eastern North American species are more closely related to *Melanopsis* (Melanopsidae H. Adams and A. Adams, 1854) than to a clade of western North American (*Juga*) and eastern Asian pleurocerids (*Semisulcospira* Boettger, 1886, *Hua* Chen, 1943).

As noted by Woodard (1934), anatomical data are critical in refining the phylogenetic relationships and classification of these species. However, all taxonomic treatments of the family have been based primarily on conchological characters in the absence of a broad comparative understanding of morphology. Although the subject of numerous ecological studies (e.g. Dillon, 2000) and comparably many descriptions exist for the radula, operculum and life history of North American pleurocerids, surprisingly little is known about their basic biology and anatomy. Scant information on the anatomy (besides radula and operculum) has been provided for *Elimia laqueata* (Say, 1829) (Woodard, 1934), *E. potosiensis* (Lea, 1841) (Jones and Branson, 1964) and *Pleurocera canaliculata* (Say, 1821) (Magruder, 1935b); among western North American forms, only reproductive anatomy is known for several species (Prozorova and Raschepkina, 2004). In addition, the

classically cited work of Dazo (1965) on the natural history, ecology, distribution and anatomy of *Pleurocera acuta* Rafinesque, 1831 and *Elimia livescens* (Menke, 1830) has long stood as the most comprehensive morphological study of any pleurocerid gastropod. As such, that study has formed the basis for hypotheses of homology in recent higher-order phylogenetic studies based on morphology (e.g. Houbrick, 1988; Glaubrecht, 1996). Yet, Dazo's study was completed long before our present understanding of the structure, function and homologies of cerithioidean reproductive anatomy was in place, particularly through the work of R. S. Houbrick on marine species. We also have a much more thorough understanding of midgut structure and its utility in revealing phylogenetic affinities of cerithioideans (Glaubrecht and Strong, 1999; Strong and Glaubrecht, 1999, unpublished data).

Given the persistent paucity of anatomical data available for the family, the goal of this contribution is to reevaluate the morphology and putative homologies of the two species described by Dazo, and to place them within the emerging framework now available for limnic cerithioideans. This is critical for ongoing morphological and phylogenetic studies of cerithioidean gastropods, and in particular for clarifying the monophyly and systematic affinity of the family Pleuroceridae.

MATERIALS AND METHODS

This study is based on collections of individuals of *Pleurocera acuta* and *Elimia livescens* living sympatrically in the Mukwonago River at the outflow from Lower Phantom Lake, Mukwonago, Waukesha County, Wisconsin (42°51.402 N; 88°19.767 W). Populations were sampled in May and June; only reproductively mature individuals were used for observations of reproductive anatomy. Individual specimens were cracked, preserved in 95% ethanol and were not relaxed. Voucher material is deposited in the National Museum of Natural History in Washington (USNM).

As stated above, Dazo (1965) provided a rather detailed account of external features (operculum, shell, ovipositor, color patterns of the head-foot) as well as of the radula and all internal organ systems (alimentary, nervous, excretory, respiratory, vascular, and reproductive systems). Baker (1928) also provided information on the operculum, jaw, radulae, and external anatomy of the two species; additional scattered accounts relating to the radula, external anatomy and life history are also available (e.g. Jewell, 1931; Howe, 1938; Goodrich, 1945). As such, the following reanalysis emphasizes anatomy of the soft parts. As the two species are overwhelmingly similar, a thorough account is provided for *Pleurocera acuta* – the type species of the type genus for the family; only details that differ are noted for *Elimia livescens*. However, the internal kidney structure of *P. acuta*, while displaying the same configuration as *E. livescens*, is too occluded with excretory tissue to allow

a clear representation. As such, only the internal structure for the latter species is illustrated.

Specimens were examined using a Leica MZ 12,5 binocular microscope with camera lucida; visualization of structures was enhanced through the use of aqueous toluidine blue. Typically four to five specimens were examined for each organ system investigated, especially for those systems showing high levels of individual and/or seasonal variation (i.e. reproductive system); a minimum of two individuals were examined for particularly complex structures (i.e. midgut, nerves). Descriptions of midgut morphology are given with the stomach opened dorsally and the style sac uppermost. Unless otherwise indicated, an incision is made along the extreme right, upper and lower margins, and the roof deflected laterally to the left. Terminology follows Strong and Glaubrecht (2002, 2003).

RESULTS

Pleurocera acuta Rafinesque, 1831

Material Examined: Wisconsin: Mukwonago River: USNM 1081522, 1081524.

External Anatomy: Operculum sub-ovate, corneous, dark reddish-brown in color, with 3.5 whorls; paucispiral with large, eccentric nucleus of approximately 2.75 to 3 whorls (Figure 1). Final whorl moderately inflated. Nucleus occupying slightly under 1/2 (~43%) of total length.

Foot ovate with narrow propodium; anterior pedal gland opening along anterior margin (Figure 2, **ap**). Ovipositor (**ovp**) located on side of neck below right cephalic tentacle. Ciliated egg groove extending short distance up side of neck from ovipositor, shallowing past mantle margin; groove fading near anal aperture. Two, partially juxtaposed, parallel folds, extending into ovipositor pore from aperture (*); one fold at upper posterior edge, second at lower anterior edge of ovipositor (when viewed laterally), forming obliquely flattened H-shaped lumen. Folds unequal in size; anterior fold along floor significantly larger than posterior fold along roof. Ovipositor pore expanding medially into head-foot, then curving and narrowing slightly posteriorly. Two vertical limbs of "H" unequal such that posterior limb forming rather narrow channel along posterior wall. Anterior limb inflated and expanding medially into foot, forming large flattened, subtriangular chamber. Folds diminishing toward blind tip of pore. Short grooved tract extending ventrally from ovipositor aperture toward foot sole, but not reaching edge of foot.

Most individuals with straight osphradium, but some with curved anterior tip (Figure 3, **os**). Hypobranchial gland highly developed with pendulous, transverse folds (Figure 4, **hg**).

Alimentary System: FOREGUT. Buccal mass short and stout, extending to base of cephalic tentacles (Figure 3,
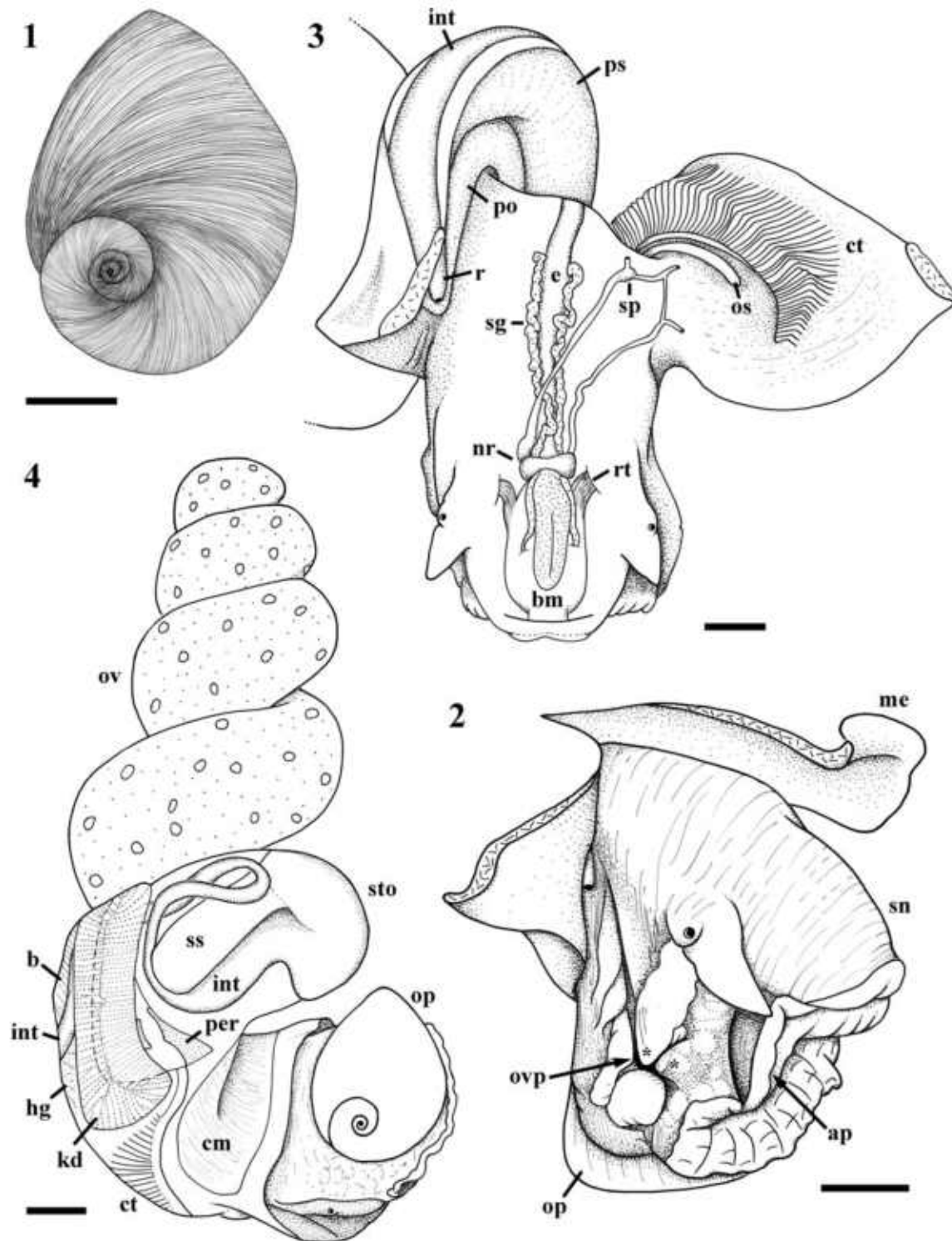
Figures 1–4. Anatomy of *Pleurocera acuta*. **1.** Operculum. **2.** Ovipositor and egg groove. Right lateral view of side of foot. Asterisks (*) indicate folds extending into ovipositor. **3.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. Hypobranchial gland removed for clarity. **4.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. Abbreviations: **ap,** anterior pedal gland; **b,** bladder; **bm,** buccal mass; **cm,** columellar muscle; **ct,** ctenidium; **e,** esophagus; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **nr,** circum-esophageal nerve ring; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **po,** pallial oviduct; **ps,** peri-intestinal sinus; **r,** rectum; **rt,** buccal mass retractor muscle; **sg,** salivary gland; **sn,** snout; **sp,** supra-esophageal ganglion; **ss,** style sac; **sto,** stomach. Scale bars = 1 mm.

bm). Odontophore occupying majority of buccal cavity with small, glandular subradular organ protruding before radula. Small jaws present at anterior ends of dorsal folds; epithelium of buccal cavity overlying dorsal folds glandular (stippled region). Shallow, non-glandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Radular sac short, curving upward behind base of buccal mass. Robust buccal retractors (**rt**) inserting onto lateral walls of cephalic hemocoel adjacent to cerebral ganglia (**nr**). Short, glandular mid-ventral fold forming small flap just behind odontophore in anterior esophagus, flanked laterally by two ventro-lateral folds. Ventro-lateral folds converging short distance behind mid-ventral fold and continuing through mid-esophagus (**e**). Mid-esophagus long, bearing paired longitudinal ventral and dorsal folds. Epithelium between dorsal and ventral folds weakly glandular and irregularly striated; septate esophageal gland lacking. Dorsal and ventral folds converging and fusing at distal end of mid-esophagus before continuing into posterior esophagus and subdividing into numerous folds equal in height. Long, tubular salivary glands (**sg**) opening dorso-laterally to buccal cavity alongside odontophore, passing through circum-esophageal nerve ring (**nr**), almost reaching posterior esophagus.

MIDGUT. Esophagus opening under ledge on left side of midgut floor (Figure 5, **e**). Marginal fold (**mf**) extending anteriorly from esophageal aperture alongside major typhlosole (**t1**), then turning posteriorly bordering right margin of sorting area (**sa**). Groove present along midline of marginal fold (**mf**) for much of its length; groove fading proximally and distally. Sorting area elongate- triangular, tapering posteriorly; posterior tip curving slightly to the left around wedge-shaped sorting area pad (**sap**). Accessory marginal fold (**amf**) emerging from esophageal aperture, paralleling marginal fold and curving around posterior tip of sorting area; fold bifurcating at posterior end of gastric chamber to form two folds. Fine parallel striations extending anteriorly from esophagus up face of major typhlosole. Midgut roof to the left of sorting area coarsely folded and cuticularized (**cu**). Gastric shield (**gs**) small and delicate, strongly concave, with narrow, tubular posterior end and more flaring, flattened anterior end; shield continuous with cuticle of stomach roof and crystalline style pocket (**p**). Glandular pad (**gp**) large and broadly rounded. Crescentic ridge (**cr**), bounding deep crescentic groove, extending from esophageal aperture and fusing to right side of glandular pad. Paired digestive gland ducts (**dd**) opening to deep pocket near proximal tip of crescentic ridge. Shallow caecum (**c**) extending ventrally under glandular pad behind gastric shield. Single longitudinal fold (**cf**) extending from caecum (**c**) around posterior end of gastric chamber. Prominent fold (**u**) extending from right side of style sac lip, along floor of crystalline style pocket, to base of major typhlosole; fold bounding u-shaped depression below lip of style sac (**ss**). Style sac

and intestinal groove communicating along entire length. Crystalline style present.

HINDGUT. Proximal intestine (Figure 4, **int**) passing below distal tip of style sac (**ss**), then extending posteriorly alongside style sac to main gastric chamber (**sto**). Intestine curving anteriorly, with broad loop overlying proximal style sac. Intestine extending under posterior end of main kidney chamber (**kd**), entering pallial roof alongside bladder (**b**) and pallial gonoduct (Figure 3, **po**), continuing forward to papillate anus near mantle margin (**r**).

Reno-pericardial System: Kidney comprising three interconnected chambers (Figure 4, 17, **kd**, **b**). Main chamber (**kd**) lying along dorsal surface of body whorl, anteriorly surrounding pericardium (Figure 4, **per**), crossing axis of body from right to left and extending short distance into pallial roof at base of mantle cavity. Chamber occluded anteriorly (within pallial roof) with excretory tubules. Posteriorly, main chamber with small, narrow lumen, dorsally enclosing intestine. Second chamber (see exposed chamber in Figure 17) extending between pericardial chamber to right body wall below intestine, forming small bladder (Figure 4, **b**). Chamber mostly occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (see Figure 17, **arv**), and communicating to mantle cavity via large nephropore (**np**). Sheets of excretory tissue branching and anastomosing, and fusing to right lateral floor, roof and walls; vertical sheets highly branched anteriorly and forming comparatively dense honeycomb of excretory tissue. Bladder penetrating connective tissue along right side of body, short distance into mantle roof. Excretory tissue separating small ventral chamber below, within pallial portion (dotted line). Size of ventral chamber, as well as branching pattern and number of excretory sheets of tissue variable between individuals. Small aperture just behind afferent renal vessel connecting main chamber and bladder (arrow). Nephridial gland absent.

Pericardium voluminous (Figure 4, **per**), extending to right side of body (dotted line).

Nervous System: Circum-esophageal nerve ring (Figure 3, **nr**) lying immediately behind buccal mass, at base of cephalic tentacles. Cerebral ganglia (Figure 6, **ce**) connected by short, stout commissure, each producing seven nerves (optic, statocyst, tentacular, and four labial 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 approximately 10–15 statoconia present dorsally alongside pedal ganglia behind pedal connectives. Sub-esophageal ganglion (**sb**) joined to left pleural ganglion by thickened connective (**co**); connec-
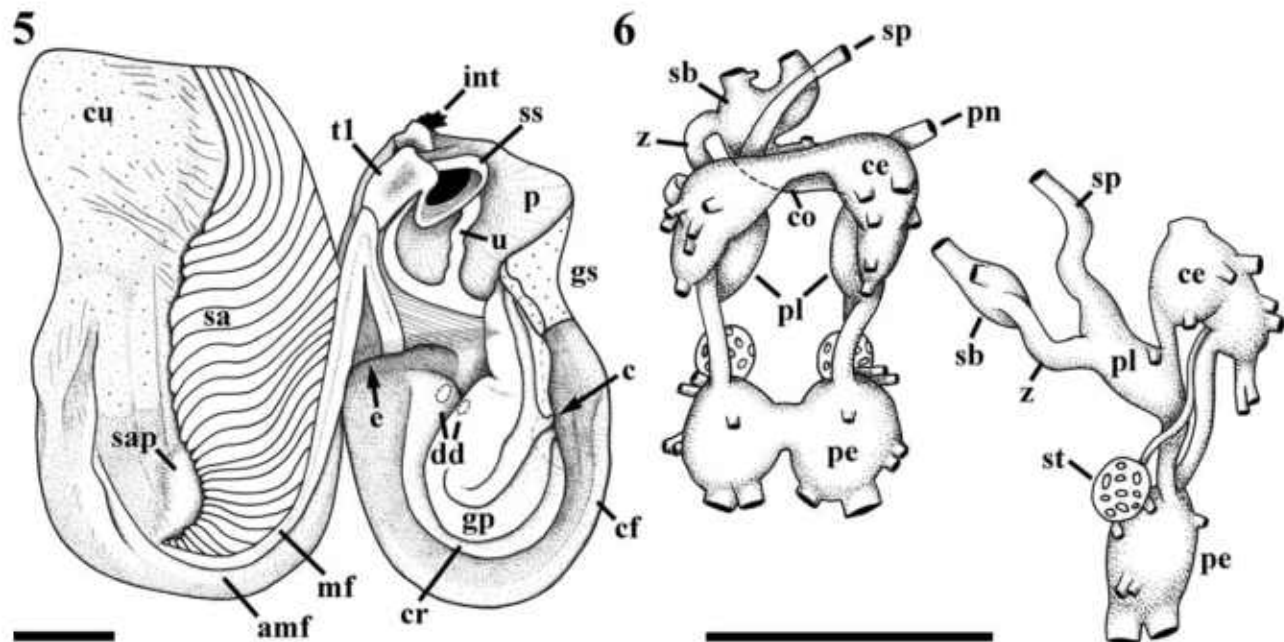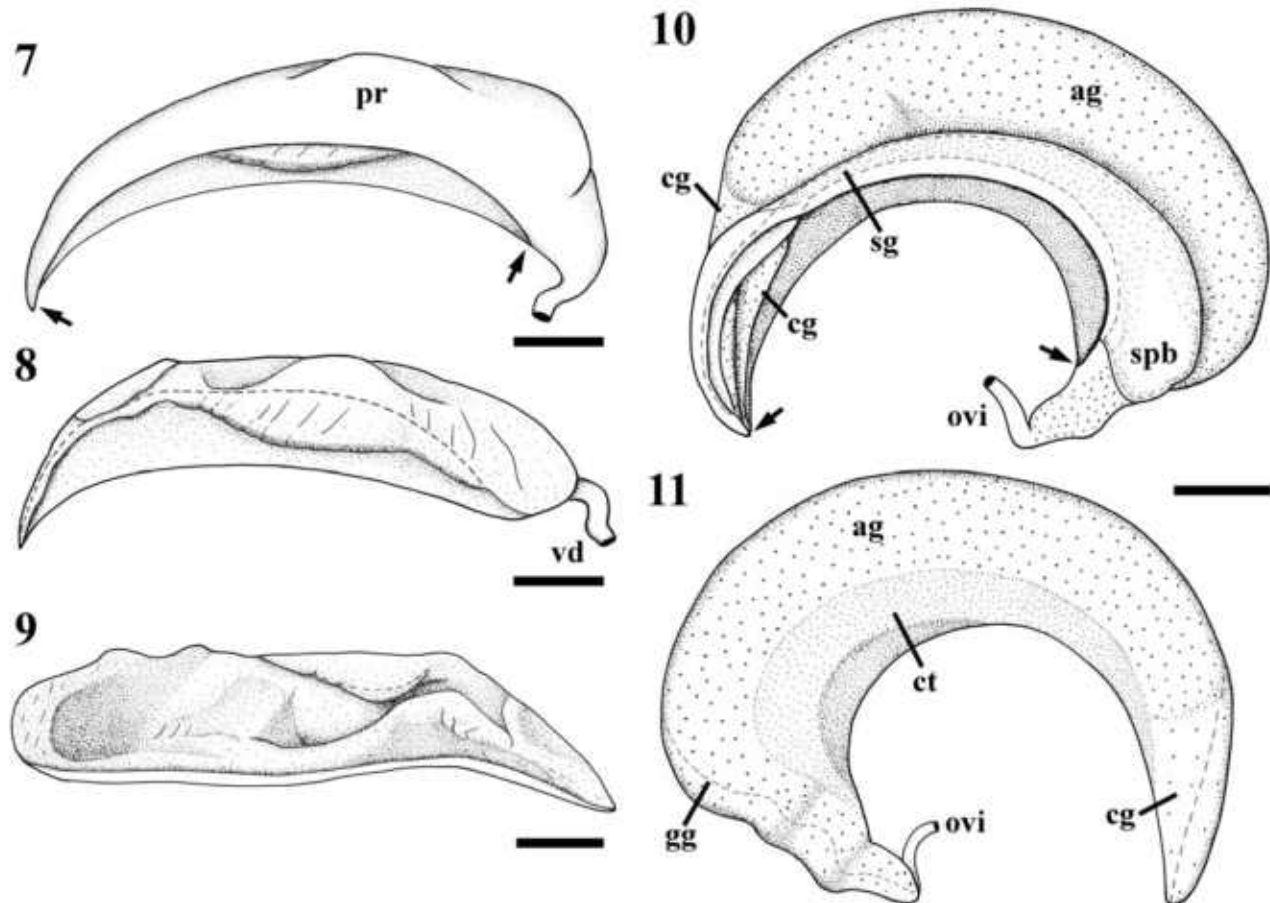
Figures 5–6. Anatomy of *Pleurocera acuta*. **5.** Midgut anatomy. Dorsal view, anterior is uppermost. **6.** Circum-esophageal nerve ring. Frontal view on the left, right lateral view on the right. Abbreviations: **amf,** accessory marginal fold; **c,** caecum; **cf,** caecal fold; **ce,** cerebral ganglion; **co,** thickened connective between left pleural and sub-esophageal ganglia; **cr,** crescentic ridge; **cu,** cuticularized region of stomach roof; **dd,** duct of digestive gland; **e,** esophageal aperture; **gp,** glandular pad; **gs,** gastric shield; **int,** intestine; **mf,** marginal fold; **p,** crystalline style pocket; **pe,** pedal ganglion; **pl,** pleural ganglion; **pn,** pallial nerve from left pleural ganglion; **sa,** sorting area; **sap,** sorting area pad; **sb,** sub-esophageal ganglion; **sp,** connective to supra-esophageal ganglion; **ss,** lip of style sac; **st,** statocyst; **tl,** major typhlosole; **u,** u-shaped fold; **z,** zygoneury. Scale bars = 1 mm.

tive producing 1–3 small nerves (n=2). Zygoneury (**z**) formed between sub-esophageal and right pleural ganglia. In addition to zygoneury (**z**), sub-esophageal ganglion (**sb**) producing one other prominent nerve and connectives to the left pleural (**pl**) and visceral ganglia. Long connective uniting right pleural and supra-esophageal ganglia (Figures 3, 6, **sp**), the latter lying on left side mantle floor near midline of osphradium. Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supra-esophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present between pericardium and kidney at base of mantle cavity, above posterior esophagus on the right. Ganglion producing two prominent nerves.

Reproductive System: MALE. Narrow vas deferens (Figure 8, **vd**) emerging ventrally from testes, continuing forward along ventral midline of whorl. Short, distal portion of vas deferens thickened and forming straight seminal vesicle. Vas deferens narrowing and curving dorsally to enter posterior end of prostate (Figure 7, **pr**) at base of mantle cavity. Prostate glandular, forming flattened tube, opening to mantle cavity through broad slit along entire length except for a short fused segment at base of mantle cavity (arrows). Lateral lamina epithelium thin along aperture; short distance into lumen, glandular tissue forming flattened longitudinal shelf. Glandular tissue diminishing in thickness at anterior and posterior ends of gonoduct. Shelf undercut along much of its length by flattened sinus (Figure 8, dotted line). Glandular tissue forming central rounded mass flanked by shallow trough along gonoductal groove. Medial lamina unevenly glandular, with irregular troughs and ridges; glandular tissue diminishing in thickness anteriorly and posteriorly (Figure 9). Epithelium of medial lamina posterior 1/5 smooth and concave, partially separated from anterior region by prominent curving ridge; ridge embracing corresponding rounded glandular mass in lateral lamina. Ridge continuous anteriorly with curving trough formed by opposing ridges of tissue. Trough fading anteriorly, and becoming flanked by short, shallow flap running along gonoductal groove.

FEMALE. Gonad (Figure 4, **ov**) dorsally surrounding digestive gland (except for a narrow ventral strip) from tip of visceral mass to posterior end of midgut (**sto**). Oviduct emerging ventrally from ovary. Renal oviduct (Figures 10, 11, **ovi**) deflected dorsally behind mantle cavity before entering base of glandular pallial oviduct. Pallial oviduct, with proximal albumen (**ag**) and distal capsule glands (**cg**). Albumen and capsule glands forming narrow bands with opposing flattened surfaces bounding gonoductal groove (Figure 11, **gg**); non-glandular portions of medial and lateral laminae formed by thickened connective tissue (**ct**). Proximal segment of albumen gland at base of mantle cavity under pallial kidney extension rather short and straight (Figures 10,

Figures 7–11. Reproductive anatomy of *Pleurocera acuta*. **7.** External, left lateral view of prostate. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **8.** Internal aspect of prostate lateral lamina. Dotted line designates extent of sinus under glandular shelf. **9.** Internal aspect of prostate medial lamina. Anterior is to the right. Note parallel folds and groove at anterior end, representing presumptive spermatophore forming region. **10.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **11.** External, right lateral view of pallial oviduct. Anterior is to the right. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **ct,** connective tissue; **gg,** gonoductal groove; **ovi,** renal oviduct; **pr,** prostate; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

11, **ag**). Anterior to pallial kidney chamber, albumen gland curving under distal tip of bursa to the right, then arcing dorsally. Capsule gland comprising approximately anterior 1/4 of pallial oviduct; externally capsule gland not inflated (Figure 10, **cg**). Broad aperture along entire length of pallial oviduct except for a short fused segment at base of mantle cavity (Figure 10, arrows). Above aperture, sperm gutter (**sg**) opening in medial lamina at anterior tip of pallial oviduct and deepening posteriorly; gutter leading to short, blind spermatophore bursa (**spb**). Seminal receptacle absent.

Elimia livescens (Menke, 1830)

Material Examined: Wisconsin: Mukwonago River: USNM 1081521, 1081523.

External Anatomy: Operculum ovate, corneous, dark reddish-brown in color, with three whorls; paucispiral with small, basal nucleus of approximately 2.5 whorls

(Figure 12). Last whorl expanding rapidly. Nucleus comprising approximately 1/5 of total length.

Foot broad and rounded, with wide propodium and long anterior pedal gland along anterior margin (Figure 13, **ap**). Ciliated egg groove extending short distance up side of neck from ovipositor; groove fading near base of tentacle. Parallel folds extending into ovipositor pore from aperture (*) roughly equal in size. Grooved tract extending ventrally from ovipositor to sole of foot at junction of propodium and mesopodium, just behind termination of anterior pedal gland.

Osphradium with curved anterior tip; some individuals with mostly straight osphradium (Figure 14, **os**). Hypobranchial gland well developed with deep, transverse folds (Figures 14, 15, **hg**).

Alimentary System: FOREGUT. Epithelium between dorsal and ventral folds glandular and irregularly to transversely striated. Dorsal and ventral folds diminish-
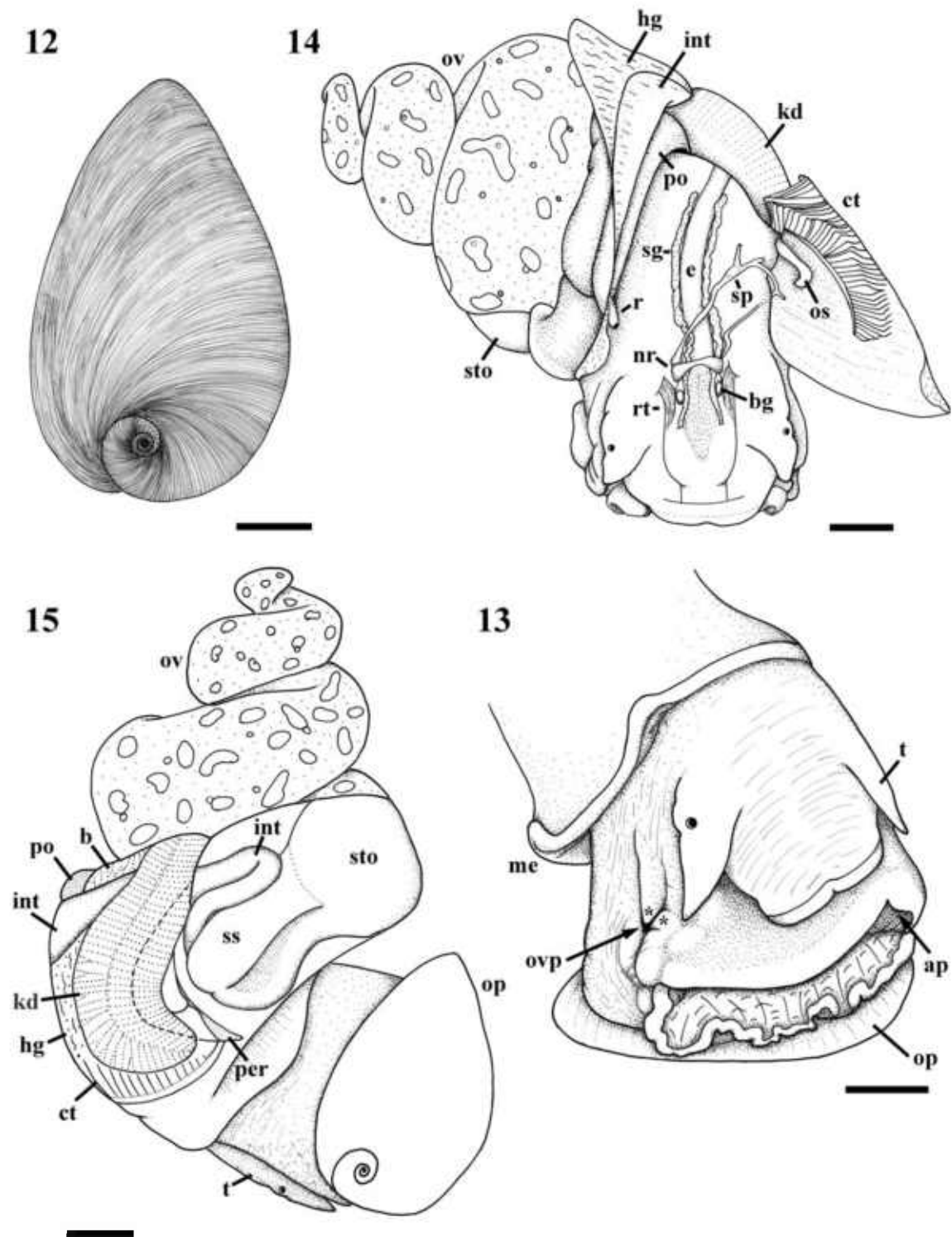
Figures 12–15. Anatomy of *Elimia livescens*. **12.** Operculum. **13.** Ovipositor and egg groove. Right lateral view of side of foot. Asterisks (*) indicate folds extending into ovipositor. **14.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. **15.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. Abbreviations: **ap,** anterior pedal gland; **b,** bladder; **bg,** buccal ganglion; **ct,** ctenidium; **e,** esophagus; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **nr,** circum-esophageal nerve ring; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **po,** pallial oviduct; **r,** rectum; **rt,** buccal mass retractor muscle; **sg,** salivary gland; **sp,** supra-esophageal ganglion; **ss,** style sac; **sto,** stomach; **t,** cephalic tentacle. Scale bars = 1 mm.
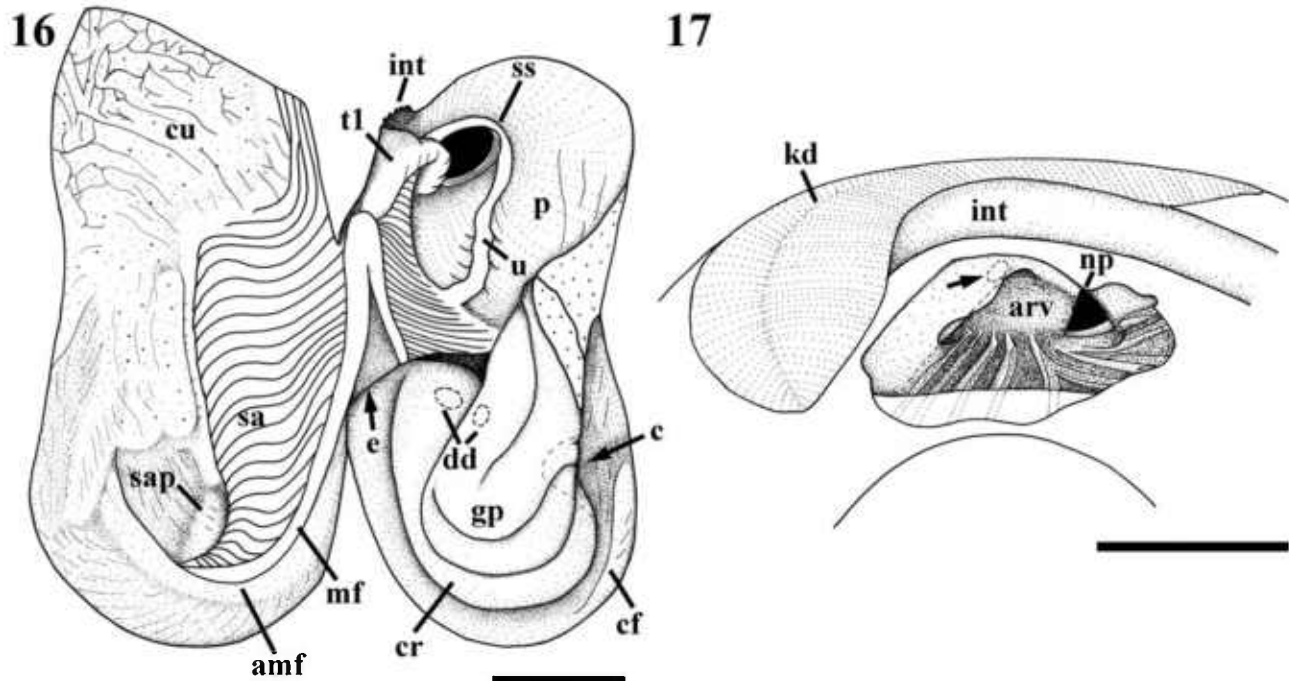
Figures 16–17. Anatomy of *Elimia livescens*. **16.** Midgut anatomy. Dorsal view, anterior is uppermost. **17.** Kidney anatomy. Internal view of bladder. Lateral view, anterior is to the right. Right wall of bladder and adhering sheets of excretory tissue removed to reveal interior; cross-hatching indicates cross-section through sheets of tissue. Arrow indicates opening in septum allowing communication between bladder and main kidney chamber. Dotted line anteriorly indicates extent of ventral chamber. Abbreviations: **amf,** accessory marginal fold; **arv,** afferent renal vessel; **c,** caecum; **cf,** caecal fold; **cr,** crescentic ridge; **cu,** cuticularized region of stomach roof; **dd,** duct of digestive gland; **e,** esophageal aperture; **gp,** glandular pad; **gs,** gastric shield; **int,** intestine; **kd,** main kidney chamber; **mf,** marginal fold; **np,** nephropore; **p,** crystalline style pocket; **sa,** sorting area; **sap,** sorting area pad; **ss,** lip of style sac; **t1,** major typhlosole; **u,** u-shaped fold. Scale bars = 1 mm.

ing at distal end of mid-esophagus (Figure 14, **e**) but continuous into posterior esophagus. Posterior esophagus narrow, bearing numerous folds of equal height. Long, tubular salivary glands (**sg**) just reaching transition to posterior esophagus.

MIDGUT. Groove along midline of marginal fold lacking (Figure 16, **mf**). Single, weak, caecal fold (**cf**) along right side of midgut behind gastric shield, opposite caecum.

HINDGUT. Proximal intestine (Figure 15, **int**) passing below distal tip of style sac (**ss**), then extending posteriorly alongside style sac almost reaching main gastric chamber (**sto**). Intestine curving anteriorly with loop partially overlying proximal style sac. Intestine extending under posterior end of main kidney chamber (**kd**), entering pallial roof alongside bladder (**b**) and pallial gonoduct (**po**), continuing forward to papillate anus near mantle margin (Figure 14, **r**).

Reno-pericardial System: Bladder (Figure 15, **b**) largely occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (Figure 17, **arv**) and fusing to right lateral floor, roof and walls. Sheets of excretory tissue loosely and regularly branching and anastomosing; posterior sheets less branched than those anteriorly.

Pericardium rather narrow and short (Figure 15, **per**), extending to intestinal loop (dotted line).

Nervous System: Buccal ganglia (Figure 14, **bg**) lying dorso-laterally at base of buccal mass between buccal retractor muscles (**rt**) and salivary glands (**sg**). Thickened connective (Figure 18, **co**) between left pleural and sub-esophageal ganglia producing 1–2 nerves (n=2). In addition to zygoneury (**z**) and connectives to left pleural and visceral ganglia, sub-esophageal ganglion producing 2–3 prominent nerves (n=2). Small statocysts (**st**) with approximately 20–30 statoconia.

Reproductive System: MALE. Flattened longitudinal shelf of glandular tissue within lateral lamina diminishing in thickness at anterior and posterior ends of prostate (Figures 19, 20, **pr**). Deep longitudinal cleft opening in glandular shelf along gonoductal groove at midpoint of gonoduct and extending anteriorly; cleft closing a short distance back from anterior tip of gonoduct (Figure 20, **cl**). Medial lamina thinly and rather evenly glandular along its length; glandular tissue slightly diminishing anteriorly (Figure 21). Epithelium of medial lamina posterior third smooth and strongly concave, separated from anterior 2/3 by prominent curving ridge; ridge embracing corresponding groove in glands of lateral lamina at proximal end of cleft. Epithelium of medial lamina anterior 2/3 irregularly and variably crossed by oblique and longitudinal ridges.
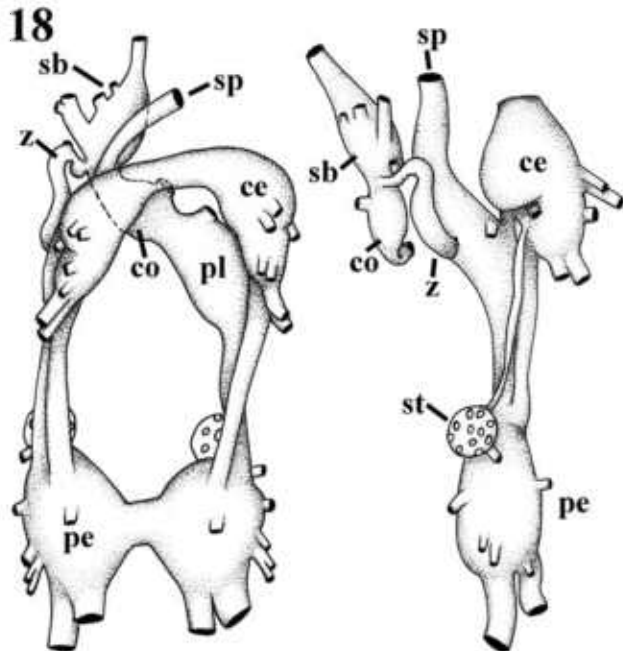
Figure 18. Circum-esophageal nerve ring of *Elimia livescens*. Frontal view on the left, right lateral view on the right. Abbreviations: **ce,** cerebral ganglion; **co,** thickened connective between left pleural and sub-esophageal ganglia; **pe,** pedal ganglion; **pl,** pleural ganglion; **sb,** sub-esophageal ganglion; **sp,** connective to supra-esophageal ganglion; **st,** statocyst; **z,** zygoneury. Scale bar = 1 mm.

FEMALE. Renal oviduct (Figures 22, 23, **ovi**) deflected dorsally behind mantle cavity before entering base of glandular pallial oviduct. Proximal albumen gland rather long and initially curved, then forming straight segment along base of mantle cavity under pallial kidney extension. Capsule gland comprising approximately anterior 1/3 of pallial oviduct; externally capsule gland markedly inflated. Above aperture, short distance back from anterior tip of oviduct ($\sim$1/5 of length), sperm gutter (**sg**) opening in medial lamina and deepening posteriorly; gutter leading to short, blind spermatophore bursa (**spb**).

DISCUSSION

Whatever may be discovered in the future regarding the structure and relationships of species currently placed within the Pleuroceridae, given that *Pleurocera acuta* is the type species of the type genus for the family, this description will necessarily remain as the standard for the application of the name.

COMPARISON OF *PLEUROCERA ACUTA* AND *ELIMIA LIVESCENS*

Baker (1928) commented on the considerable uniformity of structure in the genitalia of these two species and that

the soft parts do not seem to show the same degree of differentiation as the shells. Although this statement was based on external observations, Dazo (1965) similarly noted that, except for differences in size, the internal anatomy of the two species is quite similar or often identical in all organ systems; the most significant differences were those relating to size and shape of the operculum, snout, tentacles, foot, and radula.

Yet, notions of similarity and how similar two entities must be to be characterized as "identical" are subjective concepts. The thorough documentation of these two species has been provided to allow a more objective means of assessing the degree of similarity between the two. Of course, any anatomical rendering will maintain some element of subjectivity.

With this in mind, the present analysis confirms that *Pleurocera acuta* and *Elimia livescens* are remarkably similar, both in overall organization and in many details. This level of similarity is perhaps not unexpected given the sister group relationship between the two genera supported in one molecular analysis (Holznagel and Lydeard, 2000). However, it should be noted that monophyly of these genera has not been demonstrated unambiguously (e.g. Sides, 2005), but awaits confirmation within a more comprehensive phylogenetic framework. Thus, the present results may indicate a closer systematic affinity than currently appreciated.

Yet, a number of differences between the two species are apparent. Externally, the two differ in development of the hypobranchial gland, but this is difficult to quantify. They also differ in the position of the ovipositor and its relationship to the foot sole. This is consistent with described differences in the mode of egg capsule transfer to the substrate; in *Pleurocera acuta*, only the everted walls of the ovipositor function in oviposition (van Cleave, 1932), but in *Elimia laqueata*—a species with an ovipositor configuration identical to *E. livescens* (see below)—both the everted lips of the ovipositor and the margins of the finely grooved tract guide the ova to the substrate (Woodard, 1934).

The most significant differences in midgut structure are length of caecal fold, and the presence of a groove along the marginal fold; however, these variations may be attributable to preservation artifacts. The significance of other minor differences (size and/or shape of caecum, glandular pad, major typhlosole, gastric shield, crescentic ridge, field of parallel striations above esophageal aperture) can only be ascertained once a broader sampling of species from both genera have been examined. But these may also be attributable to preservation artifacts and/or intra-specific variation.

Internal structure of the kidney differs only in that the vertical sheets of excretory tissue are more highly and densely branched within the bladder in *Pleurocera acuta*. It was observed that the amount of such excretory tissue varied between individuals in a species and with maturity. Although a highly qualitative character, the degree of difference between the two species surpasses that of intra-specific variation.
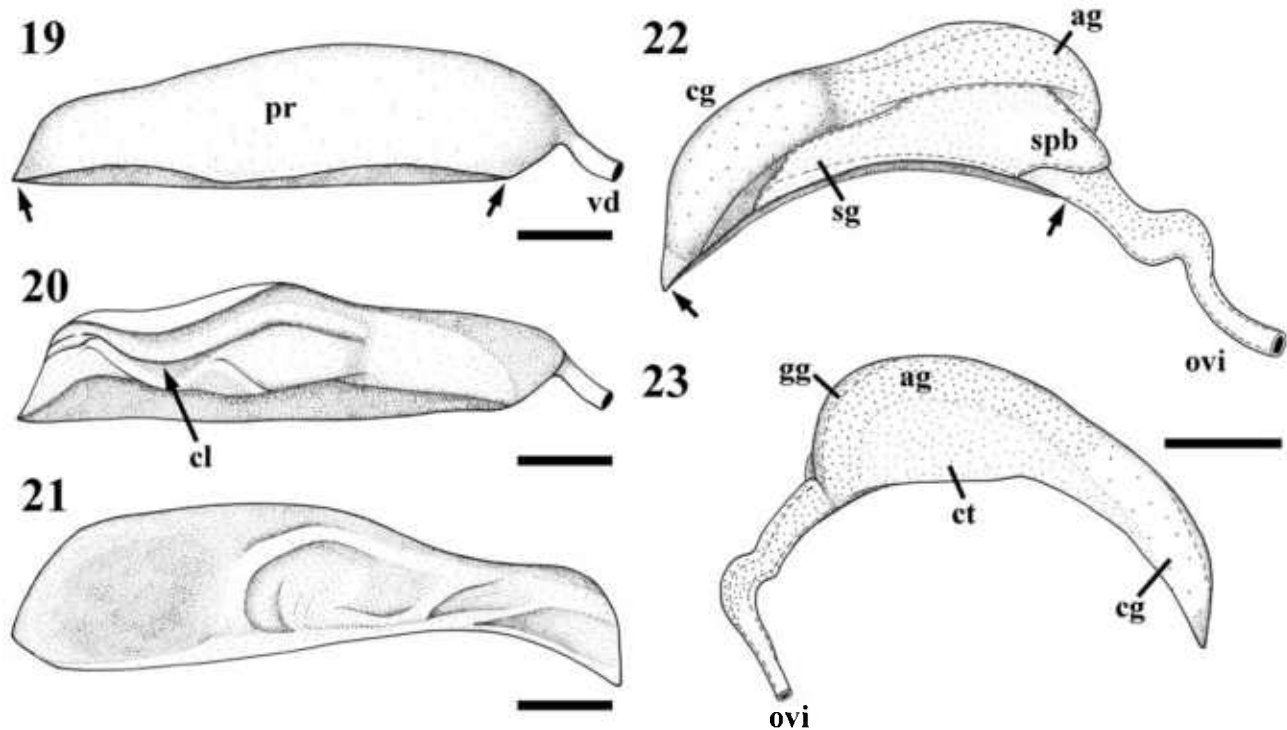
Figures 19–23. Reproductive anatomy of *Elimia livescens*. **19.** External, left lateral view of prostate. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **20.** Internal aspect of prostate lateral lamina. Note deep cleft at anterior end (**cl**), representing presumptive spermatophore forming region. **21.** Internal aspect of prostate medial lamina. Anterior is to the right. **22.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrows indicate extent of opening to gonoductal groove. **23.** External, right lateral view of pallial oviduct. Anterior is to the right. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **cl,** deep cleft; **ct,** connective tissue; **gg,** gonoductal groove; **ovi,** renal oviduct; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

The configuration of the nerve ring and visceral loop is largely identical between the two. One difference is the number of nerves issuing from the sub-esophageal/left pleural connective and from the sub-esophageal ganglion. However, given the observed intra-specific variation, these differences likely fall within the range of individual variation.

In contrast to the results presented here, Dazo (1965) reported 9 cerebral nerves, only a single nerve from the visceral ganglion, and an inconstant number of accessory pedal nerves; however, Dazo did confirm the unique thickened left pleural/sub-esophageal connective. Dazo also commented on the unlikely generality of Rosewater's (1961) findings that pleurocerids differ primarily in the lengths of the cerebral commissure and left pleural/sub-esophageal connective (n=6 for 9 species). Indeed, these lengths were found to be sometimes conspicuously different between individuals examined in the present study.

Males of the two species differed in the pattern of folds within the anterior region of the prostate. Regardless, the anterior region is inferred to be the site of spermatophore formation rather than the comparatively smoother posterior region. This conclusion seems justified given the similarity in the configuration of the folds as compared to overall form and shape of the spermatophore (Jewell, 1931; Dazo, 1965). Limnic cerithioideans in the family Paludomidae Stoliczka, 1868, have separated the glands in this anterior region to form a hollow tube that has been implicated in spermatophore formation (Glaubrecht and Strong, 2004). That discovery further supports the notion that sperm packets are produced anteriorly and suggests that this function may be homologous in different lineages.

For a summary of these and other morphological differences, see Table 1.

COMPARISON TO OTHER PLEUROCERIDS

With minor exception, published accounts agree on the main patterns of pleurocerid anatomy. Thus, pleurocerids have long been known to be dioecious and oviparous (except *Semisulcospira*) with an ovipositor involved in the deposition of the egg capsules (Stimpson, 1864). Members of the family are also aphallate, with open gonoducts, a gonad that dorsally surrounds the digestive gland, and produce crescent-shaped spermatophores (e.g. Stimpson, 1864; Jewell, 1931; Woodard, 1934, 1935; Magruder, 1935b; Jones and Branson, 1964; Dazo, 1965). Like other cerithioideans, pleurocerids possess

Table 1. Summary of morphological differences between *Pleurocera acuta* and *Elimia livescens*.

	Pleurocera acuta	*Elimia livescens*
External Anatomy:		
Propodium	Narrow	Broad
Ovipositor ventral groove	Does not extend to foot margin	Extends to foot margin
Curved anterior tip of osphradium	Sometimes present	Often present
Alimentary System:		
Ventral folds at posterior end of mid-esophagus	Fused	Unfused
Groove along marginal fold	Present	Absent
Length of caecal fold	Long	Short
Hindgut loop	Extends to main gastric chamber	Does not reach main gastric chamber
Reno-Pericardial System:		
Bladder excretory tubules	Densely and highly branched	Loosely and regularly branched
Pericardium	Extends to right body wall	Extends to intestinal loop
Nervous System:		
Buccal ganglia	Ventro-lateral	Dorsal
Statoconia	~10–15	~20–30
Nerves from sub-esophageal/left pleural connective	1–3	1–2
Nerves from sub-esophageal ganglion	2 connectives and 2 nerves (including zygoneury)	2 connectives and 3–4 nerves (including zygoneury)
Reproductive System:		
Spermatophore-forming region	Parallel folds and trough in medial lamina	Deep cleft in lateral lamina
Sperm gutter	Extends to anterior tip of oviduct	Does not extend to anterior tip of pallial oviduct
Junction of renal and pallial oviduct	Renal oviduct curves dorsally to straight segment of albumen gland	Renal oviduct ventrally joins curved portion of albumen gland
Proximal albumen gland	Short, straight segment between renal oviduct and posterior end of bursa	Initially curved, with long, straight segment to posterior end of spermatophore bursa

two types of glands within the pallial oviduct – a feature not previously documented among eastern North American species.

The gut is characterized by the presence of tubular salivary glands, a crystalline style and a style sac in restricted communication with the proximal intestine (Magruder, 1935a, b; Itagaki, 1960; Dazo, 1965). The bi-lobed nature of the kidney has been noted before (Magruder, 1935b; Itagaki, 1960), but the internal sub-division of the organ had not been previously documented.

The nervous system is consistent with many other cerithioideans (left dialyneurous, long connective between the right pleural and supra-esophageal ganglia, single visceral ganglion) (e.g. Strong, 2003; Strong and Glaubrecht, 2002, 2003), but is distinguished by the presence of an enlarged connective between the left pleural and sub-esophageal ganglia and a zygoneurous connection on the right—the latter a highly homoplastic character in the Cerithioidea (see review in Houbrick, 1988). However, the presence/absence of zygoneury among pleurocerids requires confirmation as it has been depicted as dialyneury in several other species (Magruder, 1935b; Itagaki, 1960). Only the former study confirmed the presence of the enlarged left pleural and sub-esophageal connective. Additionally, published descriptions (Magruder, 1935b;

Itagaki, 1960; Dazo, 1965; present study) disagree on the number of nerves produced by various ganglia, but as noted above, this can be highly variable even within species. However, the number of statoconia reported by Magruder (30–40; 1935b) is significantly more than the number reported herein, possibly exceeding the level of intra-specific variation and, thus may be an informative phylogenetic character.

Several significant discrepancies among previous descriptions of pleurocerid anatomy are now resolved. Woodard (1934, 1935) observed a so-called "cytophore organ" at the base of the mantle cavity, apparently confluent with the sperm duct. Similarly, Dazo (1965) reported the presence of a cytophore organ in males of both *Pleurocera acuta* and *Elimia livescens*. Based on the present analysis and Woodard's description of the internal structure and position of this organ, it is clear that Woodard misidentified the kidney bladder as a part of the reproductive tract. However, it is not clear why the cytophore organ was described as lacking in females. The intimate connection between the bladder and proximal pallial gonoduct was correctly depicted in *Hua* by Prozorova (1990).

Dazo (1965), as well as several other workers (Woodard, 1934; Jones and Branson, 1964), have

Table 2. Summary of morphological differences between *Pleurocera acuta* and *Elimia livescens* compared to other limnic gastropods classified in the Pleuroceridae and Melanopsidae. Details from Itagaki, 1960; Bilgin, 1973; Houbrick, 1988; Nakano and Nishiwaki, 1989; Glaubrecht, 1996; Strong and Glaubrecht, unpubl. data.

	Pleuraceura acuta *Elimia livescens*	*Juga*	*Semisulcospira*	*Melanopsidae*
External Anatomy:				
Ovipositor pore	Simple, weakly glandular	Simple, weakly glandular	Not applicable	Complex, highly glandular
Alimentary System:				
Salivary glands	Tubular	?	Tubular	Tubular/branched
Salivary gland position	Pass through nerve ring	?	Pass through nerve ring	Pass through/anterior to nerve ring
Esophageal gland	Absent	?	Absent?	Present
Digestive gland ducts	2	?	2	1
Caecum	Small	?	Small	Deep and spiral
Reno-Pericardial System:				
Bladder	Small, pallial	?	?	Small, pallial
Nervous System:				
Dialyneury, Zygoneury	Zygoneury	?	Dialyneury?	Zygoneury
Reproductive System:				
Seminal vesicle	Straight	?	Straight	Coiled
Pallial oviduct	Open	Open	Closed	Open
Seminal receptacle	Absent	Present	Present	Present
Reproductive strategy	Oviparous	Oviparous	Viviparous	Oviparous

reported the presence of a seminal receptacle, but no mention of a spermatophore bursa was made. The present study has confirmed that the sperm storage structure in *Pleurocera acuta* and *Elimia livescens* is a bursa based on the presence of unorientated sperm. Examination of specimens of *E. laqueata* (USNM 1081558) confirmed that the structure reported as a seminal receptacle is indeed a bursa—no seminal receptacle is present; judging from the description of Jones and Branson (1964), the same holds true for *E. potosiensis*. The pallial position of the bladder was also confirmed in *E. laqueata* (pers. obs.). It is interesting to note that the sperm gutter extends farther anteriorly in *E. laqueata* than in *E. livescens*. Additionally, the straight segment of the albumen gland between the tip of the bursa and the junction of the renal oviduct is lacking in *E. laqueata*. Instead, the albumen gland arcs dorsally to join the renal oviduct just behind the tip of the bursa. In all other respects, the overall structure of the pallial oviduct in *E. laqueata* is consistent with features described here, as well as in the close association between the ovipositor and the junction of the propodium and mesopodium.

A final discrepancy is the presumed site of spermatophore formation. Woodard (1934, 1935) described the distal prostate as smooth and the highly folded proximal portion as the site of spermatophore formation. Jones and Branson (1964) did not distinguish a spermatophore-forming region in *Elimia potosiensis*. In the present study, it is the highly folded distal region that is inferred to be the site of spermatophore formation.

SYSTEMATICS OF PLEUROCERIDAE

As mentioned above, although confusion has long existed, the distinctiveness of the Pachychilidae from other limnic lineages including the Pleuroceridae has now been clarified based on morphological and molecular data (e.g. Glaubrecht, 1996, 1999; Lydeard et al., 2002; Köhler et al., 2004). However, the paraphyly of eastern and western North American and Asian pleurocerids with respect to the Melanopsidae based on molecular data (Lydeard et al., 2002) remains at issue. The analysis of Houbrick (1988) did not include sufficient taxon sampling to adequately assess monophyly of the two families, but a sister-group relationship between the two was supported.

Although an in depth analysis of monophyly and affinity of the two families is beyond the scope of this study, several morphological features may be informative in clarifying these relationships. As noted by Prozorova (1990) the reproductive anatomy of eastern North American pleurocerids differs from species in western North America (*Juga*) and Asia (*Semisulcospira*) in that both *Juga* and *Semisulcospira* possess a seminal receptacle in addition to a spermatophore bursa. The latter genus has modified the pallial oviduct into a closed brood pouch (Itagaki, 1960; Nakano and Nishiwaki, 1989; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004).

In addition to the synapomorphies recovered in the analysis of Houbrick (weakly developed hypobranchial gland, zygoneury, long left pleural/sub-esophageal con-

nective), midgut anatomy is broadly congruent in the two families, differing in several significant respects from that of the other limnic lineages (e.g. Paludomidae, Pachychilidae, Thiaridae) (Bilgin, 1973; Köhler and Glaubrecht, 2001; Strong and Glaubrecht, 2002, 2003, unpubl. data). They also share similarities in reno-pericardial (presence of a bladder) and reproductive anatomy (open pallial gonoducts, presence of a seminal receptacle)—the latter, in particular, are undoubtedly symplesiomorphic. But other aspects of the anatomy are consistent within each family and clearly differentiate the two when sufficient information is available. Thus, in addition to features of the radula and shell, melanopsids may be distinguished by the presence of an esophageal gland, salivary glands that lie anterior to the nerve ring (although variable in the family), a single digestive gland duct and spiral caecum in the midgut, and a coiled seminal vesicle. Of course, the extent to which these features represent shared derived or homoplastic features remains to be discovered in the context of a phylogenetic analysis.

CONCLUSIONS

The present study has provided the first detailed description of the midgut and kidney for any pleurocerid snail, and has clarified the internal structure and homologies of the pallial gonoducts of eastern North American forms. This comparative analysis has confirmed the high degree of morphological similarity between *Pleurocera acuta* and *Elimia livescens*, but has also revealed a number of differences in detail; the extent to which these features support monophyly of the genera remains to be established. The fact that the presence/absence of a seminal receptacle distinguishes eastern and western North American/Asian pleurocerids is confirmed. Pleurocerids and melanopsids are broadly similar in features of the midgut and share a similar configuration of the pallial oviduct, but can be distinguished by anatomical characters of the alimentary (salivary glands, esophageal gland, digestive gland ducts, caecum) and reproductive (seminal vesicle) systems. However, comprehensive anatomical treatments of western North American and Asian pleurocerids are needed to fully assess the morphological distinctiveness of the two families. The clarification of the distribution of these features, within the context of a phylogenetic analysis, should aid in refining the monophyly of the Pleuroceridae and their affinity to other freshwater lineages.

ACKNOWLEDGMENTS

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