

On the anatomy and systematics of *Juga* from western North America (Gastropoda: Cerithioidea: Pleuroceridae)

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ABSTRACT

The family Pleuroceridae is a speciose and ecologically important family of limnic gastropods in North America and eastern Asia. *Juga* is the only native pleurocerid genus that occurs in Pacific drainage systems of Western North America, but has only recently been accepted as independent from other North American genera and may have affinities to Asian pleurocerids. As such, this genus represents a key piece to the puzzle of pleurocerid systematics. However, published accounts of *Juga* anatomy are limited to the reproductive system. Consequently, the anatomy of three species is described herein; these three taxa represent the type species of the three extant subgenera: *Juga* (*Juga*), *J.* (*Calibasis*), and *J.* (*Oreobasis*). A lectotype is designated for *Goniobasis acutifilosa* Stearns, 1890, the type species of *Calibasis*; *Melania newberryi*, the type species of *Oreobasis*, is here removed from the synonymy of *Juga bulbosa*.

This analysis confirms that *Juga* shares many anatomical features with other North American and Asian pleurocerids, but is clearly set apart from eastern North American pleurocerids in features of the ovipositor pore, radula, midgut, kidney, and pallial gonoduct. *Juga* is distinct from all other limnic cerithioideans known thus far in the form of the midgut crescentic ridge, the configuration of prostate glands, and an evagination of the kidney wall separating the main chamber and bladder. Based on information currently available, unlike molecular data, there is no morphological feature unambiguously linking *Juga* to Asian pleurocerids. Anatomically, *Oreobasis* is strikingly similar to *Juga* sensu stricto and is synonymized with it, whereas *Calibasis* is retained as a valid taxon.

INTRODUCTION

The Pleuroceridae Fischer, 1855, is a speciose and ecologically important family of limnic gastropods occurring in North America and Eastern Asia. Despite their importance, understanding of their systematics is discouragingly incomplete. The current classification of limnic lineages within the Cerithioidea Fleming, 1822, is rooted in the works of Thiele (1928, 1929), who subdivided the

heterogeneous Melaniidae Children, 1823 (an invalid name for Thiaridae Gill, 1871) into six subfamilies including the Pleurocerinae. An alternative classification advanced by Morrison (1954) distinguished only three limnic families: (i) the Pleuroceridae distributed throughout the Americas, Africa, and Asia, (ii) the Melanopsidae in Europe, and (iii) the pantropical Thiaridae. While promoting the important notion of several independent lineages, this concept heavily weighted plesiomorphic (ovipositor and oviparity) and homoplastic (brooding) features and resulted in a highly polyphyletic Pleuroceridae—a view that persisted for over three decades (e.g. Ponder and Warén, 1988). Recent work has resolved some of this confusion and supports the distinctiveness of many of Thiele's groupings (e.g. Glaubrecht, 1996, 1999; Lydeard et al., 2002; Köhler and Glaubrecht, 2001, 2003; Strong and Glaubrecht, 2002, 2003; Köhler et al., 2004; von Rintelen and Glaubrecht, 2005). However, molecular data (Lydeard et al., 2002) do not support monophyly of the Pleuroceridae as currently defined (e.g. Bouchet and Rocroi, 2005). The analysis of Houbrick (1988) based on morphological data did not include sufficient taxon sampling to adequately assess monophyly of the family.

In North America, pleurocerid diversity is highest east of the continental divide where they are represented by seven genera (*Athearnia* Morrison, 1971, *Elimia* H. and A. Adams, 1854, *Io* Lea, 1831, *Leptoxis* Rafinesque, 1819, *Lithasia* Haldeman, 1840, *Pleurocera* Rafinesque, 1818, and the extinct *Gyrotoma* Shuttleworth, 1845) and approximately 148 species currently considered valid (Johnson et al., 2005). *Juga* H. and A. Adams, 1854, with 11–12 estimated valid species (Burch, 1989; Turgeon et al., 1998; Johnson et al., 2005), is the only native pleurocerid genus that occurs in the Pacific and Interior drainages from central California to central Washington (Figure 1). Established on the basis of early teleoconch shell sculpture, four subgenera are recognized (Taylor, 1966; Burch, 1989)—three are extant: *Juga* H. and A.

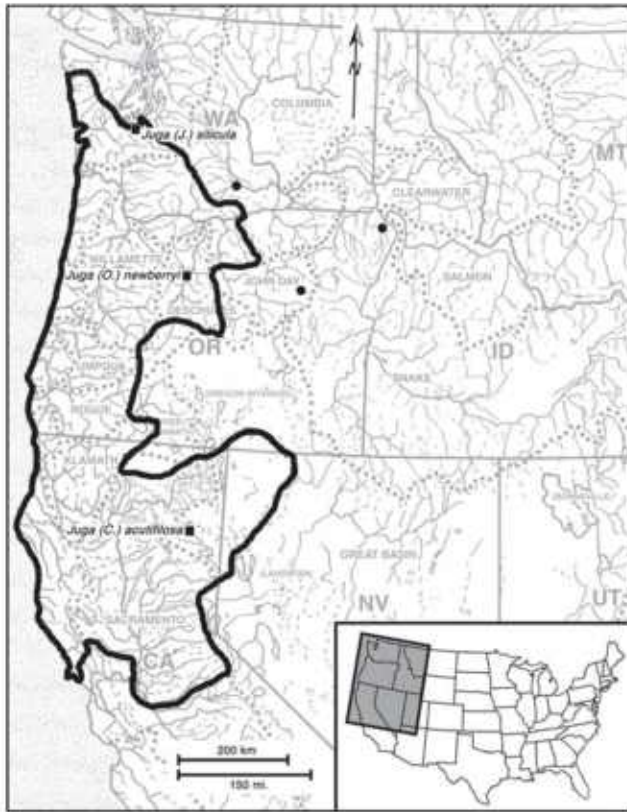


Figure 1. Distribution of *Juga*. Black line indicates currently known area of contiguous distribution. Black circles represent isolated sites beyond main distribution. Black squares are locations of extant subgeneric type localities and of material used in this investigation.

Adams, 1854 (with plicate early sculpture), *Calibasis* Taylor, 1966 (with lirate early sculpture), and *Oreobasis* Taylor, 1966 (with weak to no early sculpture). *Idabasis* Taylor, 1966 (with plicate and lirate early sculpture) is known only from fossils. Some east Asian species have also been assigned to *Juga*, but more recently these have been reassigned to *Parajuga* Prozorova and Starobogatov, 2004 (Starobogatov et al., 2004); however, this name is unavailable from a nomenclatural standpoint, as no type species was designated.

Juga has no discrete conchological feature that distinguishes it from eastern North American genera and has often been synonymized with *Goniobasis* Lea, 1862 (a junior synonym of *Elimia*) (e.g. Tryon, 1865, 1873; Pilsbry, 1899; Walker, 1918; Henderson, 1935a, b; Goodrich, 1942). Taylor (1966) was the first to restore *Juga* as a valid genus in the modern literature, primarily on the basis of its disjunct biogeographic distribution and the presence of a distinctive ovipositor (see Discussion, below). Based on recent molecular (Holznagel and Lydeard, 2000; Lydeard et al., 2002) and morphological findings (Prozorova and Raschepkina, 2004; Strong, 2005), *Juga* is supported as distinct from other North American pleurocerids and may have ties to those from eastern Asia (see Discussion, below). As such, this genus

represents an important and intriguing part of the puzzle of pleurocerid systematics.

Thus, the goal of this analysis is to establish the anatomical organization for the type species of the current extant subgeneric subdivisions within *Juga*:

Juga H. and A. Adams, 1854: type species (by subsequent designation Baker, 1963) *Melania silicula* Gould, 1847.

Calibasis Taylor, 1966: type species (by original designation) *Goniobasis acutifilosa* Stearns, 1890.

Oreobasis Taylor, 1966: type species (by original designation) *Melania newberryi* Lea, 1860.

This also represents the first comprehensive anatomical investigation of any *Juga* species; the only information published thus far concerns female reproductive anatomy (Prozorova and Raschepkina, 2004). In the context of ongoing morphological and molecular phylogenetic analyses of pleurocerids and cerithioideans in general, this information is vitally important for assessing the affinities and relationships of taxa currently placed in the Pleuroceridae.

MATERIALS AND METHODS

Specimens for morphological study were collected by hand or dip net, stored cold until evening, relaxed with menthol in shallow water from the same spring or stream in a broad, open container overnight, and transferred to dilute cold 4-5% formalin the next morning. Specimens were maintained in formalin for 48 hours then transferred to buffered 70% ethanol/10% glycerin/20% water for longer term storage. Voucher material is deposited in the National Museum of Natural History in Washington, DC, (USNM) and with Deixis Consultants in Seattle, WA.

Specimens were examined using a Leica MZ 12,5 binocular microscope with *camera lucida*; visualization of structures was enhanced with aqueous toluidine blue. Typically 2 to 4 specimens were examined for each organ system investigated, particularly for complex structures (i.e. midgut, nerves), as well as to assess intra-specific and/or seasonal variation in reproductive anatomy.

A comprehensive anatomical account is provided for *Juga (Juga) silicula*—the type species of the genus. Only discrete differences are detailed for *J. (Calibasis) acutifilosa* and *J. (Oreobasis) newberryi* with comparative remarks highlighting qualitative differences. As far as can be determined, near topotypic material was used for this investigation (see details below). A thorough systematic treatment of each species is not provided as a phylogenetic analysis and comprehensive revision of the genus are forthcoming (Frest et al., unpublished data).

Geographic names, road names and numbers, and land ownership data were confirmed using the DeLorme Mapping Washington, Oregon, and Northern California Atlas and Gazetteer, the latest available USGS 7.5' series topographic maps, and National Geographic TOPO! 2006. Universal Transverse Mercator (UTM) grid coordinates

dinates are based on NAD27 (1927 North American Datum). Locality descriptions have been downloaded from Deixis Consultants MolluscDB™. Collector abbreviations are as follows: EJ, Edward J. Johannes; TF, Terrence J. Frest.

Institution codes cited in the text are: USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC; MCZ: Museum of Comparative Zoology, Harvard.

RESULTS

Pleuroceridae Fischer, 1885

Juga (*Juga*) *silicula* (Gould, 1847)

Type Material: Three syntypes (USNM 12137) (cited as MCZ 12137 in Graf, 2001) (Figures 2-4). Johnson (1964) indicated that the largest (Figure 3) might be the specimen illustrated by Gould (1852, 1856, pl. 10, figs. 164, 164a); however, in number of whorls and overall size, the figured specimen is most likely the smallest syntype (Figure 2). As the figured specimen represents the smallest syntype, and the largest specimen mostly lacks the distinguishing axial ornament characteristic of juvenile shells, a lectotype is not here selected.

Type Locality: Indicated as “Nisqually, Oregon” (Gould, 1847) (see Figure 1). These specimens likely would have been collected by the Wilkes Expedition, 1838-1842, before the separation of Washington Territory from the larger Oregon Territory in 1853. This expedition started from Fort Nisqually, which was located in the current Washington State (still part of Oregon Territory in 1847). There was no rail station or city with the name “Nisqually” at that time. Thus, the river or the fort would be indicated. Johnson (1964) reported the type locality as “near present site of Tacoma, Washington” (also perpetuated by Graf, 2001), which is loosely true but unnecessarily vague and misleading as Tacoma lies outside the northern range of *Juga*, which ends just north of the Nisqually River (Pierce-Thurston Co. line)—by no mere coincidence near the approximate southern terminus of Late Wisconsinan glaciation.

The Nisqually River is a glacial flour stream originating on Mount Rainier with a depauperate freshwater mollusk fauna, despite various literature ascriptions. Its tributaries are comparatively rich, however, especially as they approach Puget Sound. “Nisqually” thus likely refers to Fort Nisqually, one of two trade outposts of the Hudson Bay Company, founded in 1833 on the Nisqually Reach directly south of Sequelitchew Creek (Hitchman, 1985)—a Puget Sound tributary northeast of the Nisqually River. In 1843 the operation was moved about 2 miles northeast, to approximately the present site of Dupont, Washington (Phillips, 1997), roughly in the same drainage. For quite some time, this was the only settlement in the area, so that the origin of Gould’s specimens could be Sequelitchew Creek or one of the other nearby tributaries of the Nisqually River. Attempts to

collect *Juga* from the boggy Sequelitchew Creek have been unsuccessful (Frest, unpubl. data). However, material from nearby McAllister Creek, also a Puget Sound tributary just west of the Nisqually River, has young specimens most closely resembling the types found thus far.

Remarks: Evidently a valid species (see also Goodrich, 1942; Burch and Tottenham, 1980; Burch, 1982a, b, 1989; Graf, 2001) but perhaps with a rather restricted range, confined to a few streams on the southeastern end of Puget Sound, near the Nisqually River.

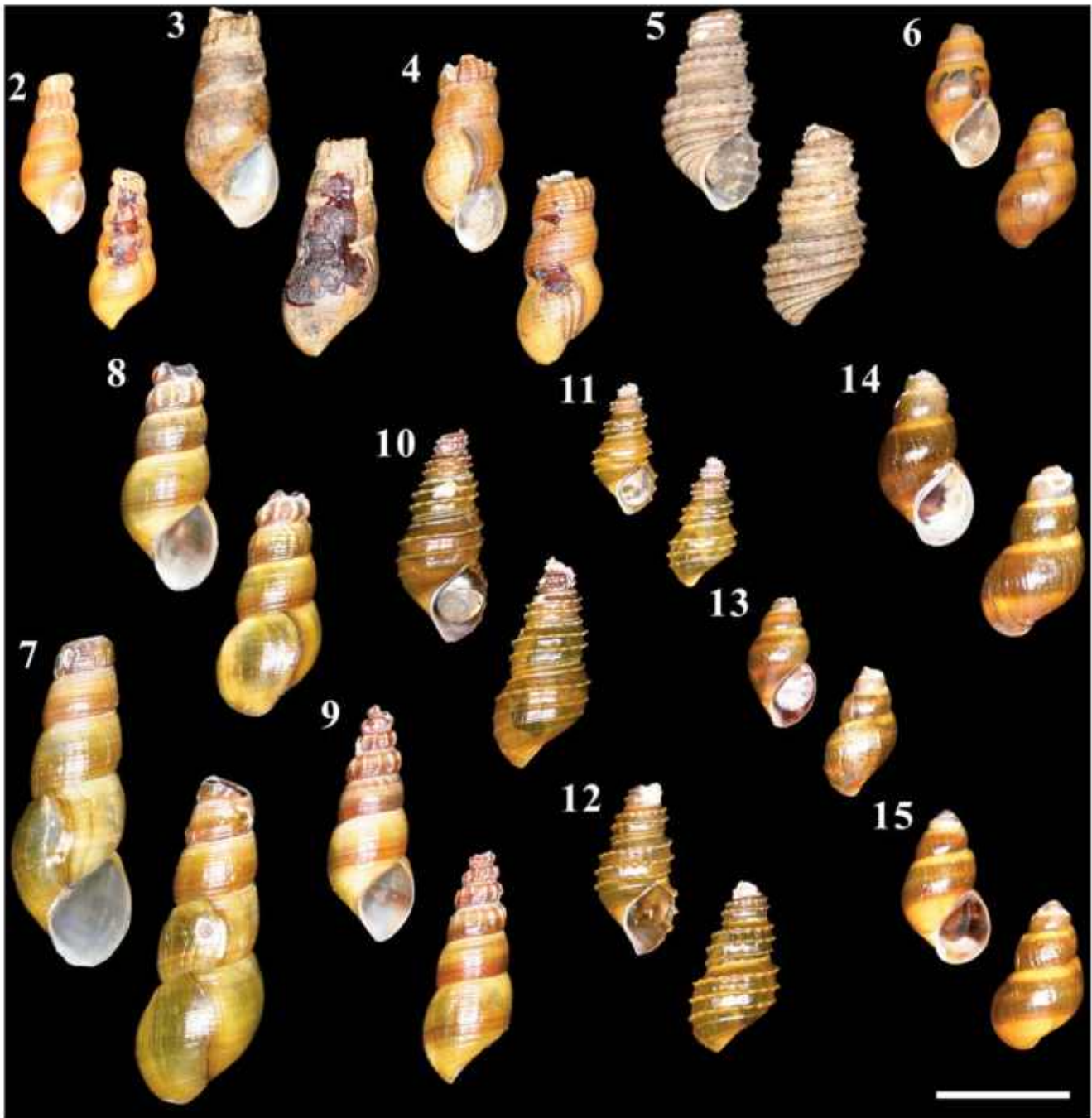
Material Examined: Washington: Thurston County: McAllister Creek at Steilacoom Road bridge, near McAllister Creek Hatchery, depth 0–1.22 m (Zone 10 520890E 5210540N [122°43'34"E, 47°02'59"N], Nisqually 1994 7.5' quadrangle, elevation 1.5 m), Deixis Consultants locality #5709, 29 Sep. 2005, collected by TF, EJ (USNM 1100657) (9 specimens dissected) (see Figures 7-9).

External Anatomy: Operculum ovate, corneous, dark reddish brown in color, with 3.5 whorls; paucispiral with eccentric nucleus of approximately 3 whorls (Figure 16). Nucleus comprising slightly less than one half of total length (~45%).

Head-foot dark gray to black in color, with lighter gray snout tip and pale foot sole; in females, ovipositor groove pale in color. Foot broad with wide propodium and long anterior pedal gland along anterior margin (Figure 17, **ap**). Ciliated egg groove forming longitudinally grooved tract extending from anterior tip of pallial gonoduct (**go**) and broadening continuously into shallow triangular shelf on side of neck below right cephalic tentacle (**ovp**). Ovipositor surface grooved, with folds directed medially into pore. Shallow grooved tract extending from pocket to edge of foot, short distance back from anterior pedal gland. Extensible snout (Figures 17, 18, **sn**) broad, squarish, with short triangular cephalic tentacles (**t**); tentacles also short in relaxed specimens.

Ctenidium (Figures 18, 19, 26, **ct**) extending from posterior end of mantle cavity to near mantle edge, anteriorly curving toward the left. Osphradium forming simple ridge alongside efferent branchial vessel, sometimes with anterior tip markedly curving toward the left; osphradium undulating slightly at anterior and posterior ends, thinning posteriorly (**os**). Hypobranchial gland moderately well developed with transverse ridges, especially at posterior end of mantle cavity (Figures 18, 19, **hg**).

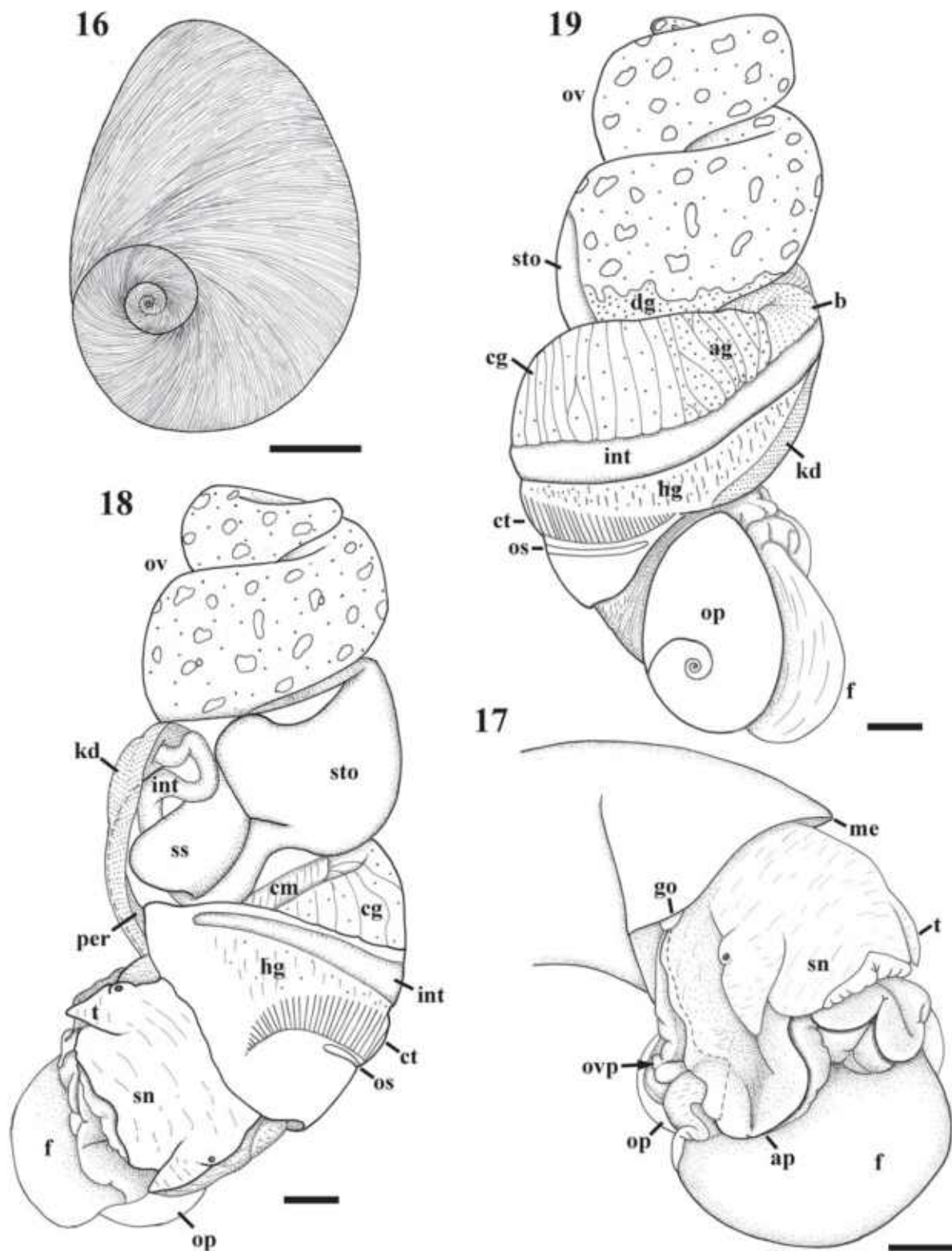
Alimentary System: RADULA: Radula comprising ~98 rows ($n = 2$) (Figures 20-25). Rachidian broadly rectangular, wider than tall, with smoothly rounded v-shaped lower margin and single small basal denticle at each lower, outer corner (Figure 22). Upper margin slightly concave with cutting edge bearing one large central triangular, spatulate cusp, and three stout, conical denticles on each side. Lateral teeth (Figures 20, 21, 23) with moderately short lateral extensions (slightly more than



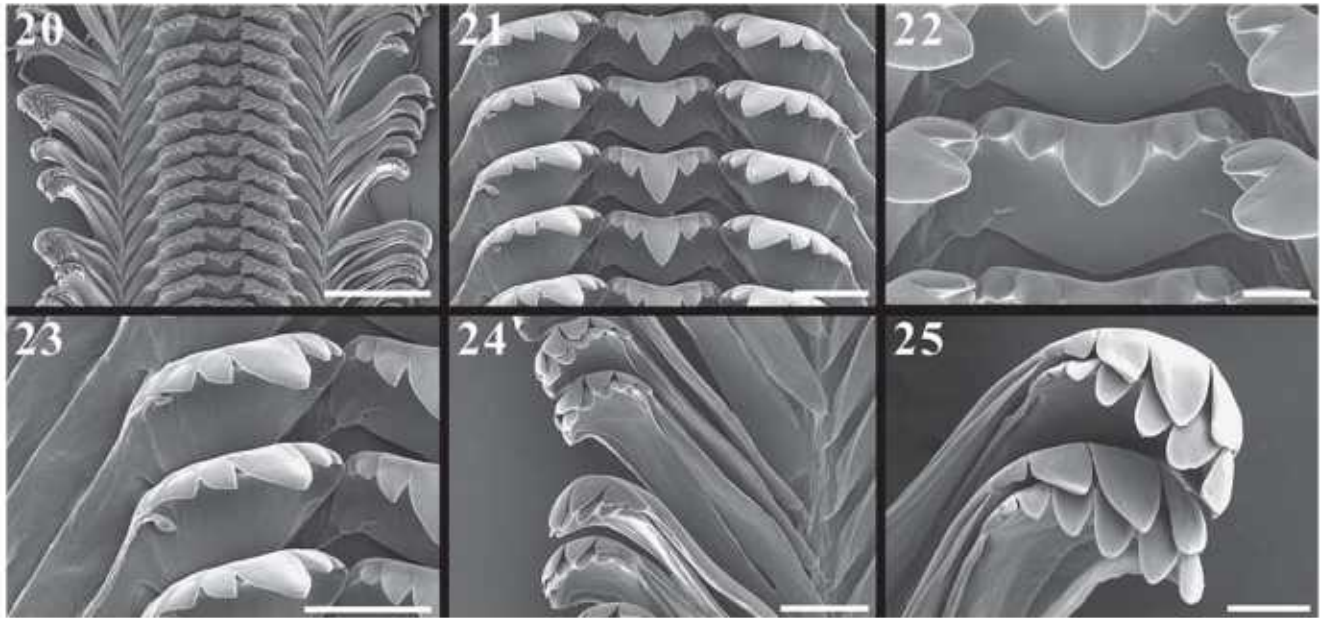
Figures 2–15. Shells of *Juga* species. **2–4.** *Juga (Juga) silicula* (USNM 12137, syntypes). Figure 2 is likely the figured specimen (Gould, 1852, 1856; pl. 10, figs. 164, 164a). **5.** *Juga (Calibasis) acutifilosa* (USNM 60596, lectotype) (Stearns, 1890; pl. 15, fig. 9). **6.** *Juga (Oreobasis) newberryi* (USNM 118961, lectotype). **7–9.** *Juga (Juga) silicula* (USNM 1100659). **10–12.** *Juga (Calibasis) acutifilosa* (USNM 1100658). **13–15.** *Juga (Oreobasis) newberryi* (USNM 1100660). Scale bar = 1 cm.

half the length of lateral cutting edge), and single, prominent spatulate cusp flanked by two inner and two to three outer denticles. Outermost denticle weakly developed and variable in shape, size, and position (Figure 23). Marginal teeth (Figures 24, 25) with broadly rounded cutting edges and long, slender shafts. Narrow flanges

developed on outer edges of marginal teeth shafts along distal one half to two thirds. Outer flange much wider and longer on inner marginal tooth; outer flange only slightly wider on outer marginal tooth. Inner marginal teeth with six and outer marginal teeth with seven flattened denticles.



Figures 16–19. External anatomy of *Juga (Juga) silicula* (USNM 1100659). **16.** Operculum. **17.** Ovipositor and egg groove. Right lateral view of head-foot. **18–19.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber (Figure 18). Abbreviations: **ag**, albumen gland; **ap**, anterior pedal gland; **b**, bladder; **cg**, capsule gland; **cm**, columellar muscle; **ct**, ctenidium; **dg**, digestive gland; **f**, foot; **go**, pallial gonoduct; **hg**, hypobranchial gland; **int**, intestine; **kd**, main kidney chamber; **me**, mantle edge; **op**, operculum; **os**, osphradium; **ov**, ovary; **ovp**, ovipositor; **per**, pericardium; **sn**, snout; **ss**, style sac; **sto**, stomach; **t**, cephalic tentacle. Scale bars = 1 mm.

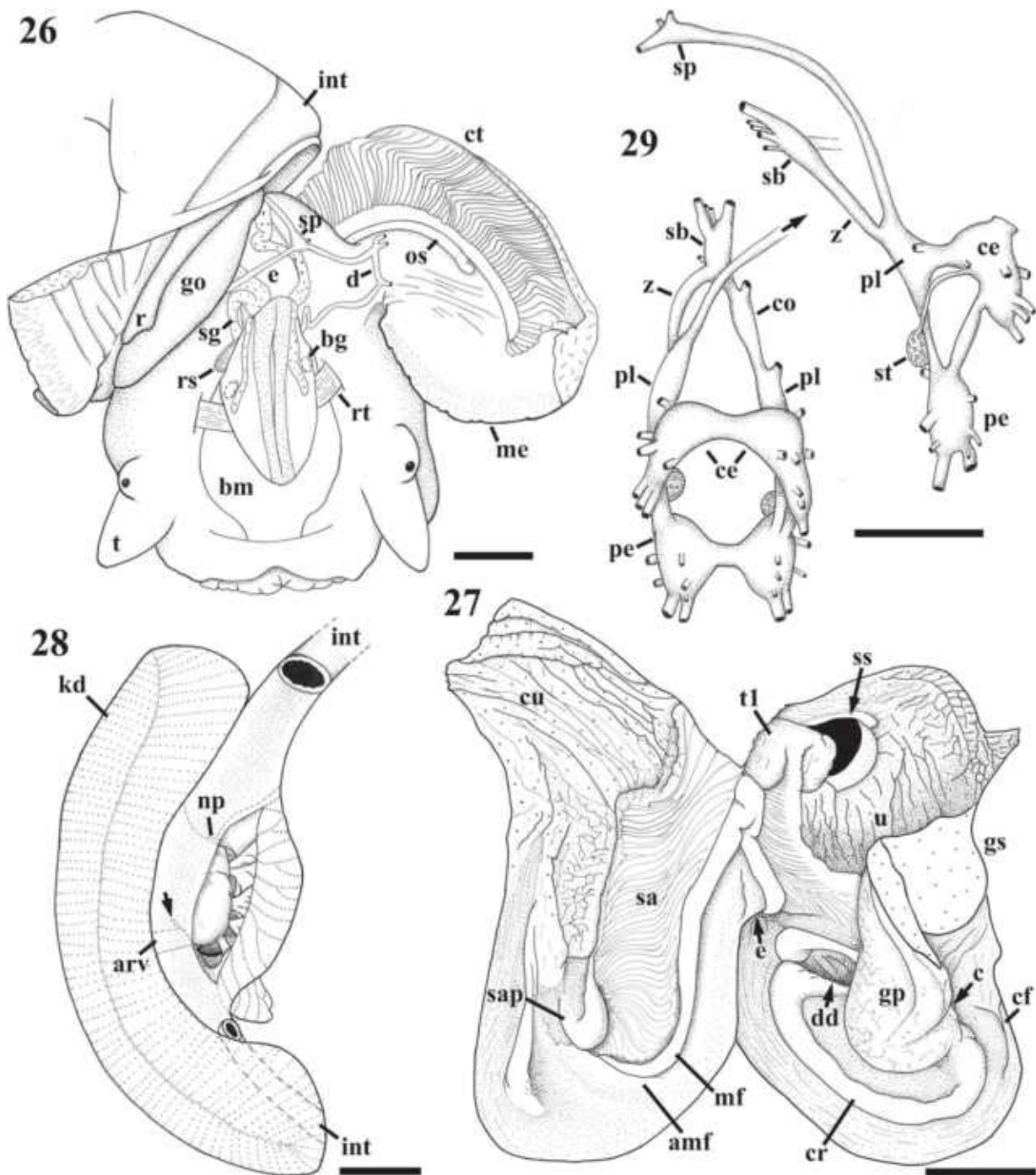


Figures 20–25. Radula of *Juga (Juga) silicula* (USNM 1100659). **20.** Section of anterior radular ribbon. Scale bar = 200 μm . **21.** Rachidian and lateral teeth. Scale bar = 50 μm . **22.** Detail of rachidian teeth. Scale bar = 20 μm . **23.** Detail of lateral teeth; note weakly formed outer third denticle. Scale bar = 50 μm . **24.** Marginal teeth. Scale bar = 50 μm . **25.** Detail of cutting edge of marginal teeth. Note unequal size of cusps on inner and outer teeth. Scale bar = 20 μm .

FOREGUT: Buccal mass short and robust (Figure 26, **bm**). Odontophore occupying posterior one half to two thirds of buccal cavity with small, glandular subradular organ protruding before radula. Small jaws present at anterior ends of dorsal folds; epithelium of buccal cavity between dorsal folds glandular (stippled). Dorsal folds deeply cleft along midline adjacent to odontophore; cleft receives salivary gland ducts at posterior end and shallows anteriorly. Very shallow, non-glandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia (**bg**) at rear of buccal cavity. Radular sac (**rs**) short (~4.4 mm), curving upward behind base of buccal mass, not passing through nerve ring, with tip resting against right posterior end of buccal mass. Robust buccal retractors (**rt**) inserting onto lateral walls of cephalic hemocoel anterior to nerve ring. Short, glandular mid-ventral fold forming small triangular ridge just behind odontophore in anterior esophagus, flanked by two ventro-lateral folds. Ventro-lateral folds converging short distance behind mid-ventral fold, forming rear-facing triangular depression surrounding mid-ventral fold. Paired dorsal and ventral folds continuing through long mid-esophagus (**e**) into posterior esophagus. Epithelium of mid-esophagus between dorsal and ventral folds longitudinally grooved; septate esophageal gland lacking. Posterior esophagus narrow, with numerous folds of approximately equal height. Long, tubular salivary glands (**sg**) passing through circum-esophageal nerve ring, extending to posterior esophagus.

MIDGUT: Esophagus opening under ledge on left side of midgut floor (Figure 27, **e**). Marginal fold (**mf**) extending anteriorly from esophageal aperture alongside major

typhlosole (**t1**), then turning posteriorly, bordering right margin of sorting area (**sa**). Sorting area elongate, rectangular, tapering posteriorly; posterior tip curving slightly to the left around crescent-shaped sorting area pad (**sap**). Accessory marginal fold (**amf**) forming weak ridge paralleling marginal fold from near esophagus, curving around posterior margin of sorting area; posterior segment of fold variable, in some specimens intersecting straight longitudinal ridge along left posterior end of sorting area (figured), in other specimens weakly bifurcate (see e.g. Figures 37, 51). Fine parallel striations extending anteriorly from esophagus up face of major typhlosole (Figure 27, **t1**). Midgut roof to the left of sorting area coarsely folded and cuticularized (**cu**). Gastric shield (**gs**) broadly concave; shield continuous with cuticle of adjacent regions of stomach roof and floor. Glandular pad (**gp**) large, rounded posteriorly, with lightly textured surface. Slight overhanging lip of glandular pad forming shallow pocket (**c**) behind gastric shield. Crescentic ridge (**cr**) bounding wide, shallow crescentic groove. Proximal end of ridge posteriorly bordering deep pouch that receives multiple openings of digestive gland (**dd**); distally, ridge fusing to right, posterior end of glandular pad. Size of opening to digestive gland duct vestibule variable. Single, weak, irregular longitudinal fold (**cf**) along floor opposite caecum. Prominent cuticularized fold (**u**) extending from beneath right side of style sac lip (**ss**), along floor, to ridge extending from base of major typhlosole; fold bounding u-shaped depression below lip of style sac. Style sac large, communicating along entire length with intestinal groove; intestine forming prominent protuberance at distal tip of



Figures 26–29. Internal anatomy of *Juga (Juga) silicula* (USNM 1100659). **26.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. **27.** Midgut anatomy. Dorsal view, anterior is uppermost. **28.** Kidney anatomy. Internal view of bladder. Lateral view, anterior is uppermost. Roof of bladder (below intestine) cut open to reveal interior; adjacent to incision, stippling indicates intersection of excretory tubules with roof of bladder. Arrow indicates opening in outpocketing of wall between bladder and main kidney chamber. **29.** Circum-esophageal nerve ring. Frontal view on the left, right lateral view on the right. Arrow indicates connective to supra-esophageal ganglion. Abbreviations: **amf**, accessory marginal fold; **arv**, afferent renal vessel; **bg**, buccal ganglion; **e**, caecum; **ce**, cerebral ganglion; **cf**, caecal fold; **co**, thickened connective between left pleural and sub-esophageal ganglia; **cr**, crescentic ridge; **ct**, ctenidium; **cu**, cuticularized region of stomach roof; **d**, dialyneury; **dd**, digestive gland duct vestibule; **e**, esophagus; **go**, pallial gonoduct; **gp**, glandular pad; **gs**, gastric shield; **int**, intestine; **kd**, main kidney chamber; **me**, mantle edge; **mf**, marginal fold; **np**, nephropore; **os**, osphradium; **pe**, pedal ganglion; **pl**, pleural ganglion; **r**, rectum; **rs**, radular sac; **rt**, buccal retractor muscle; **sa**, sorting area; **sap**, sorting area pad; **sb**, sub-esophageal ganglion; **sg**, salivary gland; **sp**, supra-esophageal ganglion; **ss**, lip of style sac; **st**, statocyst; **t**, cephalic tentacle; **t1**, major typhlosole; **u**, u-shaped fold; **z**, zygoneury. Scale bars = 1 mm.

style sac where it separates from the latter (not visible dorsally; see e.g. Figure 50, **ss**). Crystalline style present.

HINDGUT: Proximal intestine (Figures 18, 19, **int**) passing below distal tip of style sac, then extending posteriorly in broad loop, partially overlying style sac, to main gastric chamber (**sto**). Intestine continuing forward, passing under posterior end of main kidney chamber (**kd**), entering pallial roof between bladder (Figure 19, **b**) and main kidney chamber (**kd**), to papillate anus near mantle margin (Figure 26, **r**).

Reno-pericardial System: Kidney comprising two interconnected chambers (Figure 28). Main chamber (**kd**) lying along dorsal surface of body whorl, anteriorly surrounding pericardium (Figure 18, **per**, dotted line), crossing axis of body from right to left and extending short distance into pallial roof at base of mantle cavity. Main chamber occluded with excretory tubules anteriorly (within pallial roof), posteriorly, and along left margin. Central portion of main chamber with small, narrow lumen. Second chamber (exposed chamber in Figure 28) extending between pericardial chamber to right body wall below intestine, forming small bladder (Figure 19, **b**). Wall separating main chamber and bladder forming large outpocketing; small aperture within wall, just in front of afferent renal vessel, connecting main chamber and bladder (Figure 28, arrow). Bladder largely occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (**arv**). Sheets of excretory tissue branching and anastomosing, and fusing to right lateral wall, floor and roof below intestine; sheets laterally enclosing outpocketing of main chamber wall. Bladder communicating to mantle cavity via large nephropore (**np**); outpocketing of main chamber wall extending into nephropore, restricting communication with mantle cavity. Bladder penetrating connective tissue along right side of body, short distance into mantle cavity. Nephridial gland absent.

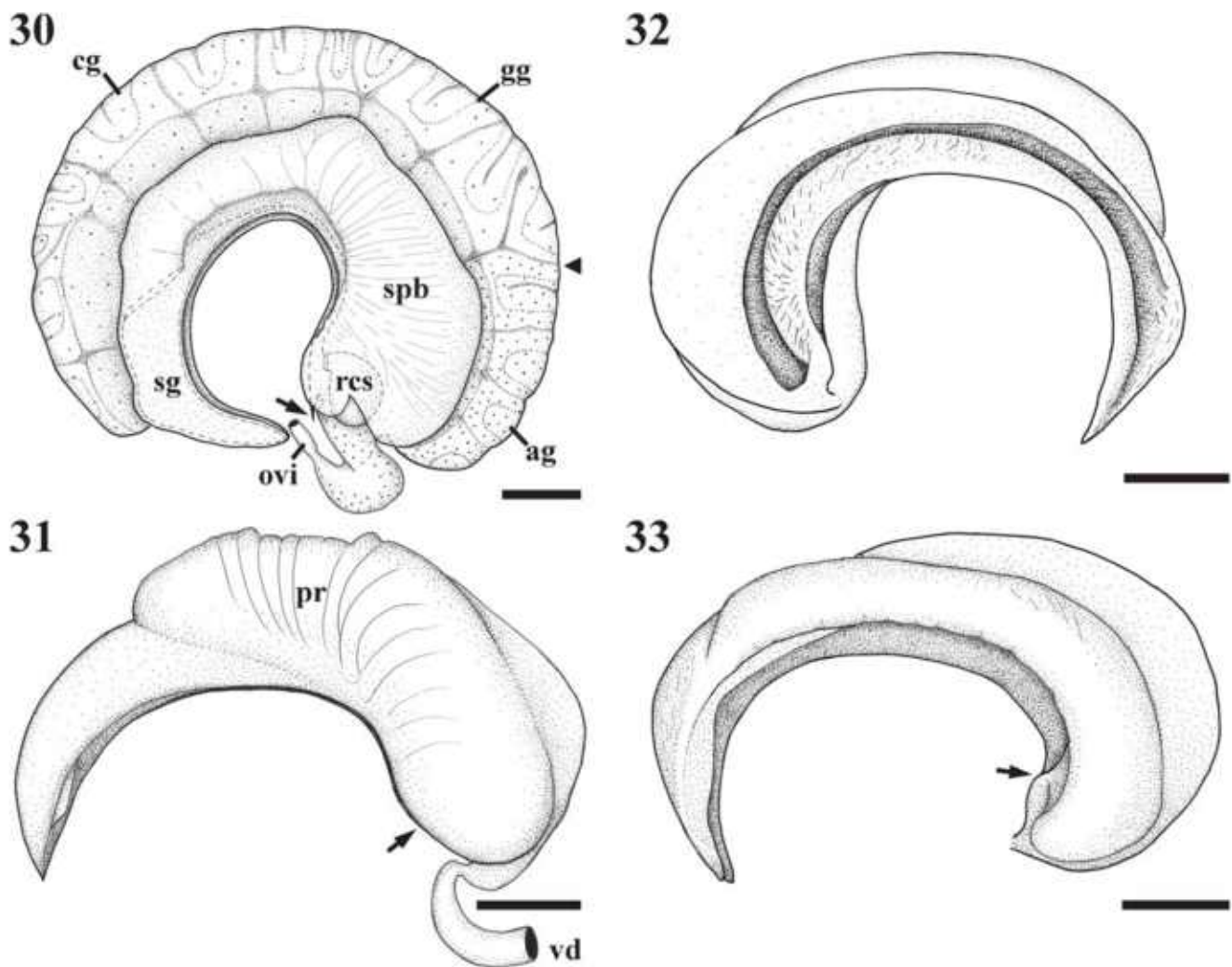
Pericardium long and narrow (Figure 18, **per**, dotted line), extending to recurved intestinal loop.

Nervous System: Circum-esophageal nerve ring (Figure 29) lying immediately behind buccal mass, well behind base of cephalic tentacles. Cerebral ganglia (**ce**) connected by short, stout commissure, each producing seven nerves (optic, statocyst, tentacular, and 4 labial nerves). Buccal ganglia (Figure 26, **bg**) lying ventrolaterally at base of buccal mass, adjacent to retractor muscles, at outer edges of esophagus where it emerges from buccal cavity. Pleural ganglia (Figure 29, **pl**) lying behind and below cerebral ganglia, connected to cerebral ganglia by short, thick connectives. Pedal ganglia (**pe**) with two prominent anterior nerves and variable number of smaller accessory nerves (five to seven). Statocysts (**st**) with numerous statoconia present dorsally alongside pedal ganglia behind pedal connectives. Sub-esophageal ganglion (**sb**) joined to left pleural ganglion by thickened connective (**co**); connective producing one small nerve. In addition to connectives to right and left

pleural and visceral ganglia, sub-esophageal ganglion producing four small nerves. Zygoneury (**z**) formed between sub-esophageal and right pleural ganglia. Long connective uniting right pleural and supra-esophageal ganglia (Figures 26, 29, **sp**), the latter lying on left side of mantle floor near midline of osphradium. Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supra-oesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present between pericardium and kidney at base of mantle cavity.

Reproductive System: FEMALE: Gonad (Figures 18, 19, **ov**) dorsally surrounding digestive gland from tip of visceral mass to posterior end of midgut (**sto**). Oviduct emerging ventrally from ovary. Renal oviduct (Figure 30, **ovi**) entering glandular pallial oviduct at base of mantle cavity. Pallial oviduct with proximal albumen (**ag**) and distal capsule glands (**cg**). Proximal albumen gland, below pallial portion of bladder, forming u-shaped tube with glands developed dorsally along axis of fold and simple gonoductal groove between opposing flattened surfaces of glands. Anteriorly, albumen and capsule glands becoming highly glandular and thrown into complex undulating folds; gonoductal groove compressed and highly convoluted (**gg**). Albumen gland approximately one third the length of capsule gland. Pallial oviduct communicating with mantle cavity through narrow aperture along entire length (arrow), except for tubular section of albumen gland at base of mantle cavity. Above aperture, along anterior ~one fourth of oviduct, deep sperm gutter (**sg**, dashed line) present within medial lamina; gutter opening broadly to long, broadly rounded spermatophore bursa (**spb**). Bursa broadening posteriorly and extending to tubular portion of albumen gland. Behind opening to bursa, sperm gutter becoming shallow abruptly and continuing posteriorly (dashed line) as shallow groove. Near posterior end of oviduct, shallow ridge entering small rounded aperture, just inside ventral edge of medial lamina, leading to small pouch-like seminal receptacle (**rcs**). Prominent glandular protuberance from opposing inner surface of lateral lamina extending into receptacle aperture, completely filling narrow proximal portion. Thin, narrow glandular ridge extending anteriorly from protuberance along inner edge of lateral lamina; glandular ridge extending to pallial oviduct tip just inside seminal groove.

MALE: Narrow vas deferens (Figure 31, **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 (**pr**) at base of mantle cavity. Prostate glandular, opening to mantle cavity through narrow aperture along entire length except for a short fused segment at base of mantle cavity (Figures 31, 33, arrow). Glands of medial and lateral laminae closely appressed, forming tightly interlocking tongue and groove arrange-



Figures 30–33. Reproductive anatomy of *Juga (Juga) silicula* (USNM 1100659). **30.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. “◄” indicates transition between albumen and capsule glands. **31.** External, left lateral view of prostate. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. **32.** Internal view of prostate medial lamina. Anterior is to the right. **33.** Internal view of prostate lateral lamina. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. Abbreviations: **ag**, albumen gland; **cg**, capsule gland; **gg**, gonoductal groove; **ovi**, renal oviduct; **pr**, prostate; **rcs**, seminal receptacle; **sg**, sperm gutter; **spb**, spermatophore bursa; **vd**, vas deferens. Scale bars = 1 mm.

ment (Figures 32, 33). Glandular tissue of medial lamina ventrally forming elongate, flattened textured fold (Figure 32), corresponding to concave ventral surface of opposing fold in lateral lamina (Figure 33). Medial lamina expanding to surround fold within lateral lamina. Dorsally and posteriorly, glands of lateral and medial laminae flaring to form flattened flange; size and shape of flange variable between individuals. Apart from fold in medial lamina, inner surface of prostate essentially smooth.

Juga (Calibasis) acutifilosa (Stearns, 1890)

Type Material: Lectotype (USNM 60596; figured specimen in Stearns, 1890, pl. 15, fig. 9) (Figure 5), by present designation, in order to enhance the stability of the nomenclature in accordance with article 74.7.3 of the

ICZN; indicated as holotype on label. Fourteen paralectotypes (USNM 60596X) in secondary type collection of USNM, indicated as paratypes on old label and as syntypes on newer label printed in 2001. Although Graf (2001) stated that the “holotype” is by original designation, Stearns figured the largest of the syntypes and provided the dimensions, but did not make an explicit type designation (designation of holotype) in the text and indicated that the description was based on examination of approximately three dozen specimens. Collected by H. W. Henshaw.

Type Locality: “Eagle Lake” (Stearns, 1890). Taylor (1981) corrected this to head of Willow Creek, Lassen Co., California (see Figure 1). There are no populations in the Eagle Lake drainage which includes several small

tributaries that flow into the lake during winter and the only outflow is through the remnants of the Bly Tunnel. Initiated during the 1920's, the Bly irrigation project diverted water from Eagle Lake to Willow Creek at Murrer's Meadows several kilometers away in the more arid Honey Lake drainage. Today, the tunnel is mostly blocked except for an 8" (~20 cm) pipe that still allows some outflow to Willow Creek. The headwaters of Willow Creek are regarded as springs along Murrer's Upper Meadow and Bly Tunnel (Moyle et al., 1996). Graf (2001) lists the type locality as "Eagle Lake, [Lassen Co.,] California".

Remarks: The species varies widely in shell morphology, from populations with several strong persistent lirae to those with lirae confined to the apical whorls. Body color also may differ drastically from population to population. Few sites show much intrapopulation variance; but adults can vary from population to population, with those at some sites highly variable and others essentially invariant. Very few populations in only a part of the range are as strongly and completely lirate as some Willow Creek (and Murrer's Upper Meadow) populations. These observations are consistent with preliminary results based on COI sequences that indicate the species, as currently recognized, is highly polyphyletic (Frest et al., unpublished data).

Material Examined: California: Lassen County: Willow Creek collected off dirt road (to E.), 0.40 km S. of Murrer's Lower Meadow, depth 0.05–0.20 m (Zone 10 695000E 4493820N [120°41'51"E, 40°34'26"N], Gallatin Peak 1989 7.5' quadrangle, elevation 1509 m), Deixis Consultants locality #1484, 10 Sep. 1993, collected by TF, EJ (USNM 1100658) (4 specimens dissected) (see Figures 10–12); southern-most of three springs at N. end of Murrer's Lower Meadow, below road on E. side of meadow, E. of Eagle Lake, depth 0–0.03 m (Zone 10 694995E 4495225N [120°41'49"E, 40°35'12"N], Gallatin Peak 1989 7.5' quadrangle, elevation 1545 m), Deixis Consultants locality #1287, 10 Sep. 1993, collected by TF, EJ (USNM 1100659) (3 specimens dissected).

External Anatomy: Operculum ovate, with slightly angular tip (Figure 34). Nucleus comprising slightly less than one half of total length (~41%).

Ovipositor pore rather deep (Figure 35, **ovp**) with deep, highly grooved tract extending to edge of foot, slight distance back from anterior pedal gland (**ap**).

Mantle edge (Figure 35, **me**) crenulated, corresponding to spiral teleoconch sculpture. Ctenidium (Figure 36, **ct**) extending from posterior end of mantle cavity to mantle edge. Hypobranchial gland weakly developed (**hg**).

REMARKS: With the exception of minor individual and/or preservational differences, the external anatomy is essentially identical to *Juga silicula*. *Juga acutifilosa* differs only in that the operculum is slightly more angular and the nucleus comprises a slightly smaller proportion of the total length, the ovipositor and groove to the edge of the

foot are significantly deeper and more grooved, the groove opens to the foot nearer the end of the anterior pedal gland, the gill extends slightly nearer the mantle edge, and the hypobranchial gland is much more weakly developed.

Alimentary System: **RADULA:** Radula comprising ~104 rows (n = 2) (Figures 38–43). Rachidian basal margin concave bordering bluntly rounded median projection; basal denticles lacking or only slightly developed (Figures 39, 40). Cutting edge bearing one large central conical cusp, and two stout, conical denticles on each side (Figure 40). Lateral teeth (Figures 38, 39, 41) with short lateral extensions (slightly less than half the length of lateral cutting edge), and single, prominent triangular cusp flanked by two inner triangular denticles and three to four outer denticles. Weakly developed outermost denticle may be present or absent (Figure 41). Marginal teeth (Figures 42, 43) with broadly rounded cutting edges and long, slender shafts. Inner marginal teeth with five and outer marginal teeth with six flattened denticles.

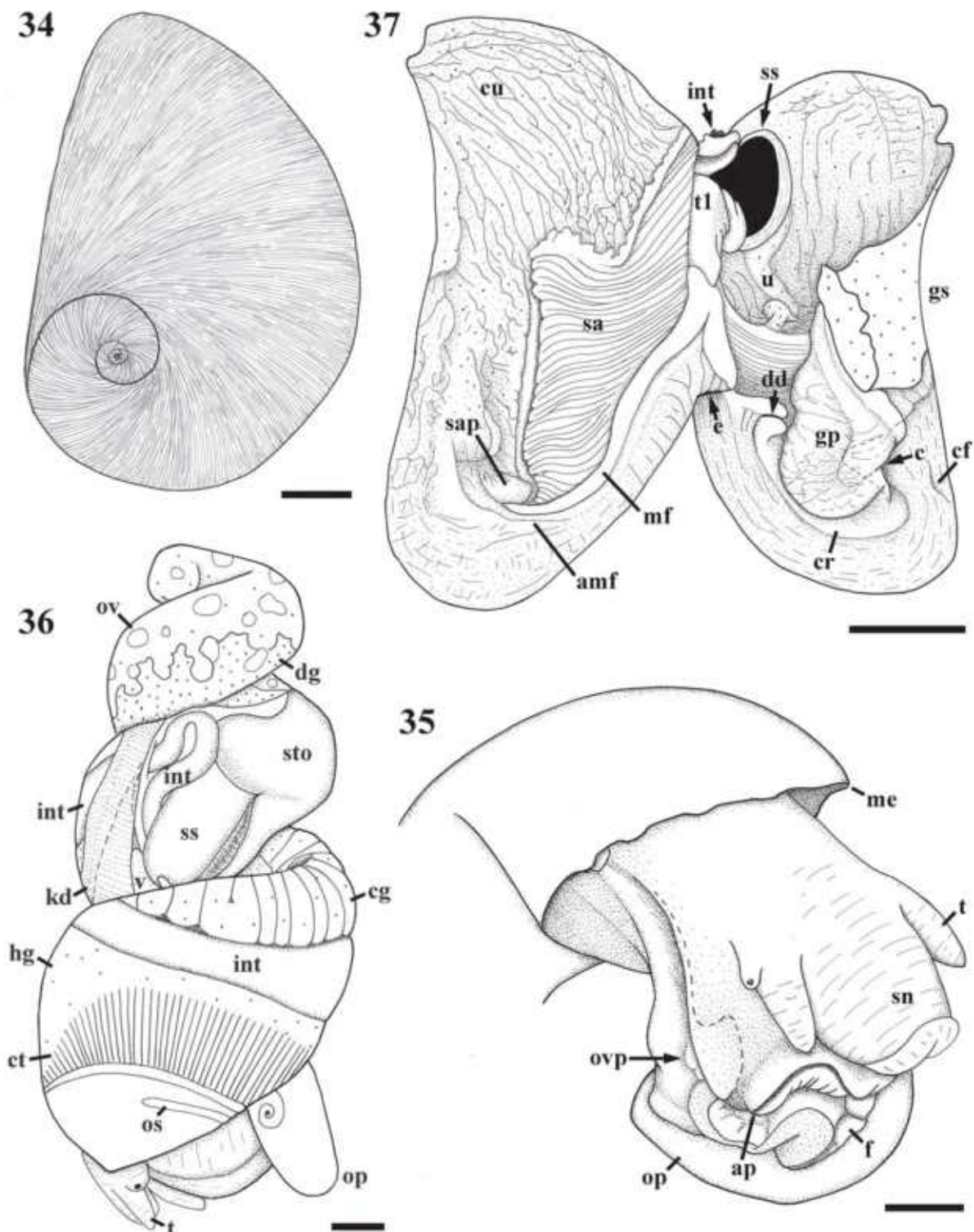
FOREGUT: Radular sac long (~6.7 mm), extending back through nerve ring approximately one half distance to supra-esophageal ganglion, then curving anteriorly with tip overlying nerve ring. Long, thin tubular salivary glands passing through circum-esophageal nerve ring, extending to posterior esophagus.

MIDGUT: Sorting area elongately triangular (Figure 37, **sa**). Accessory marginal fold (**amf**) forming weak ridge paralleling marginal fold from near esophagus, curving around posterior margin of sorting area, with weakly bifurcate posterior end. Glandular pad (**gp**) moderately large, rounded posteriorly, with coarsely textured surface. Deep pocket (**c**) extending under glandular pad behind gastric shield. Crescentic ridge (**cr**) bounding narrow, shallow crescentic groove. Style sac large; intestine forming slight protuberance at distal tip of style sac where it separates from the latter (Figure 36, **ss**).

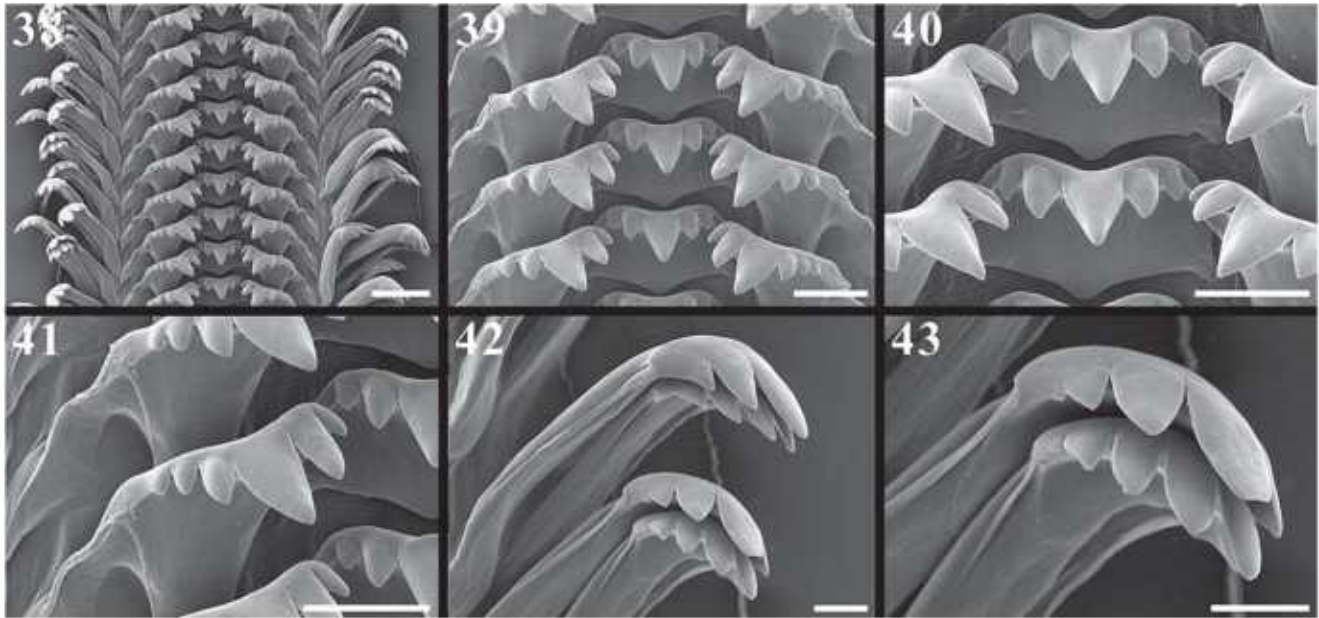
REMARKS: In comparison to *Juga silicula*, the denticles of the rachidian and lateral teeth are typically more conical, with fewer denticles present on the rachidian and marginals, but more outer denticles present on the lateral teeth. The weakly developed outermost denticle on the lateral teeth is variably developed, and only very small. Rachidian basal denticles are lacking, or only slightly developed. The radular sac is exceptionally long in this species and the salivary glands appear narrower.

Within the midgut, in spite of the differences highlighted above, overall configuration and proportions of features are very similar between *Juga silicula* and *J. acutifilosa*, with the exception that the sorting area is more elongately triangular in shape in *J. acutifilosa*.

No significant differences in the configuration of the hindgut, with the possible exception that the hindgut dramatically widens upon entering the mantle cavity in the specimens examined for *Juga acutifilosa*. However, this may be individual variation.



Figures 34–37. Anatomy of *Juga (Calibasis) acutifilosa* (USNM 1100659, except when noted). **34.** Operculum. **35.** Ovipositor and egg groove (USNM 1100658). Right lateral view of head-foot. **36.** External view of organs in visceral mass (USNM 1100658). Dotted line indicates extent of pericardium under main kidney chamber. **37.** Midgut anatomy. Dorsal view, anterior is uppermost. Abbreviations: **amf**, accessory marginal fold; **ap**, anterior pedal gland; **c**, caecum; **cf**, caecal fold; **eg**, capsule gland; **cr**, crescentic ridge; **ct**, ctenidium; **cu**, cuticularized region of stomach roof; **dd**, digestive gland duct vestibule; **dg**, digestive gland; **e**, esophageal aperture; **f**, foot; **gp**, glandular pad; **gs**, gastric shield; **hg**, hypobranchial gland; **int**, intestine; **kd**, main kidney chamber; **me**, mantle edge; **mf**, marginal fold; **op**, operculum; **os**, osphradium; **ov**, ovary; **ovp**, ovipositor; **sa**, sorting area; **sap**, sorting area pad; **sn**, snout; **ss**, style sac; **sto**, stomach; **t**, cephalic tentacle; **tl**, major typhlosole; **u**, u-shaped fold; **v**, ventricle. Scale bars = 1 mm.



Figures 38–43. Radula of *Juga (Calibasis) acutifilosa* (USNM 1100659). **38.** Section of anterior radular ribbon. Scale bar = 100 μm . **39.** Rachidian and lateral teeth. Scale bar = 50 μm . **40.** Detail of rachidian teeth. Scale bar = 50 μm . **41.** Detail of lateral teeth. Note very weak development of tiny outer fourth denticle. Scale bar = 50 μm . **42.** Marginal teeth. Scale bar = 20 μm . **43.** Detail of cutting edge of marginal teeth. Note unequal size of cusps on inner and outer teeth. Scale bar = 20 μm .

Reno-pericardial System: REMARKS: Configuration of features within the kidney and density of excretory tissue essentially identical to *Juga silicula*, with the only exception being that the central lumen within the main chamber is slightly shorter.

Nervous System: Pedal ganglia (**pe**) with two prominent anterior nerves and four smaller accessory nerves.

REMARKS: Configuration of nervous system, including number of nerves produced by major ganglia, otherwise identical to *Juga silicula*.

Reproductive System: FEMALE: Proximal albumen gland (Figure 44, **ag**), below pallial portion of bladder, forming small, flattened rounded pouch with glands developed along dorsal axis; shape of pouch somewhat variable. Along anterior ~one third of oviduct, deep sperm gutter (**sg**, dashed line) present within medial lamina; gutter opening broadly to long, broadly rounded spermatophore bursa (**spb**). Behind opening to bursa, sperm gutter shallowing abruptly to shallow groove (dashed line), then rapidly becoming obsolete. Near posterior end of oviduct, small rounded aperture, just inside ventral edge of medial lamina, leading to small narrow seminal receptacle (**rcs**). Low, flatly rounded glandular protuberance from opposing inner surface of lateral lamina slightly extending into receptacle aperture. Extremely thin, glandular ridge extending from protuberance to oviduct anterior tip along inner edge of lateral lamina opposite seminal groove; ridge thickening somewhat anteriorly.

MALE: Glands of medial and lateral laminae forming

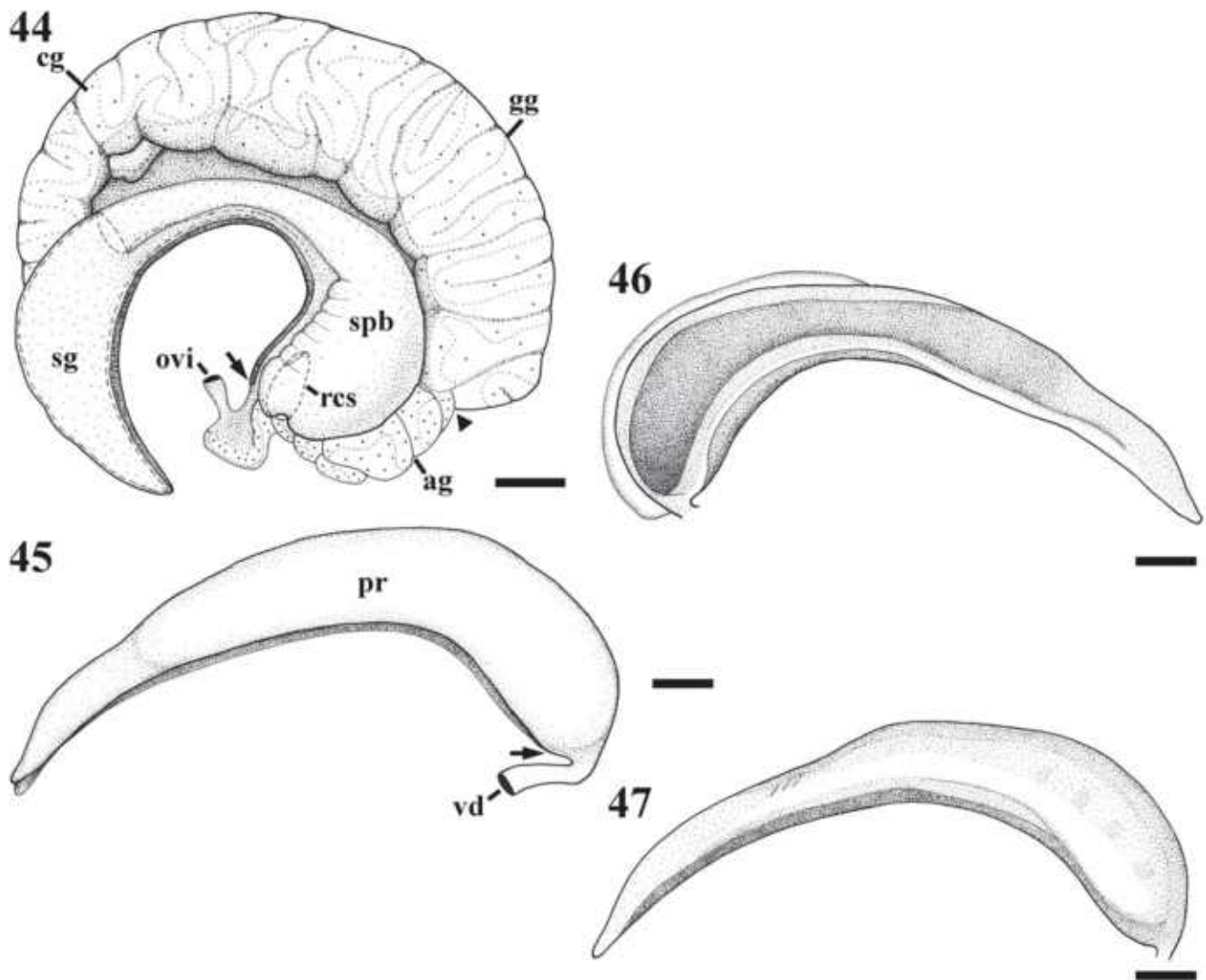
loosely interlocking tongue and groove arrangement (Figures 46, 47).

REMARKS: In contrast to *Juga silicula*, the proximal albumen gland forms a small, flattened, rounded pouch. The height and shape of the pouch is variable in *J. acutifilosa*, but is distinctly smaller and slightly less glandular than the more u-shaped tube in *J. silicula*. Overall, the capsule and albumen glands are similar in proportion, but the albumen gland is slightly shorter and not as massive as that in *J. silicula*. In addition, the seminal groove is longer and deeper anteriorly but becomes obsolete before reaching the seminal receptacle, the lateral lamina glandular ridge is much weaker and the protuberance into the aperture of the seminal receptacle is more bluntly rounded than in *J. silicula*.

Male reproductive anatomy is very similar to that of *Juga silicula* in the morphology of the folds within the prostate, but the folds are not as highly developed and hence, do not tightly interlock to the same degree. In addition, the ventral fold of the medial lamina is less textured and the dorsal and posterior flange is narrower in *J. acutifilosa*.

Juga (Oreobasis) newberryi (Lea, 1860)

Type Material: Lectotype designated by Graf (2001) (USNM 118961; figured specimen in Lea, 1863, pl. 37, fig. 135) (Figure 6); indicated as holotype on label. Twelve paralectotypes (USNM 118961X) in secondary type collection of USNM; indicated as paratypes on old label and as syntypes on newer label printed in 2001. At the time of publication, the lectotype designation of Graf



Figures 44–47. Reproductive anatomy of *Juga (Calibasis) acutifilosa* (USNM 1100659). **44.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. “◄” indicates transition between albumen and capsule glands. **45.** External, left lateral view of prostate. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. **46.** Internal view of prostate medial lamina. Anterior is to the right. **47.** Internal view of prostate lateral lamina. Anterior is to the left. Abbreviations: **ag**, albumen gland; **cg**, capsule gland; **gg**, gonoductal groove; **ovi**, renal oviduct; **pr**, prostate; **res**, seminal receptacle; **sg**, sperm gutter; **spb**, spermatophore bursa; **vd**, vas deferens. Scale bars = 1 mm.

was invalid as it did not follow strict guidelines concerning the language of lectotype designations after 1999. However, under Declaration 44, Amendment of Article 74.7.3 of the Code (Bulletin of Zoological Nomenclature 60(4) December 2003), Graf’s lectotype designation is now valid. Collected by J. S. Newberry.

Type Locality: Indicated as “Upper des Chutes River, Oregon Territory” (Lea, 1860) (see Figure 1). Most likely, the lectotype came from the Deschutes R. near Bend, Oregon, even though pleurocerids are now absent this far up the river. However, *Juga newberryi* does occur in the lower Deschutes River.

REMARKS: Lea’s (1860, 1862, 1863) description of *Mela-*

nia newberryi and 1863 illustration are quite accurate. As noted and illustrated by Lea, the most frequent color pattern is three yellow bands separated by three almost black. Occasionally, the lower band may be divided into two or more (Burch, 1989: fig. 452) or the dark bands may be tan in color. Alternatively, the shell may be band-less, in which case the color varies from yellowish-tan to dark tan. Lea (1863: 301) does not seem to have had any of the band-less form; recent field surveys have not revealed any “pure” populations of the band-less form, on the other hand, large populations are not likely to lack it (Frest, unpublished data).

This species is one of a small group of *Juga* with the whorls smooth throughout ontogeny which led Taylor (1966) to make it the type of *Oreobasis*. In the same

publication, Taylor suggested that *J. newberryi* is a "probable" synonym of *Melania bulbosa* Gould, 1847. By 1977, Taylor (1977) had accepted this synonymy without qualification, which was followed by many authors (Burch and Tottenham, 1980; Burch, 1982a, b, 1989; Graf, 2001). However, it is not clear why the two species were considered so similar. Comparison of the types indicates that, while being similar in whorl height, the two differ in shape of the aperture, whorl profile and rate of whorl expansion, particularly for the body whorl; *J. bulbosa* generally has more than three not corroded whorls while *J. newberryi* is often more severely corroded but the early teleoconch of the latter is quite distinctive when present. A search of major museum collections failed to locate many specimens aside from the types; most museum lots ascribed to *J. bulbosa* or *J. newberryi* clearly do not belong to either.

Tryon (1865) was apparently the first to reflect on the similarity of the two, indicating the presence of bands in *Juga newberryi* as the sole separating feature, but he did not synonymize them. However, Tryon's illustration of *J. bulbosa* (e.g. 1873, fig. 496) seems to use his own specimen rather than Gould's types, even though he claimed to have had them (1873: 255). In contrast to Gould's types, the specimen figured by Tryon is rather large, strongly corroded with less than 3 whorls, and the surviving whorls appear strongly convex, with a very deep suture. It is likely a band-less form of *J. newberryi*. Thus, although long considered synonyms, the perception that the two are "exactly similar in outline" (Tryon, 1865: 246) may be due to Tryon's apparent confusion between *J. bulbosa* and bandless forms of *J. newberryi*. The scarcity of museum lots may also have contributed to the confusion about the morphology and occurrence of both taxa.

Consequently, we here remove *Juga newberryi* from the synonymy of *J. bulbosa*. At present, *J. newberryi* occurs only in the lower Deschutes River, Oregon, from about Troutdale to roughly 6 miles above the mouth, where it is replaced by *J. (Juga) plicifera*. *Juga bulbosa* is likely also a valid species, but attempts to recollect this taxon anywhere in the historically identified range have been unsuccessful (Frest, unpublished data); thus, this hypothesis cannot be tested at the moment.

Material Examined: Oregon: Jefferson County: Deschutes River at RM 97.2-97.4 on E side of channel, ~0.3-0.6 km S of US 26 bridge and mouth of Shitike Creek, at Rainbow Landing, depth 0-0.41 m (Zone 10 640460E 4957320N [121°13'36"E, 44°45'26"N], Eagle Butte 1962 7.5' quadrangle, elevation 440 m), Deixis Consultants locality #2472, 13 Aug. 2000, collected by TF, EJ (USNM 1100660) (10 specimens dissected) (see Figures 13-15).

External Anatomy: Operculum ovate, with angular tip (Figure 48). Nucleus comprising about one third of total length (~34%).

Rather shallow ovipositor pore (Figure 49, **ovp**) with shallow, grooved tract extending to edge of foot, slight distance back from anterior pedal gland (**ap**).

Ctenidium (Figure 50, **ct**) extending from posterior end of mantle cavity to mantle edge. Hypobranchial gland (**hg**) moderately well developed with warty texture, particularly at posterior end of mantle cavity.

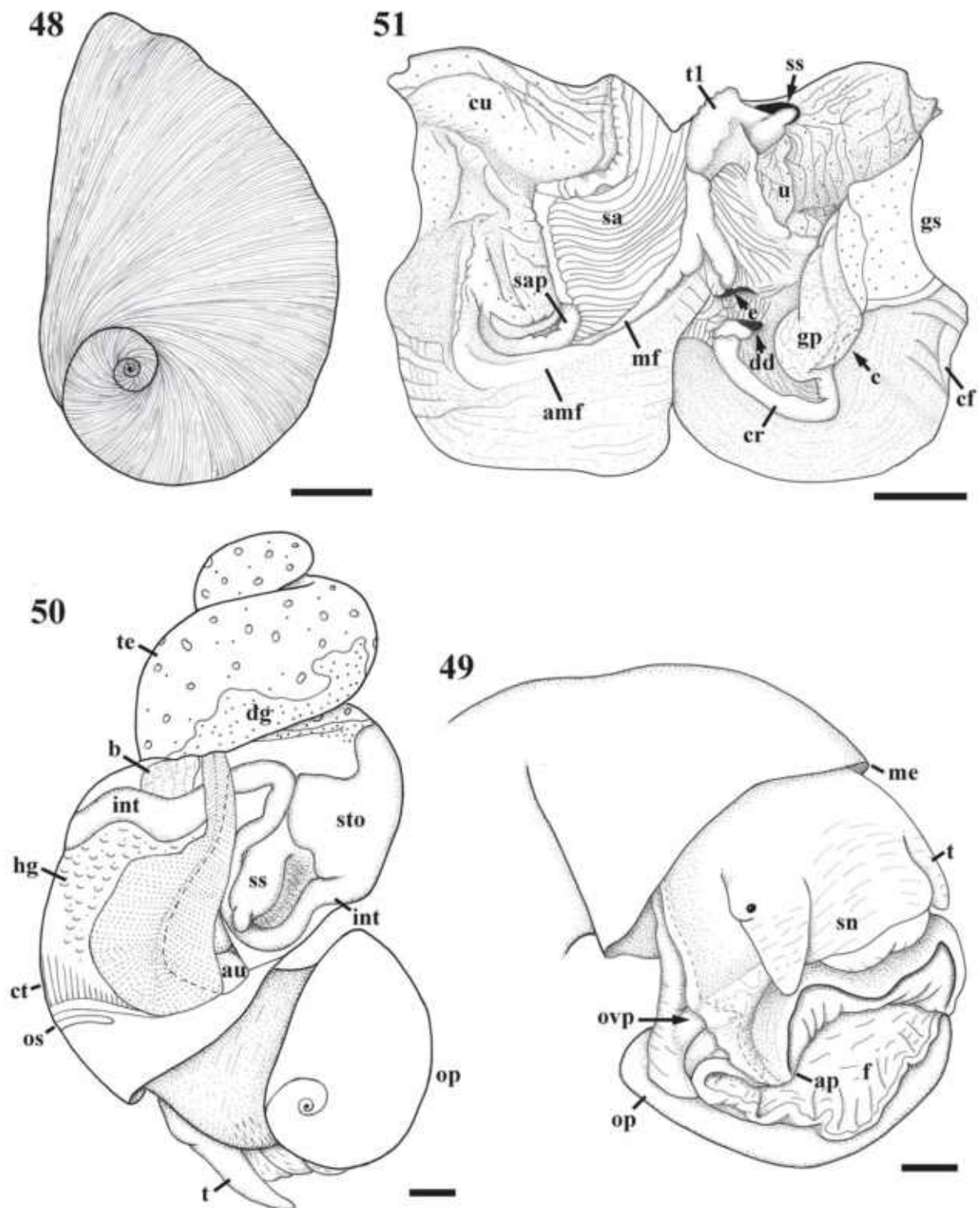
REMARKS: The external anatomy of *Juga newberryi* is almost identical to the two preceding species, and differs in that the operculum is more angular in shape and the nucleus is considerably smaller and more basal than eccentric; as in *J. acutifilosa*, the gill extends slightly nearer the mantle edge and the ovipositor groove opens nearer the end of the anterior pedal gland, but the pore and distal groove are considerably deeper in *J. acutifilosa* than in the other two species. The hypobranchial gland of *J. newberryi* is unique in having a warty texture.

Alimentary System: **RADULA:** Radula comprising ~106 rows ($n = 2$) (Figures 52-57). Rachidian with v-shaped lower margin; basal denticles lacking (Figures 53, 54). Cutting edge bearing one large central conical cusp, and two stout conical denticles on each side (Figure 54). Lateral teeth (Figures 52, 53, 55) with short lateral extensions (slightly less than half the length of lateral cutting edge), and single, prominent triangular cusp flanked by three to four inner and three to four outer denticles. Outermost denticle present, weakly developed, and variable in shape, size, and position (Figure 55). Marginal teeth (Figures 56, 57) with broadly rounded cutting edges and long, slender shafts. Inner marginal teeth with four to five and outer marginal teeth with six to seven flattened denticles.

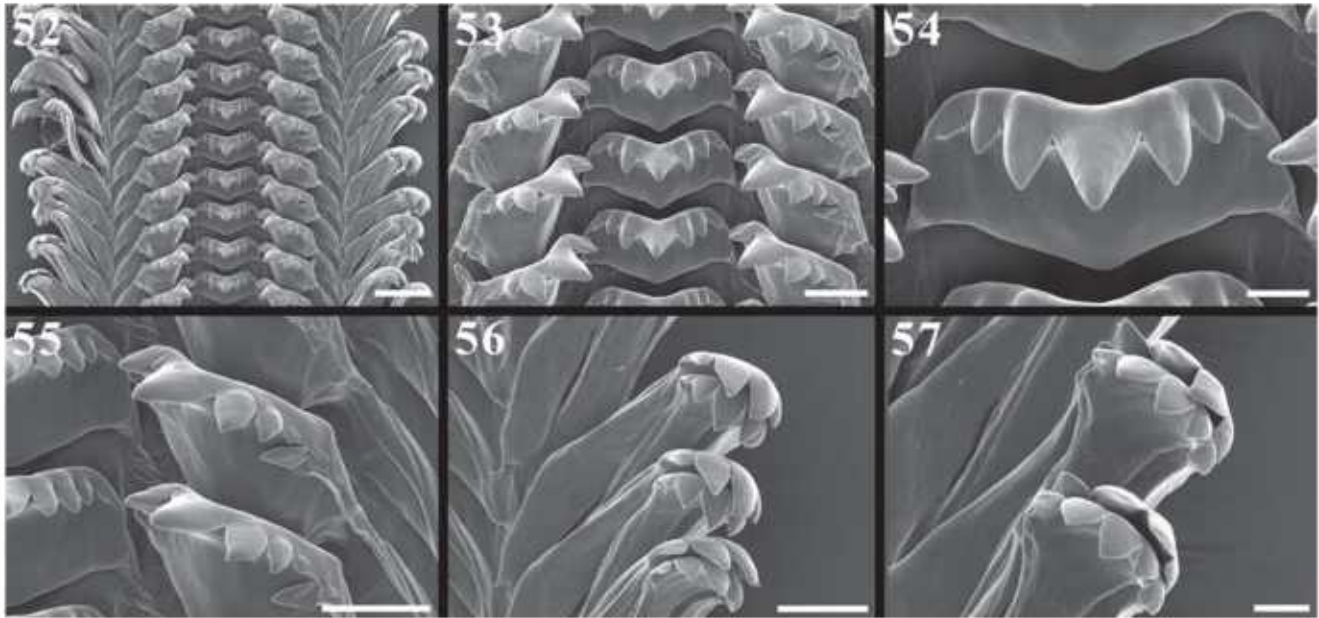
FOREGUT: Radular sac moderately long (~6.25 mm), extending back through nerve ring, then curving upward behind base of buccal mass with tip overlying left side of nerve ring. Epithelium of mid-esophagus between dorsal and ventral folds irregularly textured.

MIDGUT: Sorting area short, broadly triangular (Fig 51, **sa**). Accessory marginal fold (**amf**) forming weak ridge paralleling marginal fold from near esophagus, curving around posterior margin of sorting area, with weakly bifurcate posterior end. Glandular pad (**gp**) moderately large, rounded posteriorly, with lightly textured surface. Crescentic ridge (**cr**) bounding shallow, broad crescentic groove. Style sac small (Figure 50, **ss**); intestine forming prominent protuberance at distal tip of style sac where it separates from the latter.

REMARKS: As in *Juga acutifilosa*, the denticles of the rachidian and lateral teeth are typically more conical in *J. newberryi* than in *J. silicula*; there are only two outer denticles on each side of the central rachidan cusp, more outer denticles on the lateral teeth, the rachidian basal denticles are lacking, and the lateral extensions are proportionally smaller. However, in contrast to *J. acutifilosa*, *J. newberryi* and *J. silicula* share a similar lower margin on the rachidian and similar development of the weak, outermost denticle on the lateral teeth. *Juga newberryi* is unique in possessing three to four inner denticles on the



Figures 48–51. Anatomy of *Juga (Oreobasis) newberryi* (USNM 1100660). **48.** Operculum. **49.** Ovipositor and egg groove. Right lateral view of head-foot. **50.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. **51.** Midgut anatomy. Dorsal view, anterior is uppermost. Abbreviations: **amf**, accessory marginal fold; **ap**, anterior pedal gland; **au**, auricle; **b**, bladder; **c**, caecum; **cf**, caecal fold; **cr**, crescentic ridge; **ct**, ctenidium; **cu**, cuticularized region of stomach roof; **dd**, digestive gland duct vestibule; **dg**, digestive gland; **e**, esophageal aperture; **f**, foot; **gp**, glandular pad; **gs**, gastric shield; **hg**, hypobranchial gland; **int**, intestine; **kd**, main kidney chamber; **me**, mantle edge; **mf**, marginal fold; **op**, operculum; **os**, osphradium; **ovp**, ovipositor; **sa**, sorting area; **sap**, sorting area pad; **sn**, snout; **ss**, style sac; **sto**, stomach; **t**, cephalic tentacle; **te**, testes; **tl**, major typhlosole; **u**, u-shaped fold. Scale bars = 1 mm.



Figures 52–57. Radula of *Juga (Oreobasis) newberryi* (USNM 1100660). **52.** Section of anterior radular ribbon. Scale bar = 100 μm . **53.** Rachidian and lateral teeth. Scale bar = 50 μm . **54.** Detail of rachidian teeth. Scale bar = 20 μm . **55.** Detail of lateral teeth; note weakly formed outer fourth denticle. Scale bar = 50 μm . **56.** Marginal teeth. Scale bar = 50 μm . **57.** Detail of cutting edge of marginal teeth. Note unequal size of cusps on inner and outer teeth. Scale bar = 20 μm .

lateral teeth. The radular sac is intermediate in length relative to the buccal mass compared to *J. silicula* with a very short sac, and *J. acutifilosa* with a very long sac.

Juga newberryi differs greatly from the two preceding species in the relative proportions of features in the midgut, which is significantly longitudinally compressed. Consequently, the sorting area is broadly triangular rather than elongate and the glandular pad is disproportionately smaller. Possibly reflecting the smaller size of the style sac, the opening of the style sac to the stomach is also consistently smaller.

There are no significant differences in the configuration of the hindgut between *Juga newberryi* and *J. silicula*.

Reno-pericardial System: REMARKS: In contrast to both preceding species, the bladder of *Juga newberryi* is compressed and less voluminous, bringing the nephropore closer to the afferent renal vessel and decreasing the length of the wall between the main chamber and the bladder. Additionally, the sheets of excretory tissue in the bladder are more numerous, and more highly branched, almost entirely occluding the lumen.

Nervous System: Pedal ganglia with two prominent anterior nerves and five to six smaller accessory nerves. In addition to connections to right and left pleural and visceral ganglia, sub-esophageal ganglion producing three small nerves.

REMARKS: Apart from the differences highlighted above, configuration of the nervous system is basically identical to *Juga silicula*.

Reproductive System: FEMALE: Capsule gland (Figure 58, **cg**) comprising approximately anterior two thirds of pallial oviduct. Along anterior ~one third of oviduct, shallow sperm gutter (**sg**, dashed line) present within medial lamina; gutter opening narrowly to long, thin spermatophore bursa (**spb**). Sperm gutter continuing

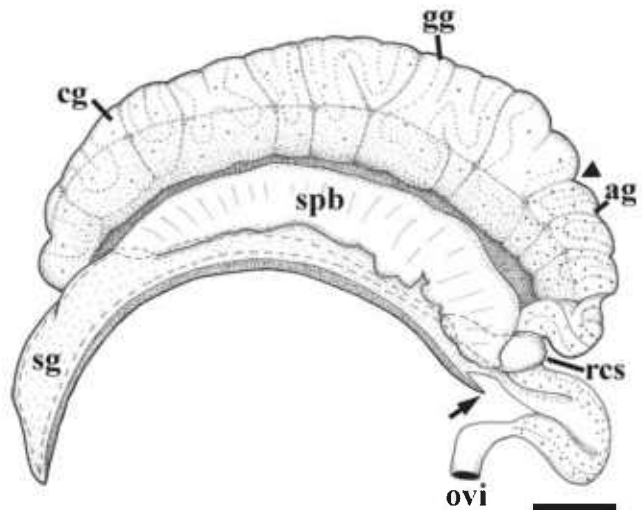


Figure 58. Reproductive anatomy of *Juga (Oreobasis) newberryi* (USNM 1100660). External, left lateral view of pallial oviduct. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. “ \blacktriangle ” indicates transition between albumen and capsule glands. Abbreviations: **ag**, albumen gland; **cg**, capsule gland; **gg**, gonoductal groove; **ovi**, renal oviduct; **rcs**, seminal receptacle; **sg**, sperm gutter; **spb**, spermatophore bursa. Scale bar = 1 mm.

posteriorly as shallow groove to small, narrow seminal receptacle (**res**). Moderate glandular protuberance from opposing inner surface of lateral lamina extending into receptacle aperture. Glandular ridge extending from protuberance to oviduct anterior tip along inner edge of lateral lamina opposite seminal groove; ridge thinning anteriorly.

REMARKS: The proximal albumen gland forms a prominent u-shaped tube that is larger than that in *Juga silicula*. The spermatophore bursa is smaller than both preceding species, but as in *J. acutifilosa*, the glandular ridge directly opposes the seminal groove and the glandular protuberance is intermediate in size between that of *J. silicula* and *J. acutifilosa*.

Apart from minor individual variation in shape and development of the prostate glands, there are no detectable discrete differences in male reproductive anatomy compared to *Juga silicula*. Some minor differences include the fact that the ventral fold of the medial lamina appears less textured as in *J. acutifilosa*, and the dorsal posterior flange appears consistently larger.

DISCUSSION

EVALUATION OF MORPHOLOGICAL CHARACTERS: Most anatomical differences among the three species investigated herein comprise qualitative variations in size and/or shape (e.g. operculum, hypobranchial gland, ovipositor, radula, and bladder). Although often emphasized in species-level systematic studies of gastropods, male and female reproductive anatomy also displays only minor differences in shape and size of the various glands, pouches, and gutters. Additional sampling within and between *Juga* species is necessary to determine if any of these comprise discrete rather than continuous character variation. Surprisingly, the midgut offers a significant source of variation, with modifications to size of the caecum, style sac, and proximal intestine, as well as overall proportions of the gastric chamber and sorting area. This is very different from eastern North American pleurocerids with species from disparate genera displaying almost identical midgut morphologies (Strong, 2005; Strong, unpublished data). For a summary of these and other differences, see Table 1.

The only published anatomical account of any North American *Juga* is that of Prozorova and Raschepkina (2004) on the female reproductive anatomy of five undetermined *Juga* species from the Willamette River system in Oregon. That study indicated the size and shape of the seminal receptacle and spermatophore bursa can vary, which was confirmed in the present study. However, Prozorova and Raschepkina reported several additional findings that could not be confirmed here, including a sperm gutter that becomes suddenly shallow (anterior one fifth to one sixth), variable length of the opening between the gonoductal groove and mantle cavity, and asymmetrical arrangement of albumen and cap-

sule glands. Indeed, the dorso-ventral axis (as defined by a plane extending between the gonoductal groove and the opening to the mantle cavity), is not correctly identified by these authors. Thus, they mistakenly conclude that the lateral lamina is glandular and the medial lamina is non-glandular, comprising the spermatophore bursa and seminal receptacle. Consequently, the glands of the oviduct are misinterpreted as a solid block penetrated by channels within the lateral lamina, rather than as a convoluted tube. This misunderstanding does not allow them to correctly identify the basic symmetry between the medial and lateral laminae, and the proportional development of the capsule and albumen glands along the antero-posterior axis. Instead, the albumen gland is often depicted as extending far anteriorly, dorsally overlying the capsule gland. Not only is this incorrect, it is difficult to imagine how such an arrangement would function.

ANATOMICAL AND SYSTEMATIC AFFINITIES OF *JUGA*: No conchological feature unambiguously distinguishes *Juga* from eastern North American pleurocerid genera; indeed, *Juga* has often been synonymized with *Elimia* (as *Goniobasis*)—a genus widespread east of the continental divide (e.g. Tryon, 1865, 1873; Pilsbry, 1899; Walker, 1918; Henderson, 1935a, b; Goodrich, 1942). However, increasing evidence not only supports the independence of *Juga*, but suggests ties to Asian pleurocerids. In an analysis of a large segment of the mitochondrial 16S rRNA gene including representatives of five eastern North American pleurocerid genera, *Juga* falls to the base of the tree rooted on *Melanopsis praemorsa* (L.) (Melanopsidae) and *Melanoides tuberculata* (Müller, 1774) (Thiaridae) (Holznagel and Lydeard, 2000). In an analysis of cerithioidean relationships using nearly full length 16S rRNA sequences (Lydeard et al., 2002), Eastern North American pleurocerids (*Elimia*, *Pleurocera*) are supported as more closely related to *Melanopsis* than to a clade uniting *Juga* with Eastern Asian pleurocerids (*Semisulcospira* Boettger, 1886, *Hua* Chen, 1943).

Available evidence from reproductive anatomy may also support a link between *Juga* and Asian pleurocerids. A recent contribution by Strong (2005) re-described the anatomy of *Pleurocera acuta* Rafinesque, 1831 and *Elimia livescens* (Menke, 1830) with a re-evaluation of pallial oviduct homologies. Despite several erroneous accounts (Woodard, 1934; Jones and Branson, 1964; Dazo, 1965), Strong's (2005) analysis confirmed Eastern North American pleurocerids described thus far lack a seminal receptacle—a feature present in all described western North American (*Juga*) and Asian (*Hua*, *Semisulcospira*) species (Itagaki, 1960; Nakano and Nishiwaki, 1989; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004, 2005). However, as stated above, the only information available on the anatomy of *Juga* concerns female reproductive anatomy. Given the detailed description of three *Juga* species herein, it is now possible to better place this unique assemblage within the emerging anatomical and phylogenetic framework for limnic cerithioideans.

Table 1. Summary of anatomical differences between three species of *Juga*.

	<i>Juga (Juga) silicula</i>	<i>Juga (Calibasis) acutifilosa</i>	<i>Juga (Oreobasis) newberryi</i>
External Anatomy:			
Operculum nucleus size (as percent of total length)	45%	41%	34%
Ovipositor pore	Shallow	Deep, highly ridged	Shallow
Hypobranchial gland	Transversely ridged	Thin	Warty
Alimentary System:			
Dentition:			
Rachidian tooth	3/1/3	2/1/2	2/1/2
Lateral teeth	2/1/2-3	2/1/3-4	3 -4/1/3-4
Marginal teeth	6/7	5/6	4-5/6-7
Rachidian basal denticle	Present	Lacking, slightly developed	Lacking
Rachidian basal margin	Bluntly v-shaped	Concave bordering rounded median projection	Bluntly v-shaped
Weakly formed outermost denticle of lateral teeth	Present	Absent	Present
Radular sac	Short	Long	Moderately long
Salivary glands	Thick, tubular	Thin, tubular	Thick, tubular
Sorting area	Elongately rectangular	Elongately triangular	Broadly triangular
Crescentic groove	Shallow, broad	Shallow, narrow	Shallow, broad
Caecum	Shallow	Deep	Shallow
Style sac	Large	Large	Small
Proximal intestine at base of style sac	Large protuberance	Small protuberance	Large protuberance
Reno-Pericardial System:			
Bladder excretory tubules	Loosely and regularly branched	Loosely and regularly branched	Densely and highly branched
Reproductive System:			
Proximal albumen gland	Moderately large, u-shaped tube	Small, rounded pouch	Large, u-shaped tube
Spermatophore bursa	Large, rounded	Moderately large, rounded	Narrow, tubular
Sperm gutter	Anterior one fourth of oviduct; extends to seminal receptacle as shallow groove within medial lamina	Anterior one third of oviduct; becomes obsolete before reaching receptacle	Anterior one third of oviduct; extends to receptacle as shallow groove within medial lamina
Lateral lamina glandular ridge	Inside seminal groove; large protuberance extending into receptacle aperture	Opposite seminal groove; low, flat protuberance extending into receptacle aperture	Opposite seminal groove; moderate protuberance extending into receptacle aperture
Prostate glands	Tightly interlocking	Loosely interlocking	Tightly interlocking

Juga, like other pleurocerids, possesses an ovipositor involved in the deposition of the egg capsules (except the viviparous *Semisulcospira*; Itagaki, 1960) (e.g. Jewell, 1931; Woodard, 1934; Magruder, 1935b; Morrison, 1954; Jones and Branson, 1964; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004, 2005; Strong, 2005). The ovipositor pore in *Juga* forms a broad, shallow triangular shelf with a highly grooved epithelium. This is very different from the deep pore that expands medially into the foot of *Pleurocera* and *Elimia*, with parallel folds that direct the movement of ova through the pore (Strong, 2005). Indeed, this feature was cited by Taylor (1966) as justifying the independence of *Juga*. Unlike *Juga*, the distal ovipositor groove extends to the foot sole in some but not all of eastern North American pleurocerids (e.g. Van Cleave, 1932; Morrison, 1954; Strong, 2005); ovipositor morphology of Asian pleurocer-

ids is unknown. In melanopsids, the pore is deep, glandular and complex and the distal groove does not intersect the foot sole (Bilgin, 1973; Glaubrecht, 1996) (Table 2).

Similar to other pleurocerids, the gut of *Juga* species is characterized by the presence of tubular salivary glands that pass through the nerve ring, the absence of a mid-esophageal gland, and a style sac in restricted communication with the proximal intestine (Magruder, 1935a, b; Itagaki, 1960; Dazo, 1965; Strong, 2005). Rachidian basal denticles are present in at least some Asian pleurocerids (Ko et al., 2001) and are apparently lacking in many eastern North American pleurocerids (e.g. Minton et al., 2004; Sides, 2005). However, they are easily overlooked in whole mounts and their absence from existing descriptions may be an error; for example, basal denticles are present in *Elimia livescens* (Glaubrecht, unpublished

Table 2. Summary of anatomical differences between *Juga* and other limnic gastropods classified in the Pleuroceridae and Melanopsidae. Details from Sunderbrink, 1929; Soós, 1936; Starmühlner and Edlauer, 1957; Itagaki, 1960; Starmühlner, 1970; Bilgin, 1973; Houbriek, 1988; Nakano and Nishiwaki, 1989; Glaubrecht, 1996; Strong and Glaubrecht, unpubl. data. NA = not applicable.

	<i>Juga</i>	<i>Elimia livescens</i> <i>Pleurocera acuta</i>	<i>Semisulcospira</i>	Melanopsidae
External Anatomy:				
Ovipositor pore	Shallow, simple, weakly glandular	Deep, simple, weakly glandular	NA	Complex, highly glandular
Alimentary System:				
Salivary glands	Tubular	Tubular	Tubular	Tubular/branched
Salivary gland position	Pass through nerve ring	Pass through nerve ring	Pass through nerve ring	Pass through/anterior to nerve ring
Esophageal gland	Absent	Absent	Absent?	Present
Digestive gland ducts	1	2	2	1
Caecum	Shallow/Deep	Shallow	Shallow	Deep and spiral
Reno-Pericardial System:				
Bladder	Small, pallial	Small, pallial	?	Small, pallial
Evagination of bladder wall	Present	Absent	?	?
Nervous System:				
Dialyneury, Zygoneury	Zygoneury	Zygoneury	Dialyneury?	Zygoneury
Accessory ganglion between left pleural and sub-esophageal ganglia	Present	Present	Absent?	Present?
Reproductive System:				
Ovipositor distal groove intersects foot sole	Present	Present/Absent	NA	Absent
Seminal vesicle	Straight	Straight	Straight	Folded
Proximal albumen gland	U-shaped	Straight	?	?
Gonoductal groove	Convoluted	Simple	Simple?	Simple?
Seminal receptacle	Present	Absent	Present	Present
Reproductive strategy	Oviparous	Oviparous	Viviparous	Oviparous

data), but have not been described in the literature (e.g. Baker, 1928; Dazo, 1965). The phylogenetic significance of these features is unclear as they occur sporadically among many cerithioidean groups, including batillariids, planaxids, melanopsids, thiarids (see e.g. Thiele, 1928; Houbriek, 1987; Glaubrecht, 1996). Melanopsids differ in possessing an esophageal gland, and the salivary glands may be tubular or branched and variably pass through or by-pass the nerve ring; the radula is variable and may present a rachidian that is similar to that of pleurocerids, or may be quadrangular, robust with conical denticles and with a marked glabella (Sunderbrink, 1929; Thiele, 1928; Bilgin, 1973; Glaubrecht, 1996).

The midgut of *Juga* species diverges from eastern North American pleurocerids and other putatively closely related limnic lineages most noticeably in size and shape of the glandular pad and configuration of the crescentic ridge. In *Juga*, the glandular pad is rather narrow with a crescentic ridge that is often separated from it by a wide, shallow groove; the proximal end of the crescentic ridge borders a vestibule that receives several ducts of the digestive gland. Typically, melanopsids, paludomids, and thiarids have a broadly rounded glandular pad and a deep, narrow crescentic groove such that the crescentic ridge closely adheres to the outer edges of the pad. Al-

though the midgut has demonstrated great utility in reconstructing relationships among cerithioidean lineages (Strong, unpublished data), midgut characters of *Juga* do not provide unambiguous evidence of affinity to any one freshwater family; the small, narrow glandular pad is rather similar to that of *Semisulcospira*, but the configuration of the crescentic ridge, particularly in *J. silicula* and *J. newberryi*, is unique among cerithioideans known thus far. The presence of a single digestive gland duct vestibule is shared between *Juga* and melanopsids, but is also found in a number of cerithioideans; other pleurocerids and paludomids have two digestive gland ducts (Strong and Glaubrecht, 2002, 2003, 2007, unpublished data; Strong, 2005).

As in paludomids (e.g. Strong and Glaubrecht, 2002, 2003) and melanopsids (Bilgin, 1973), the kidney of pleurocerids penetrates the pallial cavity (Magruder, 1935b; Itagaki, 1960; Strong, 2005), but the pallial portion of the bladder is smaller than that in the former taxa. The branching pattern of excretory tubules within the bladder is essentially identical between *Juga* and eastern North American pleurocerids, but *Juga* is unique in the outpocketing of the wall separating the main chamber and the bladder (Strong, 2005). Kidney anatomy is currently unknown for Asian pleurocerids and melanopsids.

Although published accounts of pleurocerid nervous systems disagree on the number of nerves produced by various ganglia (Magruder, 1935b; Itagaki, 1960; Dazo, 1965; Strong, 2005; present study), this is often variable within species. However, the present account agrees with that of Strong (2005) that the cerebral ganglia produce seven nerves, and that there are two prominent anterior pedal nerves with a variable number of small accessory nerves (typically four to seven). The thickened connective between the left pleural and sub-esophageal ganglia, representing a small accessory ganglion, was found to give off only a single large nerve in the present study, but was found by Strong (2005) to produce one to three nerves in *Elimia* and *Pleurocera*. Strong (2005) also found the sub-esophageal ganglion to give off one to three nerves, whereas three to four nerves were found in the present study.

The most intriguing aspect of the nervous system is the presence of the accessory ganglion. It is known only from eastern North American pleurocerids (Magruder, 1935b; Strong, 2005) and now *Juga* (present study), and has not been depicted in most accounts of melanopsid (Bouvier, 1887; Soós, 1936; Starmühlner and Edlauer, 1957; Starmühlner, 1970; Bilgin, 1973; Glaubrecht, 1996) and Asian pleurocerid (Itagaki, 1960) nervous system anatomy. However, the illustration of the nerve ring of *Melanopsis frustulum* Morelet, 1856-57 (Starmühlner, 1970) and that of *M. doriae* Issel, 1866 (Starmühlner and Edlauer, 1957) clearly show a thickened connective between the left pleural and sub-esophageal ganglia, indicating that it is most likely present in melanopsids as well. Paludomids and thiarids have a much more concentrated nerve ring with the left pleural and sub-esophageal ganglia fused or in close contact (e.g. Seshaiya, 1934; Glaubrecht, 1996; Strong and Glaubrecht, 2002, 2003).

Pleurocerids and melanopsids share the same basic layout of the pallial oviduct to the exclusion of paludomids and thiarids, including the presence of a long opening to the mantle cavity, and a deep sperm gutter opening anteriorly to a spermatophore bursa and posteriorly to a seminal receptacle; as mentioned above, eastern North American pleurocerids are unique in lacking the seminal receptacle (Bilgin, 1973; Nakano and Nishiwaki, 1989; Prozorova, 1990; Glaubrecht, 1996; Raschepkina, 2000; Prozorova and Raschepkina, 2001, 2004, 2005; Strong, 2005). Whereas in *Juga* and *Semisulcospira* the sperm gutter becomes obsolete or continues posteriorly as a shallow groove within the medial lamina (Prozorova and Raschepkina, 2004, 2005; herein), in melanopsids the sperm gutter is continuous along the ventral edge of the medial lamina and contains the opening to the receptacle at the posterior end of the oviduct (Bilgin, 1973; Glaubrecht, 1996). In *Elimia* and *Pleurocera*, a deep sperm gutter is present above the opening to the mantle cavity along its entire length, and closes posteriorly to form a short, blind spermatophore bursa.

One aspect of cerithioidean reproductive anatomy that

is routinely overlooked is the configuration of the capsule and albumen glands. Strong and Glaubrecht (2002, 2003) have found that the shape of the albumen gland in paludomids is quite distinctive, and likely a synapomorphy of the family. In *Juga*, the glands and intervening gonoductal groove of the pallial oviduct are highly convoluted with a proximal albumen gland that is pouch-like or u-shaped (present study), while eastern North American pleurocerids possess glands that form two narrow bands with smooth opposing surfaces and an essentially linear proximal albumen gland (Strong, 2005). However, such potentially informative characters are undescribed for other pleurocerids and melanopsids.

Male reproductive anatomy of *Juga* is apparently quite distinct as no other male pleurocerid (indeed, no other cerithioidean) has been described with a tightly interlocking arrangement of glands (e.g. Woodard, 1934; Itagaki, 1960; Prozorova, 1990); however, a large fold within the lateral lamina may be present (Nakano and Nishiwaki, 1989; Strong, 2005). Among eastern North American pleurocerids, both the highly folded proximal portion (Woodard, 1934) and distal region of the prostate Strong (2005) have been inferred as the site of spermatophore formation. In *Juga*, there is no differentiated anterior or posterior region, but intuitively the tightly interlocking folds of the lateral and medial laminae must function in molding the spermatophore.

CONCLUSIONS

While sharing many similarities, numerous features clearly set *Juga* apart from eastern North American pleurocerids: ovipositor pore, lateral outer cusps, midgut glandular pad and crescentic ridge, digestive gland duct vestibule, evagination of kidney wall, convoluted gonoductal groove, proximal albumen gland, seminal receptacle, interlocking prostate glands. However, as is often the case for ancient lineages, it is difficult to identify uniquely shared features that more or less unambiguously demonstrate affinity to any one limnic lineage. *Juga* is particularly difficult as many of these features not only set the genus apart from other pleurocerids, but are undocumented (ovipositor pore, kidney, pallial oviduct glands) or apparently autapomorphic among cerithioideans (crescentic ridge, evagination of the kidney wall, prostate). Nevertheless, this analysis has revealed some characters that are shared with Asian pleurocerids (midgut glandular pad, seminal receptacle), but some that are also shared with melanopsids (digestive gland duct). However, the presence of the seminal receptacle is undoubtedly plesiomorphic and uninformative in delineating relationships. Others are so heterogeneously distributed among limnic lineages, it is difficult to determine if there may be an underlying phylogenetic signal (ovipositor ventral groove, rachidian basal tentacles). Unlike molecular data, given the available morphological evidence, there is no overwhelming signal linking *Juga* to Asian pleurocerids, nor for that matter linking eastern North

American pleurocerids to melanopsids (Table 2). While part of this pattern may be due to the high rate of autapomorphies, it may simply be an artifact of missing data. Clearly, one of the more significant impediments in assessing pleurocerid affinities is that comprehensive anatomical accounts of pleurocerids and melanopsids are rare, leaving many potentially informative characters unknown. Thus, it is clear that further anatomical studies within the context of ongoing morphological and molecular cladistic analyses are necessary to unambiguously resolve the question of pleurocerid monophyly and their affinities to melanopsids.

These results also have implications for the systematics of *Juga*, particularly with regards to the validity of current subgeneric subdivisions. Although all three taxa possess unique features that clearly distinguish them from one another, *J. silicula* and *J. neuberryi* are strikingly anatomically similar and share many features to the exclusion of *J. acutifilosa*: 1) shallow, weakly ridged ovipositor pore, 2) similar rachidian basal margin, 3) similar development of weak, outermost denticle of the lateral teeth, 4) thick, tubular salivary glands, 5) shallow, broad crescentic groove, 6) shallow caecum, 7) large proximal intestine protuberance on base of style sac, 8) u-shaped proximal albumen gland, and, 9) tightly interlocking prostate glands (Table 1). In conclusion, the anatomical data do not support separation of *Juga* sensu stricto and *Oreobasis* and *Oreobasis* is thus here synonymized with *Juga* sensu stricto; *Calibasis* is sufficiently distinct to merit retention as a valid taxon. The question of the rank of these taxa is, of course, highly subjective. But given what is known about anatomical differentiation among other pleurocerid genera, it could reasonably be argued that *Juga* sensu stricto and *Calibasis* be recognized at the rank of genus.

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