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REDESCRIPTION OF *PALUDINA INTEGRA* SAY, 1821, TYPE SPECIES OF GENUS *CINCINNATIA* (GASTROPODA: HYDROBIIDAE)

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ABSTRACT

We present evidence that *Paludina integra* Say, 1821, an early described species of North American freshwater snail which has been previously placed in either of two families (Hydrobiidae, Viviparidae), is the hydrobud snail known as *Cincinnatia cincinnatiensis* (Anthony, 1840). We provide a description for this snail, which is the type species of the genus *Cincinnatia* Pilsbry, 1891, and select a neotype to ensure nomenclatural stability. Features of genitalia (including a second female bursal duct which has not been recorded previously for members of the family Hydrobiidae) distinguish this species from all other members of the North American subfamily Nymphophilinae. At the present time, insufficient data are available to support allocation of other species to *Cincinnatia*. *Paludina cincinnatiensis* Anthony, 1840, *Amnicola scarboroughi* Tryon, 1870, *Amnicola peracuta* Pilsbry & Walker *in* Pilsbry, 1889, *Amnicola judayi* Baker, 1922, and *Cincinnatia cincinnatiensis chicagoensis* Baker, 1930 are junior synonyms of *Cincinnatia integra* (Say, 1821)

INTRODUCTION

One of the long unresolved problems in North American freshwater malacology involves the identity of one of the earliest described taxa, *Paludina integra* Say, 1821. Say compared this species to *Campeloma decisa* (Say, 1817a), but recorded the shell length as 1/4 inch (6.35 mm), which is much smaller than any (adult) North American member of the Viviparidae. The majority of students treating this species (beginning with Haldeman, 1840:11–12) have assumed that this measurement is incorrect or pertained to an immature specimen, and placed *integra* in the viviparid genus *Campeloma*. Others (e.g., Berry, 1943.35–36; Thompson, 1968:116), however, accepted the small size of the snail and asserted that Say described the hydrobiid known as *Cincinnatia cincinnatiensis* (Anthony, 1840). In several recent works (e g , LaRocque, 1968; Burch & Tottenham, 1980) *integra* was referred to both families, highlighting the confusion as to generic allocation of this snail.

Say did not figure this species and his original material is lost. Topotypes cannot be collected as the type locality was only vaguely described. Nevertheless, we believe that evidence supporting allocation of *integra* to the Hydrobiidae is very strong We argue that Say's comparison between the hydrobiid *integra* and *Campeloma decisa* was understandable given the similarity in shell shape between these species, and the state of knowledge of the North American freshwater snail fauna in the early 19th century. To ensure nomenclatural stability, we select a neotype for *integra*. We also provide the first thorough morphological description of this widespread species, and discuss its implications for systematics of *Cincinnatia*.

MATERIALS AND METHODS

Institutional repositories of examined material are indicated by the following acronyms. ANSP: Academy of Natural Sciences, Philadelphia, CM: Carnegie Museum, Pittsburgh; FMNH: Field Museum of Natural History, Chicago, MCZ Museum of Comparative Zoology, Harvard University, Cambridge; UF Florida Museum of Natural History, University of Florida, Gainesville; UIMNH University of Illinois at Urbana-Champaign Museum of Natural History; UMMZ: University of Michigan Museum of Zoology, Ann Arbor; USNM former United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D C.

Anatomical study was of ethanol-preserved snails that had been relaxed with menthol crystals and fixed in dilute formalin. Methods of dissection were of Hershler (1994). Anatomical study was principally

Table 1. Freshwater prosobranch snails recognized from North America as of January, 1821 and listed as in Say's publications. Current allocations of these species are given in parentheses.

[Family] VIVIPARIDAE
Lymnaea vivipara (Linnaeus, 1758) (misidentified; *Viviparus georgianus* [Lea, 1834])
Paludina ponderosa Say, 1821 (= *Campeloma crassula* Rafinesque, 1819)
Lymnaea subcarinata Say, 1817a (*Lioplax*)
Lymnaea decisa Say, 1817a (*Campeloma*)

PLEUROCERIDAE
Lymnaea virginica Say, 1817a (*Elimia*)
Melania canaliculata Say, 1821 (= *Pleurocera canaliculata canaliculata*)
Melania elevata Say, 1821 (= *Pleurocera canaliculata canaliculata*)
Melania conica Say, 1821 (= *Pleurocera canaliculata canaliculata*)
Melania praerosa Say, 1821 (*Leptoxis*)
Melania armigera Say, 1821 (*Lithasia*)
Palundina [sic] *dissimilis* Say, 1819 (= *Leptoxis carinata carinata*) [Bruguiere, 1789])

HYDROBIIDAE
Paludina integra Say, 1821 (*Cincinnatia*)
Paludina limosa Say, 1817c (= *Amnicola limosa limosa*)
Paludina porata Say, 1821 (= *Amnicola limosa porata*)
Paludina lustrica Say, 1821 (*nomen dubium*; condition of embryonic whorls must be assessed to resolve generic allocation, yet type specimen is lost. Name suppressed per ICZN, Opinion 1108, 1978.)

POMATIOPSIDAE
Cyclostoma lapidaria Say, 1817b (*Pomatiopsis*)

VALVATIDAE
Cyclostoma tricarinata Say, 1817b (= *Valvata tricarinata tricarinata*)

of a single sample (UF 77151, seepage spring, Van Buren, Carter County, Missouri 5 males and 5 females dissected), although specimens from the neotype locality (UF 35319) and all other available alcohol-preserved material (indicated with asterisks in 'Material Examined' section) were consulted for confirmation of important details.

IDENTITY OF *PALUDINA INTEGRA* SAY, 1821

Say (1821) described *integra* as follows: 'Shell olivaceous, pale, conic; whirls [sic] six, wrinkled across; spire rather elongated, entire at the apex; suture profoundly indented; aperture sub-ovate, less than half of the length of the shell.' He gave the length as 1/4 inch (6.35 mm) and compared the species to *P. decisa*, although he noted that the spire (of *integra*) is more elongated and never truncate at the apex, but always acute. This description clearly fits the hydrobiid known as *Cincinnatia cincinnatiensis*, which resembles '. . . an uncorroded *Campeloma decisum*, but in miniature' (Clarke, 1981:56). There is little that distinguishes the shells of the two species aside from size, sculpture of the protoconch, whorl convexity, and fact that the hydrobiid has a complete apex. Also note that this widespread hydrobiid occurs in the Missouri River basin, from which Say collected *integra* (see below).

When Say published his description in January, 1821, only 17 species of freshwater prosobranch snails were recognized from North America (Table 1). Only three North American hydrobiids had been described at this time, none of which resembles *integra*. Shells of *Amnicola* differ from those of *integra* in their small size, turbinate shape, thin and translucent parietal wall, wide umbilicus and blunt apex. Thus it was logical for Say to have compared *integra* instead with *Campeloma decisa*, which it more closely resembles in shell features.

TAXONOMY

Cincinnatia Pilsbry, 1891

Cincinnatia Pilsbry, 1891:327 [footnote]. [Type species, *Paludina cincinnatiensis* Anthony, 1840 (= *Paludina integra* Say, 1821); original designation]

Diagnosis. Medium-large sized North American freshwater hydrobiids having sub-globose to ovate-conic shells with protruding apex, rounded whorls, impressed sutures and wide umbilicus. Distinguished from other taxa currently assigned to the subfamily Nymphophilinae Taylor, 1966 by the large number of superior tubercles on the dorsal surface of the penis and presence of a second (posterior) duct issuing from the female bursa copulatrix. The massive, cylindrical bursa copulatrix having very short (anterior) duct also may be unique to this genus within the subfamily.

Remarks. Pilsbry (1891) proposed this genus (as a 'sectional term' under *Amnicola*) based on the minute radula and fine denticulation of radular teeth of the type species. Early workers followed Pilsbry's diagnosis and allocated additional species (some now placed in *Probythinella* Thiele, 1928) to *Cincinnatia* based on their similarly small radula and large shells with rounded whorls. Baker (1928) later separated *Cincinnatia* from *Amnicola* based on the radular features given above. Thompson (1968) recognized the significance of the glandular fields on the penis of these animals and later (Thompson, 1979) placed the genus in the subfamily Nymphophilinae. Other details of nomenclatural history of the genus can be found in Thompson (1968) and Kabat & Hershler (1993).

Given that the penial morphology of *C. integra* closely resembles a number of other North American nymphophilines, whereas the distal female genitalia of this species is strikingly different from all other members of the subfamily thus far studied, it is clear that the existing generic classification of this group, largely based on patterns of penial ornamentation (e.g., Thompson, 1968), must be re-examined with fuller anatomical data in hand. We defer assessment of the relationship between this unusual snail and other nymphophilines until such data are obtained.

Cincinnatia integra (Say, 1821)

Paludina integra Say, 1821:174. [neotype selected herein, USNM 860651, 4.8 mm, 5.0 whorls; type locality, Meramec River, 2.9 km NNW of Steelville, Crawford County, Missouri.]

Paludina cincinnatiensis Anthony, 1840:279, pl. III, fig. 3. [4 syntypes, MCZ 142813, shell most closely resembling Anthony's figure selected as lectotype, MCZ 315776, 5.1 mm, 5.0 whorls; type locality, canal near Cincinnati].-Lea, 1844:16.-Küster, 1852:52, pl. 10, figs. 13, 14.

Amnicola cincinnatiensis.-Haldeman, 1845:9, pl. 1, fig. 4.-Frauenfeld, 1863:1030.-Binney, 1865:85-86, fig. 168.-Tryon, 1870:54.-Call, 1885:117–118.-Dall, 1885:257.-Keyes, 1888:73.-Walker, 1893:139.-Shimek, 1904:379 (Nebraska record).-Dall, 1905:118, fig. 87 (Alaskan record?).-Sterki, 1907:387 (Ohio records).-Sampson, 1913:72 (Missouri records).-Over, 1915.93 -Winslow, 1921:15 (North Dakota record).-Henderson, 1927.20 (South Dakota record).-Tuthill, 1962:16.

Amnicola integra.-Troschel, 1857:107–108, pl. VIII, fig. 4.-Leonard, 1959:33–35, fig. 20; pl. 1, fig. 1 (Kansas records).-Murray & Roy, 1968.32 (Texas records).-Harman & Berg, 1971.47–48, figs. 173, 174, 180 (New York records).

Amnicola scarboroughi Tryon, 1870:54 [type not found; type locality, Walnut Creek, Kansas, and Rocky Mountains; not further restricted subsequently.]

Amnicola peracuta Pilsbry & Walker *in* Pilsbry, 1889:88, pl. III, fig. 20. [4 syntypes, ANSP 58292, shell most closely resembling figured specimen of Pilsbry & Walker selected as lectotype, 4.6 mm, 5.0 whorls; type locality, Spivey's Lake, Navarro Co., Texas.]-Singley, 1893:312 (in part).-Walker, 1918:136.-Clench, 1925:12.-Strecker, 1935:39.-Murray & Roy, 1968.32.

Amnicola (Cincinnatia) cincinnatiensis.-Baker, 1906:93–94 (Illinois records).-Baker, 1922:61.

Cincinnatia cincinnatiensis.-Walker, 1918:136.-Baker, 1928:122–124, fig. 53; pl. VI, figs 40, 41; pl. VII, figs 15–17.-Clarke, 1973:241–244, pl. 21, fig. 4; map 46.-Taylor, 1975:57.-Fullington, 1978:36, fig. 3g,h-Clarke, 1981:56, fig. 10, unlabelled distribution map (Canada) -Cvancara, 1983:62, fig. 42 (North Dakota distribution).-Burch & Jung, 1988:246, fig. 18.-Jokinen, 1992:26–27 (New York records).

Amnicola judayi Baker, 1922:19 [2 syntypes, UIMNH Z12651, specimen labelled male selected as lectotype, 5.0 mm, 5.5 whorls, type locality, off Doemel Point, Lake Winnebago [Wisconsin], on a sandy bottom, in nine feet of water.]-Clarke, 1973:241 (as synonym of *cincinnatiensis*).

Cincinnatia cincinnatiensis judayi.-Baker, 1928. 124–126, pl. VI, figs. 42, 43.

Cincinnatia cincinnatiensis chicagoensis Baker, 1930:189, figs. 2, 12–15 [holotype, UIMNH Z28329, 5.4 mm, 4.5 whorls; type locality,

shore of Lake Michigan at the foot of Division Street, Chicago, Illinois].

Amnicola (Cincinnatia) integra.-Berry, 1943: 32–36, map 4, fig. 4 (penis), pl. I, fig. 7 (shell); pl. III, fig. 4 (radula); pl. VI, fig. 1 (whole animal, cleared).-Robertson & Blakeslee, 1948:85 (New York records), plate x, fig. 15.-LaRocque, 1953:269.-Tuthill, 1962:16.-LaRocque, 1968:394, pl. 10, fig. 7; fig. 247 (distributional maps).

Amnicola integer [sic] -Goodrich & Schalie, 1944:300 (Indiana records).-Dawley, 1947: 693 (Minnesota records).

Cincinnatia integra -Branson, 1961:42, pl. IV, fig. 29 (Oklahoma records).-Taylor, 1975: 103.-Thompson, 1977:fig. 4B (SEM of protoconch).-Thompson & McCaleb, 1978:357.-Turgeon et al., 1988:60.

Cincinnatia peracuta.-Taylor, 1975:149 -Burch & Tottenham, 1980.110 (fig. 225).

Cincinnatia scarboroughi.-Taylor, 1975:171.

Neotype: Say gave the type locality for *integra* as '. . . waters of the Missouri'. He probably (*fide* Say, 1821:149) collected this material while he participated (as zoologist) in the 1819–1820 Long Expedition to the Rocky Mountains. Original narratives of this exploration (James, 1823; Bell, 1973) do not mention this or other recent species of freshwater mollusks collected by Say and hence provide no further information regarding type locality Say's field party explored much of the lower Missouri River basin between 22 June 1819–October 1820 (see Barber, 1928:16, for map of this journey). During August 1820, the field party divided into two groups. The group led by Major Bell, and including Say, proceeded down the Arkansas River. Three army deserters robbed this group of various possessions, including Say's journals from 1819–August 1820 (Say's biotic collections were not stolen). It is thus likely that Say himself could not further restrict the type locality (beyond 'waters of the Missouri'), which could have been any such site visited during about a year of fieldwork. Specific localities along the Missouri are mentioned in the journal of Say's field party, including Council Bluffs, Iowa, where the group camped for a long time period (October 1819–June 1820).

The Secretary of War (James Calhoun) declared that specimens collected by the Long Expedition were United States property and ordered that these be deposited in the Philadelphia Museum (Weiss & Zeigler, 1931:85), which refers to the Titian Peale Museum (not the Academy of Natural Sciences of Philadelphia). Say (1821:149) stated that his specimen(s) of *integra* was deposited in that institution. The Philadelphia Museum was a private institution which entered bankruptcy in 1848. Collections of this institution were offered at a sheriff's auction and were purchased in a joint venture by M. Kimball and P. T. Barnum, both of whom were engaged in theatrical management. The sheriff's catalogue listed among the numerous geological, ethnological, historical and natural history items, 13 cases of shells (Sellers, 1980:314). The collection was divided between Kimball and Barnum and it is not known what happened to the cases of shells. Some of the less spectacular natural history specimens were donated by Kimball to the Lyceum of Natural History (in New York) and the Boston Museum of Natural History. The Lyceum of Natural History and its collections were destroyed by fire in 1851. The Boston Museum collection was transferred to the Boston Society of Natural History in 1893, and soon thereafter remnants of this were transferred to the Museum of Comparative Zoology (Faxon, 1915). Say's material for *integra* has not been located at this institution (T. Kausch, personal communication, October, 1994). Another possibility is that the types were deposited at the ANSP, which retains other Say shell collections (Weiss & Zeigler, 1931:211). Binney (1865:48, fig. 96) figured a *Campeloma* from the ANSP collection which he claimed was Say's type. We have not located this specimen, but we see no reason for accepting this figure as a type, given the complete absence of supporting documentation and arguments offered above for placement in Hydrobiidae. Ironically, Pilsbry (*in litt.*, Berry, 1943:35–36) also claimed to have seen the type at the ANSP, and indicated that it was the same species as *Paludina cincinnatiensis*. Baker (1964:167) was unable to find this material during his review of nonmarine mollusk types at the ANSP, and we have also searched and failed.

Given that type material for *integra* is lost (or destroyed) and that a complex taxonomic problem exists concerning this species, we believe it appropriate to select a neotype for the purpose of establishing stability of nomenclature (per ICZN Article 75(b)). As explained above, the type locality cannot be pinpointed beyond Say's original, vague description. This species is widespread throughout the Missouri River basin and we thus have selected the neotype from a lot collected from the

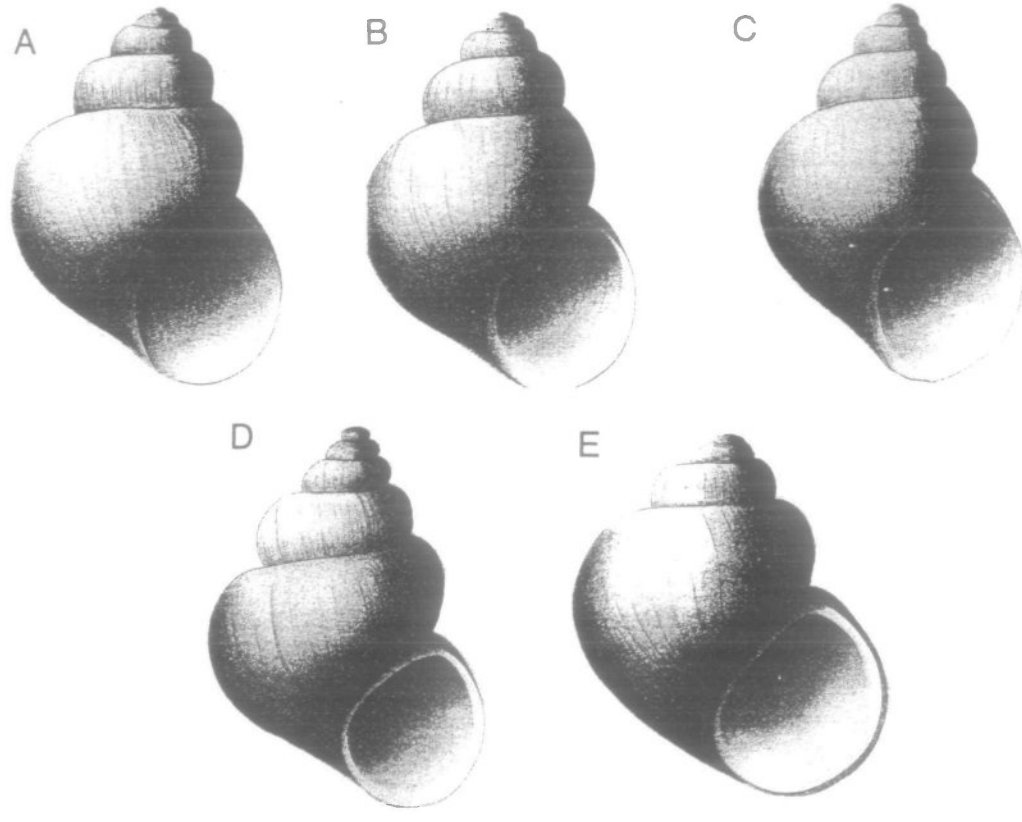
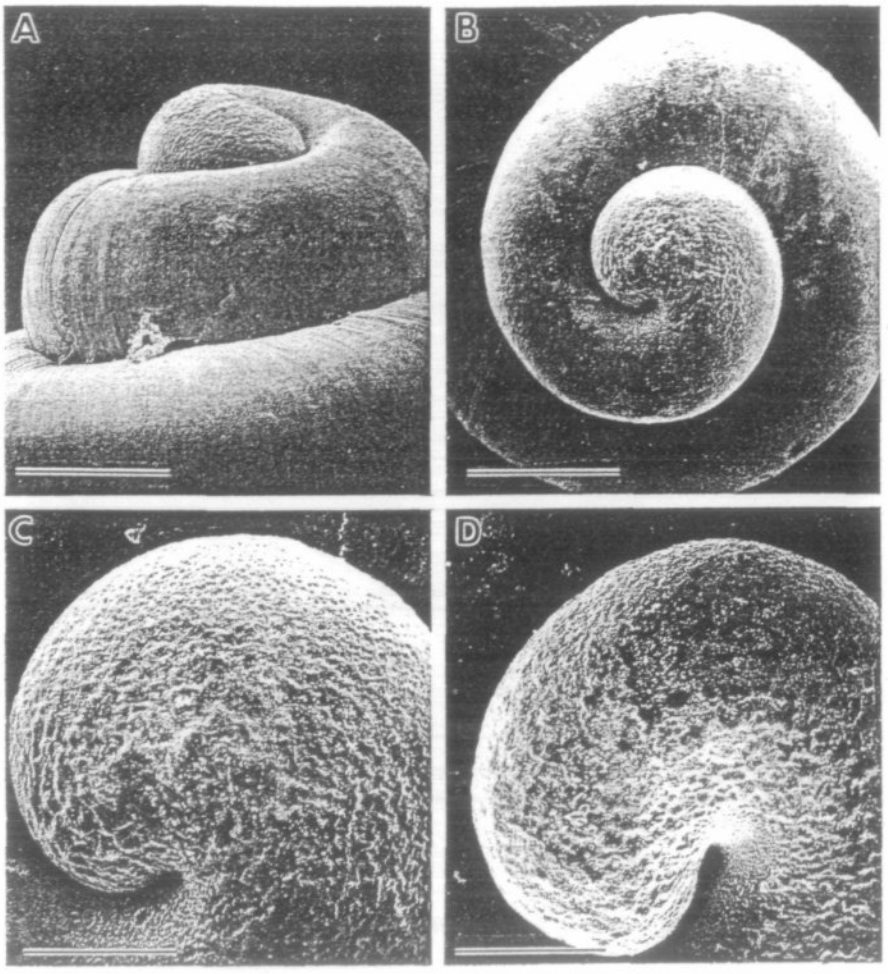


Figure 1. Type specimens of *Cincinnatia integra* and junior synoyms. **A.** *Paludina integra* Say, 1821 (neotype, USNM 860651); shell 4.8 mm tall. **B.** *Paludina cincinnatiensis* Anthony, 1840 (lectotype, MCZ 142813); 5.1 mm. **C.** *Amnicola peracuta* Pilsbry & Walker *in* Pilsbry, 1889 (lectotype, ANSP 58292); 4 6 mm. **D** *Amnicola judayi* Baker, 1922 (lectotype, UIMNH Z12651a), 5.0 mm. **E.** *Amnicola cincinnatiensis chicagoensis* Baker, 1930 (holotype, UIMNH Z28329); 5.4 mm.

Meramec River, a tributary to the Missouri, by F. G. Thompson, 2 June 1969. Other specimens from this lot are deposited in the Florida Museum of Natural History (UF 35319, [8 specimens in alcohol], UF 77067 [51 dry shells]).

Description: Shell (Fig. 1) sub-globose to ovate-conic; height typically about 5.5 mm, ranging from 3.9–7.7 mm; width/height usually about 0.72–0.73. Whorls 4.25–6.0, strongly inflated, with pronounced shoulder, often flattened around periphery; suture deeply impressed. Umbilicus widely perforate (compared to other congeners), only partially obscured by columellar lip. Shell apex (Fig. 2A) acute, slightly convex. Protoconch (Fig. 2B-D) 1.1–1.3 whorls, dome-like, slightly tilted, with strongly impressed suture; diameter about 415 μm. Early (first 0.75 whorl) protoconch surface strongly wrinkled in reticulate-irregular fashion, later portion with much weaker relief; sculpture sometimes crossed by weak spiral striae. Teleoconch sculptured with distinct, irregularly spaced collabral striations extending from suture to base of whorl; and sometimes with very fine, irregularly spaced, incised spiral striations. Aperture weakly prosocline; broadly ovate to broadly ellipsoidal. Columellar base of aperture sometimes protracted, especially in immature specimens with an incomplete peristome. Peristome complete across parietal wall at maturity, usually broadly adnate. Outer lip straight or weakly sinuate adapically. Outer and columellar lip often thin, sometimes internally thickened in larger, mature specimens. Shell clear-white, transparent. Periostracum tan.

Operculum (Fig. 2E,F) ovate, paucispiral,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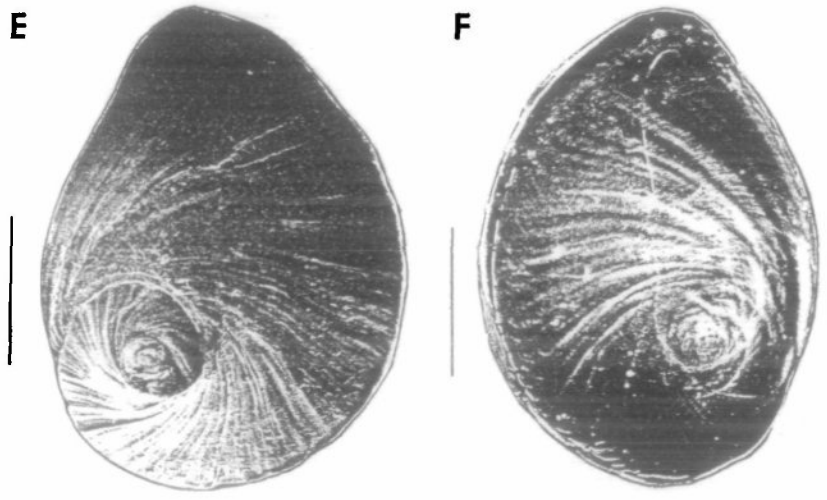
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Figure 2. Shells and opercula of *Cincinnatia integra*. **A.** Shell apex (USNM 507274); scale bar = 150 μm. **B** Protoconch (ibid.); scale bar = 150 μm. **C, D.** Detail of protoconch microsculpture (ibid.); scale bar = 60 μm. **E.** Operculum, outer surface (UF 77151), scale bar = 0.75 mm. **F.** Operculum, inner surface (ibid.), scale bar = 0.75 mm.

slightly concave, medium thickness, light amber, transparent, with eccentric nucleus. External surface smooth or slightly frilled, with weak spiral scratches near outer edge. Attachment scar margins without obvious thickening. Attachment area slightly thickened in nuclear region.

Snout, head pale-brown, sometimes with dark sub-epithelial pigment. Tentacles with brown-black longitudinal stripes on dorsal and ventral surfaces (otherwise pale). Sides of head pale-light grey, sometimes with dark sub-epithelial pigment. Dorsal surface of foot pale or light grey, sometimes black along edges. Pallial roof usually with black streaks fringing sides of ctenidium and gonoduct; streaks sometimes coalescing to form uniform pigment cover. Visceral coil brown-black dorsally. Penis usually entirely pale, rarely having black epithelial pigment on filament.

Tentacles (Fig. 3A-D) with well-developed longitudinal ciliary tracts on dorsal and ventral surfaces, and along forward edges. Left tentacle (Fig 3A,C) also with scattered tufts of cilia arranged in a weakly transverse manner. Distal snout moderately lobate, with broad band of cilia all around; groove surrounding lips unciliated. Eyes present. Foot ovate, anterior end weakly indented, lateral wings well developed, posterior end rounded. Anterior pedal mucus gland of numerous small-sized units.

Ctenidium well-developed, occupying nearly entire length of pallial cavity, extending to near pallial edge. Ctenidium slightly overlapping pericardium posteriorly; efferent vein short. Filaments about 28, broadly triangular (about as tall as wide), weakly plicate, free edge weakly convex. Osphradium between posterior end and middle of ctenidium, narrow, rather elongate (ca. 40% of length of ctenidium), anterior end simple. Hypobranchial gland covering pallial roof and rectum, thin, but somewhat thicker on posterior portion of pallial roof. Renal organ with 1/4 to 1/3 of length in pallial roof. Renal aperture with white lips. Renal gland well developed, longitudinal, on left side of renal organ and abutting pericardium. Pericardium slightly in pallial roof. Body spaces with little connective tissue.

Circum-oesophageal ganglia pigmented. Cerebral commissure more than 1/2 width of ganglion; pedal commissure ca. 1/5 to 1/3 width of ganglion; pleural-supraoesophageal commissure as long or longer than combined lengths of ganglia; left pleural and sub-oesophageal ganglia abutting.

Jaws present. Buccal mass very small, positioned well anterior to nerve ring. Radular ribbon about 680 μm long, protruding behind buccal mass as very short coil, about five times as long as wide, with about 45 rows of teeth.

Central teeth (Fig. 4A,B) trapezoidal, width about 27 μm; dorsal edge concave; basal region with medium excavation; basal tongue broadly V-shaped, about as long as lateral angles. Basal cusps 1–2; innermost cusps larger, arising from lateral angles. Cutting edge with 4–5 lateral cusps; median cusp pointed-rounded, slightly longer than lateral cusps. Lateral teeth (Fig. 4C,F) clavate, without distinct flexure of outer margin; basal tongue short, often weakly rounded. Outer wing about 200–250% longer than cutting edge. Lateral cusps 5 (inner side) to 6–7 (outer side); median cusp pointed-rounded, slightly longer than lateral cusps. Cusps on inner marginal teeth slightly larger than those on outer teeth. Inner marginal teeth (Fig. 4D,F) with about 24–28 cusps extending along outer side for about 1/3 length of tooth at upper end; teeth with weak flange on inner side. Outer marginal teeth (Fig. 4E,F) with about 20 cusps extending along inner side for about 1/3 length of tooth at upper end; teeth with weak flange on outer side. Dorsal folds of oesophagus simple, medium length. Salivary glands elongate, nearly straight, entirely anterior to nerve ring. Stomach and style sac about equal in length; stomach chambers about equal in size. Stomach with single opening to digestive gland. Posterior caecum of stomach broadly triangular, large. Rectum straight within pallial cavity. Anus simple, slightly anterior to female genital aperture and near pallial edge.

Females oviparous. Egg capsules hemispherical, coated with sand grains. Ovary occupying 1.0 whorl (animal 3.5 whorls), overlapping posterior and part of anterior stomach chambers, filling most of length of visceral coil behind stomach. Ovary of vertical lobes, which become somewhat branched anteriorly. Oviduct leaving ovary from ventro-anterior

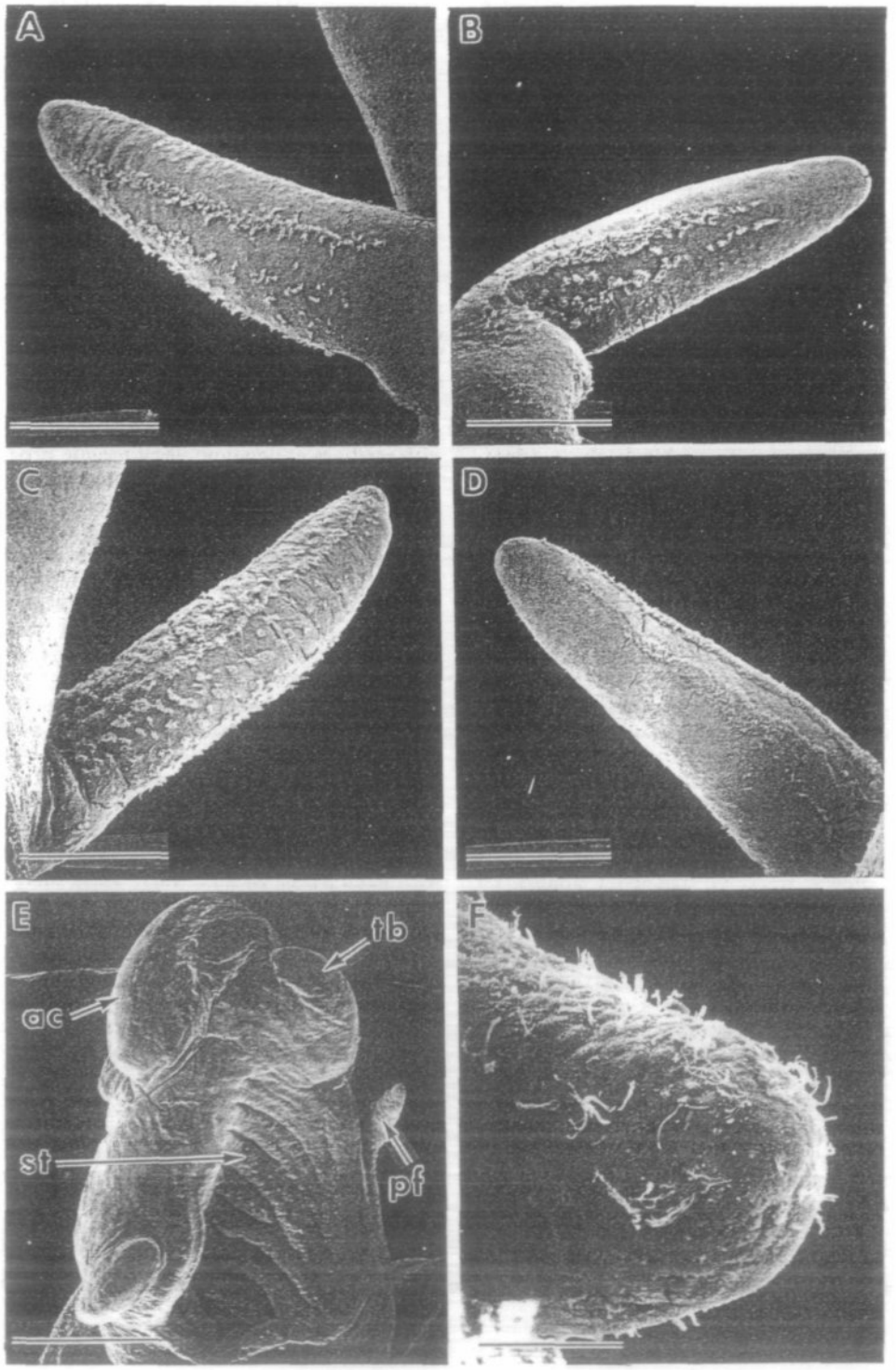
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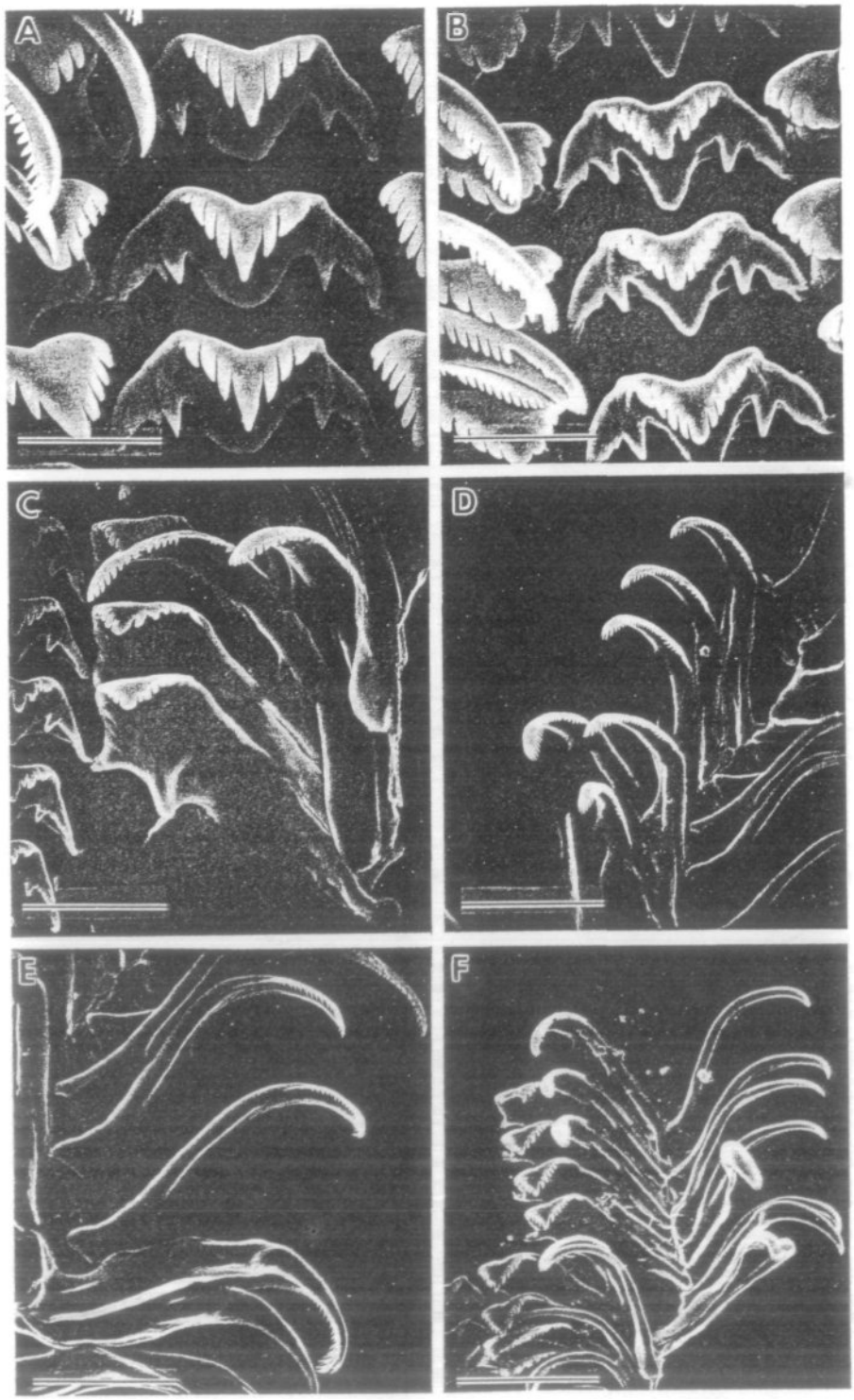
Figure 3. Critical point dried cephalic tentacles and penis of *Cincinnatia integra*. **A.** Left tentacle, dorsal surface (UF 235543); scale bar = 231 µm. **B.** Right tentacle, dorsal surface (ibid.); scale bar as above. **C.** Left tentacle, ventral surface (ibid.); scale bar as above. **D** Right tentacle, ventral surface (ibid.), scale bar = 200 µm. **E.** Penis, dorsal surface (UF 77151); scale bar = 0.5 mm. **F.** Tip of penial filament, showing sparse ciliation (ibid); scale bar = 13.6 µm Abbreviations: ac, accessory crest; pf, penial filament, st, superior tubercle, tb, terminal bulb.

edge. Coiled oviduct (Fig 5A; co) a single, narrow U-shape to circular coil, usually tightly bound in a sheath of connective tissue. Oviduct opening to albumen gland ventrally at junction between albumen and capsule glands. Anterior bursal duct (Fig. 5B; abd) joining oviduct at or slightly in front of posterior pallial wall. Seminal receptacle (Fig 5A, sr) pyriform, having thin muscular coat, opening to distal 'arm' of coiled oviduct; lumen containing oriented sperm abutting inner walls. Seminal receptacle duct extremely short. Seminal receptacle positioned on left side of middle of bursa copulatrix. Seminal receptacle much smaller than bursa copulatrix. Bursa copulatrix (bc) on left side of main part of albumen gland (ag), sometimes extending slightly posterior to gland; albumen gland wrapping around bursa copulatrix anteriorly (Fig. 5A,D). Bursa copulatrix almost as long as but narrower than albumen gland; near-cylindrical, slightly expanded posteriorly. Anterior bursal duct distinctly narrowed compared to bursa, very short, surrounded by albumen gland. Bursa also having a second, narrow, ciliated duct (pbd; lined with columnar epithelium similar to that of bursa) containing oriented sperm, which exits from the middle of the organ ventrally and loops on (or slightly embedded within) the left side of the albumen gland before joining the oviduct slightly behind the posterior pallial wall (Fig. 5B). Glandular gonoduct comprised of complexly folded cells (*sensu* Ponder, 1988:146). Albumen gland of simple shape, about as large as capsule gland, behind or very slightly within pallial cavity. Capsule gland (cg) of simple shape, with two distinct glandular zones (posterior, cream-coloured; anterior, clear); opening by a short, subterminal slit. Ventral channel (Fig. 5C, vc) with thin, non-glandular ventral wall; longitudinal fold well-developed on left side. Glandular gonoduct with pronounced rectal furrow. Genital aperture (Fig. 5A, go) with anterior expansion (ax).

Testis occupying 1.75 whorls (animal 3.0 whorls), broadly overlapping stomach, sometimes abutting posterior edge of prostate gland, filling most of length of visceral coil behind stomach. Testis of grape-like, compound lobes draining to a narrow vas efferens. Vas deferens exits from near anterior end of testis, and strongly undulates (as seminal vesicle) beneath testis and on posterior stomach Prostate gland (Fig. 6C; pr) having complex histology, bean-shaped, broadly oval in transverse section; about 1/4 of length in pallial roof. Rectal furrow of prostate gland pronounced. Pallial vas deferens (pvd) exiting from mid-distance between posterior pallial wall and anterior end of prostate gland. Posterior pallial vas deferens with large horizontal loop on pallial roof and columellar muscle, duct loosely bound in connective tissue. Anterior pallial vas deferens narrow, opening to 'neck' near posterior end of pallial cavity, coursing anteriorly as straight tube forming raised ridge covered by connective tissue.

Penis (Fig. 3E,F, 6A-C) positioned well behind right eye. Penis very large relative to head; broadly rectangular to almost square, flattened in cross-section, base slightly narrowed. Penis surface smooth except for few weak folds near base. Distal penis distinctly bifurcate, with large lobate process and short, narrow, tapering penial filament (Fig. 3E). Filament shorter than lobate process. Inner side of lobate process with large, stalked apical crest (Fig. 3E, 6A; ac) bearing glandular field distally; outer side of process with protruding terminal bulb (tb). Dorsal surface of penis having prominent, U-shaped superior tubercle (glandular field) extending from terminal bulb back along outer edge to mid-penis and then coursing back distally to base of lobe. Arms of gland occasionally fused distally, forming complete ellipse. Gland often fragmented along outer edge, forming two or more elongate, adjacent units. Space between two arms of gland filled by numerous (10–20) transverse superior tubercles, usually elongate and often abutting arms of above, but often fragmented into smaller units. Large, stalked superior tubercle positioned just outside above loop, from proximal to near mid-penis along the inner edge. Ventral penis having swollen distal region extending from base of filament onto lobate process Swelling bearing large, sub-


A
B
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F

Figure 4. Radula, *Cincinnatia integra* (UF 77151) **A, B** Central teeth, scale bars = 13.6 µm, 15 0 µm, respectively C Lateral and inner marginal teeth; scale bar = 23.1 µm. **D.** Inner marginal teeth; scale bar = 38 µm. **E.** Outer marginal teeth; scale bar = 27 µm. **F** Portion of radula ribbon, scale bar = 50 µm.

terminal, transverse, stalked parapical crest (Fig. 6C; pc) flanked by second, smaller, transverse, stalked inferior crest (ic) proximally; and one or more small accessory crests either distally or proximally Ventral penis also bearing narrow, stalked, longitudinal accessory crest (rarely multiple fields) along outer edge just distal to filament. Distal penis without obvious ciliation. Penial opening terminal. Penial duct (pd) with thin muscular coat, narrow, coursing along straight path near outer edge before looping inwards to enter neck.

Variation. Shell variation in *C. integra* is pronounced, reflecting the broad distribution and ecological tolerance of this species Obesity of shells is especially variable, even within single populations, some of which (from the middle and lower Mississippi drainages) range in form from rather slender to nearly globose. The contour of the whorls usually is evenly rounded, but in some populations from the Ouachita River drainage, whorls have a distinct spiral shoulder, and are flattened laterally. Populations living in lentic habitats tend to vary more in shell shape, whorl contour, and aperture development than those from lotic waters.

Distribution (Fig 7): Broadly distributed within drainage of Mississippi River and large tributaries (e.g., Missouri, Ohio Rivers). Also in Great Lakes-St Lawrence River, southern Great Plains, and Gulf Coastal (from Texas through western Alabama) drainages. Almost all records are from east of the Continental Divide. The highly disjunct Northeast Atlantic coastal records require confirmation (we have not seen any anatomical material from this region). We have not seen any material confirming the Utah records provided by Pilsbry (1899:122), Hannibal (1912:191) and other workers.

Remarks: Anthony's (1840) figure and types clearly indicate that *Paludina cincinnatiensis* (ibid.:279, '. . . spire entire at the apex and prominent; suture deeply impressed. . .') is the same species as *integra*, as has been recognized by several earlier workers (see above). Note that this species has sometimes been incorrectly attributed to Say, 1829 (e.g., Burch & Tottenham, 1980:110; Turgeon et al., 1988:60). Tryon's (1870) introduction of *scarboroughi* probably was inadvertent (he indicated that he once 'contemplated' describing this species, but later concluded that his material was not distinct from *cincinnatiensis*), but was valid as he provided a brief diagnosis ('larger and more robust' [than the above]). Types for this species were not located by Baker (1964), and we have not found any of the specimens that Tryon distributed under this name, although we found one lot (Walnut Creek, Kansas, *ex* Scarborough, ANSP 27868) that corresponds to his description and may represent part of this material (although the original label identifies this material as *cincinnatiensis* and not *scarboroughi*). Tryon did not provide a figure, but nevertheless it is clear from his comments that *scarboroughi* is merely large-sized *integra*. We have not been able to further pinpoint the type locality for *scarboroughi* as there are at least two separate Walnut Creeks in Kansas (Rand, McNally & Company, 1956:177, and associated map) and we have not seen any anatomical material from this region. Pilsbry & Walker (*in* Pilsbry 1889) stated that *peracuta*, while closely similar to *cincinnatiensis* (with similar radula), is smaller, more slender, more narrowly perforate, with flatter whorls, longer spire, and thinner, more adnate peristome. Type material for *peracuta* nevertheless falls within the range of shell variation exhibited by *integra* elsewhere. While we have not seen anatomical material from the type locality area (note that Pilsbry's specific locality is not locatable on any maps that we have studied), snails from Arkansas and south-central and southwestern Texas (Fig. 6B) conform to *integra* in all anatomical respects. Baker (1922) stated that *judayi* resembles *cincinnatiensis* (and has an acute apex), but is smaller with more convex whorls and a wider umbilicus. He later (Baker, 1928:125–126) decided that his species was a lacustrine form of *cincinnatiensis* and noted the occurrence of intermediate forms. The type locality, Doemel Point, Lake Winnebago (Wisconsin), is just northeast of Oshkosh, Winnebago County (Juday, 1914·

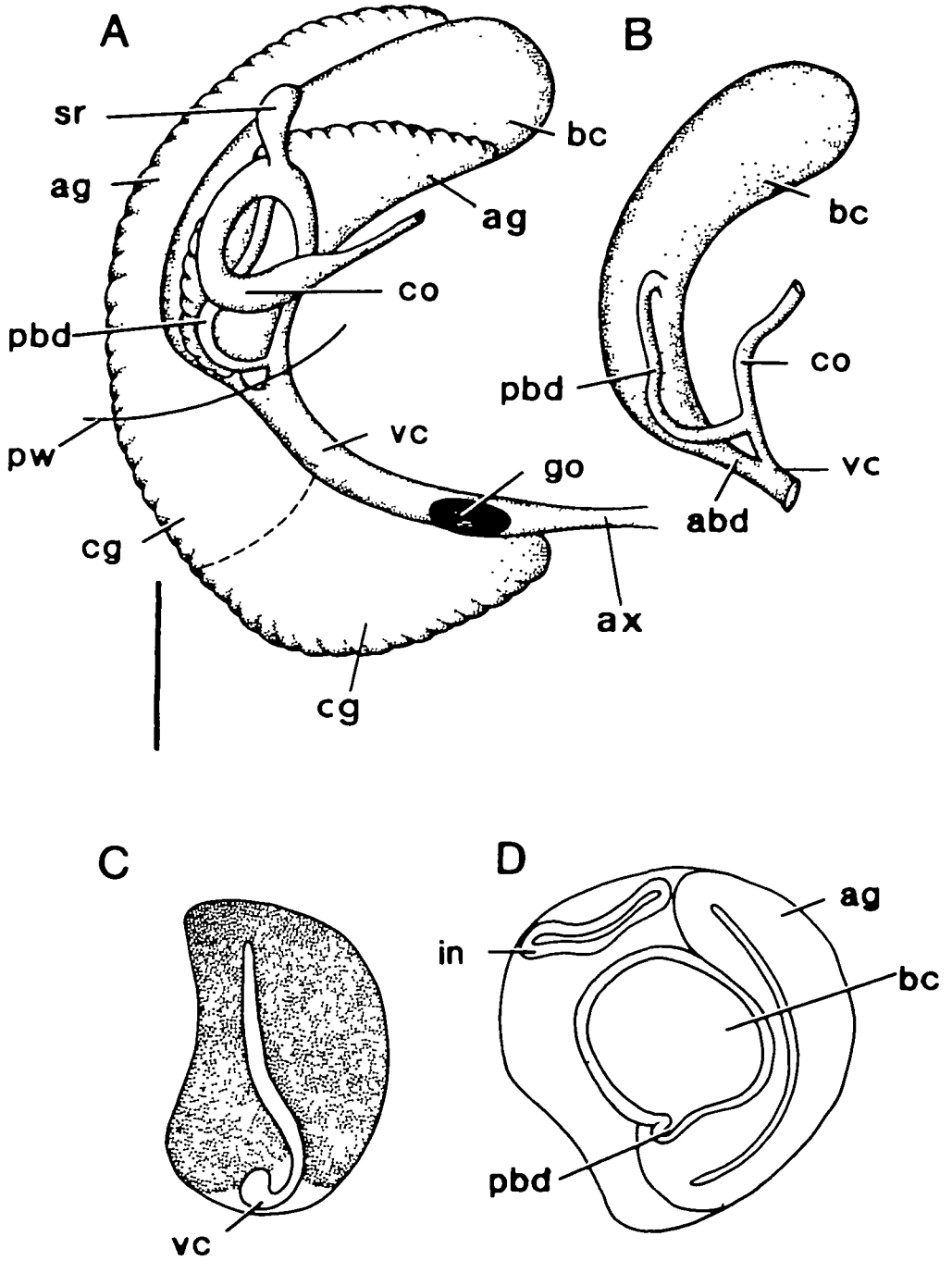

Figure 5. Female genitalia, *Cincinnatia integra;* scale bar = 250 μm. **A.** Pallial oviduct and associated organs and structures, viewed from left side (UF 77151). **B.** Bursa copulatrix and its ducts (USNM 874079). **C.** Transverse section of capsule gland, near mid-length. Glandular portion stippled. **D.** Transverse section through albumen gland (near mid-length) and associated structures (UF 77151). Abbreviations: abd, anterior bursal duct; ag, albumen gland; ax, anterior expansion; bc, bursa copulatrix; cg, capsule gland; co, coiled oviduct, go, genital opening; in, intestine; pbd, posterior bursal duct; pw, pallial wall; sr, seminal receptacle; vc, ventral channel.

map XXVI). Baker (1930:189) stated that *chicagoensis* is a 'shortened-up race of the river form *cincinnatiensis*, differing in being more globose, with shorter spire and wide umbilicus' and indicated that its radula is exactly like the above. Again, we see no merit in providing taxonomic distinction between the lacustrine and riverine forms of *cincinnatiensis* based on morphological criteria.

Given the extremely broad distribution of this snail we acknowledge that molecular studies may reveal significant differentiation of groups of populations. Note, however, that isolated drainage units now occupied by this species were more fully integrated in the recent past. For instance, prior to the Wisconsin glaciation the Hudson Bay drainage was connected to north-flowing drainages that now comprise headwaters of the Mississippi River (Lemke et al., 1965), and during low sea level stands associated with this same glaciation the lower courses of some of the western Gulf Coastal rivers were confluent (Conner & Suttkus, 1986).

Material examined: **Canada**. ONTARIO Wapuaga Beach, Georgian Bay (UMMZ 43903) *Algoma District:* Hamilton (ANSP 62654, ANSP 67568). *Huron District:* Lake Huron, Grand Bend (UMMZ 42261). *Lambton District.* drift, Lake Huron at Kettle Point (UMMZ 13700). *Northumberland District:* Presqu'ile Point, Lake Ontario, near Brighton (USNM 464548). *Prince Edward District.* Lake Ontario (UMMZ 138769) -Wellington Harbor, Lake Ontario (USNM 464532).

United States. ALABAMA *Clarke County:* Leatherwood Creek, ca. 24 km SSE of Jackson, just above confluence with Tombigbee River (UF 230747, UF 231750). ARKANSAS. *Ashley County:* Ouachita River, 12.5 km W Crossett (UF 77194). -slough 3.5 km NE Hwy 189/Hwy 133 crossing (UF 77195). *Baxter County* White River, Cotter (UF 77199, UMMZ 119428) -North Fork White River, Norfolk (UF 77200, UMMZ 119436).-White River, 4 8 or 6.4 km above Norfolk (USNM 272175) *Benton County·* Sagar Creek, Siloam Springs (*USNM 883646) *Bradley County·* Saline River, 3 2 km E Warren (UF 77094, UF 77192).-Saline River, 5.1 km E of Johnsville (UF 77093).-Saline River, 10.2 km NNE of Warren (UF 77091, *UF 77092) -Ouachita River, Morobay (UF 77190). *Calhoun County·* Moro River, 8.2 km E Fordyce (UF 77087, *UF 77088) -Moro Creek, 10 2 km E Harrell (UF 77191) *Chicot County* Grand Lake (UF 77196, UMMZ 13327) *Clark County·* Big Deciper Creek, Gum Springs (UF 77197, UF 206949, UMMZ 119428).-Ouachita (River), Arkadelphia (*UF 35317). *Craighead County·* St Francis River, Lake City (UF 206857). *Dallas County* Ouachita River, 5.0 km W Sparkman (UF 77089, UF 77090) *Fulton County·* Spring River, 1 1 km S Mammoth Spring (UF 77193). *Prairie County* White River, NE DeValls Bluff (UF 77198, UMMZ 197620) ILLINOIS. *Cass County:* Illinois River, Beardstown (UF 77170, UMMZ 197633, FMNH 14571). *Cook County·* Palos Park (FMNH 28028) -Summit (FMNH 71847).-Salt Creek (UF 77171, UMMZ 119407).-Lake Michigan, Lincoln Park (UF 77166, UMMZ 119408).-Little Muddy Creek, near Schiller (UF 88875).-Lake Michigan, Division Street, Chicago (ANSP 147793, UIMNH Z28329). *DeKalb County* Kishwaukee Creek (MCZ 46578). *DuPage County·* DuPage River (FMNH 17428).-Dupage River, Pioneer Park (FMNH 17460). *Fulton County·* Canton (numerous). *Henry County* Blue River (UF 77144). *Jackson County·* Big Muddy River, just S of Murphysboro (UF 77174, UMMZ 197634) *LaSalle County:* canal, Utica (UF 77172, UMMZ 119408, UMMZ 69814).-Utica (UF 77169).-Starved Rock (ANSP 72036). *Mason County·* Crystal Lake, Havana (FMNH 71849, FMNH 19973) -Havana (ANSP 27855). *Mercer County* Mississippi' River (MCZ 2076, MCZ 2099) *Perry County.* Beaucoup Creek, 1.6 km E Matthews (UF 77167, UMMZ 197644). *Randolph County* Plum Creek, 6.9 km NW Sparta (UF 77168, UMMZ 197642). *Rock Island County·* Mississippi River, Moline (UF 77165, UF 88726).-Mississippi River, below mouth of Rock River, Frahms Island (ANSP 96668). *St Clair County* Pittsburg Lake, 1.6 km W Edgemont (UF 77164, UMMZ 197640) *Tazewell County·* Spring Lake (ANSP 27858). *Washington County.* Beaucoup Creek (FMNH 59983) -Beaucoup Creek, W of Dubois (UF 88877, UF 206951).-Puncheon Creek, Dubois (UF 88873).-Locust Creek, W Dubois (UF 88876) *Will County* Joliet (FMNH 58860) -Lilycache Creek, Joliet (FMNH 59928, UF 77173, UMMZ 119410, CM 62 26320) -Fox River, Plainfield (USNM 762936) INDIANA. *Henry County·* Blue River (UMMZ 119443). *Lake County·* Lake Michigan, Miller (FMNH 87864, FMNH 111563, MCZ 71275) *Posey County* Bayou W Upton (UF 77143, UMMZ 119439). IOWA. *Calhoun County·* Racoon River, Lake City (USNM 534140). *Cerro Gordo County·* Lime Creek, Mason City (USNM 507779). *Cherokee County:* Little Sioux River, Cherokee (USNM 527964). *Clinton County* Mill Creek (USNM 539842).-drift of. creek, Dewitt (ANSP 91943). *Dickinson County* Lake Okoboji (numerous).-Orleans (numerous).-Spirit Lake (numerous).-Millers Bay (USNM 525917) -Little Sioux River, W of Milford (USNM 478451).-Arnolds Park, Millers Bay (UF 77160).-Gar Lake (numerous).-bay N of Arnolds Park (USNM 478415).-Hottes Lake (USNM 525230). *Dubuque County:* Dubuque (ANSP 27859) *Emmet County:* Des Moines River, Estherville (USNM 478454, USNM 478455, USNM 507678). *Floyd County·* Shell Rock River, Nora Springs (USNM 478450) *Franklin County* Hampton (ANSP 91942) *Greene County·* drift, Cedar Creek (USNM 539877). *Hamilton County·* river drift, Webster City (USNM 520605). *Hardin County* Eldora (ANSP 107444, UF 22879). *Jasper County·* Newton (USNM 511809, USNM 514784) *Johnson County.*

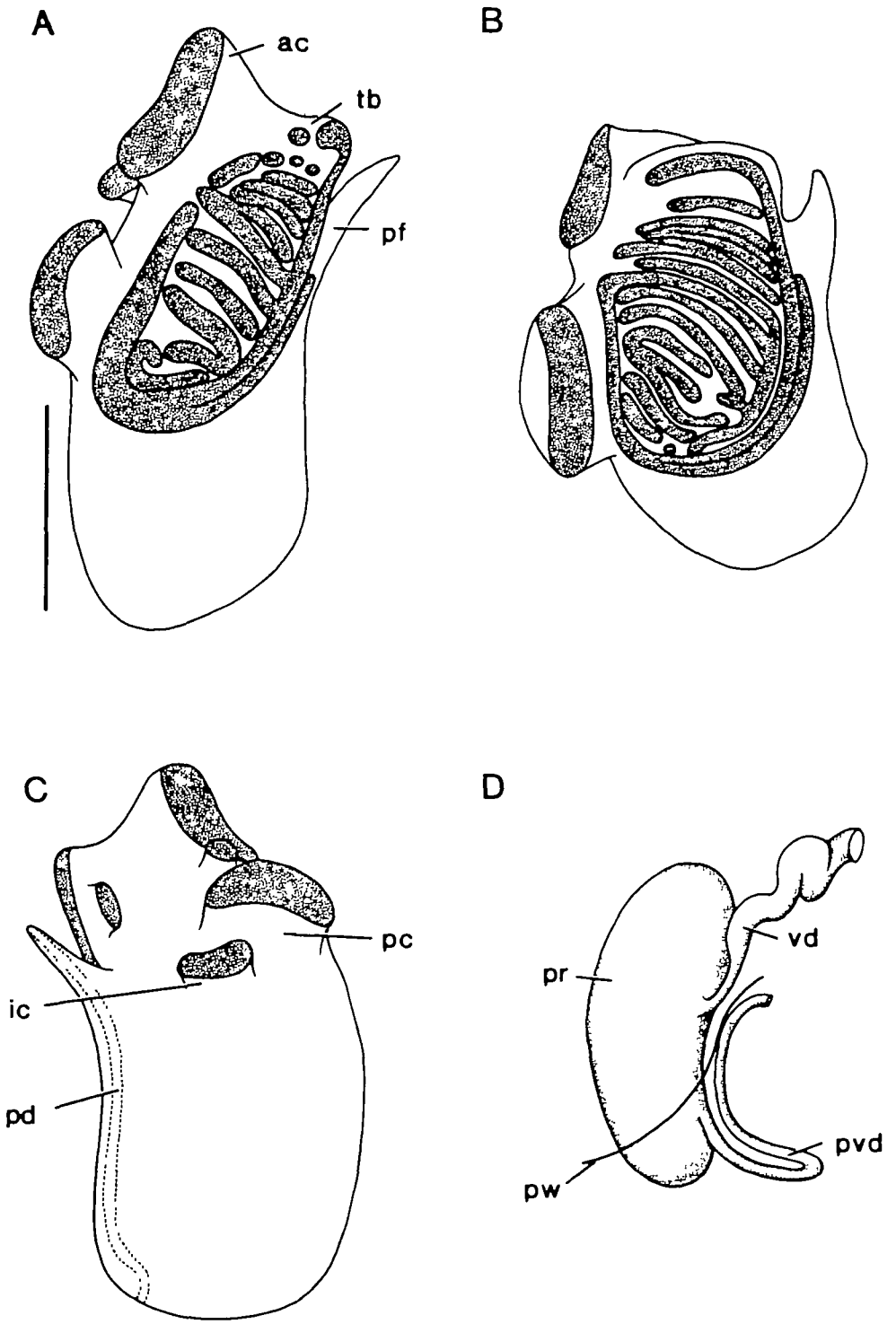
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Figure 6. Male genitalia, *Cincinnatia integra*; scale bar = 1 0 mm. **A** Penis, dorsal aspect (UF 35319) **B** Penis, dorsal aspect (USNM 874079). **C.** Penis, ventral aspect (UF 35319). **D** Prostate gland, viewed from left side (UF 77151). Glandular areas on the penis are stippled Abbreviations ac, accessory crest; ic, inferior crest, pc, parapical crest; pd, penial duct; pf, penial filament; pr, prostate gland; pvd, pallial vas deferens; pw, pallial wall; tb, terminal bulb; vd, vas deferens.

Iowa City (numerous) -pond along Illinois River, Iowa City (FMNH 130407).-catfish pond, Iowa City (USNM 527962).-Iowa River (USNM 525150) -small stream, near Iowa City (ANSP 27865).-pond, near Iowa City (ANSP 27862) -ox-bow pond, near Iowa City (ANSP 161551) *Lee County:* Keokuk (USNM 535168, USNM 508368, USNM 508370).-Mississippi River, 4.6 km N Keokuk (UF 77085, *UF 77086) -Mississippi River, Ft. Madison (UF 77155) -lagoon, Montrose (UF 77153). *Linn County·* Cedar Rapids (ANSP 161565, USNM 527985). *Lyon County* Rock Rapids (USNM 527963) -pond, west of Granite (USNM 527975). *Muscatine County* Muscatine (numerous) -Mississippi River, Muscatine (MCZ 2078, MCZ 2100) -1.6 km W Coles Ferry (USNM 478422) *O'Brien County* Floyd River, Sheldon (USNM 534606). *Pymouth County.* Dalton (USNM 520608).-Broken Kettle Creek at #6, Big Sioux River (USNM 478453). *Polk County:* Des Moines (numerous) -Old zoo park, Des Moines (UF 77159, UMMZ 119446) -Pond, Des Moines (MCZ 2079, UF 77154).-Des Moines River, Des Moines (numerous) -Herrold (UF 77157).-vicinity of Des Moines (UF 88862, UF 88870, UF 88872) *Sac County·* Beach Wall Lake, Lake View (USNM 520595, 520599), *Scott County* Davenport (ANSP 27867, ANSP 91939) -drift on Tom Creek, Rock Rapids (USNM 478448). *Sioux County* Big Sioux River, Hawarden (USNM 514461) -Rock Valley (USNM 506207). KANSAS *Allen County* Neosho River, W of Edgetown (USNM 742061). *Douglas County·* Lone Star Lake (USNM 738059, USNM 742063) *Pottawatomie County·* Onago (USNM 33562) *Riley County·* Kansas River, Ft Riley (USNM 508431). *Shawnee County* Silver Lake (ANSP 64450). LOUISIANA *Ascension Parish:* Bayou Manchac at US HWY 61, near Prairieville (UF 175882). *Desoto Parish.* Frierson (CM 62 25394). *Iberville Parish.* borrow pit, near levee, 3 2 km S Ramah (UF 175867).-drainage canal, 1.6 km E Rosedale, LA HWY 76 (UF 175871) *Lafourche Parish.* Bayou Boeuf, Kraemer (UF 223555) *Livingston Parish* Tickfaw River, 1.6 km W Holden (UF 77081, UF 77082).-head of Island Pond, 0 4 km N of island (UF 35073) *Ouachita Parish:* Little River, mouth of Hurricane Bayou (ANSP 98510) *Pointe Coupee Parish:* Old River, ca 1 6 km N Morganza Spillway, LA HWY 1 (*UF 175869) -Flase River, New Roads (UF 35077). *Rapides Parish.* Alexandria (USNM 121354). *West Baton Rouge Parish.* drainage ditch, near Carey, US HWY 190 at LA HWY 983 (UF 175873) -Grand Bayou, near Carey, 1.6 km W US HWY 190 at LA HWY 983 (UF 175877). MAINE. *York County* Kennebunk (UF 77131). MARYLAND *Harford County* Havre de Grace (ANSP 161337) MICHIGAN *Alpena County* Alpena (FMNH 64233). *Bay County* Saginaw Bay drift, Bay City Park (UMMZ 43149, UF 77135). *Berrien County·* Galien River (UMMZ 119458, UF 77133). *Calhoun County·* Brigham Lake, 4.8 km E Battle Creek (UMMZ 197621). *Charlevoix County* Sandy Bay, Beaver Island, Lake Michigan (UMMZ 142515, UF 77140). *Gladwin County.* Mill Pond, Beaverton (UMMZ 36784, UF 77141) *Gratiot County·* Pine River, Alma (UMMZ 119458, UF 77139). *Houghton County:* Sturgeon River (MCZ 53274, FMNH 12113).-Sturgeon Bay (USNM 52768) *Kent County* Rockford (FMNH 137932) *Livingston County.* Whitewood Lake (UMMZ 21494, UF 77136). *Manistee County* Onekama (FMNH 64233) *Monroe County* La Plaisence (sp.?) Bay (UMMZ 21494, UF 77138) *Ottawa County·* Ottawa Beach (UMMZ 31597, UF 77132).-Black Lake, Holland (UF 25079) *Roscommon County* Denton Creek. Prudenville (UF 88878) *Saginaw County·* East Saginaw (UF 88860) *Wayne County* River Rouge (UMMZ 119448, UF 77137).-Detroit River, Belle River (UMMZ 119452, UF 77134). MINNESOTA *Aitkin County* Rice Lake, Kimberly (USNM 347728) *Anoka County·* Rum River, Anoka (MCZ 2083, UF 77142, UMMZ 156531). *Blue Earth County:* Eagle Lake (numerous).-Watonwan River, 19.2 km S of Mankato (ANSP 98709). *Douglas County* Lake Mary, Alexandria (USNM 347706) *Jackson County* Heron Lake (USNM 104458). *Lake of the Woods County·* Lake of the Woods, NW of Angle (USNM 347749) *Rice County* Roberts Lake (MCZ 46600). *St Louis County* Grand Lake (USNM 473487, USNM 124526) *Stearns County·* Lake Koronis, Paynesville (USNM 347721).-Sauk Lake (USNM 519932) (Stearns-Todd Counties) MISSISSIPPI *Coahoma County.* Sunflower River, 5.6 km WSW Roundaway (UF 77126).-Sunflower River, 11 0 km S Clarksdale (UF 77075, UF 77076) *Clarke County* Souinlove River, 5 0 km ESE Pachuta (UF 77108, UF 77109, UF 77122). *Green County·* Leaf River, 2.1 km SE McLain (UF 77110). *Hinds County* Pearl River, Jackson (UF 77121, UMMZ 119424) -Fourteen Mile Creek, 4.8 km NE Newman (UF 77069, UF 77070) *Holmes County·* Tombigbee River, Durant (UF 77125, UMMZ 119421) -Durant (UF 88865, UF 88871). *Leflore County* Quiver River, 11.2 km E Doddsville (UF 77073, UF 77074) *Lowndes County·* James Creek, 16.8 km E Crawford (*UF 77095). *Newton County·* Chunky River, 1 8 km E Chunky (UF 77118) *Noxubee County* creek, 3.2 km E Macon (UF 77071, UF 77072) -Woodward Creek, 2 1 km E Cooksville (UF 128864).-Broken Pumpkin Creek, 4 0 km NW Bigbee Valley (UF 128865) *Perry County:* Leaf River, 1.3 km N Beaumont (UF 77113). *Quitman County.* Coldwater River, 1.4 km

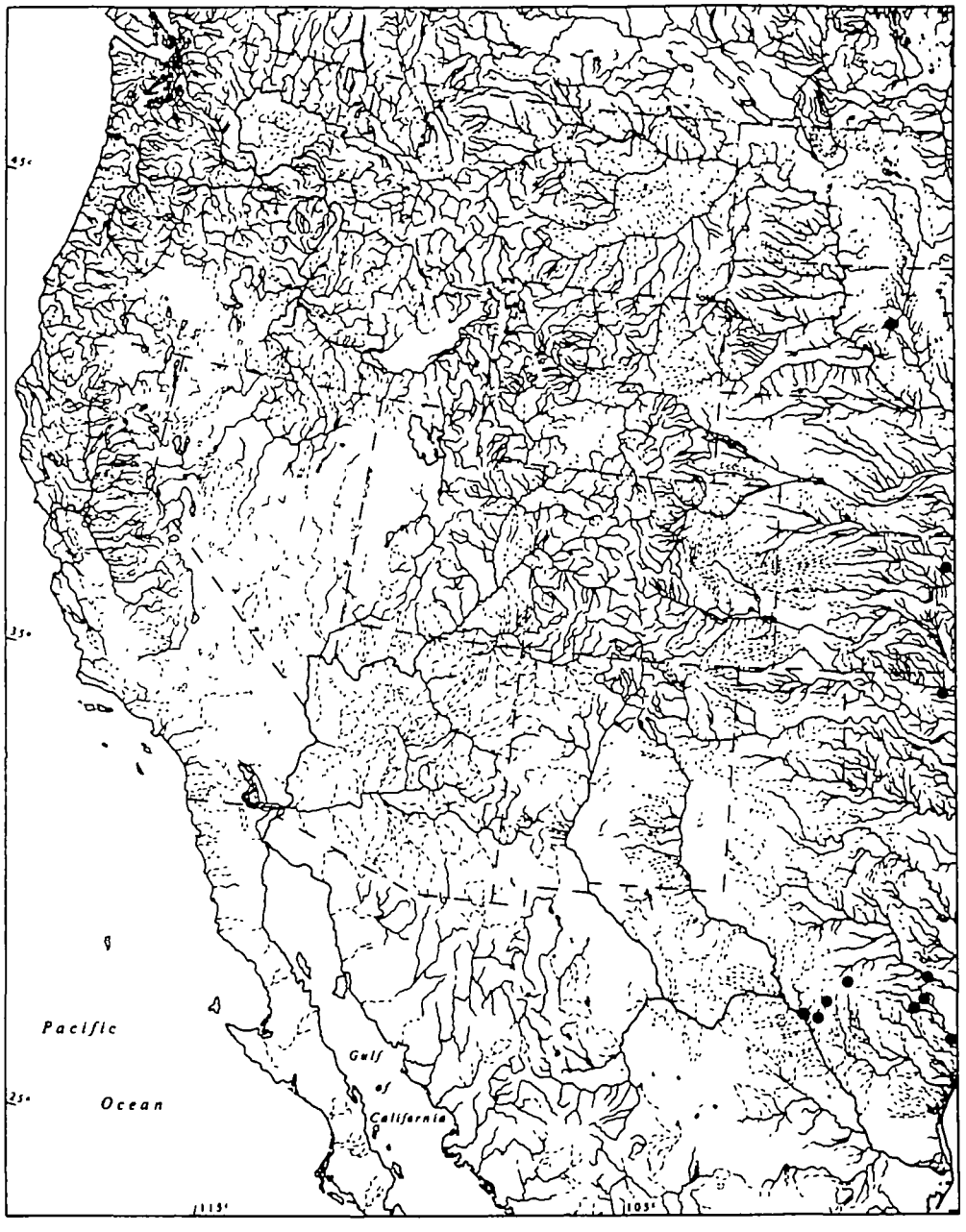
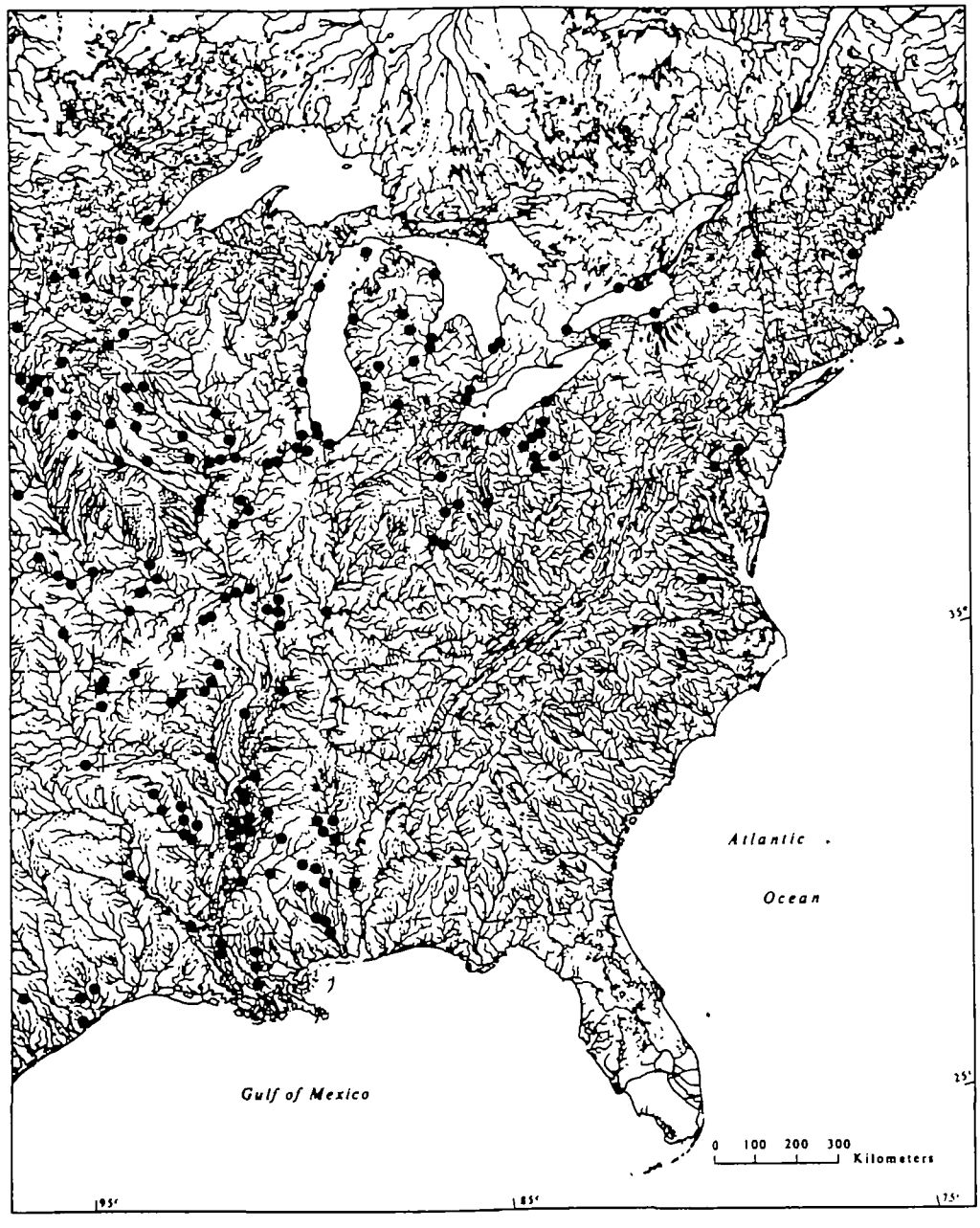


Figure 7. Map showing distribution of *Cincinnatia integra*.

W Birdie (UF 77119). *Scott County:* Warrior Creek, 1.3 km W Lake (*UF 77096). *Sharkey County.* Rolling Fork Creek. Rolling Fork (UF 77117) *Smith County:* Ish Creek, 2.4 km W Sylvarena (UF 77097). *Sunflower County:* Sunflower River, 11.2 km WSW Inverness (UF 77120).-Quiver River, 6.1 km S Sunflower (UF 77123). *Warren County.* creek on Hwy 27, 1.8 km W, 1.8 km WNW Newmans (UF 77114). *Washington County:* Black Bayou, 5.1 km W Arcola (UF 77112).-slough, Arcola (UF 77079, UF 77080, UF 77124).-Bogue Phalia River, 3.2 km E Arcola (UF 77065, UF 77066, UF 77116).-Black Bayou, 6.6



km W Hollandale (UF 77115). *Wayne County*: Chickasawhay River, 6.7 km W state line (UF 77077, UF 77078). MISSOURI. *Carter County*: seepage spring, Van Buren (*UF 771551).-pond on island in Current River, 4.8 km S Van Buren (numerous) *Cooper County*: Blackwater (FMNH 145478). *Crawford County*: Meramec River, 12 km SE Leasburg (UF 77183).-Meramec River, 2.9 km NNW Steeleville (*UF 35319, UF 77067, USNM 860651).-Meramec River, 14.2 km W Steeleville (UF 77149). *Franklin County*: Meramec River, 16 km W Robertsville (UF 77185, UMMZ 197626) *Henry*

County Artesian Lake, Clinton (numerous).-water station, Clinton (FMNH 50144). *Howard County* Glasgow (UF 88922) *Jackson County:* Kansas City (MCZ 15925). *Jefferson County.* slough at base of bluff, 3.2 km SE Pacific (UF 77186, UMMZ 197625) *Laclede County·* Gasconade River (CM 62.24919). *McDonald County·* Sugar Creek, Sugar Island Camp, E Pineville (*UF 85885).-Elk River, Mt. Shira Public Fishing Access, Ginger Blue (UF 128868). *Oregon County·* Warm Fork, 2.4 km N Thayer (UF 77152). *Pettis County:* Artesian Lake, Sedalia (UF 77150, UMMZ 69813).-Muddy Creek, Sedalia (UF 77180, UMMZ 69811) -Flat Creek, Sedalia (MCZ) - Sedalia (USNM 124526) *Saline County.* Blackwater River (UF 77187). *Shannon County:* Jacks Fork (MCZ 2081). *St Louis County·* Meramec River, Hunters Ford, 6.4 km S Allenton (UF 77188, UMMZ 197639).-Meramec River, Kirkwood (MCZ 94687, UF 77181, UMMZ 197646). *Stone County.* James River, Galena (UF 77189, UMMZ 119435).- pond, Galena (USNM 272176). NEBRASKA. *Cass County·* (USNM 134547). *Lancaster County·* Lincoln (UF 77100, USNM 526151).-Salt Creek, Lincoln (UF, USNM 528040) -Dead Mans Run, Lincoln (USNM 508404).-Platte River Jct. (USNM 526405). NEW YORK *Herkimer County·* Mohawk (numerous).-Mohawk River (ANSP 122879, USNM 47533) *Jefferson County.* Watertown (ANSP 88619). *Ontario County·* N end Seneca Lake, Geneva (USNM 217672). *Orleans County·* Erie Canal (USNM 73418). Wayne County: Sodus Bay, Lake Ontario (USNM 536642). *Yates County·* (USNM 473987) OHIO. *Ashtabula County·* small ditch NW Geneva (CM 62.25093). *Auglaize County:* Auglaize River, Wapakoneta (CM 62.26321) *Clark County* Springfield (USNM 121315). *Columbiana County·* Sandy Creek, Bayard (CM 62.24921, CM 62 25093) *Franklin County·* Columbus (numerous) *Hamilton County* canal near Cincinnati (MCZ 142813, MCZ 315776) -Cincinnati (numerous).-Ohio River, Cincinnati (FMNH 87857, FMNH 87883).-Clear Creek (FMNH 3724, FMNH 9855).-Miamitown (MCZ 161879). *Lorain County.* Elyria (USNM 28091). *Montgomery County.* Stillwater River, at Ridge Avenue, Dayton (*UF 235543) *Ottawa County:* drift of Sandusky Bay, Bay Point (UF 77130, UMMZ 27492). *Portage County:* Congress Lake outlet, Ravenna (CM 62.26314).-Cuyahoga River, near Hiram (CM 62.26323). *Stark County:* race from Ohio Canal, Navarre (UF 77128) -Tuscarawas River, Navarre (UF 77129, UMMZ 119416, CM 62.26315). *Summit County.* Hudson (USNM 53570).-Clinton (USNM 437646).-Old channel of Chippowa Creek, Warwick (ANSP 104632). *Tuscarawas County:* New Philadelphia (USNM 117751).-Tuscarawas River, New Philadelphia (CM 62.26326, CM 62.26220). OKLAHOMA. *Cherokee County:* Illinois River (FMNH 32865). *Le Flore County:* Poteau River, Slate Ford (UMMZ 138585). *Payne County:* Perkins (ANSP 112842). PENNSYLVANIA *Delaware County·* just below Addingham (ANSP 110399).- Pond on Darby Creek, Addingham (ANSP 106834) SOUTH DAKOTA. *Moody County.* Sioux River (UF 1076). *Roberts County.* Lake Transverse (UMMZ 69815, MCZ). *Spink County* Turtle River (FMNH 87848, MCZ 68992). *Turner County:* Park Creek, Vermillion River (MCZ 2082). *Union County:* Otis Mill (FMNH 109388, USNM 109383).- Devils Lake (FMNH 71848, FMNH 59982).-Clear Lake, Springhale (CM 62.25394). TENNESSEE. *Lake County·* outlet of Reelfoot Lake at spillway (UMMZ 197619). *Obion County* Reelfoot Lake (USNM 605804) TEXAS *Brazoria County:* Angleton (USNM 535712) *Chambers County.* Old River (USNM 464844). *Colorado County* drift, Colorado River, Columbus (USNM 527581). *Comal County:* Guadalupe River, New Braunfels (USNM 123754).- Guadalupe River, 6.4 km above New Braunfels (USNM 525934, USNM 526942) -New Braunfels (numerous) -Comal Creek, New Braunfels (USNM 97451). *Goliad County·* Cardenas Creek (USNM 128517, USNM 464898). *Harris County·* White-oak Bayou, Houston (USNM 134366).-Buffalou Bayou, Houston (USNM 127395). *Hays County:* San Marcos River, San Marcos (*USNM 874079). *Jackson County:* Ware (sp.?) Lake (USNM 465121, USNM 465124). *Milam County* Brazos River, Smileys Bluff (USNM 516318). *Kerr County:* Ellebracht Springs, E Mountain Home (*USNM 883418) -Guadalupe River, HW 39, W of Ingram (*USNM 874916).- spring, S fork Guadalupe River (*USNM 874920, *USNM 874924). *Kinney County.* Pinto Creek, 12.8 km W of Bracketville (*USNM 874921).-Pinto Creek, 5.8 km W of Bracketville (*USNM 883419) - Pinto Creek, HW 277, SE of Del Rio (*USNM 874914) -Las Moras Creek, Fort Clark (Bracketville) (USNM 151543). *McLennan County* Hog Creek (USNM 198483) *Navarro County* Spivey's Lake (ANSP 58292). *Real County.* Old Faithful Spring, N of Camp Wood (*USNM 883417). *Travis County:* Barton Springs, Austin (USNM 125671, USNM 464776, USNM 464869) *Victoria County·* Ripley Lake (USNM 151520, USNM 564043) -Garcetas Creek (USNM 465037).-Guadalupe River (USNM 465006) VERMONT *Addison County·* Chimney Point, Lake Champlain (USNM 336414, USNM 435902) VIRGINIA *Prince George County:* James River, City Point (ANSP 68801) WISCONSIN *Brown County·* Green Bay (UMMZ 137975) *Door County:* Kangaroo Lake (FMNH 64020) *Milwaukee County.* Milwaukee (ANSP 122880, USNM 27897, USNM 24802) *Winnebago County·* Lake Winnebago, off Doemel Point (UIMNH Z12651a, UIMNH Z12651b)

DISCUSSION

In the recent literature, 13 species (listed in Table 2; 10 from Florida, one from Maine, and two from the mid-West) have been described as or allocated to *Cincinnatia.* On the basis of penial morphology, *C. integra* most closely resembles members of the Floridian *vanhyningi* group (*fide* Thompson, 1968:119),

Table 2. Species described as or assigned to genus *Cincinnatia* in the recent literature.

Amnicola comalensis Pilsbry & Ferriss, 1906[1]
Amnicola floridana Frauenfeld, 1863[2]
Cincinnatia fraterna Thompson, 1968
Cincinnatia helicogyra Thompson, 1968
Cincinnatia mica Thompson, 1968
Bythinella monroensis Dall, 1905[2]
Cincinnatia parva Thompson, 1968
Amnicola peracuta Pilsbry & Walker *in* Pilsbry, 1889[1] (synonym of *Cincinnatia integra*)
Cincinnatia petrifons Thompson, 1968
Cincinnatia ponderosa Thompson, 1968
Lyogyrus vanhyningi Vanatta, 1934[2]
Cincinnatia wekiwae Thompson, 1968
Amnicola winkleyi Pilsbry, 1912[3]

[1]Transferred to *Cincinnatia* by Taylor (1975).
[2]Transferred to *Cincinnatia* by Thompson (1968)
[3]Transferred to *Cincinnatia* by Davis & Mazurkiewicz (1985).

which also have a circular or U-shaped pattern of fused superior tubercles on the dorsal penis, parapical crest borne on a fleshy pedicel (not a low ridge), and multiple ventral glands. However, *C. integra* differs from members of this group by having a large number of superior tubercles which are transversely arranged. Apart from the type species, none of the species now placed in *Cincinnatia* has been described beyond shell, operculum, radula, and penis, with the exception of *winkleyi*, which was thoroughly depicted by Davis & Mazurkiewicz (1985). We note the following differences between this species and *C. integra*. The protoconch is not strongly wrinkled, but nearly smooth (Davis & Mazurkiewicz, 1985: fig. 1c-f). The stomach has an external ridge near mid-length (Davis & Mazurkiewicz, 1985:fig. 17), which is absent in *integra*. The bursa copulatrix is ovate (not elongate), with a substantial portion posterior to albumen gland (as opposed to being about even with the posterior edge of the gland), and is not imbedded in the gland, but lies on its left side (Davis & Mazurkiewicz, 1985:fig. 9a). The bursa has a single, anterior duct (confirmed by the first author, who dissected Davis' material, ANSP A10246). The seminal receptacle opens to the oviduct distal to (as opposed to from the posterior edge of) the coiled portion (Davis & Mazurkiewicz, 1985:fig. 8). Our preliminary dissections of alcohol material of four Floridian species allocated to *Cincinnatia* (*floridana, parva, petrifons, wekiwae*; e.g., members of both species groups described by Thompson, 1968) showed that their distal female genitalia closely conform to that described for *winkleyi*, which agrees in general topology to that described for other North American nymphophiline genera such as *Birgella* Baker, 1926 (Thompson, 1984: figs. 83, 84), *Nymphophilus* Taylor, 1966 (Thompson, 1979:fig 15); *Pyrgulopsis* Call & Pilsbry, 1886 (Hershler, 1994:figs. 4,5), and *Stiobia* Thompson & McCaleb, 1978 (Thompson & McCaleb, 1978:fig. 4B). (Several alcohol series of *comalensis* also have been studied—this species closely resembles eastern American members of the genus *Pyrgulopsis*.)

Distinctive features of the type species set it apart from all of these taxa and suggest that the genus *Cincinnatia*, as currently constituted, probably is non-monophyletic. The distinctiveness of this species was noted by Thompson & McCaleb (1978:357), who treated *integra* as a species group in *Cincinnatia* separate from the two Florida groups described by Thompson (1968). For the time being, we thus treat *Cincinnatia* as monotypic although we note that many other North American nymphophiline taxa (including some taxa that have been allocated to this genus and all members of the eastern genera *Notogillia* Pilsbry, 1953; *Rhapinema* Thompson, 1969; and *Spilochlamys* Thompson, 1968) still have not yet been thoroughly studied anatomically, and acknowledge that some of these may ultimately prove to belong to the *Cincinnatia* clade.

To our knowledge, the configuration of the distal female genitalia in *Cincinnatia integra* has no parallel within the family Hydrobiidae. Some members of the family Pomatiopsidae also have two ducts opening to the bursa copulatrix (Davis, 1979:figs. 9, 13A), but given the

otherwise very different groundplans of female genitalia in these two groups (e.g., in pomatiopsids, one of these ducts serves as a sperm tube separated from the glandular gonoduct) we see little reason to assume homology The function of this novel, second bursal duct is problematic. It was early conjectured (based on observed ciliary currents) that at least in prosobranchs, sperm are first deposited by the male into the female's bursa copulatrix and then from this storage structure are transported to the seminal receptacle (Fretter, 1941, 1946). Given the large size and elongate shape of the bursa in *C. integra*, the presence of a second, posterior duct opening from this structure to the oviduct could thus facilitate passage of sperm to the posterior seminal receptacle. If, on the other hand, one ascribes a primarily gametolytic function to the bursa copulatrix (Runham, 1988:153–154), the posterior duct might instead transport 'old' sperm to this organ from the seminal receptacle for digestion. The fact that this duct often contained oriented sperm supports the latter hypothesis, although it is possible that the duct (and perhaps even the portion of the bursa to which it opens) also may serve as an additional site for storage of this sperm. Study of the ciliary currents within this duct will be needed to address further this question.

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