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Review of the North American aquatic snail genus *Probythinella* (Rissooidea: Hydrobiidae)

Robert Hershler

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA

Abstract. The aquatic gastropod genus *Probythinella* THIELE is redefined and proposed as a monophyletic subunit (sister to *Cincinnatia*) within the North American component of the family Hydrobiidae (Prosobranchia: Rissooidea) on the basis of synapomorphies of blunt shell apex, presence of two seminal receptacles, short albumen gland, and blunt terminus of penis. *Probythinella* is composed of two parapatric species that are distinguished by derived modifications of the outer edge of the operculum and pigmentation of the pallial roof and cephalic tentacles, and also differ in shell shape, thickness of outer shell lip, size of buccal mass (relative to shell height), and number of cusps on the lateral and marginal radular teeth. Species recognized are *Probythinella emarginata* (KÜSTER), distributed throughout the Mississippi River drainage and drainages of Great Lakes, Hudson Bay, and Mackenzie River; and *P. protera* PILSBRY, found in brackish waters along the eastern Gulf of Mexico.

Additional key words: systematic malacology, Prosobranchia, Mollusca, North America

Aquatic snails of the genus *Probythinella* THIELE 1928 comprise a small group of North American hydrobiids recognizable by the cylindrical spire and extremely blunt apex of their shells. Members of the genus are found throughout much of eastern North America in both inland freshwater habitats and brackish waters along the Gulf of Mexico. Despite the small size of the genus, its systematics remains confused and, in addition, neither monophyly of *Probythinella* nor its relationships to other hydrobiid genera have been established.

This study was prompted by my long-term interest in the systematics of Hydrobiidae in North America. These small prosobranch snails are ubiquitous members of fresh- and brackish-water communities, in which they often are among the more abundant benthic invertebrates (e.g., Noel 1954; Wells 1978), and comprise a significant element of taxonomic diversity in the region, with more than 45 genera (Kabat & Hershler 1993) and 170 Recent species (Turgeon et al. 1988) in current usage. This old (early Mesozoic; Kabat & Hershler 1993) group of obligately aquatic, poorly dispersing snails is tightly linked with drainage history (Taylor & Bright 1987), yet has not been used for studies of vicariance biogeography because of an absence of rigorous phylogenetic hypotheses. The inland hydrobiid fauna of North America, which includes many narrowly localized species, also is assuming importance in concert with efforts to protect and manage aquatic ecosystems: several species have already been added to the Federal List of Threatened and Endangered Wildlife, and more than 100 others currently are candidates for addition to this list (USDI 1994).

The purposes of this study were to determine, describe, and assess the distribution of the recognizable species of *Probythinella*; and to delineate character states that help define the genus as a monophyletic unit. The latter is proposed on the basis of a cladistic analysis of *Probythinella* and several possibly allied North American taxa. The resulting hypothesis of evolutionary relationships is tentative, as much of the North American hydrobiid fauna is poorly studied and the state of systematics of this huge family is chaotic (Kabat & Hershler 1993).

Thiele (1928) introduced *Probythinella* and designated the type species as *Paludina emarginata* KÜSTER 1852. The validity of this species name has proven controversial as some workers have argued that Küster did not describe a new taxon, but instead misidentified or transferred *Lymnaea emarginata* SAY 1821. Opinion also has been divided as to whether *emarginata* sensu KÜSTER is conspecific with an earlier described snail, *Paludina obtusa* LEA 1841. Although the type species of *Probythinella* was described during the middle of the 19th century and is one of the most widespread hydrobiids in North America, its anatomy still has not been thoroughly depicted. Although Baker (1928) and others illustrated the radula, while Berry (1943) figured the penis, even these few details have not been reported without errors, to wit, the assertion that the outer marginal radular teeth of the type species lack cusps (Berry 1943:38, plate III, fig. 5; Clarke 1981: 58). A second, distinctive species, *Probythinella protera* PILSBRY 1953, was later described from putative Pliocene beds in St. Petersburg, Florida. Solem (1961) documented an extant population in Lake Pontchartrain which he referred to this species, whereas Morrison (1965) named a new genus and species for this population, *Vioscalba louisianae*. The possible conspecificity of the extant coastal populations and fossil *protera* remains unresolved (Heard 1979).

Methods

Types and other dry shell lots from major museum collections were examined during the course of this review. In addition, living snails (of the type species) and preserved material (for both species) were studied for anatomical details. Animals were dissected in dilute Bouin's Solution using fine forceps and minute insect pins mounted on wooden sticks. Sections were cut at 4 μm and stained with hematoxylin and eosin. Shells, opercula, radulae, and dried heads and penes were studied using a Hitachi S-570 scanning electron microscope (SEM). Tissue was dried using a Denton DCP-1 critical point drier. A complete morphological description that applies to both recognized species is provided in the genus account. Species descriptions focus only on features useful in distinguishing between these taxa. Anatomical study of the type species was more detailed than that of *P. protera,* owing to the paucity of suitable material for the latter. See Appendix for listing of material examined and abbreviations for institutions. Many of the characters used in the phylogenetic analysis were from a comprehensive list that is being prepared for the family Hydrobiidae (Hershler & Ponder, unpubl.). Data used in this analysis were obtained by direct observations as well as from the following literature sources: *Cincinnatia* (Thompson 1977; Hershler & Thompson, in press); *Fluminicola* (Hershler & Frest, in press); *Hydrobia* (Muus 1963; Bandel 1975; Fish & Fish 1977, 1981; Hershler & Davis 1980; Davis et al. 1982, 1989); *Nymphophilus* (Taylor 1966b; Thompson 1979; Hershler 1985); *Pristinicola* and *Taylorconcha* (Hershler et al. 1994); and *Tatea* (Ponder et al. 1991). Phylogenetic hypotheses were generated using HENNIG86 (Farris 1988) for parsimony analysis. Multistate characters were unordered. Owing to the relatively small size of the data set, an exact method was used ("ie*"), which is guaranteed to find all minimum-length trees. The "nelsen" option was used to generate a consensus cladogram. CLADOS 1.3 (Nixon 1992) was used to study character state evolution and generate the published cladograms.

Systematics

Genus *Probythinella* THIELE

Probythinella THIELE 1928:370, 378. Type species, *Paludina emarginata* KÜSTER 1852; monotypy.

Vancleaveia BAKER 1930:189. Type species, *Paludina emarginata* "KÜSTER" (SAY 1821); subsequent designation, Pilsbry 1935:562.

Vioscalba MORRISON 1965:217. Type species, *Vioscalba louisianae* MORRISON 1965; original designation.

Diagnosis. A North American brackish- and freshwater group of medium-sized hydrobiid snails having a smooth shell with medium spire and blunt apex. Operculum thin, simple. Cephalic tentacles having well-developed ciliary tracts. Ctenidium well developed, osphradium fairly large. Radula typically hydrobiid, but very small, with numerous cusps on all teeth. Stomach with large posterior caecum. Male and female genital glands having complex histology. Female oviparous, having simple coiled oviduct, two seminal receptacles, and a posterior bursa copulatrix. Albumen gland much shorter than capsule gland. Bursal duct opening to closed ventral channel. Male having large prostate gland. Penis gently tapering, lacking specialized glands, having prominent lobe along inner edge. Distal penis blunt, with terminal papilla.

Description. Shell (Figs. 1, 2A, 7A): sub-globose to narrow-conic, sub-cylindrical, or pupoidal; having narrow umbilicus. Apex (Figs. 2B,C, 7B) flat or slightly depressed; protoconch (Figs. 2D–G, 7C) near planispiral, surface having well-developed reticulate wrinkled pattern in early portion. Peristome complete across body whorl at maturity. Aperture markedly constricted in one species (Fig. 7A). **Operculum** (Figs. 2H,I, 7D,E): ovate, having eccentric nucleus, slightly concave, transparent, clear-light brown. Outer surface smooth or weakly frilled, sometimes having weak spiral scratches near outer edge; inner surface lacking obvious thickenings or muscle scar. **General anatomy**: animal moderately pigmented. Tentacles considerably longer than snout, slightly tapered distally. Dorsal snout having numerous small clusters of cilia; distal portion moderately lobate. Oral lips fringed with thick ciliary tufts (Fig. 7F). Portion of head behind right tentacle strongly ciliated (Fig. 4A). Foot ovate, anterior end indented, lateral wings well developed, posterior end rounded. Cephalic tentacles (Figs. 4A–E, 7G,H) having well-developed longitudinal ciliary tracts on dorsal surfaces; left tentacle also having weakly developed transverse ciliary bands. Ventral surfaces of tentacles densely ciliated throughout. Eyes present. Anterior pedal gland of numerous small units. Body spaces with little connective tissue. Cerebral and pedal commissures fairly short (40–50% of ganglion width); pleuro-supraoesophageal commissure medium length; left pleural and suboesophageal ganglia connected by short commissure. **Pallial cavity**: ctenidium extending to near pallial edge, overlapping pericardium posteriorly, efferent vein short. Filaments numerous, broadly triangular (slightly wider than tall), plicate, free edge weakly convex, apices on right. Osphradium elongate (ca. 35–40% of ctenidium length), anterior end simple, positioned between posterior end and middle of ctenidium. Hypobranchial gland medium thickness, covering rectum, pallial genital ducts, and right side of posterior pallial roof. Renal organ having little or no pallial bulge. Renal gland well developed, longitudinal, on left side of renal organ, abutting pericardium. Pericardium without bulge in pallial roof. **Digestive system**: jaws present. Radula protruding behind buccal mass as short coil. Central radular teeth (Figs. 3B, 8A) trapezoidal; basal region medium excavated; basal tongue rounded, about as long as lateral angles; basal cusps, several, innermost cusps slightly enlarged, arising from intersection of lateral angles and tooth face. Lateral teeth (Figs. 3C,D, 8B) clavate, with elongate outer wing, dorsal edge straight. Central cusps of central and lateral teeth pointed, slightly enlarged. Later and marginal teeth having numerous small cusps. Inner marginal teeth (Figs. 3F,H, 8C,D) having weak flange along inner edge; outer marginal teeth (Figs. 3H,I, 8C,E) having short flange along outer side near base. Dorsal folds of oesophagus simple, medium length. Salivary glands short, nearly straight. Stomach and style sac about equal in length; stomach chambers equal in size. Stomach with single opening to digestive gland and large posterior caecum. Rectum nearly straight within pallial cavity. Anus simple, positioned well anterior to female genital aperture near pallial edge. **Female reproductive anatomy** (Fig. 5A–D): ovary of simple vertical lobes, overlapping posterior and part of anterior stomach chambers, filling most of length of visceral coil behind stomach. Oviduct exiting ovary slightly behind anterior edge. Coiled oviduct a simple loop lacking a sheath of connective tissue. Oviduct opening to albumen gland ventrally at junction between albumen and capsule glands. Bursal duct joining oviduct slightly behind posterior pallial wall. Posterior seminal receptacle usually medium-sized (66–80% of length of bursa copulatrix) and ovate, pressed against left side of bursa copulatrix, opening to distal arm of coiled oviduct near ventral edge; duct short. Wall of posterior seminal receptacle internally folded, comprised of cuboidal cells, covered with thin muscular coat; lumen containing oriented sperm. Anterior seminal receptacle small, pouch-like, having histology similar to posterior seminal receptacle, lying against left side of albumen gland, opening to oviduct just distal to oviduct coil and just posterior to opening of bursal duct; duct medium length (about 1/4–1/2 length of body of seminal receptacle). Bursa copulatrix orange, as long or longer and as wide as albumen gland, positioned almost entirely posterior to albumen gland (anteriormost portion on left side of gland), pyriform to nearly lenticular, anterior edge blunt. Bursa copulatrix comprised of columnar cells having basal nuclei, lined with thin muscular coat. Bursal duct medium-elongate, exiting from anterior edge dorsal to mid-line, medium width, lying against left side of albumen gland. Albumen gland white, simple shape, only 1/2 length of capsule gland (but equal in width), lacking pallial component. Capsule gland green, simple shape; anterior portion staining darker in section; opening a short slit. Ventral channel of capsule gland having thin, non-glandular ventral wall (Fig. 5D); longitudinal fold weakly developed on left side. Albumen gland with distinct rectal furrow. Genital aperture without anterior expansion. **Male reproductive anatomy** (Fig. 5E,F): testis of compound vertical lobes overlapping both stomach chambers, filling most of length of visceral coil behind stomach, draining to narrow vas efferens. Vas deferens exiting from testis about 1/3 distance back from anterior edge; coursing posteriorly (for 1/2 whorl) as narrow, straight tube; and then bending back anteriorly (and dorsally) as thickened seminal vesicle that undulates along entire length to near prostate gland. Prostate gland (Fig. 5E) bean-shaped, broad or elongate, oval in transverse section, ventral wall glandular; about 1/3 of length in pallial roof. Pallial vas deferens exiting from midway between posterior pallial wall and anterior end of prostate gland. Posterior pallial vas deferens wrapping around edge of prostate gland, coiling alongside rectum in front of gland (covered by hypobranchial gland), and bending back and weakly coiling on columellar muscle; duct loosely bound in connective tissue. Anterior pallial vas deferens opening to "neck" about mid-length of pallial cavity, strongly undulating beneath epithelium. Penis (Figs. 4F,G, 5E, 7H) large relative to head; positioned slightly behind head, centrally or slightly to left of mid-line, gently tapering, flattened in transverse section, base slightly expanded. Penis surface smooth or weakly folded proximally. Penis bearing large, strongly tapering lobe along inner edge slightly distal to mid-length; distal edge of penis blunt. Dorsal penis variably ciliated proximally; distal tip (Figs. 4H, 7I) strongly ciliated. Penial opening a short, broadly triangular, terminal, non-eversible papilla. Penial duct having medium thickness muscular coat, lined internally with long cilia; rather broad, near outer edge, undulating along most of length.

Remarks. Thiele (1928) described *Probythinella* as a "section" under *Cincinnatia* (p. 370; later in the same paper he placed it under *Hoyia*, p. 378), and placed the genus in the tribe Lyogyreae, subfamily Hydrobiinae. He conjectured a close relationship with *Cincinnatia* on the basis of shared small radula and finely denticulate teeth, but distinguished *Probythinella* by its blunt apex, straight anterior (dorsal) edge and three basal cusps on central radular teeth, and feeble, finely cuspate lateral teeth. Baker (1930) separated *Probythinella* from *Cincinnatia* based on the larger number of basal cusps on the central radular tooth and blunt apex of shell. Baker (1930) did not explicitly indicate a type species when describing *Vancleaveia*, although he placed *emarginata* and its junior synonyms in the genus. Pilsbry (1935) later designated *emarginata* as the type species of *Vancleaveia*, and placed the genus in synonymy with *Probythinella*. Pilsbry (1935) compared *Probythinella* to western American (fossil) *Brannerillus*, also having blunt apex. Morrison (1965) later described *Vioscalba* and placed this genus in the Hydrobiinae, using his earlier (1949) broad definition of this subfamily as all hydrobiids having a simple (i.e., with single internal duct) penis. Morrison emphasized the unusual *Stenothyra*-like shell when describing *Vioscalba* and did not compare this novelty to *Probythinella*, but instead to the eastern North American genus *Notogillia*. Heard (1979) later suggested that *Vioscalba* is a junior synonym of *Probythinella*. Taylor (1966b) reiterated placement in the Hydrobiinae, and noted the similarity of penes of *Probythinella* and brackish-water species of *Hydrobia*. This placement was followed in the recent compendium of Vaught (1989). Starobogatov (1970) later placed *Probythinella*, without justification, in the subfamily Nymphophilinae, which he inexplicably allocated to the family Bithyniidae. Andrews (1977) transferred the genus *Vioscalba* to the Stenothyridae, presumably based on Morrison's (1965) observation that the constricted aperture of one of the species resembled that of the genus *Stenothyra*. Hershler & Holsinger (1990) allocated *Probythinella* to the Littoridininae (= Cochliopinae; also see Bernasconi 1992:14), based on the supposed presence of a separated sperm tube in the distal female genitalia (diagnostic of this subfamily), but this observation was later discovered to be in error (Hershler & Thompson 1992).

Probythinella emarginata (Küster)

(Figs. 1B–D, 2–5)

Paludina emarginata Küster 1852:50, plate 10, figs. 3, 4. [North America; holotype, MZC 105, Fig. 1B].—Binney 1865:85, fig. 169 (in synonymy of *Amnicola cincinnatiensis*).—Pilsbry 1935:562 (footnote; in synonymy of *binneyana*).—Berry 1943:36 (in synonymy of *binneyana*).—Morrison 1947:27 (in synonymy of *limafodens*).—La Rocque 1968:394 (in synonymy of *lacustris*).

Amnicola emarginata.—Frauenfeld 1863:1030.—Frauenfeld 1864:603.—Baker 1902:336-337 (in part).—Dall 1905: 118 (in part), fig. 86 (Canada records).—Baker 1906:94 (Illinois records).—Chadwick 1906:23 (Wisconsin record).—Sterki 1907:387 (Ohio records).—Over 1915:93 (South Dakota records).—Winslow 1921:15 (North Dakota records).—Whittaker 1924:11 (Canadian records).—Henderson 1927:20 (South Dakota record).—Goodrich & Schalie 1944:300 (Indiana records).—Dawley 1947:693 (Minnesota record).—Tuthill 1962:16 (North Dakota record).

Amnicola cincinnatiensis.—Binney 1865:85 (in part).

Bythinella obtusa.—Tryon 1870:48.—Keyes 1888:73 (Iowa records).—Walker 1893:139 (Michigan records).—Call 1900:414 (Indiana records), plate 8, fig. 18.—Shimek 1904:379 (Nebraska record).

Bithynella obtusa.—Nutting 1893:292 (Canadian record).

Cincinnatia emarginata.—Walker 1901:32 (in part).—Baker 1928:126–127 (in part), fig. 54 (1, 2).—Thiele 1928:369-370, fig. 22 (radula).—Hoff 1943:226 (Tennessee record).—Hibbard & Taylor 1960:80 (in synonymy of *lacustris*).

Amnicola (*Cincinnatia*) *emarginata*.—Walker 1918:136 (in part).

Hoyia (*Probythinella*) *emarginata*.—Thiele 1928:378.—Thiele 1929:140, fig. 115.

Cincinnatia emarginata lacustris Baker 1928:127–130, plate VII, figs. 20, 21; [text] figs. 54 (3, 4) [Winnebago Lake, near Oshkosh; holotype, UMMZ 216532; paratype, UIMNH Z12676, Fig. 1C].—Franzen 1957:31.

Cincinnatia emarginata canadensis Baker 1928:130–131, fig. 54 (7, 8) [Lake Kakisa near mouth of Beaver River, west of Great Slave Lake, about latitude of 61°N (emended to Lake Kakisa near mouth of Kakisa River; Clarke 1973:250); holotype, UIMNH Z22510a, Fig. 1D; paratype, UIMNH Z22510b].—Franzen 1956:23.—Hibbard & Taylor 1960:80 (in synonymy of *lacustris*).—Clarke 1973: 250 (in synonymy of *lacustris*).

Vancleaveia emarginata canadensis.—Baker 1930:189–191, fig. 2, parts 3–5,10, fig. 3 (in part).

Vancleaveia emarginata emarginata.—Baker 1930:191, fig. 2, parts 1, 2, 9; fig. 3 (in part).

Vancleaveia lacustris.—Baker 1930:191, fig. 2, part 10, fig. 3 (in part).

Amnicola (*Probythinella*) *binneyana*.—Berry 1943:36–41 (in part; anatomical and ecological details), map 5 (Michigan records); fig. 5; plate I, figs. 8–12; plate III, fig. 5; plate VI, fig. 2; plate VII, fig. 5.

Probythinella lacustris lacustris.—Morrison 1947:27.
Probythinella lacustris canadensis.—Morrison 1947:27.
Probythinella lacustris limafodens MORRISON 1947:27 [Proposed as replacement name for *Paludina emarginata* sensu KÜSTER 1852.]—Branson 1959:225 (Oklahoma records).—Hibbard & Taylor 1960:80 (in synonymy of *lacustris*).—Clarke 1973:250 (in synonymy of *lacustris*).—Rosewater 1984:5.
Amnicola (Probythinella) binneyana.—La Rocque 1953:269 (in part; Canada records).—Robertson & Blakeslee 1948: 85 (in part; New York records), plate X, fig. 15.
Amnicola (Probythinella) emarginata emarginata.—La Rocque 1953:269 (in part; Canada records).
Amnicola (Probythinella) emarginata canadensis.—La Rocque 1953:270 (Canada records).
Amnicola (Probythinella) lacustris.—La Rocque 1953: 270.—La Rocque 1968:394–396 (in part; Ohio records), plate 10, figs. 8–12, fig. 248.
Probythinella emarginata.—Pilsbry 1953:445.—Taylor 1975:79.
Probythinella lacustris.—Hibbard & Taylor 1960:80–84 (in part; Pleistocene Kansas records; ecological details), plate IV, figs. 1, 2, 5, 6; fig. 5).—Miller 1966:225 (Pleistocene Oklahoma record).—Miller 1970:41 (Pleistocene Kansas record).—Clarke 1973:250–253 (in part), plate 21, fig 5; map 48 (Canada records).—Taylor 1975:108.—Burch & Tottenham 1980:100, figs. 107, 129–131.—Clarke 1981: 58, figure and map (Canada records) on p. 59.—Smith 1981:177.—Cvancara 1983:63, fig. 43 (North Dakota records), plate 4, fig. 13.—Taylor 1985:300, fig. 28 (in part; western records).—Pip 1986:tables 1–7 (ecological details).—Burch & Jung 1988:247–248, fig. 21.—Turgeon et al. 1988:62.—Jokinen 1992:25 (New York records), fig. 9b.
Amnicola binneyana.—Tuthill 1963:30 (North Dakota record).—Bickel 1968:23 (Tennessee records).—Harman & Berg 1971:49 (in part), figs. 178, 180 (New York distribution).
Amnicola lacustris.—La Rocque 1967:plate 8, figs. 1, 2, 5, 6.
Amnicola (Probythinella) lacustris.—La Rocque 1968:394–396, fig. 247, plate 10, figs. 8–12.
Probythinella limafodens.—Taylor 1975:113.
Probythinella binneyana.—Gordon 1982:350 (Arkansas record).

Diagnosis. Distinguished from *P. protera* by deeper sutures of the shell whorls, and unconstricted aperture with fairly thin lip. Also differs by presence of longitudinal pigment stripes on tentacles and dark bands along the pallial roof, rim along outer edge of operculum, smaller buccal mass, and more numerous cusps on lateral and marginal radular teeth.

Description (anatomical details principally from UF 175879, UF 224044, USNM 883915). Shell (Figs. 1B–D, 2A) sub-globose to narrow-conic or sub-cylindrical; height, typically about 4.0 mm, ranging from 2.4–5.0 mm; width/height, 0.61–0.71. Whorls, 4.0–5.25, inflated, slightly convex to well rounded, often strongly angled or shouldered below suture, rarely with weak angulation at periphery; suture impressed. Umbilicus near absent or narrow slit to perforate, slightly obscured by columellar lip. Apex blunt or depressed, often tilted, convex. Body whorl rarely abruptly descending toward end of growth. Protoconch 1.3–1.5 whorls, near planispiral, suture impressed; diameter about 270 μm. Protoconch sometimes having weak spiral scratches; reticulate sculpture weakening near beginning of teleoconch. Teleoconch sculptured with strong, regularly spaced collabral striations extending from suture to base of whorl. First whorl sometimes planorboid, depressed. Aperture prosocline, sometimes weakly so; ovate, sometimes weakly angled above, sometimes slightly expanded along columellar base. Peristome usually narrowly adnate, sometimes slightly separated. Outer and columellar lips thin or moderately thickened internally; columellar lip slightly reflected. Shell clear-white, transparent. Periostracum light tan.

Outer edge of operculum having weak rim. Snout brown-black proximally, pigment weaker distally; lips pale; snout also containing large white granules near sides. Head, buccal mass dark. Dorsal surfaces of tentacles having two black longitudinal bands near edges flanking narrow pale strip containing white granules; pigment bands weakly developed on ventral surfaces. Bases of tentacles containing large cluster of yellow granules. Sides of head pale. Dorsal surface of foot pale or light gray. Pallial roof usually having black bands along sides of ctenidium; areas covering ctenidium and glandular gonoducts pale. Visceral coil grey-black dorsally. Penis pale or grey-black on portion of dorsal surface. Ctenidial filaments 32–37. Renal organ with little or no pallial bulge. Opening of renal aperture pale. Circum-oesophageal ganglia lightly pigmented. Pleural-supraoesophageal commissure about 130–150% combined lengths of ganglia.

Buccal mass small, positioned well anterior to nerve ring. Radular ribbon about 400–500 μm, about 3–3.5 times as long as wide, with about 45–55 rows of teeth. Central teeth trapezoidal, width about 15–18 μm; dorsal edge slightly concave. Basal cusps, 2–3. Cutting edge with 5–6 lateral cusps. Basal tongue of lateral teeth weakly developed. Outer wing about 230–270% longer than cutting edge. Lateral cusps 7 (inner side) to 18–20 (outer side). Inner marginal teeth with about 33 cusps extending along outer edge for about 50% length of tooth at upper end; teeth with weak flange along inner edge. Outer marginal teeth with about 18 cusps extending along inner side for about 40% of length of tooth at upper end. Salivary glands entirely anterior to nerve ring.

Testis 1.5 whorls (animal 3.5 whorls). Prostate gland broad. Ovary about 1.75 whorls (animal 3.0 whorls). Coiled oviduct a single narrow U-shape to almost circular loop. Bursa copulatrix about as large as albumen gland. Bursal duct 66–80% of bursa length. Genital aperture simple.

Distribution. Lotic and lentic inland habitats throughout the Mississippi River basin; drainages of Great Lakes, Hudson Bay, and Mackenzie River to the north (Fig. 6).

Remarks. Küster (1852) described *Paludina emarginata* SAY, which he also listed as *Limnaeus emarginatus* SAY teste BRONN. He did not explicitly state that he was describing a new species, and the validity of his name has remained controversial. Küster's types have never been studied as a unit, and are not known to be concentrated in a single repository. In the case of *emarginata,* Küster indicated that his material was from Director v. Charpentier (Jean de Charpentier, 1786–1855), whose shell collection was deposited at the Musée Zoologique de Lausanne (Forcart 1950). A single, one-specimen lot (MZC 105; Fig. 1B) corresponding to this material was found at this institution. The label reads *Paludina* (originally "*Limnaea?*" but crossed out) *emarginata,* and below, "Bronn, 1844." Further notes indicated that the material came from Heidelberg (where Bronn worked), and thus I conclude that this was Bronn's material and identification. Küster's Latin description (translated in Binney [1865:86]) indicated a small, narrowly rimate, ovate-conic shell with deep sutures and eroded apex. Additional German text reiterated this and also gave the dimensions of the specimen as 1.67‴ tall and 1‴ wide (= 3.6 × 2.2 mm; fide conversion of German linie provided by Abbott [1974, flyleaf]), which corresponds to the size of the "natural" [actual-sized] figure of Küster. The MZC specimen is 3.8 × 2.1 mm, closely resembles Küster's figure, and almost certainly is his specimen. Although the shell has an eroded apex, it is nevertheless identifiable as a slender example of the widespread inland species of *Probythinella.* Walker (1901:31–32) suggested that Cuming material in the British Museum (referred to by Frauenfeld 1863) corresponds to Küster's figure. I have examined this lot (BMNH 1994135), and corroborated its identity as *emarginata,* but see no reason for supposing that it represents Küster types.

Several workers (notably Pilsbry 1935; Berry 1943; Morrison 1947; Clarke 1973; Burch 1982) rejected *emarginata* KÜSTER as a valid name for this hydrobiid and instead treated his usage as a misidentification or transfer of *emarginata* SAY. Morrison (1947) introduced a new name, *Probythinella lacustris limafodens* for the hydrobiid which Küster described and illustrated. Clarke (1973:253) explicitly pointed to ICZN Article 49 as grounds for rejection of *emarginata* KÜSTER. Note, however, that under this Article an exception is made (and the name in question remains available) when a previous misidentification is deliberately used in fixing the type species of a new nominal genus (ICZN Article 11i), which one may argue is what Thiele (1928) did when listing *Paludina emarginata* (obviously sensu) KÜSTER as the type species of *Probythinella* (although authorship of the species would be attributed to Thiele in this situation; fide above article). Given that Küster, a malacologist having considerable knowledge of freshwater snails, had hydrobiid material before him, I concur with Walker (1901, 1918) that it seems very unlikely that he either misidentified this as the well-known North American lymnaeid (*Stagnicola emarginatus*) or that he meant to transfer the latter to *Paludina.* Instead, it is clear (from the above paragraph) that he was restricting his description to the material he had in hand, which he referred to as *emarginata* SAY teste BRONN. The fact that he did not propose a new specific name, and first attributed the species solely to Say, may be viewed as a lapse, and thus I view *Paludina emarginata* "SAY" KÜSTER 1852, as a validly described species meeting the criteria of ICZN Article 12. Given that Küster evidently based this species on a single specimen, I identify this shell (MZC 105) as the holotype by monotypy (per ICZN Article 73(a)(ii)).

Baker (1928) divided *Cincinnatia emarginata* into several subspecies. He introduced *lacustris* as a small, globose, lacustrine form from Lake Winnebago, Wisconsin; and *canadensis* as a large, elongate lacustrine form from drainage of Great Slave Lake in Canada. He identified the nominotypical form (under which he subsumed *obtusa*) as riverine, medium-sized, elongate, but wider and more convex than *canadensis.* He also referred to shape of protoconch and number of planispiral apical whorls in distinguishing these taxa. Baker (1928) gave the type locality of *canadensis* as Lake Kakisa, near mouth of Beaver River, and indicated that the material was collected by Whittaker. As noted by Clarke (1973:250), it is likely that this collection instead was from a locality referred to by Whittaker (1924:9) as "south shore of Lake Kakisa, near mouth of Kakisa River." Modern maps do not show a Beaver River near the west side of Great Slave Lake, but it is listed as equivalent to Kakisa River in USDI (1953:28). Baker (1930) later elevated *lacustris* to a separate species, based on its wide shell and larger number of planispiral apical whorls. Regarding the status of Baker's taxa, I see no reason to dispute Berry (1943), who noted that transitional specimens could be found linking the lacustrine and riverine forms, and suggested that these should be regarded as ecological variants not requiring formal treatment. This opinion was later echoed by Morrison (1947) and Clarke (1973). Hibbard & Taylor (1960) pointed out that variation within the widespread inland species is not consistently correlated either with habitat or geography.

Fossil records from Lake Pleistocene lake beds of southeastern Idaho reported by Miller (1963:703) and others (Bright 1967:2; Taylor 1985:300; as *Probythinella lacustris*) are well westward of other known occurrences. Smith (1981:177) mentioned this occurrence with reference to a putative early hydrographic connection between the Bonneville Basin and the Hudson Bay drainage. Neither Miller nor subsequent workers illustrated this material and I have not been able to locate the USGS collections that formed the basis of this discovery. I have, however, examined two lots of Pleistocene material collected by Bright from this region and attributed to this species (UMMZ 230061, UMMZ 230259). Although this material is somewhat similar to *Probythinella,* these shells have a more acute spire and frequently protruding apex. Given these differences, I am reluctant to accept these shells as *Probythinella* in the absence of additional evidence. It is worth noting that the genus *Pyrgulopsis* is common in late Cenozoic lake deposits of the Bonneville Basin (Taylor 1966a, 1985; Taylor & Bright 1987; as *Fontelicella*) and sometimes resembles *Probythinella* in overall appearance of shell.

Species confused with *Probythinella emarginata.* *Paludina obtusa* Lea (type locality, "Ohio") is similar to the widespread inland species of *Probythinella,* but is smaller (2.3–2.5 mm), has a much larger protoconch (diameter ca. 0.55 mm), and has strongly angled shoulders on the whorls (Hibbard & Taylor 1960:83). Additionally, the protoconch (from SEM study of paralectotype, USNM 853167), which is flat but not depressed, has well-developed spiral striae (overlapping a background of weak wrinkles), which are not known in *Probythinella.* Placement of this species by early workers varied and more recently Morrison (1947; also see Hubricht 1976; Burch 1982) transferred the species to *Fontigens,* which has a somewhat similar shell shape, including an occasionally blunt apex and spirally striated protoconch (see Hershler et al. 1990, figs. 2a,c, 13g, etc.). Although the only record for *Fontigens* from Ohio is a single sample of the type species, *F. nickliniana,* from along the Ohio River (Hershler et al. 1990), I now contend (contra Hershler et al. 1990: 43) that *obtusa* probably does belong in this genus, and certainly not in *Probythinella.*[1]

[1] Lea (1841) described *Paludina obtusa* from "Ohio" and indicated that the material was provided by Dr. Kirtland, a frequent correspondent (Scudder 1885) who collected throughout the state (Silliman 1878). Kirtland's published works provide no details on the type locality. Lea later (1844) further described this species, emphasizing the blunt apex and pupiform aspect of the shells, and indicated that his material comprised a two-specimen lot. Morrison (1947) identified USNM 121394 as these syntypes. Original labels are lacking for this lot, but given that it consists of two specimens, was collected from "Ohio" and is from the Lea collection (*ex* Kirtland), and conforms to Lea's description, it may be assumed to be Lea's syntypes. Lea did not figure this species, but gave the (shell) length and width as 0.1 inch (2.25 mm) and .07 inch (1.6 mm), very close to measurements of the two shells comprising this lot. I selected the larger of the two specimens (which corresponds to that figured by Binney [1865, fig. 138]) as the lectotype (Fig. 1A). I have not seen any other material referable to this species and thus view it as represented by the unique type series. Early workers recognized *obtusa* Lea as a junior homonym (not Troschel 1837; Viviparidae), for which Hannibal (1912) later provided a replacement name, *Cincinnatia binneyana.*

Probythinella protera Pilsbry

(Figs. 1E,F, 7, 8)

Amnicola emarginata.—Clench 1925:12 (Texas record).
Probythinella protera Pilsbry 1953:444–445, plate 64; fig. 6 [Pliocene of St. Petersburg; holotype, ANSP 18589; Fig. 1E].—Solem 1961:158–159.—Clench & Turner 1962: 124.—Thompson 1968:12.—Richards 1968:178.—Heard 1979:310.—Vittor 1979:table 2 (Alabama records).
Vioscalba louisianae Morrison 1965:217–220, figs. 1, 2 [off Frenier Beach, in the southwestern part of Lake Pontchartrain](St. John the Baptist Parish, LA); holotype, USNM 635627; Fig. 1F; paratypes, USNM 635628, various lots distributed to many institutions].—Taylor 1975: 115.—Andrews 1977:85, unnumbered figure.—Rosewater 1984:5.
Vioscalba protera.—Morrison 1965:220.—Taylor 1975: 160.—Andrews 1977:85.
Probythinella profera [sic].—Ode 1965:4 (Texas record).
Probythinella louisianae.—Heard 1979:310–312 (eastern Gulf of Mexico records), figs. 1, 2.—Heard 1982:15.—Britton & Morton 1989:209, 211, fig. 8-4H.

Diagnosis. See that of *P. emarginata.*

Description (anatomical details principally from UF 231759, USNM 874156). Shell (Fig. 1E,F, 7A) ovate-conic to pupiform; height 2.5–3.5 mm; width/height, 0.56–0.71. Whorls, 4.5–4.75, slightly convex, rarely with slight shoulders; sutures shallow. Umbilicus absent or narrow, slit-like. Apex blunt or slightly protruding, rarely depressed, much more convex than later whorls. Body whorl abruptly descending near end of growth. Protoconch about 1.3 whorls, diameter about 240 µm. Early portion of protoconch surface wrinkled,

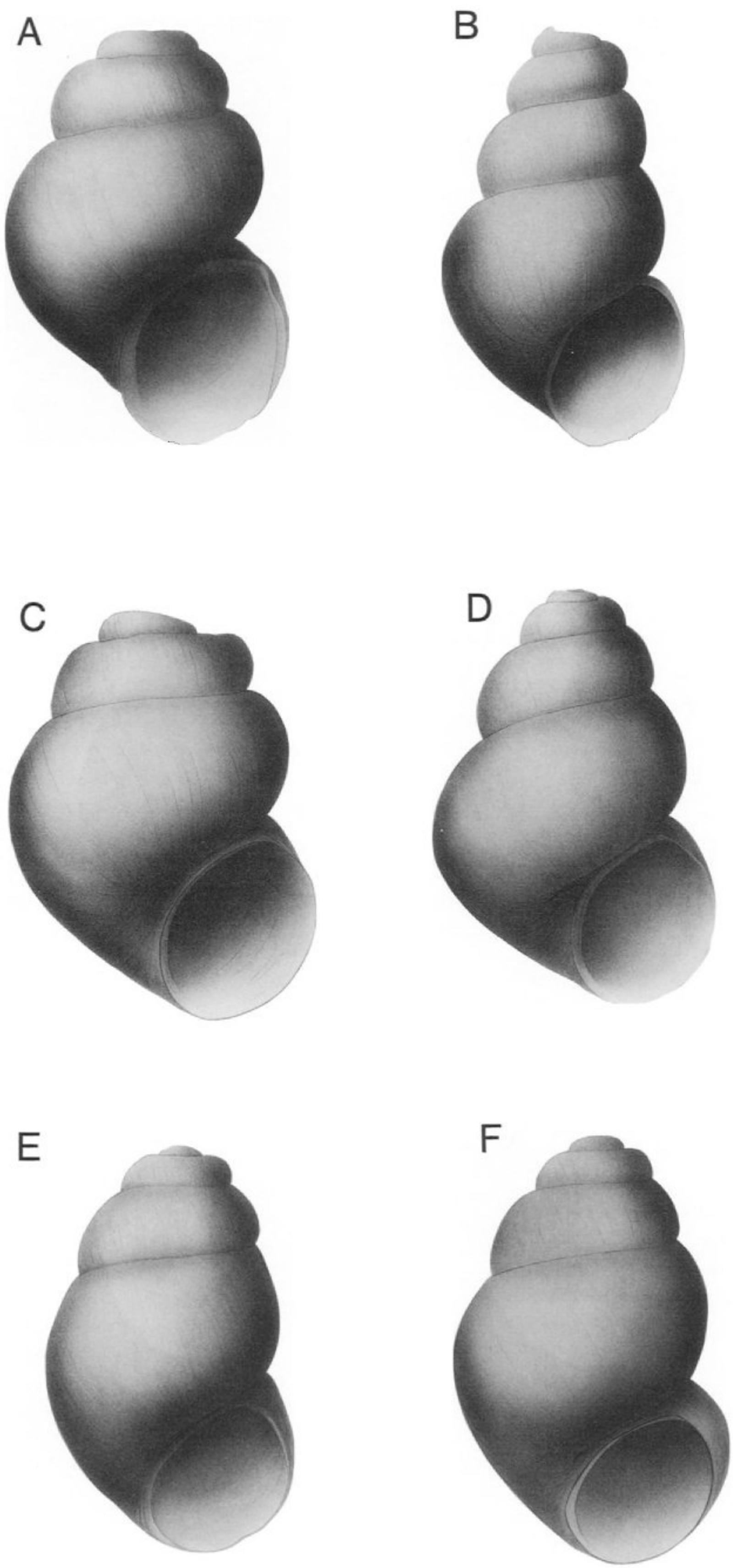


Fig. 1. Type material (shells) of taxa allocated to *Probythinella* in the literature. **A.** *Paludina obtusa* LEA 1841, lectotype, USNM 121394, 2.6 mm tall. **B.** *Paludina emarginata* KÜSTER 1852, holotype, MZC 105, 3.8 mm. **C.** *Cincinnatia emarginata lacustris* BAKER 1928, paratype, UIMNH Z12676, 3.2 mm. **D.** *Cincinnatia emarginata canadensis* BAKER 1928, holotype, UIMNH Z22510, 4.0 mm. **E.** *Probythinella protera* PILSBRY 1953, holotype, ANSP 18589, 3.1 mm. **F.** *Vioscalba louisianae* MORRISON 1965, holotype, USNM 635627, 3.5 mm.

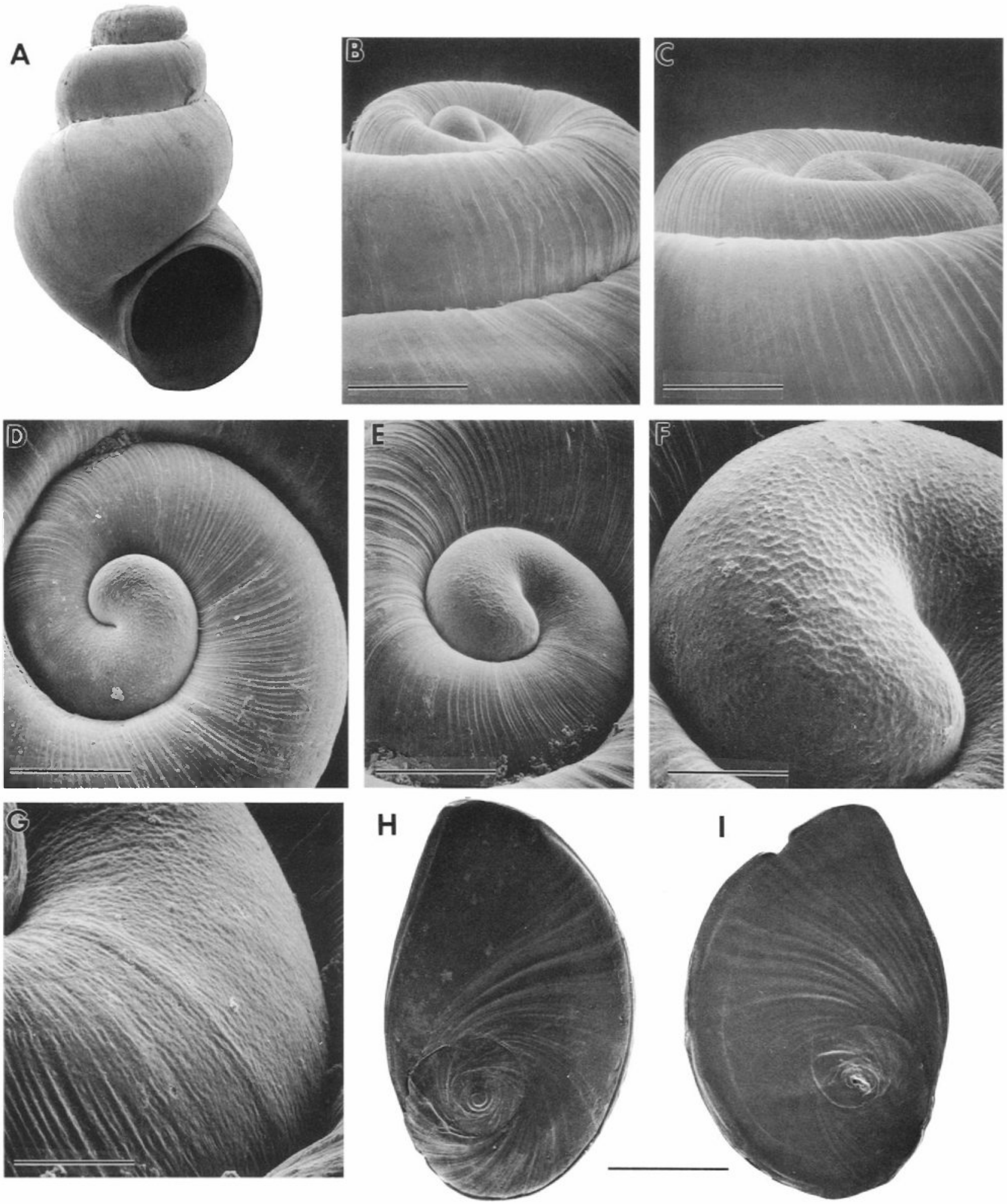


Fig 2. Shell and operculum of *Probythinella emarginata.* SEM. **A.** Shell, USNM 742064, 3.9 mm tall. **B.** Shell apex, showing sunken and tilted protoconch, USNM 27883, bar = 250 μm. **C.** Shell apex, showing slightly sunken protoconch, USNM 27883, bar = 150 μm. **D, E.** Shell apex, showing wrinkled protoconch, USNM 27883, bars = 150 μm, 136 μm. **F.** Close-up of early protoconch, showing microsculpture, USNM 27883, bar = 50 μm. **G.** Close-up of late protoconch-early teleoconch, showing microsculpture, USNM 27883, bar = 38 μm. **H, I.** Operculum, outer and inner sides, USNM 874884, bar = 0.5 mm.

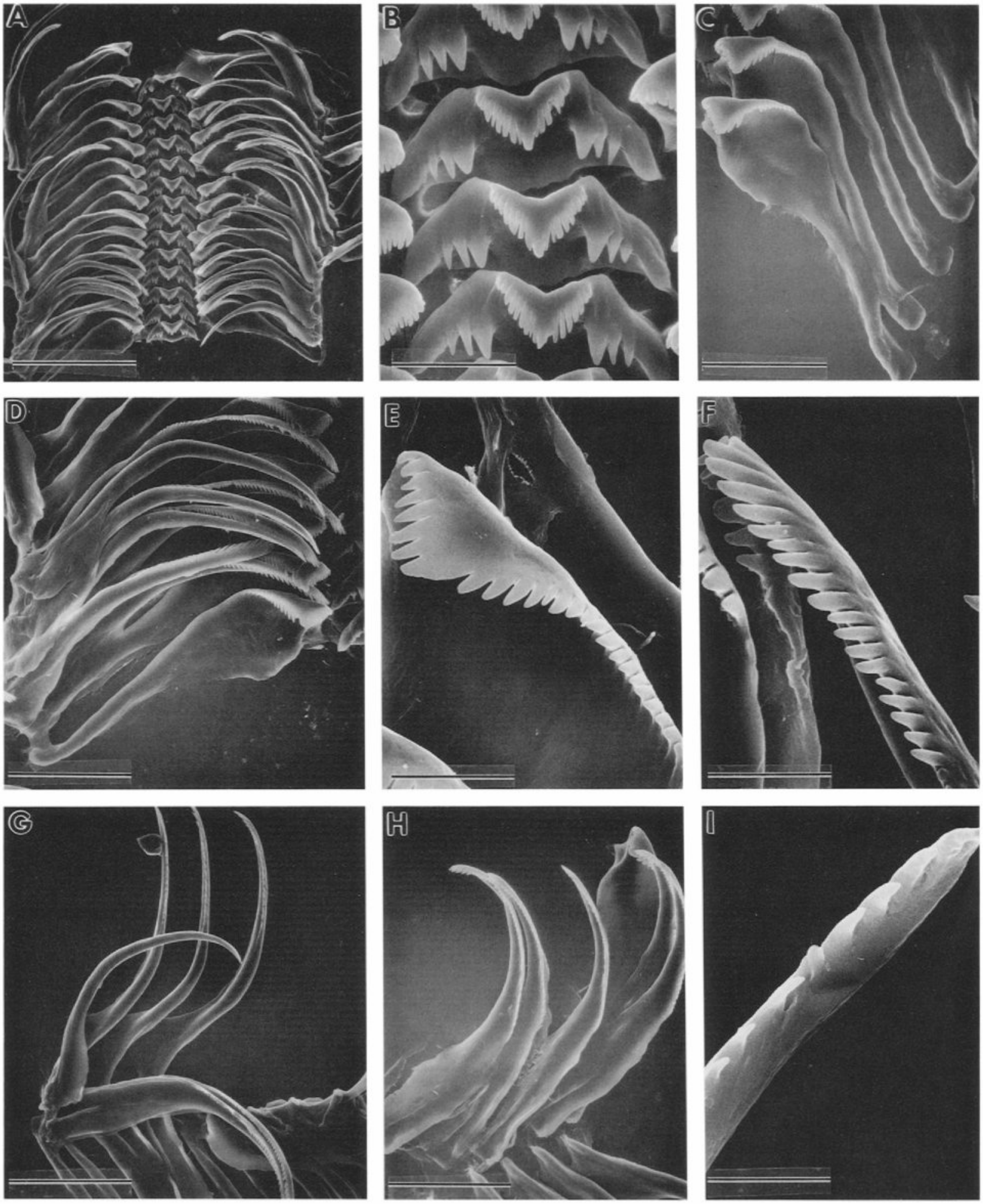
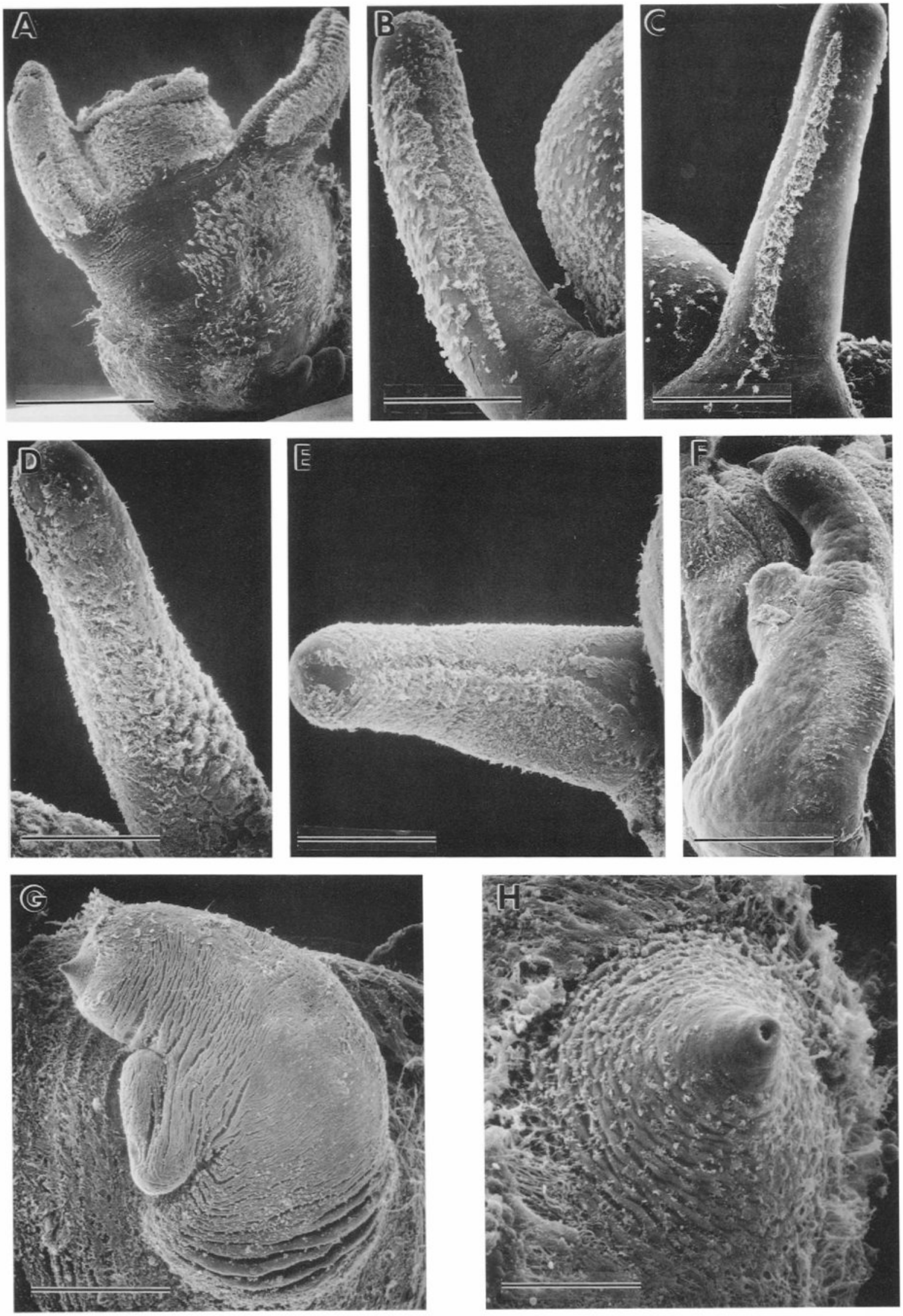


Fig. 3. Radula of *Probythinella emarginata.* SEM. **A.** Section of radular ribbon, showing all four tooth types, USNM 883915, bar = 60 μm. **B.** Central teeth, USNM 883915, bar = 10 μm. **C.** Lateral teeth, USNM 883915, bar = 20 μm. **D.** Lateral and marginal teeth, USNM 883915, bar = 20 μm. **E.** Close-up of cutting edge of lateral tooth, UF 224044, bar = 4.3 μm. **F.** Close-up of cutting edge of inner marginal tooth, UF 224044, bar = 3.8 μm. **G.** Marginal teeth, USNM 883915, bar = 25 μm. **H.** Lateral and inner marginal teeth, USNM 883915, bar = 25 μm. **I.** Close-up of cutting edge of outer marginal tooth, UF 224044, bar = 3.8 μm.


A
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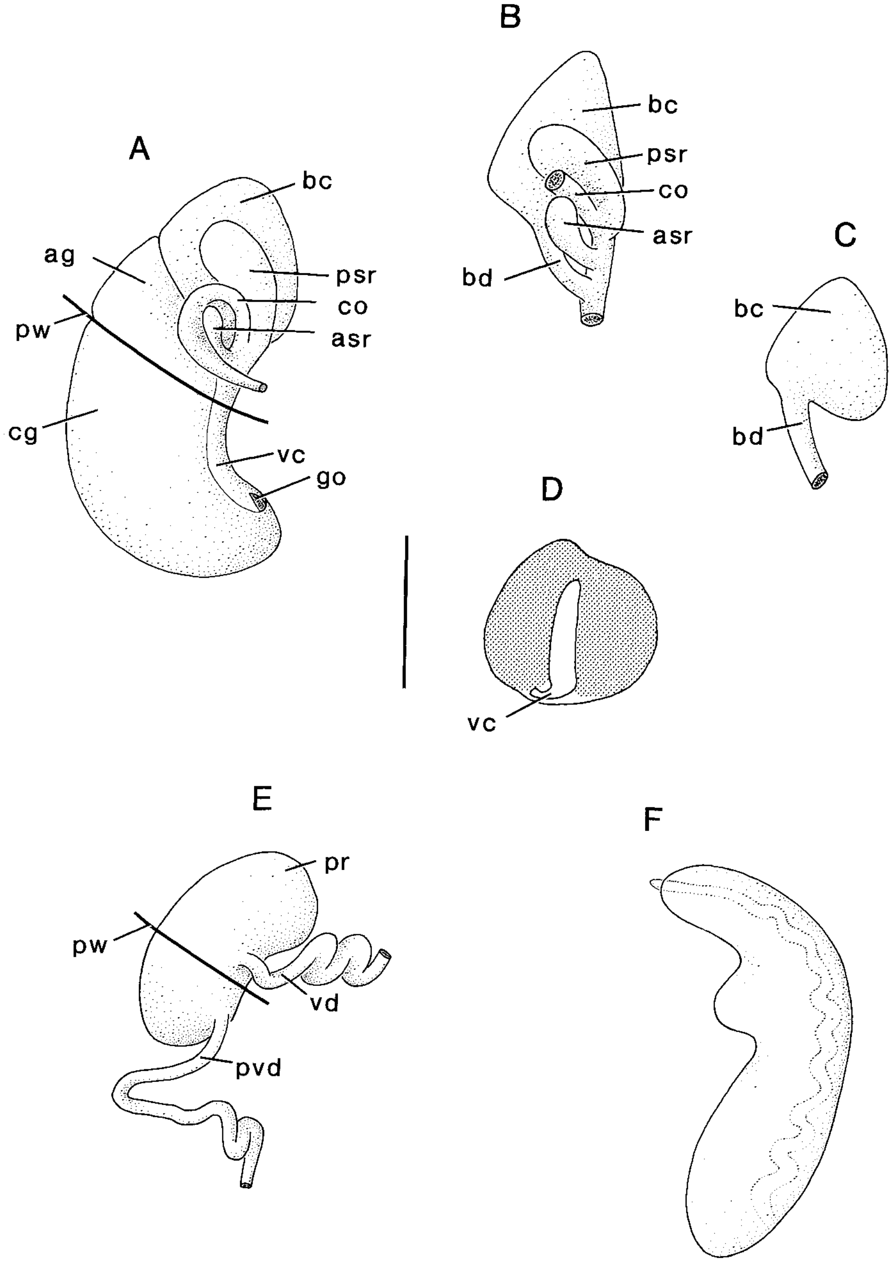

Fig. 5. Reproductive anatomy of *Probythinella emarginata.* **A.** Pallial oviduct and associated organs and structures, viewed from the left side, USNM 883915. **B.** Bursa copulatrix and associated structures, viewed from the left side, USNM 883915. The coiled oviduct has been cut to expose the anterior seminal receptacle. **C.** Bursa copulatrix and duct, USNM 883915. **D.** Transverse section of capsule gland, near mid-length, UF 175879. **E.** Prostate gland and vas deferens, viewed from the left side, USNM 883915. **F.** Penis, viewed from dorsal aspect, UF 224049. Scale bar = 0.5 mm. Abbreviations: ag = albumen gland, asr = anterior seminal receptacle, bc = bursa copulatrix, bd = bursal duct, cg = capsule gland, co = coiled oviduct, go = genital opening, pr = prostate gland, psr = posterior seminal receptacle, pvd = pallial vas deferens, pw = pallial wall, vc = ventral channel, vd = vas deferens.

←

Fig. 4. Heads and penes of *Probythinella emarginata,* critical point dried. SEM. **A.** Dorsal view of snout, cephalic tentacles, and head (note penis near bottom of picture), USNM 883915, bar = 380 μm. **B.** Left tentacle and portion of snout, dorsal aspect, UF 224044, bar = 176 μm. **C.** Right tentacle and portion of snout, dorsal aspect, UF 224044, bar = 231 μm. **D.** Left tentacle, ventral aspect, UF 224044, bar = 136 μm. **E.** Right tentacle, ventral aspect, UF 224044, bar = 176 μm. **F.** Penis, dorsal aspect, UF 224044, bar = 300 μm. **G.** Penis, dorsal aspect, USNM 883915, bar = 200 μm. **H.** Close-up of penis tip, USNM 883915, bar = 27 μm.

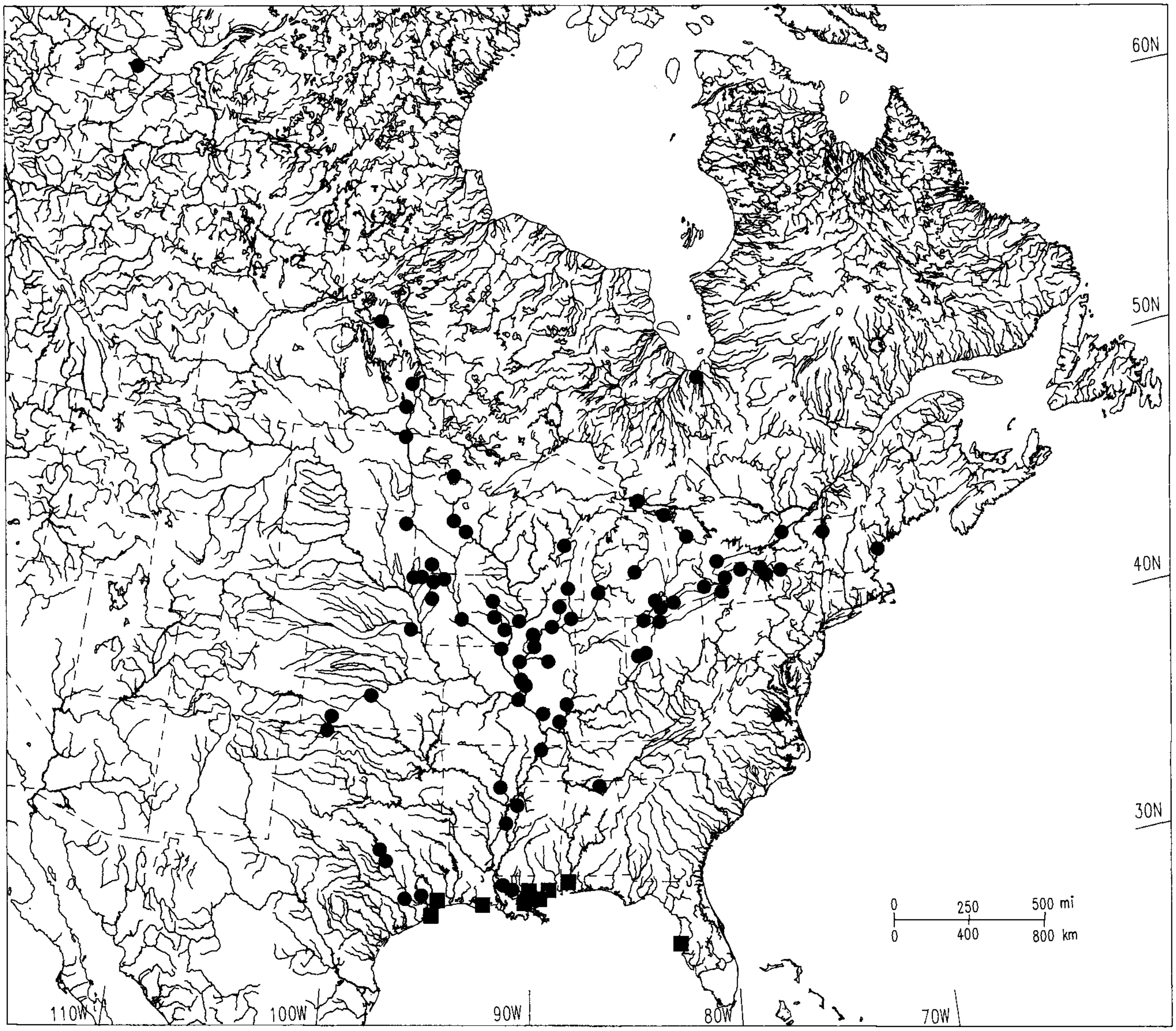

Fig. 6. Map of North America showing distributions (Recent and fossil localities) of *Probythinella emarginata* (●) and *P. protera* (■).

later portion smooth. Collabral striations on teleoconch weak, often crossed by faint spiral scratches. First whorl near planorboid. Aperture prosocline, ovate, strongly constricted. Peristome adnate or slightly separated. Outer lip strongly thickened, sometimes forming a pronounced varix just behind the aperture; columellar lip medium to thick, unreflected. Shell clear-grey, transparent, glassy when cleaned. Periostracum light tan.

Outer edge of operculum lacking rim. Snout pale-medium reddish brown; pigment weaker distally; lips pale. Tentacles pale or light, lacking longitudinal pigment stripes. Sides of head pale or light. Dorsal surface of foot pale or light. Pallial roof often nearly uniformly pigmented (apart from pale gonoducts), usually lacking pigment bands alongside ctenidium. Visceral coil dark. Ctenidial filaments about 35. Kidney bulge small. Renal aperture slightly thickened, almost white. Circum-oesophageal ganglia unpigmented. Pleural-supraoesophageal connective about 150–180% combined lengths of ganglia.

Buccal mass medium-sized, abutting nerve ring posteriorly, darkly pigmented. Radula ribbon about 440 μm, about 4.5 times as long as wide, with about 45 rows of teeth. Central teeth broadly trapezoidal, width about 19–20 μm, dorsal edge distinctly notched; basal cusps 3–5. Cutting edge with 4–5 lateral cusps, central cusp not noticeably broader than laterals. Basal tongue

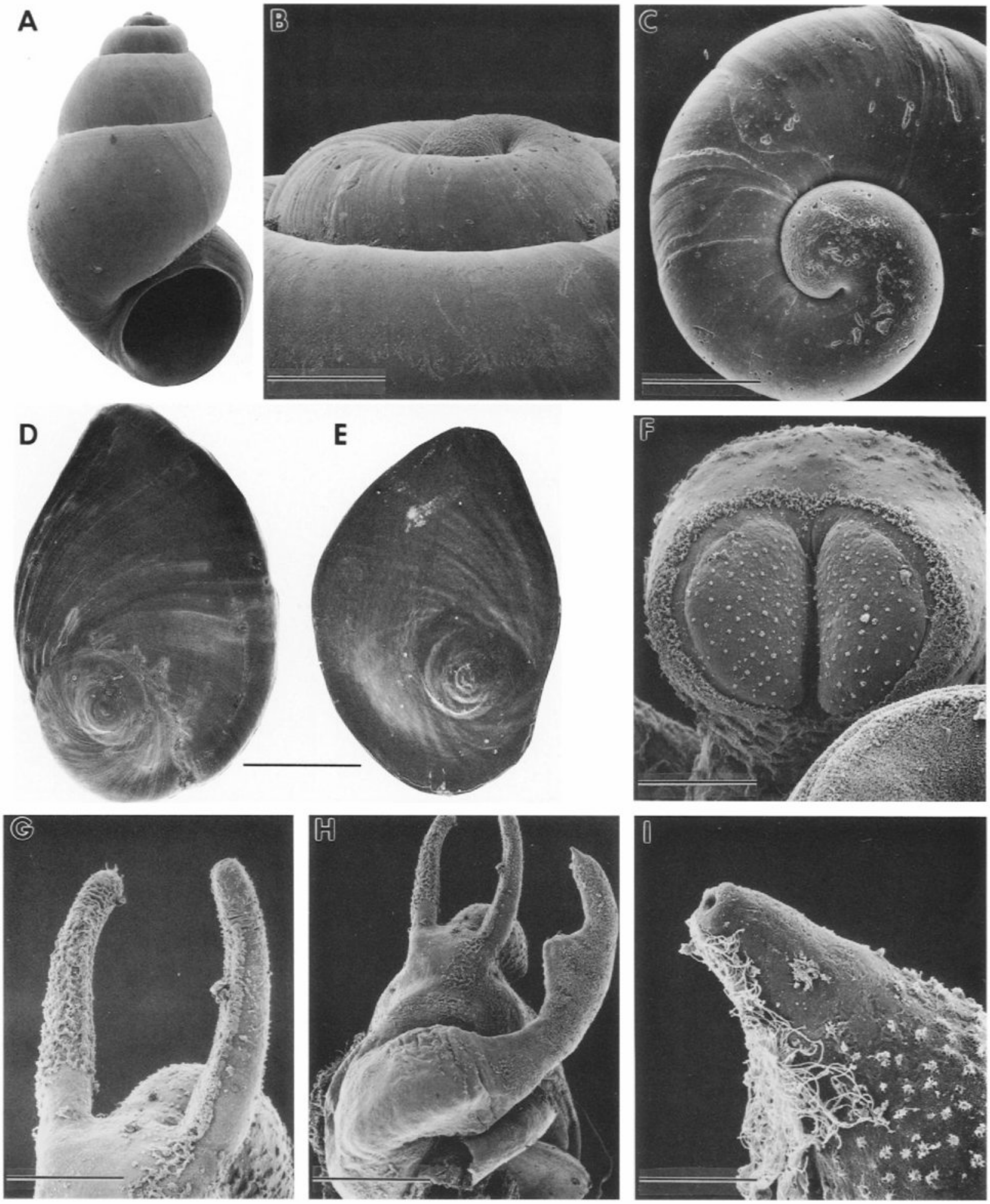

Fig. 7. Morphology of *Probythinella protera.* SEM. **A.** Shell, USNM 635629, 3.1 mm. **B.** Shell apex, showing blunt aspect of protoconch, USNM 635629, bar = 100 μm. **C.** Shell apex, showing wrinkled protoconch surface, USNM 635629, bar = 120 μm. **D, E.** Operculum, outer and inner sides, UF 231759, bar = 300 μm. **F.** Anterior edge of snout, showing cilia fringing oral lips, UF 231759, bar = 100 μm. **G.** Cephalic tentacles, dorsal aspect, UF 231759, bar = 200 μm. **H.** Head and penis, dorsal aspect, UF 231759, bar = 430 μm. **I.** Close-up of penis tip, UF 231759, bar = 17.6 μm.

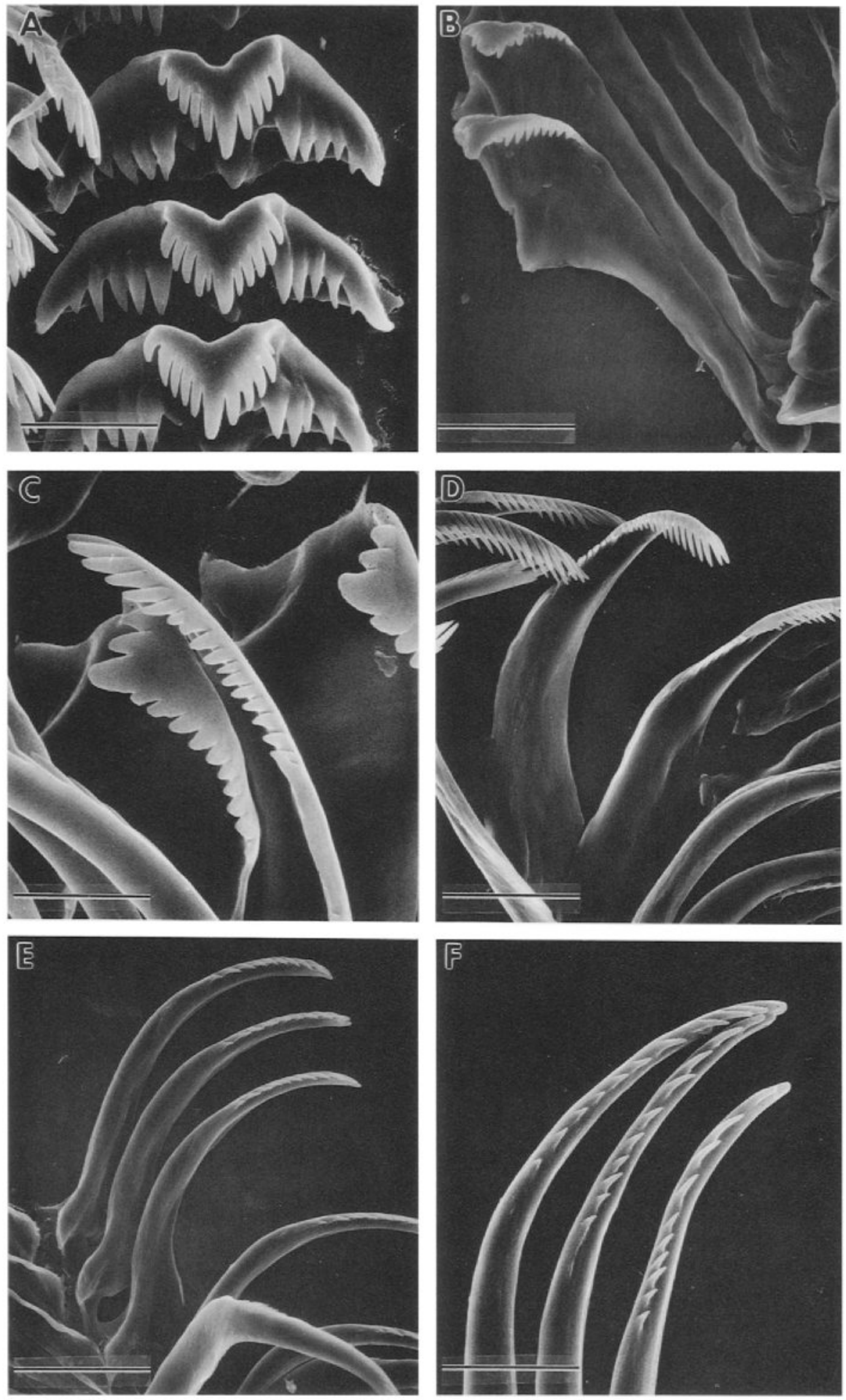

Fig. 8. Radular teeth of *Probythinella protera*. SEM. **A.** Central teeth, UF 231759, bar = 7.5 μm. **B.** Lateral teeth, USNM 874156, bar = 13.6 μm. **C.** Close-up showing cutting edges of lateral and inner marginal teeth, UF 231759, bar = 5.0 μm. **D.** Inner marginal teeth, USNM 874156, bar = 13.6 μm. **E.** Outer marginal teeth, USNM 874156, bar = 16.6 μm. **F.** Close-up showing cutting edges of outer marginal teeth, UF 231759, bar = 8.6 μm.

of lateral teeth weak to moderately developed. Outer wing about 220% longer than cutting edge. Lateral cusps 4–6 (inner side) to 8–10 (outer side). Inner marginal teeth with 16–23 cusps extending along outer edge for about 40–50% of length of tooth at upper end. Outer marginal teeth with 10–15 cusps extending along inner side for about 1/4 to 1/3 of length of tooth at upper end. Salivary glands partly overlapping nerve ring.

Testis 1.5 whorls (animal 3.75 whorls). Prostate gland elongate. Ovary, 1.25 whorls (animal, 3.75 whorls). Coiled oviduct posterior-oblique, narrow. Bursa copulatrix often larger than albumen gland. Bursal duct narrow, length about 40–65% that of bursa copulatrix, sometimes exiting lateral (dorsal) to midline of bursa. Genital aperture sometimes mounted on small papilla.

Distribution. Brackish waters along the eastern Gulf of Mexico coast (Fig. 6). The sole inland record for this species is from Reelfoot Lake, Tennessee, but was from a bird's stomach.

Remarks. The age of the St. Petersburg fossil remains somewhat conjectural as the type locality apparently contains a mixture of Recent and fossil spoil (Olsson & Harbison 1953; Heard 1979). Hazel (1983) indicated that the "Caloosahatchee" of St. Petersburg is not contemporaneous with this formation elsewhere and probably is somewhat older. Pilsbry (1953) distinguished this species from *emarginata* by the less convex later whorls, smaller aperture, and narrower umbilicus. Solem (1961) placed Recent snails from Lake Pontchartrain in this species, and pointed out that six freshwater members of the same Pliocene fauna remain extant. Morrison (1965) later introduced a new genus and species for the Lake Pontchartrain population, *Vioscalba louisianae,* and also transferred *protera* to this genus. He differentiated *protera* from *louisianae* by its more abruptly truncate spire, narrower shell, and whorls that are flatter toward the suture. Heard (1979) treated *protera* and *louisianae* as distinct, but acknowledged their closeness. Scrutiny of available recent material and Pilsbry's holotype clearly indicates that a single Gulf Coastal species is involved, united by the relatively flat whorls and constricted aperture of the shell.

Distributions of the two species of *Probythinella* appear to be contiguous, but non-overlapping. Note, for instance, that in the southern end of its distribution, *P. emarginata* occurs in Bayou Manchac, which drains to Lake Pontchartrain, which in turn harbors *P. protera.* Both of these populations are morphologically uniform and without obvious evidence of introgression.

Phylogenetic Relationships

Phylogenetic relationships among the two species of *Probythinella* and other North American hydrobiids (conjectured to be closely related to this genus) were assessed. Owing to paucity of anatomical data for most members of the large North American fauna, only representative taxa (particularly those also characterized by females having a capsule gland with an enclosed ventral channel) were included in the analysis and consisted of the following: *Nymphophilus minckleyi* TAYLOR 1966b (type species of Mexican *Nymphophilus,* which includes one other closely similar species) and *Cincinnatia integra* (SAY 1821) (type species of North American *Cincinnatia*; possibly monotypic [Hershler & Thompson, in press], representing a large group of snails traditionally placed in the subfamily Nymphophilinae; *Fluminicola coloradensis* MORRISON 1940 and *Fluminicola virens* (LEA 1838), representing a smaller group of snails assigned to the Lithoglyphinae; and *Pristinicola hemphilli* (PILSBRY 1890) and *Taylorconcha serpenticola* HERSHLER ET AL. 1994, monotypic western genera of uncertain affinities. North American representatives of the subfamilies Amnicolinae, Cochliopinae, and Fontigentinae (Hershler & Thompson 1988, 1992; Hershler et al. 1990) were not included because these groups, which may comprise separate clades from the Hydrobiidae, are distinguished by synapomorphies involving fundamental features of the anatomical groundplan (e.g., presence of spermathecal duct and posteriorly looped albumen gland in female cochliopines; trifid penis having tubular glands and absence of female seminal receptacle in fontigentines) and cannot readily be compared with *Probythinella* and other North American taxa. Similarly, several subterranean genera (*Antrorbis, Holsingeria, Phreatodrobia*) were excluded because of their highly reduced morphologies, which also hamper meaningful comparisons in this preliminary analysis.

The estuarine genus *Hydrobia* (data mostly from the single North American species), usually considered among the more primitive hydrobiids (Ponder et al. 1993), was used as primary outgroup (occupying basal positions on generated trees). Character states found in *Hydrobia* were treated as plesiomorphic. While I concur with Ponder et al. (1993) that various morphological features of *Hydrobia* may ultimately prove to be derived, I nevertheless prefer to polarize character states on the above basis for an analysis of this scale rather than to pursue other options such as derivation of a hypothetical ancestor; or to use as outgroups more distantly related taxa such as other rissooidean families, whose morphological groundplans often differ substantially from hydrobiids and whose evolutionary relationships to this group remain poorly resolved (Ponder 1988). The Australian estuarine genus *Tatea* (data mostly from the type species), also considered a primitive member of the family (Ponder et al. 1993), was used as an additional outgroup.

Characters

The data set consisted of 47 characters (105 states) scored for 10 taxa. Characters are discussed below

Table 1. Matrix of 47 characters for eight North American hydrobiid taxa and two outgroups (*Hydrobia, Tatea*). "?" refers to missing data. Both "N" (inapplicable) and "?" were treated as unknown in the analysis.

	Character									
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–47
Hydrobia	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
Tatea	02011	00000	10011	01110	?1001	01111	02021	1001?	03?01	N0
Cincinnatia integra	00011	10001	11001	01011	11111	10110	02001	11011	10100	11
Probythinella emarginata	10001	10202	11011	01111	11111	10110	12000	10110	12010	00
Probythinella protera	10011	00203	11011	01111	11111	10110	12000	10110	12010	00
Taylorconcha serpenticola	01010	00012	20001	12000	00012	11110	01NNN	NN011	00101	N0
Pristinicola hemphilli	00010	N221N	10001	10000	01012	10111	02001	10011	00011	N0
Nymphophilus minckleyi	00010	01113	11011	10110	10000	10100	02120	01011	00100	11
Fluminicola coloradensis	03100	02213	11101	10110	00012	11110	02120	11011	01001	N0
Fluminicola virens	03100	02211	11101	10010	01012	11110	02111	01011	01011	N0

("0" indicates plesiomorphic state, "N" indicates inapplicable character state) and character states for each taxon are listed in Table 1.

1. Shell apex. 0=protruding, 1=flat or depressed.

2. Protoconch sculpture: wrinkles. 0=reticulate, 1=coalesced into crude spiral elements, 2=pit-like (steep-sided), 3=absent. In *Hydrobia,* at least two species have reticulate sculpture (Bandel 1975: fig. 12; Fish & Fish 1977: plate Ia; Fish & Fish 1981: fig. 3) whereas another has a more pustulose condition (Fish & Fish 1981: fig. 2). In this analysis, *Hydrobia* is scored as reticulate. The pattern of wrinkling is finer in *Pristinicola* than in the other taxa, but these conditions are treated as a single state. Species of *Fluminicola* have a smooth protoconch except for strong spiral elements (lacking any indication of wrinkles); see character 3.

3. Protoconch sculpture: spiral elements. 0=absent, 1=present.

4. Outer edge of operculum. 0=with rim, 1=lacking rim.

5. Dorsal surface of operculum. 0=edges of whorls frilled (slightly elevated above surrounding surface), 1=edges of whorls flush with operculum surface.

6. Pallial roof pigmentation. 0=uniform, 1=well-developed bands flanking sides of ctenidium (superimposed on an otherwise pale surface), N=pigment absent.

7. Longitudinal ciliary tracts on dorsal surfaces of tentacles. 0=tract(s) elongate and few, 1=tracts short and numerous, 2=ciliation uniform.

8. Longitudinal ciliary tracts on ventral surfaces of tentacles. 0=tract(s) elongate and few, 1=tracts short and numerous, 2=ciliation uniform.

9. Transverse ciliary tracts on dorsal surface of left tentacle. 0=present, 1=absent.

10. Dorsal tentacle pigmentation. 0=short central distal band, 1=elongate central band, 2=elongate bands along edges (central area pale), 3=uniform, N=pigment absent.

11. Anterior pedal mucus gland. 0=central glandular unit enlarged, 1=units about equal-sized, 2=units few, weakly developed.

12. Osphradium shape. 0=elongate, 1=ovate.

13. Hypobranchial gland development. 0=uniform appearance, 1=posterior region arched or humped.

14. Extent of pallial kidney. 0=large (1/3 or more of overall length of organ), 1=small.

15. Pallial tentacle. 0=present, 1=absent.

16. Shape of radular ribbon. 0=rectangular (about 3–5× as long as wide), 1=elongate (7–10×).

17. Size of radular ribbon. 0=medium (length=20–35% of shell length), 1=small (10–15%), 2=large (ca. 75%).

18. Basal excavation of central radular teeth. 0=moderate to high (at least half of tooth height excavated), 1=weak.

19. Number of basal cusps on central radular teeth. 0=single pair, 1=two or more pairs.

20. Shape of dorsal edge of lateral teeth. 0=distinctly flexed, 1=straight.

21. Basal process of lateral teeth. 0=well developed (knob-like), 1=simply rounded or angled. Character not documented for *Tatea.*

22. Length of shaft of lateral teeth. 0=short (<1.5× length of cutting edge), 1=long (>2× length of cutting edge).

23. Number of cusps on lateral teeth. 0=few (6–8), 1=many (10–27).

24. Dorsal folds of mid-oesophagus. 0=strongly recurved, 1=straight.

25. Posterior caecum of stomach. 0=small, 1=large, 2=absent.

26. Mode of development. 0=with pelagic larval phase, 1=direct.

27. Anterior extent of ovary. 0=overlaps stomach anteriorly, 1=positioned behind stomach.

28. Pigmentation of coiled oviduct. 0=present, 1=absent.

29. Number of oviduct coils. 0=two or more, 1=one (sometimes preceeded by a slight twist or bend).

30. Position of coiled oviduct. 0=lies against middle or anterior portion of albumen gland, 1=lies against posterior edge of albumen gland.

31. Number of seminal receptacle(s). 0=one, 1=two. *Probythinella* has two such pouches, one opening to the posterior arm of the coiled oviduct (as is usual for hydrobiids) and one opening anterior to the coiled portion of the oviduct. Characters 32 and 33 apply to the posterior (or primary) seminal receptacle.

32. Shape of seminal receptacle. 0=globular, 1=elongate, 2=ovate-pyriform.

33. Position of seminal receptacle. 0=partly overlapping bursa copulatrix, 1=anterior to bursa copulatrix. This character (and 34–37) cannot be scored for *Taylorconcha* as these snails lack a bursa copulatrix.

34. Position of bursa copulatrix. 0=lies against left side of albumen gland, 1=lies against right side of albumen gland, 2=mostly or entirely posterior to albumen gland.

35. Orientation of bursa copulatrix. 0=long axis perpendicular (or nearly so) to length of albumen gland, 1= parallel to albumen gland.

36. Length of bursal duct. 0=long (at least as long as bursa copulatrix), 1=short. *Cincinnatia* has two such structures, a thick anterior duct and a very slender duct opening to the middle of the bursa copulatrix. The anterior duct is assumed to be primary and was used to score this character.

37. Position of bursal duct. 0=lies on albumen gland, 1=at least partly embedded within albumen gland.

38. Size of albumen gland. 0=sub-equal or longer than capsule gland, 1=much shorter than capsule gland.

39. Capsule gland. 0=uniform, 1=differentiated into at least two distinct glandular zones.

40. Course of seminal vesicle. 0=extends posteriorly as a straight tube before bending anteriorly and coiling, 1=does not extend posteriorly or does so for a short distance as an undulating tube. Character not documented for *Tatea.*

41. Pallial vas deferens. 0=straight or undulating tube, 1=with pronounced coil(s).

42. Shape of distal penis. 0=tapered, 1=pointed, 2=blunt, 3=truncate.

43. Penial duct. 0=undulating, 1=straight. Character not documented for *Tatea.*

44. Distal terminus of penis. 0=simple, 1=with papilla.

45. Accessory lobe of penis. 0=present (along inner side), 1=absent.

46. Orientation of penial lobe. 0=medial and extending laterally, 1=distal and almost parallel to the length of the penis; N=lobe absent.

47. Glandular fields on penis. 0=absent, 1=present.

Analysis

The analysis yielded three equally parsimonious trees having length of 101 steps, consistency index (CI) of 0.59, and retention index of 0.56. Note that this CI (an inverse measure of homoplasy) was somewhat less than that predicted (0.7) for data sets having this number of taxa (Sanderson & Donoghue 1989:fig. 1 and associated equation). One of these trees is shown in Fig. 9. (The consensus tree is shown in Fig. 10.) In all three trees the North American taxa comprised a paraphyletic group owing to the non-basal position of *Tatea* (which as "non-primary" outgroup was permitted to "float" in this program). All three trees contained two main clades, one of which included *Cincinnatia* and *Probythinella,* and the other *Pristinicola* and *Fluminicola.* In one of the alternative trees, *Nymphophilus* was shifted from the latter clade to a basal position within the other main clade; in the other, *Nymphophilus* and *Taylorconcha* occupied positions basal to the splitting off of the two main clades. Topology was otherwise identical in all three trees. Deployment of *Tatea,* instead of *Hydrobia,* as the primary outgroup yielded three equally parsimonious trees having the same length and consistency as the above. In all three of these trees the two species of *Probythinella* and *Cincinnatia* again comprised a clade.

Cincinnatia and *Probythinella* are sister groups united by unreversed synapomorphies of lateral teeth having straight dorsal edge and numerous cusps, and coiling of pallial vas deferens.[2] However, this hypothesis

[2] *Cincinnatia* and *Nymphophilus,* traditionally placed together in the Nymphophilinae, do not appear closely related in this analysis, further supporting the opinion that this subfamily as traditionally defined (i.e., on basis of three characters involving penial form, penial glands, and protoconch microsculpture; Thompson 1979) is non-monophyletic (Bodon & Giusti 1991; Hershler & Thompson, in press).

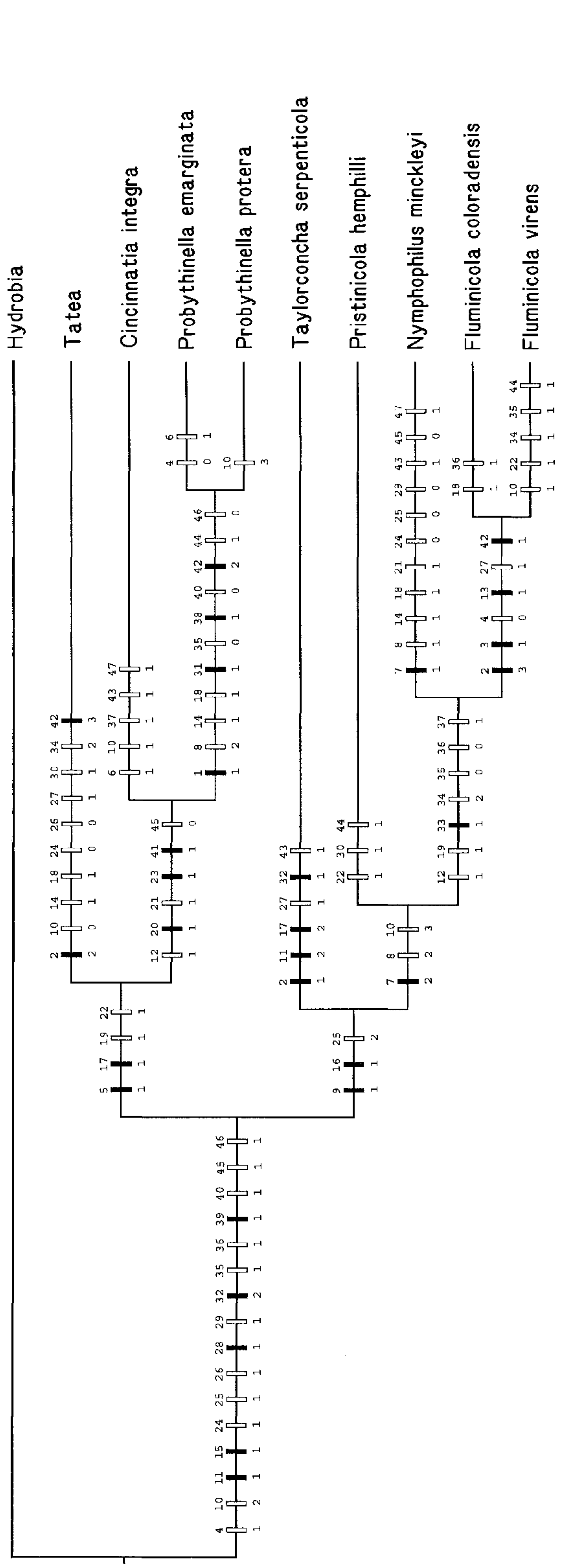

Fig. 9. Cladogram for species of *Probythinella* and other members of the North American hydrobiid fauna, plus two outgroups (*Hydrobia, Tatea*). Bars indicate character state transformations supporting nodes, with character number given above and state indicated below. Black bars indicate unique, unreversed synapomorphies.

will require further testing with a larger set of taxa: some species allocated to the subfamily Lithoglyphinae, for instance, also have numerous cusps on the lateral teeth (Thompson 1984:figs. 17, 21, 25). This preliminary result, which supports earlier contentions of Thiele (1928) and others (see above), is perhaps surprising given that these taxa differ significantly in various features, notably penial morphology and distal female genitalia. Too much reliance may have been placed on penial characters (such as presence-absence of glandular fields) in hydrobiid classification. It is also intriguing to speculate that the unusual aspects of the female genitalia of these taxa (*Cincinnatia,* second bursal duct; *Probythinella,* second seminal receptacle) could actually be homologous as both of these structures open to the same region of oviduct (i.e., distal to the coiled portion). The clade comprising the two species of *Probythinella* is differentiated from sister taxon *Cincinnatia* by unique and unreversed synapomorphies of flattened shell apex, two seminal receptacles, short albumen gland, and blunt terminus of penis. The two species of *Probythinella* are rather weakly distinguished from one another by several homoplastic transformations. *Probythinella emarginata* is distinguished from *P. protera* by derived modifications of operculum having a rim along outer edge and pallial roof having distinct pigment bands; the latter species also is distinguished by a derived character state of uniform tentacle pigmentation (each transformation paralleled once elsewhere on the cladogram). In one of the alternative trees, dorsal tentacle pigmentation has a different pattern of evolution and appears as a derived (but paralleled once) modification (i.e., possession of elongate bands along sides) for *emarginata.* Note, however, that autapomorphic characters (such as the thickened shell lip of *P. protera*) were deliberately excluded from this analysis.

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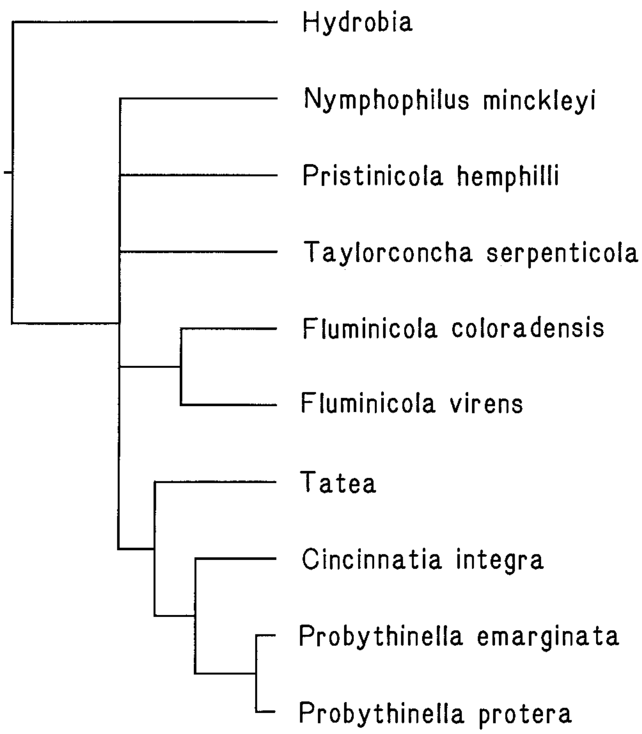

Fig. 10. Strict consensus cladogram for species of *Probythinella* and other members of the North American hydrobiid fauna, plus two outgroups (*Hydrobia, Tatea*).

mcnclatural and othcr issues. D. Lindberg, W. Pondcr, and the editor provided helpful comments on the manuscript.

Appendix: Material Examined

Lots containing anatomical material (all of which were dissected during the course of this study) are highlighted with an asterisk. The following abbreviations for institutions are used:

ANSP	Academy of Natural Sciences, Philadelphia
BMNH	The Natural History Museum, London
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MZC	Musée Zoologique Cantonal, Lausanne (Switzerland)
UF	Florida Museum of Natural History, University of Florida, Gainesville
UIMNH	University of Illinois at Urbana-Champaign Museum of Natural History
UMMZ	Museum of Zoology, University of Michigan
USNM	former United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UWZM	University of Wisconsin Zoological Museum, Madison

Probythinella emarginata (Küster)

CANADA. Manitoba. Saskatchewan River, Lake Winnipeg, Grand Rapids (USNM 180310).—Winnipeg (Clay) (UMMZ 121249, USNM 471385).—Winnipeg (Thompsons Clay Bed) (UMMZ 119896).—Winnipeg (ANSP 137533, UMMZ 119893, UMMZ 183842). **Northwest Territories.** Lake Kakiska near mouth of Beaver River, west of Great Slave Lake (UIMNH Z22510). **Ontario.** Moose Factory, James Bay (USNM 28083).—Den Valley beds, Toronto (USNM uncat.).—North channel, Gravelly Point, St. Josephs Island, Lake Huron (ANSP 153109).—Moose River, Shipsands Island (ANSP 139570).—Lake Erie, Port Dover (UMMZ 42232).—Wiarton (UMMZ 37482).—Kingsville, beach (UMMZ 119887).—Lake Simcoe (UMMZ 119898).—St. Lawrence River, west of Brockville (UMMZ 183912).—Mindemoya Lake, southeast side, Manitoulin Island (UMMZ 52632).—Rondeau Bay (drift) (UMMZ 42243).—Lake Erie, Locust Point (UMMZ 119890) (not found on maps).

UNITED STATES. Alabama. *Madison County*: Huntsville (UMMZ 69852). **Arkansas.** *Chicot County*: Grand Lake (UMMZ 133328). *Prairie County*: White River, northeast of De Valls Bluff (UMMZ 197609). **Illinois.** North Branch, Chicago River (FMNH 3013, FMNH 3014). *Cass County*: Illinois River, Beardstown (FMNH 155697, UMMZ 197616). *Cook County*: Lake Michigan, Chicago (ANSP 166086).—Lake Michigan, 57th Street, Chicago (FMNH 105686).—Lake Michigan, shore, foot of Elm Street, Chicago (MCZ 89395).—Calumet (UF 88634). *Fulton County*: Canton (MCZ 2070, MCZ 175793, UMMZ 119882). *Jackson County*: Big Muddy River, just south of Murphysboro (UMMZ 197615). *Kane County*: Fix River, Elgin, 0.8 km S Hwy 90. *La Salle County*: Utica (several FMNH lots, UMMZ 69823, UMMZ 119877). *Logan County*: 1.6 km east of Griggs (USNM 166664). *Madison County*: Mississippi River, Alton (UF 88553, UMMZ 197752). *Mason County*: Havana (ANSP 27880).—Illinois River, Havana (several FMNH lots). *Mercer County*: Mississippi River (MCZ 2069). *Pope County*: Ohio River, Golconda (UMMZ 197617). *Rock Island County*: mouth of Rock River (ANSP 75761).—Milan (ANSP 117460). *Rock Island County*: Mississippi River, Moline (several UF lots, MCZ 2068). *St. Clair County*: Cahokia Creek, 2.4 km east Brooklyn (UMMZ 197614). *Will County*: Joliet (UMMZ 119892). **Indiana.** *Posey County*: Wabash River, Grand Chains (UF 88883, UMMZ 51542, UMMZ 119883). **Iowa.** Eastport (USNM 506388) (not found on maps). *Cherokee County*: sandbar, Cherokee (USNM 520292). *Dickinson County*: Lake Okoboji (various USNM lots).—Little Sioux River, west of Milford (USNM 506393). *Emmet County*: Des Moines River, Estherville (USNM 526539).—Estherville (USNM 511010). *Johnson County*: Iowa River, Iowa City (USNM 525148).—Iowa City (ANSP 92029, MCZ 315781, UMMZ 119897). *Lee County*: Mississippi River, 2.9 miles (4.7 km) north of Keokuk (*UF 224044).—Keokuk (USNM 535167).—lagoon, Montrose (UF 224045). *Linn County*: Cedar Rapids (USNM 507619).—Cedar River, Cedar Rapids (USNM 539459). *Lyon County*: Rock Rapids (USNM 506381).—

west of Granite (USNM 506390). *Muscatine County*: (USNM 526368).—Muscatine (ANSP 92034, UMMZ 119874, USNM 526577).—Rock Island (USNM 514556).—Keokuk Lake (USNM 600747). *Polk County*: Des Moines River, Des Moines (ANSP 92093, MCZ 2066, USNM 742064).—Des Moines (UF 224046). *Scott County*: Mississippi River, Le Claire (MCZ 2067).—Davenport (UMMZ 119891). *Sioux County*: Big Sioux River, Hawarden (USNM 514460). **Kansas.** *McPherson County*: Sandahl gravel pit (Pleistocene) (UMMZ 230695). *Meade County*: Pleistocene deposits, vicinity of Butler Springs (UMMZ 197551). **Louisiana.** *Ascension Parish*: Bayou Manchac, near Prairieville (*UF 175879, *USNM 874884, *USNM 874885, *USNM 874886, *USNM 883416, *USNM 883915). *Pointe Coupee Parish*: False River, New Roads (UF 35078). **Maine.** *York County*: Scarboro (USNM 515801). **Michigan.** *Ottawa County*: Black Lake, Holland (ANSP 75663). *Saginaw County*: East Saginaw (ANSP 27878). *Wayne County*: Detroit River, Ecorse (USNM 198893). **Minnesota.** Mississippi River, 0.4 km above mouth of Clearwater River (Sherburne-Stearns Counties) (ANSP 67351).—Eagle Lake (ANSP 67211). *Cass County*: Lake Winnibigoshish, Bena (UMMZ 197610). *Hennepin County*: Minnesota River, Fort Snelling (MCZ 2071). *Jackson County*: Heron Lake (USNM 104459). *Stearns County*: (UMMZ 119875). *Wright County*: Clearwater (UF 206869). **Mississippi.** *Sunflower County*: Sunflower River, 2.5 miles (4.0 km) west of Ruleville (*UF 224043).—Quiver River, 6.1 km south of Sunflower (UF 224048). **Missouri.** *Osage County*: Osage River, 4.8 km west of Loose Creek (UMMZ 197613). *St. Louis County*: Kirkwood (USNM 519982).—Meramec River, Kirkwood (FMNH 136931, MCZ 94688, UMMZ 54626, UMMZ 197612).—Creve Coeur Lake, east side (UMMZ 197611). **Nebraska.** *Lancaster County*: Salt Creek, Lincoln (USNM 526817 [mixed with *Cincinnatia integra*], FMNH 121180). **New York.** Erie Canal (numerous lots).—Mohawk River (USNM 27883, and numerous other lots).—Erie Canal and Mohawk River (ANSP 124769).—Hudson River, drift (UMMZ 119881). *Erie County*: shore of lake Erie, near Buffalo (ANSP 164893).—Niagara River drift, Grand Island (FMNH 107619). *Essex County*: Lake Champlain, Crown Point (ANSP 129274).—Crown Point, near monument (ANSP 131167). *Herkimer County*: Mohawk (several ANSP, UF, UMMZ lots).—Mohawk River, Mohawk (several ANSP lots).—Erie Canal (UF 88635, UF 88636). *Monroe County*: shore of Lake Ontario, Rochester (ANSP 145904). *Oneida County*: Mohawk Valley, near Stanwix (ANSP 134986). *Onondaga County*: Baldwinsville (USNM 506361).—Liverpool (USNM 592787).—Harbor Brook and Avery Avenue, Syracuse (ANSP 134987). *Oswego County*: Burge Canal cut, 0.8 km southeast of Hinmansville (ANSP 113116). *Wayne County*: Sodus Bay (USNM 536643).—near Clyde (USNM 251446). **North Dakota.** (UMMZ 10844, UMMZ 10963). *Pembina County*: Red River, Pembina (UMMZ 30002). **Ohio.** North Ohio (USNM 117752). *Clark County*: Springfield (USNM 121328). *Lucas County*: Maumee River (UMMZ 27499).—Toledo, Hocking Valley fill in Maumeer River (UMMZ 27498). *Montgomery County*: Stillwater River at Ridge Avenue, Dayton (*UF 224049). *Ottawa County*: Sandusky Bay (UF 1129).—Upper Sandusky Bay, Danbury (UMMZ 27504).—Lower Sandusky Bay, Sandusky (UMMZ 27505).—Sandusky Bay, Bay Point (UMMZ 27506, UMMZ 119886). **Oklahoma.** *Harper County*: Pleistocene deposits, west of Buffalo (UMMZ 213789). **South Dakota.** *Clay County*: Vermillion River (ANSP 112874). *Codington County*: Lake Kampeska (ANSP 110794). *Deuel County*: (USNM 217950). *Roberts County*: Lake Transverse (UMMZ 69822). **Tennessee.** *Obion County*: Reelfoot Lake (USNM 605806). **Texas.** *Austin County*: Brazos River, drift, Sealy (MCZ 217984). *Burleson County*: Brazos River, Burleson Bluff, 12.8 km northeast of Cooks Point (MCZ 223925). *Harris County*: Lake Houston, near Humble (MCZ 214899). *Menard County*: San Saba River, Peg Leg Crossing (UMMZ 119876) (not found on map). *Robertson County*: Brazos River, Black Shoals, 8 km W of Calvert (MCZ 222394). **Virginia.** *Prince George County*: James River, City Point (ANSP 68802, UMMZ 119878). **Wisconsin.** *Brown County*: Green Bay (ANSP 60103, USNM 105135).—East River (UMMZ 137988). *Milwaukee County*: Milwaukee (USNM 27898). *Winnebago County*: Winnebago Lake, near Oshkosh (UWZM 4531).

Probythinella protera Pilsbry

UNITED STATES. Alabama. *Mobile County*: Fowl River, 1.9 km west of Mon Lewis, 1.6 km northeast of Bellingrath (*UF 224042).—west coast Mobile Bay, just south of mouth of Dog River (USNM 680257). **Louisiana.** Lake Pontchartrain, at mouth of Tchefuneta River (*USNM 874156) (Tangipahoa-St. Tammany Parishes). *Orleans Parish*: Chef Menteur (USNM 219657). *Plaquemines Parish*: Carlisle (USNM 341561). *St. John the Baptist Parish*: Lake Pontchartrain, off Frenier Beach (MCZ 255918 [paratypes]). *Vermilion Parish*: Fearman Lake, Vermillion Bay (USNM 701404). **Mississippi.** *Jackson County*: Davis Bayou (*UF 231758).—Simmons Bayou, 6.4 km ESE Ocean Springs (UF 224041). **Tennessee.** Reelfoot Lake (USNM 605807) (from stomach contents of waterfowl) **Texas.** *Chambers County*: upper end of Trinity Bay, Galveston Bay (USNM 708167).—Anahuac Lake (*UF 231759).—Lake Charlotte (MCZ 56164, UMMZ 119895) *Galveston County*: Galveston (UF 224041).

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