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First record for springsnails (Mollusca: Hydrobiidae: *Pyrgulopsis*) from the northern Rocky Mountains

Robert Hershler and Daniel L. Gustafson

(RH) Department of Invertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560-0118
(DLG) Department of Ecology, Montana State University, Bozeman, Montana 59717-0346

Abstract. *Pyrgulopsis bedfordensis,* new species, from southwest Montana, differs from other congeners having an enlarged penial lobe by its unique pattern of penial ornament, consisting of a transverse terminal gland and a raised gland on the inner edge of the lobe. This species is locally endemic in the headwater region of the Missouri River basin. Origin of this novelty is attributed to vicariance associated with Neogene migration of the continental divide.

Pyrgulopsis is the largest genus of inland aquatic mollusks in North America, with 123 described species in common usage. Although phylogenetic structure within *Pyrgulopsis* has not been well established, the genus is divisible into non-overlapping eastern and western subunits which are well differentiated morphologically (Hershler 1994). The large western fauna is restricted to the region extending from the southern Great Plains to the Pacific Coast, and from the Columbia Plateau to the Basin and Range of northern Mexico. The much smaller eastern fauna ranges from the Central Lowlands to the Atlantic Coast.

Snails conforming morphologically to the western group have been collected east of the continental divide only in the Pecos-Rio Grande drainage of the southern Great Plains (e.g., Taylor 1987). One of us (DLG), however, recently discovered a population of *Pyrgulopsis* living in a thermal spring in the upper Missouri River drainage just east of the continental divide which also conforms to the western group. Herein we describe this new species, which represents the first record of *Pyrgulopsis* in the Northern Rocky Mountains.

Specimens are deposited in the Florida Museum of Natural History (UF), and National Museum of Natural History, Smithsonian Institution (USNM). Terminology and methods of morphological analysis are of Hershler (1994, 1998) and Hershler & Ponder (1998). Measurements of shells of the holotype and a series of paratypes are in Table 1.

Pyrgulopsis bedfordensis, new species

Type material.—The holotype (UF 271731) is a dried shell (3.37 mm shell length, Fig. 1) from Warm Springs Creek (also known as Bedford Hot Spring), Townsend Valley, Broadwater County, Montana, T. 7N, R. 1E, sections 14, 23, elevation about 1,200 m (46.3537°N, 111.5641°W); collected by D. L. Gustafson and M. M. Hooten, 26 Jan 1991. The location of the type locality is shown in Fig. 2. Paratypes (USNM 854975, USNM 854976, USNM 892153, USNM 892154, UF 184057, UF 184058, UF 193049, UF 193050) consist of several series of dry shells and alcohol-preserved specimens collected from the type locality at the same time. Two additional series (USNM 892151, USNM 892152), which are not designated as paratypes, were collected at the type locality by D. L. Gustafson during 1995 and 1999.

Table 1.—Morphometric and meristic shell features of holotype and ranges of values for 10 paratypes of *Pyrgulopsis bedfordensis*, new species. Morphometric parameters are expressed in mm.

	Holotype	Paratypes
Shell height	3.37	2.94–3.69
Shell width	2.10	1.99–2.30
Body whorl height	2.42	2.22–2.70
Body whorl width	1.91	1.71–2.10
Aperture height	1.39	1.31–1.59
Aperture width	1.35	1.27–1.47
Shell width/shell height	0.62	0.58–0.70
Number of whorls	>5.0	>4.0–5.0

Diagnosis.—A medium-sized species of *Pyrgulopsis* with trochiform to ovate-conic shell having an eroded apex and well-developed columellar shelf. Penis large; filament medium length, lobe long. Penial ornament of a curved gland along the distal edge of the lobe (terminal gland) and a smaller unit (Dg3) borne on the distal edge of a well-developed swelling on the inner edge of the lobe.

Description.—Shell (Fig. 3A–E) clear-white, trochiform to ovate-conic, width/height, 58–70%; height (larger adults), about 2.9–3.7 mm; width, 1.9–2.3 mm; whorls about 5.0. Apex usually eroded in adult specimens. Protoconch valvatiform, whorls about 1.25, diameter about 260 μm, earliest 0.5 whorl slightly wrinkled, surface otherwise smooth (Fig. 3F, G). Teleoconch whorls of low to medium convexity, narrowly shouldered. Aperture ovate to pyriform, broadly adnate to slightly disjunct. Inner lip completed, slightly thickened, columellar lip strongly reflected in most adult specimens. Outer lip usually thin, orthocline or weakly prosocline, sometimes weakly sinuate. Umbilicus narrowly perforate, often obscured by columellar lip. Periostracum brown or tan. Shells of males forming distinctly smaller size class (about 2.5–2.6 mm) than those of females.

Operculum (Fig. 3H–K) medium thickness, light amber with darker red hue in nuclear region, ovate, paucispiral, nucleus ec-

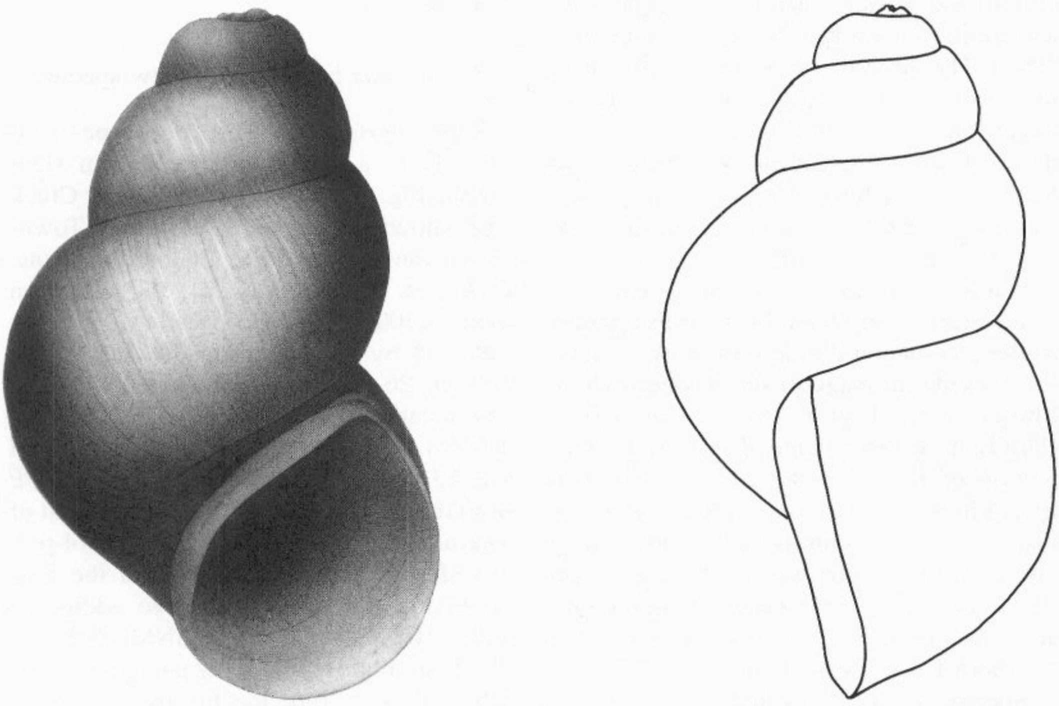

Fig 1. Holotype of *P. bedfordensis*, new species, from Warm Springs Creek, Broadwater County, Montana.

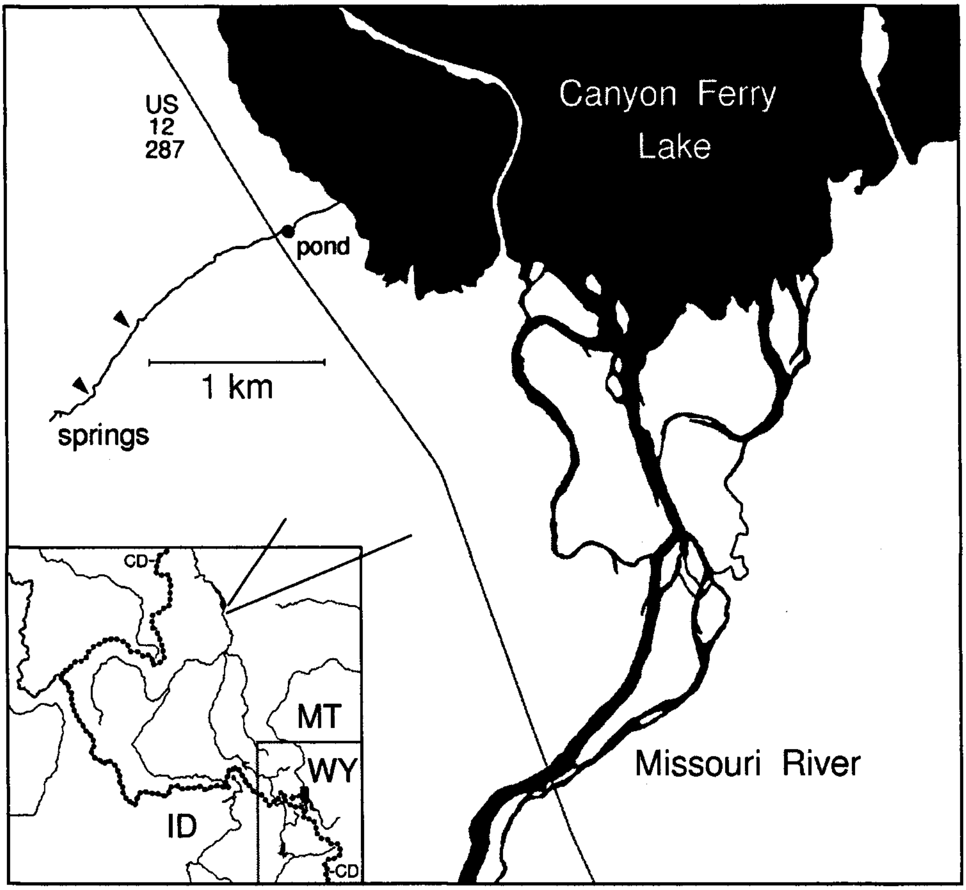

Fig. 2. Map showing location of Warm Springs Creek. Sampling sites are indicated by thick arrows. cd, continental divide.

centric. Edges of whorls without frills on outer surface (Fig. 3H); outer margin without rim. Attachment scar margin thickened between inner edge and nucleus (Fig. 3I–K).

Buccal mass large; radular sac extending behind buccal mass as small loop. Radula about 885 × 142 μm, with about 57 rows of teeth. Central teeth (Fig. 4A–C) trapezoidal, 33–39 μm wide, dorsal edge medium indented; lateral cusps 3–4; central cusp medium width, narrowly pointed, considerably longer than lateral cusps; basal cusp 1, large, arising from intersection of tooth face and lateral margin. Basal tongue of central teeth broad V-shaped or U-shaped, basal sockets medium depth. Lateral teeth (Fig. 4C, D) with 2–3 cusps on inner side and 2–4 cusps on outer side, central cusp large, spoon-shaped; neck weakly flexed; outer wing 135–145% width of tooth face. Inner marginal teeth (Fig. 4D–F) with 23–31 cusps, often bearing noticeably enlarged cusp proximally (Fig. 4F). Outer marginal teeth (Fig. 4D–F) with 34–38 cusps. Style sac about as long as remainder of stomach; stomach with very small posterior caecum.

Cephalic tentacles grey, dark brown, or black, pigmented lighter around eyespots. Snout usually dark brown (rarely lighter), distal lips often lightly pigmented. Foot medium to dark brown. Opercular lobe brown or black all around, central area pale. Neck with light to medium cover of grey gran-

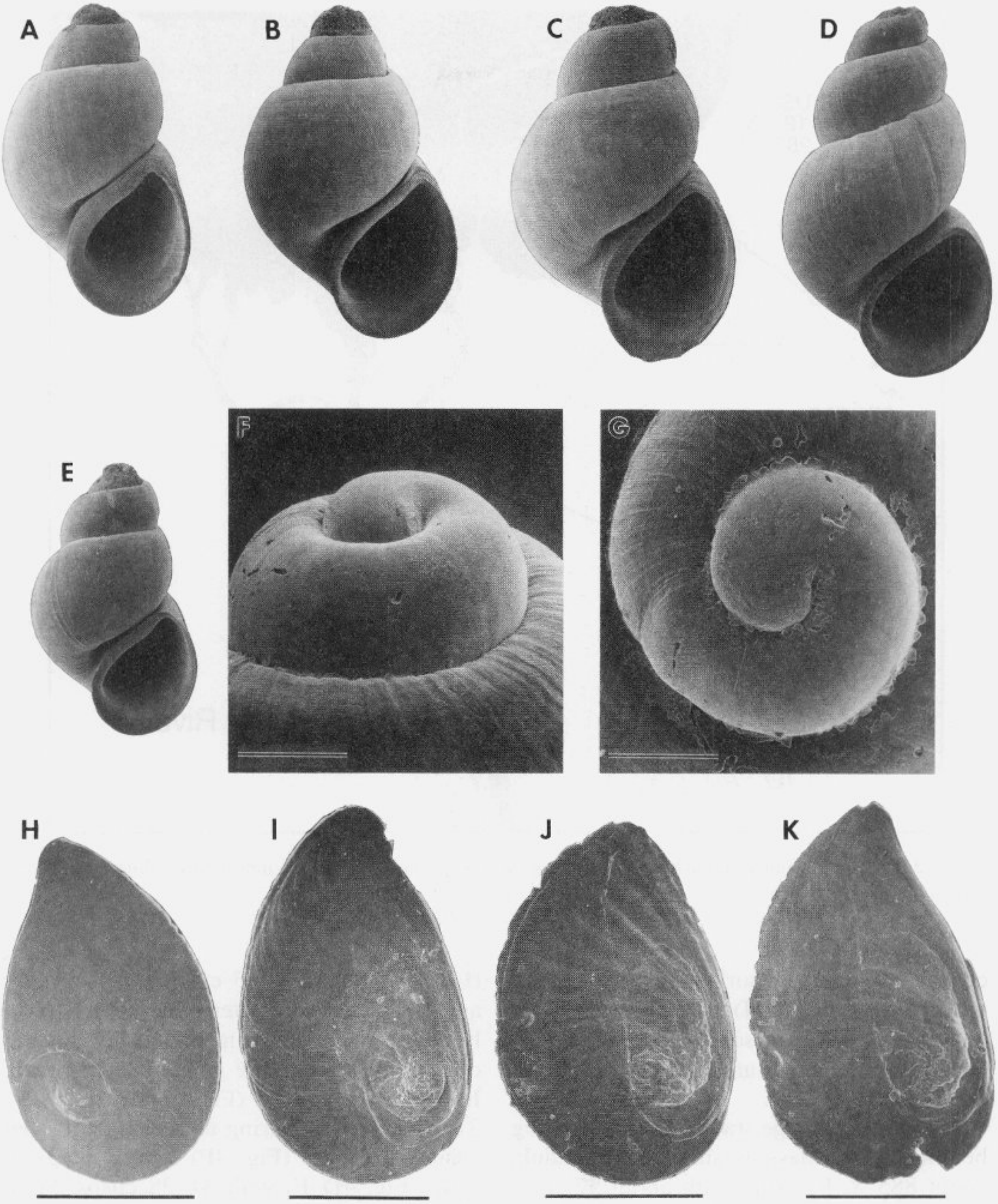

Fig. 3. Scanning electron micrographs of shell and opercula of *P. bedfordensis,* USNM 854976. A–E. Variation in shell shape (shell height, 2.86, 3.10, 3.26, 3.69, 2.66 mm, respectively). F. Shell apex, viewed from side (bar = 100 μm). G. Shell apex, viewed from above (bar = 100 μm). H. Outer surface of operculum (bar = 500 μm). I–K. Inner surface of operculum (bars = 500 μm).

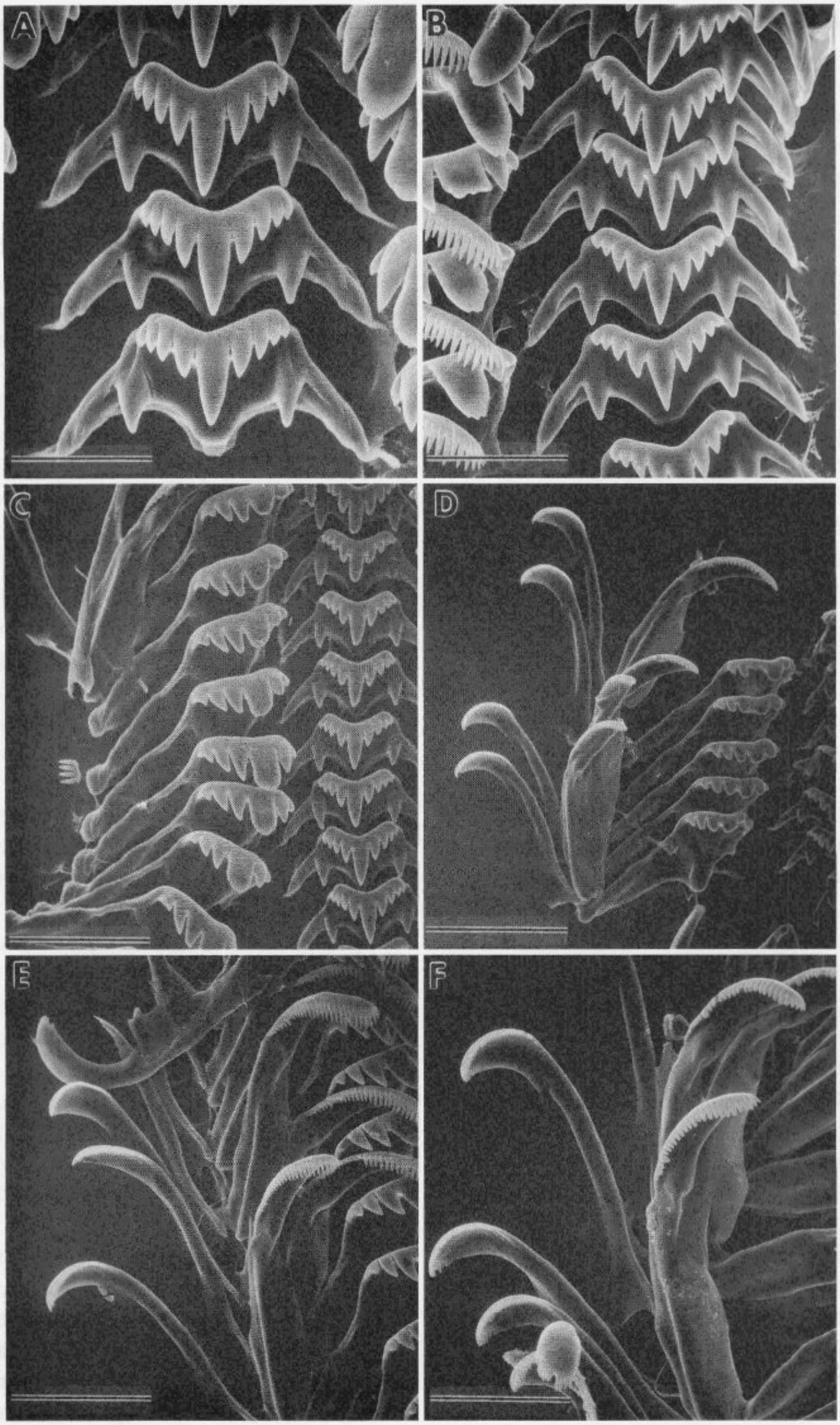

Fig. 4. Scanning electron micrographs of radula of *P. bedfordensis,* USNM 854976. A, B. Central radular teeth (bars = 17.6 μm). C. Section of ribbon showing central and lateral radular teeth (bar = 38 μm). D, E. Sections of ribbons showing lateral and marginal radular teeth (bars = 43, 30 μm, respectively). F. Marginal radular teeth (bar = 27 μm).

ules. Pallial roof, visceral coil black on dorsal surfaces, lighter ventrally. Penial filament having dark melanin core.

Ctenidium with about 18 medium sized filaments (not extending to rectum); filaments with pleats, broadly triangular, apices centrally positioned; ctenidium abutting pericardium posteriorly. Osphradium small, intermediate width, centrally positioned. Renal gland slightly oblique; kidney with small pallial bulge and simple opening. Rectum straight, slightly overlapping capsule gland, abutting prostate gland.

Ovary a single yellow mass, weakly lobate dorsally, 0.5–0.75 whorl, filling slightly less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Albumen gland clear-white, having very short pallial component (Fig. 5A). Capsule gland yellow, about as long as but narrower than capsule gland, divided into two sub-equal tissue sections (anterior section smaller and lighter), ovate in section, right lobe thicker than left; rectal furrow absent. Ventral channel moderately overlapping capsule gland; longitudinal fold well-developed. Genital aperture a terminal slit positioned slightly posterior to anus. Coiled oviduct of a single anterior-oblique loop; gonopericardial duct not evident in dissection. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix small relative to albumen gland, narrow to ovate, longitudinal, extending slightly posterior to albumen gland, sometimes slightly overlapped by albumen gland dosrally (Fig. 5B). Bursal duct originating from anterior edge at mid-line, considerably longer than bursa copulatrix, medium to wide, usually broadening distally, surficial or slightly embedded in albumen gland proximally. Seminal receptacle small relative to bursa copulatrix, narrow or ovate, positioned near ventral edge of albumen gland slightly to well anterior to bursa copulatrix, duct slightly shorter than body (Fig. 5C).

Testis 1.25 whorls, composed of numerous compound lobes, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers anteriorly. Seminal vesicle a small mass of tight coils opening from and positioned alongside the anterior portion of testis. Prostate gland small, sub-globular, pallial portion very short or absent, ovate in section (Fig. 5D). Pallial vas deferens curving on columellar muscle. Penis large relative to head, base rectangular, smooth; filament about 67% length of base, tapering, distally pointed, narrow, longitudinal or oblique (Fig. 5E). Lobe about as long and wide as base, rectangular, longitudinal. Terminal gland transversely positioned along edge of lobe, narrow, curved, rarely split into two units. Dg3 borne on prominent stalk arising from inner edge of lobe, stalk often clearly demarcated from lobe; glandular unit shorter than terminal gland, slightly curved. Penial duct narrow, curved, coursing from close to inner edge proximally to near medial position distally.

Etymology.—An adjectival geographical name referring to location of the type locality near the historical site of Bedford, Montana. Gender female. We propose the vernacular name, "Bedford springsnail," for this species, also in reference to its single known locality.

Comparisons.—This novelty conforms morphologically to the western fauna of congeners, which share weak protoconch microstructure, surficial position of the female bursal duct relative to the albumen gland, and connection of the bursal duct and oviduct at the posterior pallial wall (Hershler 1994). *Pyrgulopsis bedfordensis* has an unique pattern of penial ornament, which consists of a transverse terminal gland and well-developed gland on the inner edge of the lobe (Dg3). Although not closely similar to any other member of the genus, this species uniquely shares with several other congeners living in western thermal springs an elongate-rectangular penial lobe that is much larger than the filament (e.g., *P. isolata, P. nana*; Hershler & Sada 1987, figs. 32, 38).

Habitat.—The type locality (Fig. 6A, B)

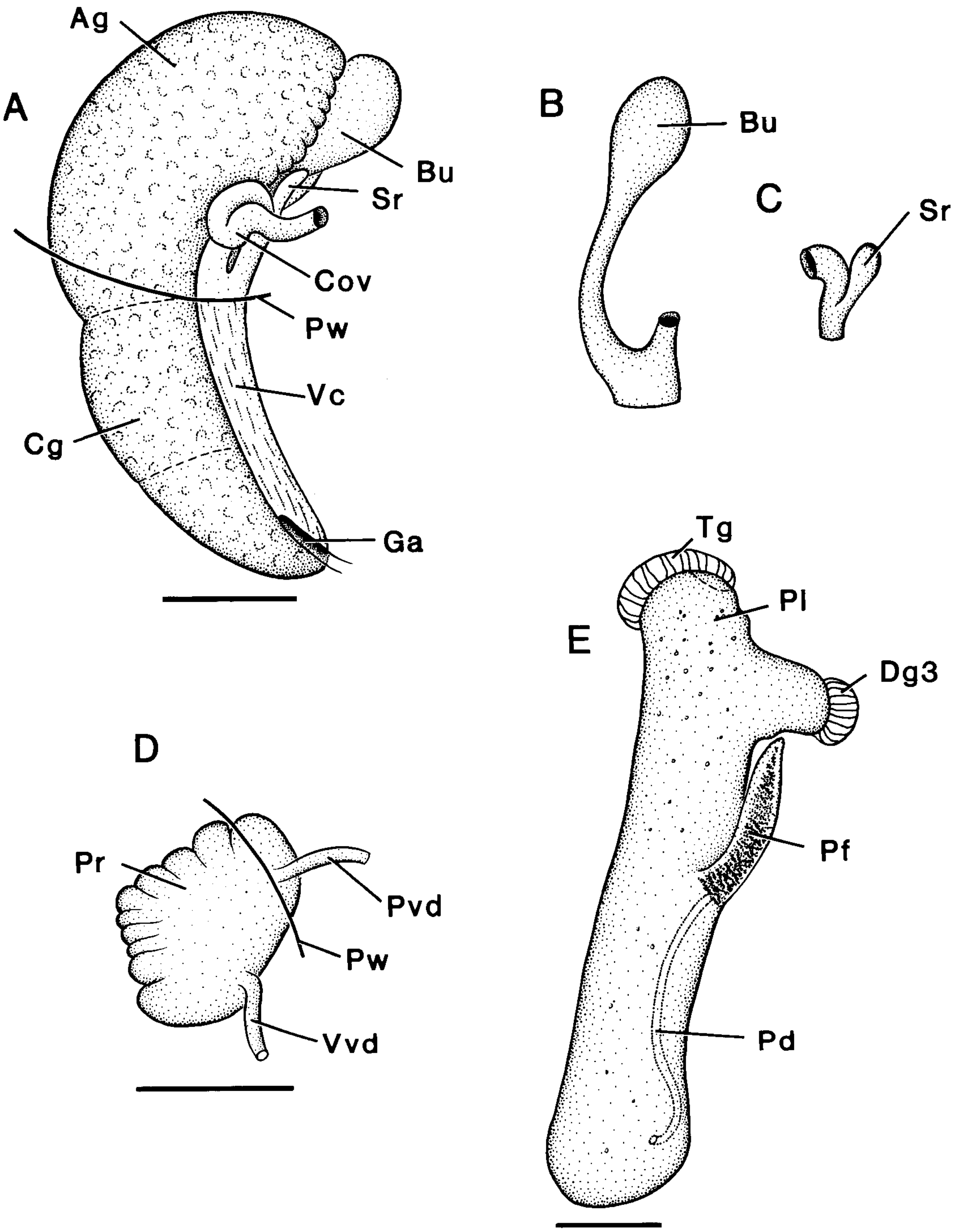

Fig. 5. Genitalia of *P. bedfordensis*, USNM 892152. A. Left side of female glandular oviduct and associated structures. B. Bursa copulatrix and its duct. Scale as in A. C. Seminal receptacle and its duct. Scale as in A. D. Left side of prostate gland, showing insertion of vas deferens. E. Penis. Bars—250 μm. Ag, albumen gland; Bu, bursa copulatrix; Cg, capsule gland; Cov, coiled oviduct; Dg3, gland along inner edge of penial lobe; Ga, genital aperture; Pd, penial duct; Pf, penial filament; Pl, penial lobe; Pvd, pallial vas deferens; Pw, posterior wall of pallial cavity; Sr, seminal receptacle; Vc, ventral channel of capsule gland; Tg, terminal gland; Vvd, visceral vas deferens.

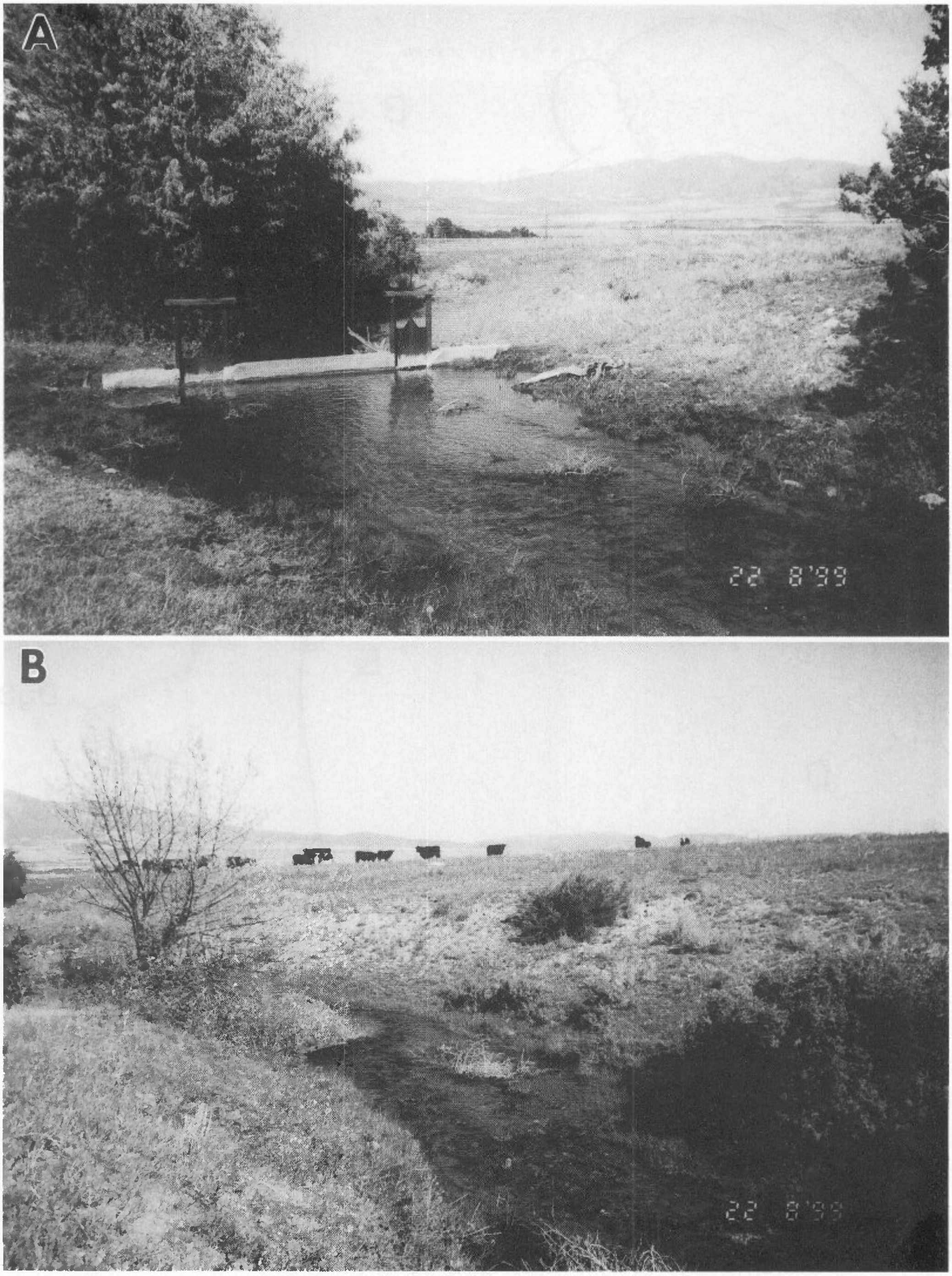

Fig. 6. Type locality of *P. bedfordensis*. A. Lower end of sampling area, with diversions structure used to irrigate nearby fields. Riparian area badly trampled by livestock. B. Typical reach of spring run (above diversion structure). Photographs, 22 August 1999.

is a large thermal spring which flows for about 2.0 km (dropping 56 m in elevation) before entering the western pond at the upper end of Canyon Ferry Reservoir just east of Bedford. (There are three more ponds to the east.) This creek drained directly to the Missouri River prior to construction of the original Canyon Ferry Dam in 1901. The water temperature was 21°C near the source on 26 January 1991 (when the air temperature was well below zero) and 23°C on 22 August 1999. (Mean annual air temperature at nearby Townsend is 6.74°C.) Sonderegger et al. (1981) indicated a temperature of 23.6°C for this spring, along with pH, 7.2; specific conductivity, 467 μmho/cm; and 350 mg/L TDS.

Pyrgulopsis bedfordensis was abundant throughout the sampled section of spring run and snail shells made up a large component of substrate in many areas. Snails were collected by sweeping a fine aerial insect net underneath riparian vegetation which lined the stream margins. (Snails released from the vegetation with the slightest disturbance.) Snails were also found on all other available substrates; mud, rocks, wood, mosses, aquatic and submerged vascular plants, and filamentous algae. This new species was collected along with another gastropod snail (*Fossaria* sp.) and 31 other invertebrates, most of which have broad geographic distributions. The other invertebrates include various species commonly found in thermal waters; e.g., *Libellula saturata* Uhler and *Argia vivida* Hagen (Odonata), *Ambrysus mormon* Montandon (Hemiptera), *Chimarra utahensis* Ross and *Protoptila erotica* (Trichoptera), and *Microcylloepus* sp. (Coleoptera). Three species of fishes were collected—*Rhinichthys cataractae* (Valenciennes), *Gambusia affinis* (Baird and Girard), and *Xiphophorus variatus* (Meek)—the latter two of which are introduced in Montana.

Distribution.—This species is thus far known only from the type locality. Local endemism is likely given that over the past 18 years one of us (DLG) has extensively sampled aquatic habitats throughout Montana and adjacent states (Fig. 7) without finding this snail elsewhere. This sampling included 30 of the Montana warm springs listed by Sonderreger et al. (1981), including all five of the springs in close proximity to Warm Springs Creek.

Discussion

Origin of *Pyrgulopsis bedfordensis* is conjectural given the poorly resolved phylogenetic relationships within the genus, and the incompletely known history of drainage in the northern Rocky Mountan region. An origin associated with upstream penetration of the Missouri River basin appears unlikely given the distinctiveness of the eastern and western faunas of *Pyrgulopsis* (see above). The well documented Pleistocene rerouting of the ancestral Missouri River, which coursed north to the Hudson Bay prior to blockage by the Laurentide ice sheet and assumption of the modern path to the Mississippi River (Howard 1958, Lemke et al. 1965), probably had no bearing on this issue as *P. bedfordensis* represents the northernmost record for the genus (living and fossil) in the West. We instead attribute origin to vicariance of an earlier paleodrainage implied by the close geographical proximity of this species of poorly dispersing snail to fauna living across the continental divide in the upper Snake River basin (e.g., *P. robusta*; Hershler 1994). Note that *Pyrgulopsis* has not been found in the upper Colorado River basin (Green River drainage), which also is in close proximity to the Missouri headwaters.

Extensional faulting responsible for development of the basin and range of southwest Montana began during the middle Miocene and profoundly disrupted an ancestral landscape that consisted of broader, shallower basins (Reynolds 1979, Fields et al. 1985, Boronsky et al. 1993, Sears & Fritz 1998). (The Townsend pull-apart graben, to which *P. bedfordensis* is endemic, lies along the boundary between this zone

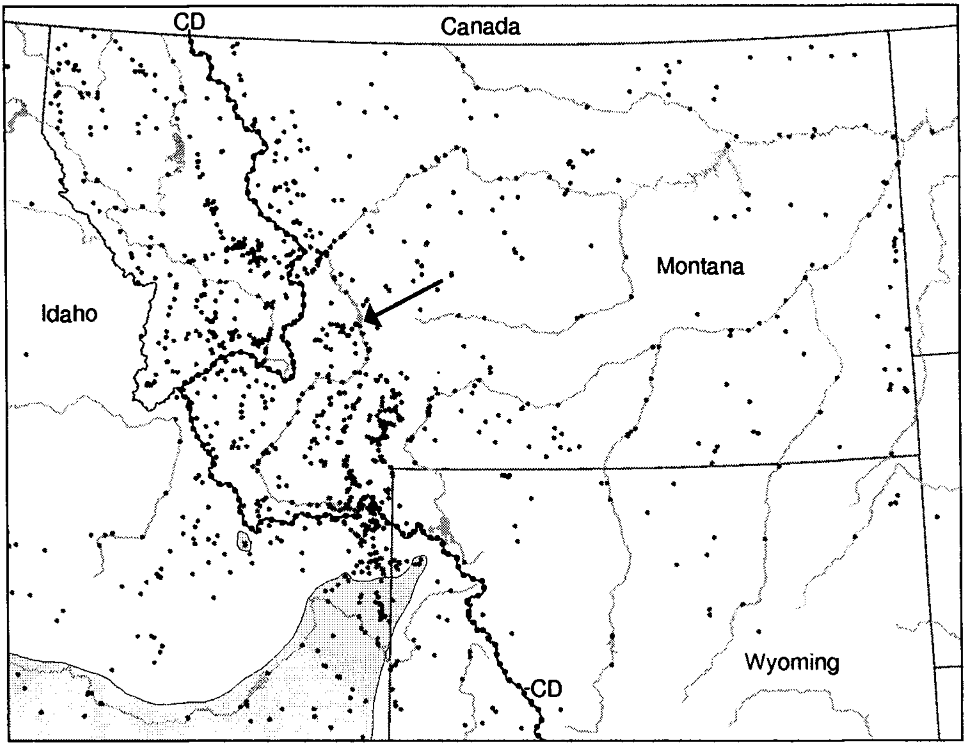

Fig. 7. Map showing location of sampling sites in Montana and adjacent states. The shaded area depicts the regional distribution of *Pyrgulopsis*, with the disjunct occurrence of *P. bedfordensis* indicated by the arrow. CD, continental divide.

of deformation and more stable crust to the north [Reynolds 1977].) The continental divide probably had a complex history in this region (Fields et al. 1985) and the modern north-trending Missouri headwater drainage may not have been assembled until the Quaternary (Robinson 1963, Fritz & Sears 1993). Anderson (1947) presented physical evidence that the continental divide shifted about 161 km to the east during the late Tertiary, with associated severence of a paleodrainage that integrated southwest Montana and southeast Idaho (also see Ruppel 1967). The development and migration of volcanic centers and a topographic swell in association with passage of the North American plate across the Yellowstone Hot Spot (beginning ca. 16 Ma) has provided a cogent explanation for such an eastward shift of the divide (Pierce & Morgan 1992, 1999; Smith & Braile 1994). Fritz & Sears (1989, 1993; also see Kreps et al. 1992) recently proposed that during the early middle Miocene, the portion of southwestern Montana now comprising the upper Missouri River basin drained south to the present site of the Snake River Plain, with tectonic break-up of this landscape and reversal of flow direction occurring about 6.5 Ma in association with local passage of the hotspot. While some of the stratigraphic interpretations of this proposal have been challenged, the hypothesized drainage reversal has been accepted (Cheney et al. 1994, Fritz & Sears 1994).

The western fossil record of *Pyrgulopsis* dating to the late Miocene (Hershler & Sada 2001) is congruent with the above time frame of physical events contributing to vicariance of a postulated Missouri-Snake paleodrainage. This hypothesis is also consistent with other organismal distributions suggesting prior connections across the Pacific divide in this region, including those of fishes (Miller 1959, Smith 1981, Behnke 1992, Smith 1999), mollusks (Taylor 1985), and a recently described oligocheate, *Rhynchelmis gustafsoni,* which is narrowly endemic to headwaters of the Missouri and Snake river basins and is the only member of its species group that ranges east of this divide (Fend & Brinkhurst 2000). Note, however, that for some of these cases (e.g., Cutthroat Trout) it has been argued that biotic pattern reflects montane headwater transfers effected by Pleistocene or younger faulting or landslides rather than an earlier disruption of through-going basinal drainage. The possibility that, in accordance with our hypothesis, this snail may have long persisted locally in southwest Montana and endured the harsh conditions of the Quaternary is supported by its endemism slightly south of the continental Wisconsin ice sheet and by the minimal record of alpine glaciation in the ranges enclosing Townsend Valley (Alden 1953). Furthermore, this valley was not inundated by glacial Lake Great Falls, which was ponded further downstream in the Missouri River Valley against the southern edge of the ice sheet (Calhoun 1906, Alden 1932). The large discharge (88.3 l/s; Waring 1965), high temperature, and long, high-gradient outflow of this spring also may have contributed to local persistence of *P. bedfordensis.*

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