A NEW SPECIES OF *EREMOPYRGUS* (HYDROBIIDAE: COCHLIOPINAE) FROM THE CHIHUAHUAN DESERT, MEXICO: PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY

ROBERT HERSHLER[1], HSIU-PING LIU[2] AND J. JERRY LANDYE[3]

[1]*Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0118*
[2]*Department of Biological Sciences, University of Denver, Denver, Co 80208*
[3]*New Mexico Fishery Resources Office, U. S. Fish & Wildlife Service, 2105 Osuna Road NE, Albuquerque, NM 87113-1001*

ABSTRACT

A new species of hydrobiid gastropod, *Eremopyrgus elegans*, is described from northwestern Chihuahua state, Mexico. This new species inhabits a single spring more than 1000 km south-southeast of waters occupied by its sole congener (*E. eganensis*), which lives in east-central Nevada. *Eremopyrgus elegans* differs from its congener in its narrower shell, larger number of shell whorls, tilted shell apex, location of glandular lobe on the outer edge of the penis, presence of a terminal penial papilla, and 12 additional anatomical features. Although well differentiated, these two species share an unique type of glandular penial lobe and distinctive female genitalic organs, and their monophyly within the Cochliopinae is supported by a phylogenetic analysis based on a partial sequence of the mitochondrial COI gene. Our phylogenetic analysis depicts *Eremopyrgus* as sister to *Zetekina*, which is distributed along the Pacific Coast of southern Central America. We conjecture that the broadly disjunct distribution of *Eremopyrgus*, which cuts across the structural grain of western North America, may reflect the trace of a prior inland 'invasion' by coastal progenitors.

INTRODUCTION

Hydrobiid snails of Mexico remain poorly known as much of this large, geographically complex country has not been thoroughly surveyed for aquatic invertebrates. In northeastern Mexico aquatic habitats of the Chihuahuan Desert (*sensu* Schmidt, 1979, fig. 1) became isolated through inception of modern basin and range topography in the Oligocene (Henry & Aranda-Gomez, 1992; Stewart, 1998) and onset of aridity during the late Quaternary (Metcalfe, O'Hara, Caballero & Davies, 2000), providing an ideal scenario for extensive local diversification of hydrobiids and other poorly dispersing biota. Yet, aside from the largely endemic fauna of the Cuatro Cienegas basin (Taylor, 1966b; Hershler, 1985), only four nominate hydrobiids have been recorded from the region (Pilsbry, 1895, 1928; Drake, 1953, 1956), although the presence of undescribed taxa has been known for some time (Williams, Brown, Brooks, Echelle, Edwards, Hendrickson & Landye, 1985; Landye in Minckley & Minckley, 1986; Taylor, 1987).

Our ongoing survey of aquatic habitats in the Chihuahuan Desert is revealing a diverse fauna of undescribed hydrobiids. As part of a projected series in which we will review this fauna genus by genus, herein we describe a new species of *Eremopyrgus* which we collected from a spring in northwestern Chihuahua state more than 1000 km south-southeast of waters occupied by its congener (*E. eganensis* Hershler). *Eremopyrgus* has not been collected in intervening western areas despite extensive field-work (e.g., Taylor, 1987; Hershler, 1998), nor have we found it elsewhere in the Chihuahuan Desert region (Hershler & Landye, unpublished). We present morphological and mtDNA evidence supporting recognition of these broadly disjunct species as a monophyletic group within the hydrobiid subfamily Cochliopinae and we further explore these data insofar as they provide an additional perspective on the regional biogeographic history of the Cochliopinae.

METHODS

Outline drawings of shells were prepared using a camera lucida attached to a dissecting microscope (25× magnification). A standardized series of points were then digitized from these drawings using a SummaSketch III tablet linked to a personal computer and resulting data were then converted into standardized shell measurements using a MS-DOS program, NEW-CONCH (Chapman, unpublished). Animals used for anatomical study were relaxed in the field with menthol crystals, and then fixed in dilute formalin (10% of stock solution) and preserved in 70% ethanol. Prior to dissection, shells were removed from animals by soaking in dilute hydrochloric acid. Animals were dissected using a WILD M8 research microscope and drawings were made with the aid of a camera lucida attachment. Methods of preparation of material for scanning electron microscopy are of Hershler (1998). Counts of radular cusps and tooth rows were determined from scanning electron images. Terminology of anatomical features follows Hershler (2001) and character state delineations are from Hershler & Ponder (1998). Institutional abbreviations follow Leviton, Gibbs, Heal & Dawson (1985).

Partial sequences of the mitochondrial cytochrome c oxidase subunit I (mtCOI) gene were obtained from four specimens of the new species of *Eremopyrgus* using methods of Liu, Hershler & Thompson (2001). Sequences were deposited under Genbank accession numbers AF388167–AF388170. These were incorporated into a phylogenetic analysis along with previously analyzed mtCOI sequences of members of cochliopine sub-clades III, IV, and V (Liu *et al.*, 2001), which represent the portion of the subfamily topology that contained *E. eganensis*. In our earlier analysis, sub-clade V was sister to the lineage containing *E. eganensis*, and thus we used its most basal member (*Mexipyrgus carranzae* Taylor) for rooting in the current study. Analyses were conducted using the maximum parsimony option of PAUP*4.0 (Swofford, 2000). All characters were weighed equally based on a mutational saturation test (see Liu *et al.*, 2001). The heuristic search option with 10 replications of random stepwise additions was used to search for minimum length trees. Bootstrapping (Felsenstein, 1985) with 1,000 replications was performed to assess branch support on the resulting trees.

SYSTEMATICS

Family *Hydrobiidae* Troschel, 1857

Subfamily *Cochliopinae* Tryon, 1866

Eremopyrgus Hershler, 1999

Type-species: *Eremopyrgus eganensis* Hershler, 1999, by original designation.

Diagnosis: (modified from Hershler, 1999): Shell medium-sized, elongate-conic or conical with weakly convex teleoconch whorls, shallow sutures, and pyriform aperture. Protoconch weakly sculptured. Prostate gland elongate, with large pallial section. Distal portion of penis darkly pigmented; penial ornament of 1–2 squat, glandular lobes. Females ovoviviparous; capsule gland a thin-walled brood pouch, folded posteriorly; bursa copulatrix medium-sized to large relative to brood pouch; seminal receptacle minute, without obvious duct; sperm duct located in front of duct to albumen gland, opening to bursa copulatrix; renal oviduct with posterior-oblique bend.

Remarks: *Eremopyrgus* is recognizable as a member of the hydrobiid subfamily Cochliopinae based on the presence of a female spermathecal duct and a connection between the oviduct (as opposed to the spermathecal duct) and albumen gland (*fide* Liu *et al.*, 2001).

Eremopyrgus elegans new species

Diagnosis: A narrow-shelled *Eremopyrgus* with 5.25 or more whorls. Apex tilted relative to teleoconch axis; teleoconch whorls almost flat to weakly convex. Penial ornament of a single medial lobe on outer edge of penis.

Description: Shell (Fig. 1A,B) 1.9–4.4 mm tall, elongate-conic, whorls 5.25–6.25. Periostracum tan, thin. Initial 1.0 whorl well rounded, flattened above, strongly inclined relative to teleoconch (Fig. 1C). Protoconch ca. 0.8 whorl, initial portion corrugated, otherwise sculptured with weak spiral ornament (Fig. 1D,E). Early teleoconch with well rounded whorls and sculpture of weak spiral lines, demarcation at 1.75 whorls reflecting cessation of growth in brood pouch. Remaining teleoconch whorls almost flat or weakly convex, smooth apart from growth lines. Spire outline usually slightly convex. Aperture small, apertural lip thin, complete across parietal wall in largest specimens. Outer lip orthocline or weakly prosocline, often sinuate in profile; columellar lip sometimes narrowly reflected. Shell imperforate or with rimate umbilicus. Shell parameters are in Table 1.
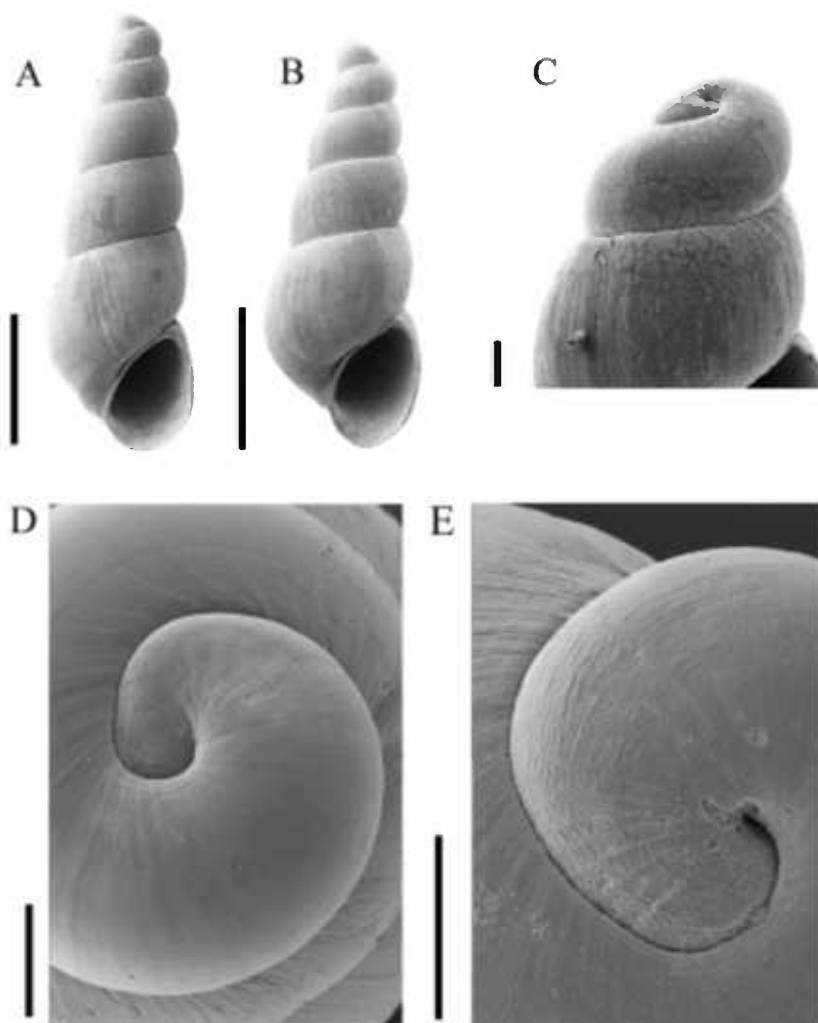

Figure 1. Scanning electron micrographs of shells of *Eremopyrgus elegans*, USNM 905324. **A, B.** Standard views of shells; scale bars = 1.0 mm. **C.** Apical whorls, showing tilted state of initial whorl; scale bar = 100 μm. **D, E.** View of protoconch, showing weak spiral sculpture; scale bars = 100 μm.

Operculum thin, flat, clear or light amber, ellipsoidal, multi-spiral, nucleus highly eccentric Fig. 2A), outer margin without rim; attachment scar margin thickened all around on inner side, especially along inner edge and in nuclear region (Fig. 2B).

Foot generally light gray or pale, opercular lobe often darkly pigmented internally. Snout pale to medium gray or dark brown. Cephalic tentacles usually pale, sometimes light gray. Visceral coil medium gray, often black in part (e.g., over testis). Pigment over pallial genital ducts lighter than elsewhere.

Ctenidium well developed, connected to pericardium by long efferent vein; ctenidial filaments about 21, lightly pigmented, broadly triangular with central apices, lateral surfaces weakly ridged. Osphradium small relative to ctenidium, centrally positioned along ctenidial axis. Renal organ with small pallial portion; renal opening simple; pericardium with small pallial portion. Anterior stomach chamber slightly larger than posterior chamber; style sac slightly longer than remaining stomach, posterior caecum of stomach absent.

Radula with about 60 well-formed rows of teeth; ribbon length 486 μm, ribbon width 76 μm; central tooth width 16 μm. Dorsal edge of central teeth (Fig. 3A) strongly indented, basal tongue broad V-shaped, base even with lateral margins, median cusps elongate, distally pointed, basally parallel-sided, lateral cusps 5–7; the single basal cusp is well-developed. Lateral teeth (Fig. 3B) having 3–4 cusps on inner side and 4–7 cusps on outer

Table 1. Shell parameters for paratypes of *Eremopyrgus elegans* (USNM 905324). Measurements are in mm. NW = number of whorls, SH = shell height, SW = shell width, SS = SW/SH, HBH = height of body whorl, WBW = width of body whorl, APH = height of aperture, APW = width of aperture, N= number of specimens, CV = coefficient of variation.

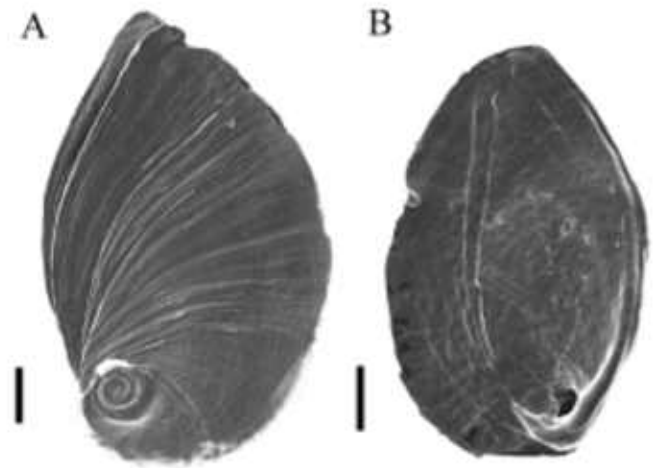|	NW	SH	SS	HBH	WBW	APH	APW	SW
N	14	15	15	15	15	15	15	15
Minimum	5.25	3.08	0.34	1.16	1.58	1.09	0.95	0.67
Maximum	6.25	3.68	0.39	1.32	1.85	1.21	1.15	0.76
Mean	5.64	3.34	0.37	1.23	1.68	1.16	1.01	0.72
CV	0.05	0.04	0.04	0.04	0.04	0.03	0.05	0.04

Figure 2. Scanning electron micrographs of operculum of *Eremopyrgus elegans*, USNM 905324. **A**, outer side. **B**, inner side. Scale bars = 100 μm.
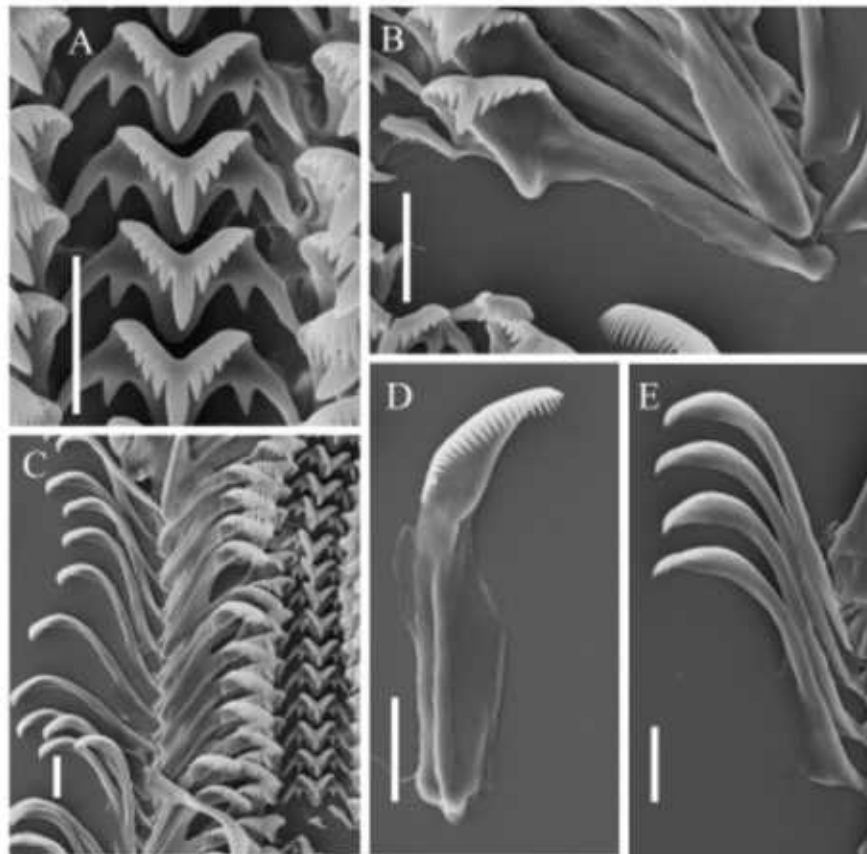

Figure 3. Scanning electron micrographs of radula of *Eremopyrgus elegans*, USNM 905324. **A.** Central radular teeth. **B.** Lateral radular teeth. **C.** Portion of radular ribbon. **D.** Inner marginal teeth. **E.** Outer marginal teeth. Scale bars = 10 μm.

side; outer wing weakly flexed, length 200–230% width of tooth face; central cusp weakly pointed or rounded distally, dorsal edge weakly concave; basal tongue well developed. Inner marginal teeth (Fig. 3D) with 22–26 cusps, cutting edge on outer side of tooth, occupying about 40% of tooth length. Outer marginal teeth (Fig. 3E) with 25–32 cusps, cutting edge on inner side of tooth, occupying about 30% of tooth length. Cusps on inner marginal teeth larger than those on outer marginals (Fig. 3C).

Testis 0.5 whorl, of 8–10 compound lobes, positioned entirely posterior to stomach, filling <50% of digestive gland behind stomach. Seminal vesicle exiting from testis near mid-length, consisting of a few loose coils abutting left side of testis. Prostate gland (Fig. 4A, Pr) medium-sized, about 50% of length

in pallial roof, banana-shaped, ovate in section, walls thickened all around. Visceral vas deferens (Vvd) opening near postero-ventral edge of prostate gland; pallial vas deferens (Pvd) exiting a little behind anterior edge, in front of posterior pallial wall, duct having distinct bend on columellar muscle. Penis (Fig. 4B) small, narrow, weakly tapering distally, with rounded tip. Penial duct (Pd) narrow, positioned centrally to near outer edge, near straight to strongly undulating, opening through small terminal papilla. Single glandular lobe (Pl) tapering distally, borne along outer edge of penis near mid-length. Penis near pale to medium gray almost throughout; pigment especially dense near tip and along mid-line.

Oviduct terminating blindly as narrow tube just behind stomach. Glandular oviduct large, mostly consisting of thin-walled
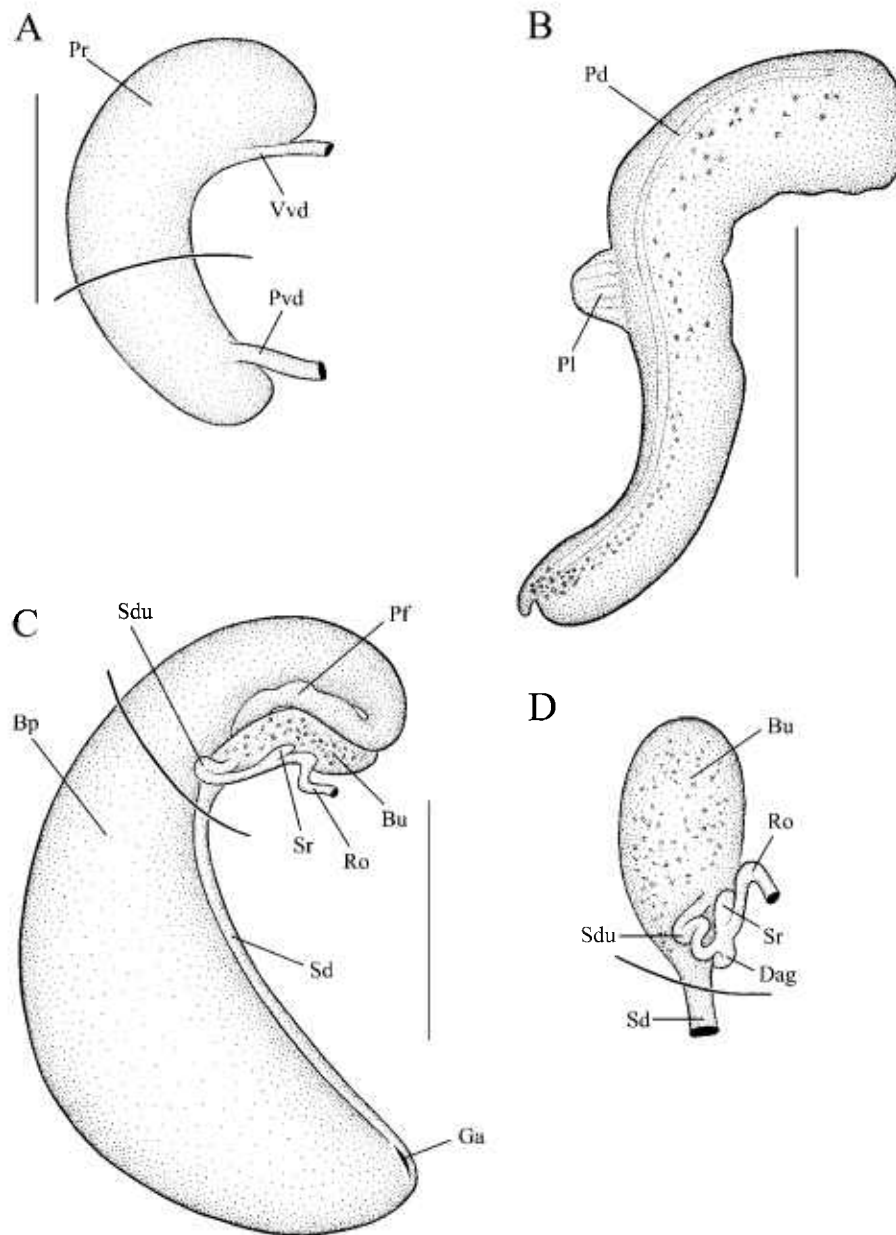

Figure 4. Genitalia of *Eremopyrgus elegans*, USNM 905324. **A.** Prostate gland, left side; scale bar = 250 μm. **B.** Penis; scale bar = 250 μm. **C.** Distal female genitalia, left side; scale bar = 500 μm. **D.** Bursa copulatrix and associated structures; scale as in C. The albumen gland is hidden behind the bursa copulatrix (Bu). Abbreviations: Bp, brood pouch; Bu, bursa copulatrix; Dag, duct to albumen gland; Ga, common genital aperture; Pf, posterior fold of brood pouch; Pd, penial duct; Pl, penial lobe; Pr, prostate gland; Pvd, pallial vas deferens; Ro, renal oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle; Vvd, visceral vas deferens.

brood pouch (Fig. 4C, Bp) having a single narrow folded section lying against dorsal edge of bursa copulatrix (Bu); anterior opening a terminal slit (Ga) positioned slightly behind anus. Brood pouch containing 1–2 embryos having up to 1.75 shell whorls. Albumen gland very small relative to brood pouch, narrow, abutting right side of bursa copulatrix. Bursa copulatrix medium-sized relative to brood pouch, narrow ovate, lightly pigmented (brown), extending to near posterior edge of brood pouch, duct short, narrow, exiting anterior edge. Seminal receptacle (Sr) much smaller than bursa copulatrix, ovate, positioned along left side of bursa copulatrix in anterior half near ventral edge, opening to oviduct at point where duct to albumen gland (Fig. 4D, Dag) issued. Sperm duct (Sdu) entirely visceral (e.g., positioned behind posterior pallial wall), narrow, coursing anteriorly before turning back posteriorly to open to anterior bursa copulatrix near ventral edge; distal section having 1–2 small vertical coils. Renal oviduct (Ro) a single, small, inverted L-shaped bend, opening to posterior edge of albumen gland. Oviduct and pericardium having narrow connection originating at distal end of oviduct coil. Spermathecal duct (Sd) narrow, extending to anterior

portion of pallial cavity, opening fused with that of brood pouch.

Type material: A large series of specimens was collected by Robert Hershler and J. Jerry Landye on 6 Dec. 1998 from a large spring known locally as Ojo Vareleño (*fide* Henrickson & Straw, 1976), 2.4 km NW of Casas Grandes, Chihuahua, Mexico (30° 24′ N, 107° 59′ W), elevation ca. 1514 m (Fig. 5). The holotype (USNM 892119, Fig. 6) is a dried shell (3.93 mm height, 5.75 whorls) selected from this series, while remaining material (composed of dried shells and alcohol-preserved snails) is deposited as paratypes (UF 281620, USNM 905324). An additional series (USNM 883255) was collected in the type locality area by J. Jerry Landye and P. Hines in 1990.

Etymology: The species name is derived from New Latin *elegans*, meaning tasteful or choice, and referring to the slender, flat-whorled shell.

Habitat: In the type locality area (Fig. 7) multiple spring sources coalesce into a broad cienega which drains to the Rio Casas
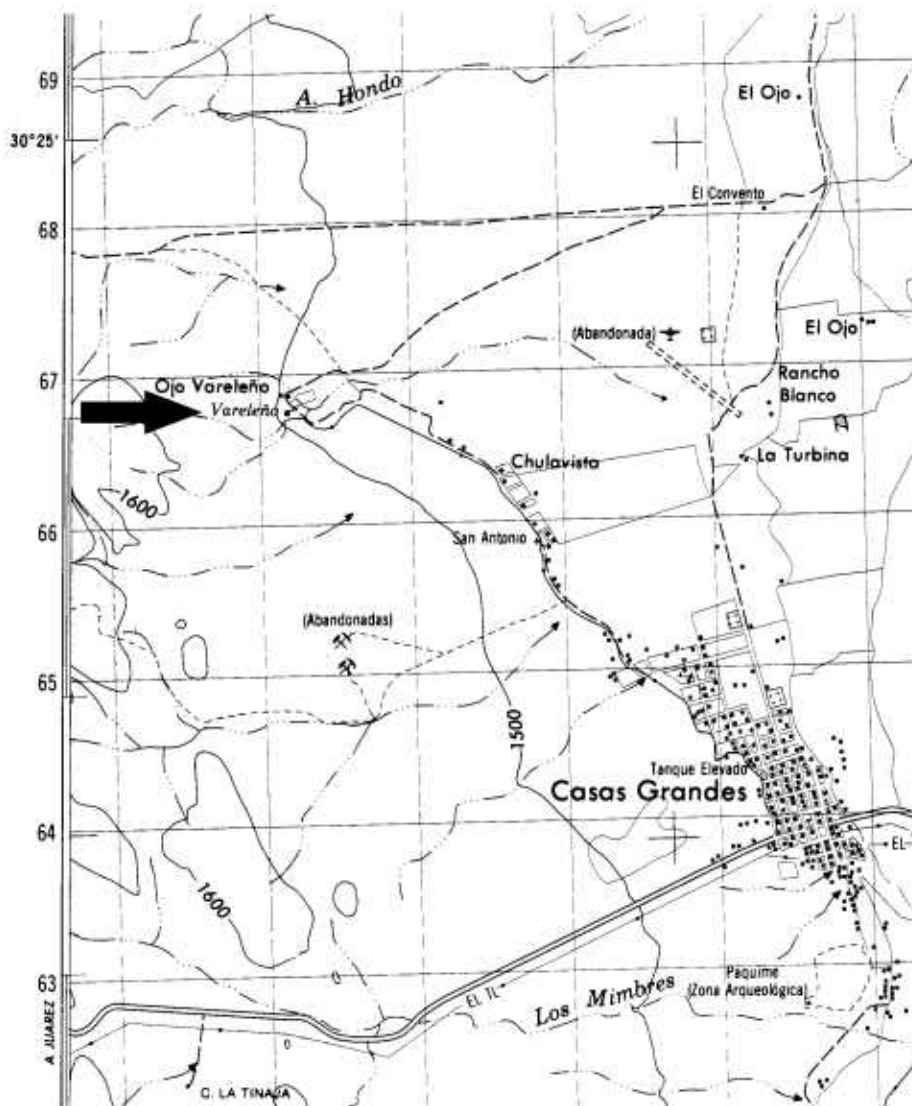

Figure 5. Map showing location of the type locality of *Eremopyrgus elegans* (from Nuevo Casas Grandes H13A71, Carta Topografica 1:50,000 sheet). Quadrants are 1.0 km^2.

Grandes, although a portion of the flow is diverted into an irrigation canal which provides water for the town of Casas Grandes. Water temperature at the spring sources was 30°C on 16 September 1990 and on 6 December 1998. *Eremopyrgus elegans* was moderately common in fine detritus and sand near the spring sources. Associated molluscs in this section of the spring run were another hydrobiid snail (*Pyrgulopsis* sp.), which was common on watercress and on rocks in swift current, and a planorbid snail (*Planorbella* sp.). An aquatic isopod also was found under rocks.

Comparisons: *Eremopyrgus elegans* is easily separable from *E. eganensis* by its narrower shell, larger number of shell whorls, tilted shell apex, location of the glandular lobe on the outer (not inner) edge of the penis, and presence of a small terminal penial papilla. This snail is further distinguished from its congener by the narrower central cusps, deeper notch of the dorsal edge, and narrower basal tongue of the central radular teeth; posterior shortening of the ctendium, smaller pallial portion of the renal organ, restriction of sperm duct to the left side of the bursa copulatrix, more dorsal position of the posteriorly folded section of the brood pouch relative to the bursa copulatrix,

Figure 6. Holotype of *Eremopyrgus elegans*, USNM 892119; shell height = 3.93 mm.

pigmentation of the bursa copulatrix, simple female genital aperture, smaller number of shell whorls of brooded embryos, smaller testis positioned entirely posterior to the stomach, and simply rounded condition of the distal section of the penis. The strong morphological differentiation of these congeners is paralleled by a relatively large mtCOI sequence divergence of 10.02%.

Although the two species of *Eremopyrgus* are well differentiated morphologically, they nonetheless are closely similar in shell features and anatomical groundplan. Among the character-states that they share is a distally tapered penial lobe, containing multiple glandular units distally that discharge through a small terminal opening, which is unique within the Cochliopinae (Hershler, 1999) and probably within the Hydrobiidae more generally, and thus may represent a defining synapomorphy for the genus. The minute female seminal receptacle opening to the oviduct without an intervening duct also may represent a uniquely shared condition within the subfamily. A similar sperm pouch has only been described for one other taxon, *Paludiscala caramba* Taylor, and in that case the structure was considered to be an outpocketing of the albumen gland rather a true seminal receptacle (Hershler, 1985). Our phylogenetic analysis of mtCOI sequences (Fig. 8) strongly supported monophyly of *Eremopyrgus*, as the clade composed of *E. eganensis* and four specimens of *E. elegans* had a 100% bootstrap value. No sequence variaton was observed among four specimens of *E. elegans*.

Hershler (1999) suggested that *E. eganensis* was not closely related to other cochliopines of the Great Basin (which belong to the genus *Tryonia*) and instead compared this snail with members of the '*Heleobia* group' (*fide* Hershler & Thompson, 1992) based on similarities of their glandular penial lobes. In a subsequent analysis of cochliopine phylogeny based on mtCOI sequences (Liu *et al.*, 2001), a close relationship was not evident between *E. eganensis* and either of these groups, and instead this species was sister to and formed a sub-clade with two species of *Zetekina*, a cochliopine genus which is distributed along the Pacific coast of southern Central America (Hershler & Thompson, 1992). *Zetekina* has non-glandular penial lobes, and this topology implies that the penial glands of *Eremopyrgus* are uniquely derived within the Cochliopinae. A sister relationship between *Eremopyrgus* and *Zetekina* is retained in our present analysis (in which *E. elegans* has been added), although boot-

Figure 7. Photograph of type locality area of *Eremopyrgus elegans*, 6 December 1998 (from 35 mm color slide).
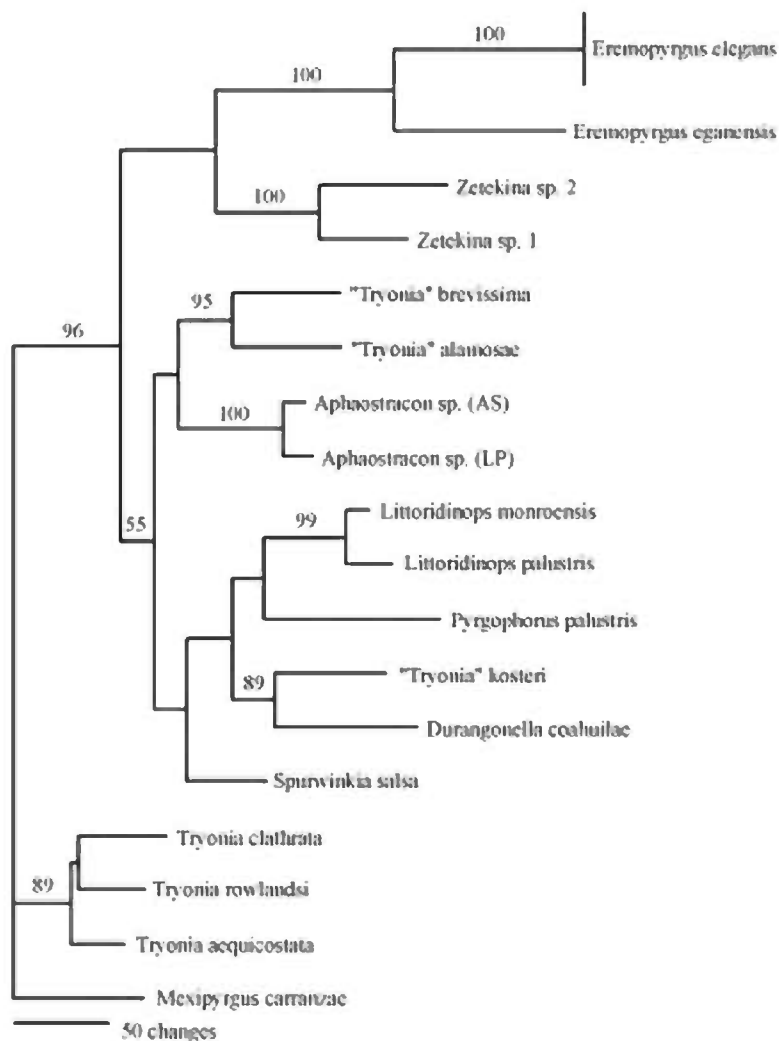
Figure 8. Single shortest length tree based on maximum parsimony analysis of mtCOI sequence data. CI, 0.59; TL, 1462. Bootstrap percentages are given when >50%. The four specimens of *E. elegans* were identical in their sequences. Samples of *Aphaostracon* sp. were from Alexander Springs, Lake Co, FL (AS); and Lake Panasoffkee, Sumter Co., FL (LP). Species of *Tryonia* positioned outside of the clade containing the type species (*T. clathrata* Stimpson) are being transferred to additional genera (Hershler, 2001).

strap support is weak. Although we have not identified anatomical features which may serve as unifying synapomorphies for a clade composed of *Eremopyrgus* and *Zetekina*, a sister relationship is consistent with the narrow shells with weakly convex whorls and shallow sutures shared by these taxa.

Biogeographic considerations: Hershler & Thompson (1992) ascribed a Tethyan origin for the Holarctic and Neotropical Cochliopinae and speculated that freshwater habitats have been invaded several times by coastal progenitors during the history of the group. Modern coastal cochliopines live in a variety of habitats and tolerate a broad range of salinity regimes, ranging from freshwater to hypersaline (e.g., *Heleobops carrikeri* Davis & McKee [Davis & McKee, 1989]; *Spurwinkia salsa* (Pilsbry) [Davis, Mazurkiewicz & Mandracchia, 1982]). These snails typically range hundreds of kilometers along shorelines (e.g., *Texadina sphinctosoma* Abbott & Ladd [Taylor in Andrews, 1977]; *Tryonia imitator* (Pilsbry) [Kellogg, 1985]), reflecting their broad salinity tolerance (as well as the frequent possession of pelagic larvae). Together, these features suggest that euryhaline progenitors could have dispersed broadly across inland regions through estuaries and other coastal drainages. We conjecture such an origin for *Eremopyrgus*, which is distributed

across the structural grain of inland western North America (Fig. 9) that has been in place since the mid-Tertiary (Christiansen & Yeats, 1992) and includes dominant elements dating to the Cretaceous (e.g., Mogollon Highlands; Bilodeau, 1986).

The two species of *Eremopyrgus* are distributed in proximity to an early Tertiary continental divide which extended southwards along the Sevier arch in easternmost Nevada, across the Mogollon Highland in southern Arizona, and along a structural high in western Mexico (Christiansen & Yeats, 1992, fig. 15). There is no physical evidence of inland paleodrainages or ancient sedimentary basins that could have integrated areas now inhabited by these snails, however coastal progenitors could have colonised the region during the late Cretaceous, when the Western Interior Seaway transgressed into Chihuahua and also lapped against the eastern flanks of the Sevier cordilleran belt in Utah (Elder & Kirkland, 1993). Alternatively, access could have been afforded during the Eocene-Oligocene, when long Pacific coastal streams penetrated inland from the Great Basin region south to northern Mexico (Christiansen & Yeats, 1992; Howard, 1996, 2000). Origin of *Eremopyrgus* in conjunction with severence of a coastal link is supported by the sister relationship between this genus and *Zetekina*, which lives

Figure 9. Drainage map of western North America showing broadly disjunct distribution of *Eremopyrgus*.

in tidal zones of rivers (Hershler & Thompson, 1992; F. G. Thompson, pers. com, November, 2000) and was previously distributed well north of its modern Central American range based on Neogene fossils from the Central Valley of California (Taylor, 1966a).

Subsequent diversification of *Eremopyrgus* may be attributed to severence of the coastal linkage and fragmentation of an ancestral inland distribution in association with the complex geological history of the region during the Tertiary. Vicariance of a southern element could reflect capture of the Rio Casas Grandes (and other Chihuahuan Desert drainages) across the Pacific divide of northern Mexico, as was previously suggested on the basis of fish evidence (Hendrickson, Minckley, Miller, Siebert & Minckley, 1980; Minckley, Hendrickson & Bond, 1986). The 10–15° of post-Eocene counter-clockwise tectonic rotation of northeast Mexico proposed by Urrutia-Fucugauchi (1981; also see Nowicki, Hall & Evans, 1993) on the basis of paleomagnetic evidence also would have effected separation of the Chihuahuan Desert region from the southwestern Great Basin.

Although *Eremopyrgus* has no fossil record (as far as we know), narrow-shelled hydrobiids of uncertain affinities (*Hydrobia* sp.) from the Late Cretaceous-Eocene Sheep Pass Formation (Good, 1987) suggest the possibility of an early presence of the group in east-central Nevada (where *E. eganensis* now lives). While we do not have a calibrated molecular clock for the cochliopines, the relatively large mtCOI sequence divergences between the two species of *Eremopyrgus* (10.02%) and between these and the two species of *Zetekina* analyzed (12.95–14.11%) suggest that branching events within this clade may be ancient.

Several members of additional cochliopine sub-clades also range broadly across the structural grain of western North America (e.g., *Durangonella*, *Tryonia*; Hershler & Thompson, 1992, maps 5,13), suggesting that these similar distributions may have resulted from a single inland invasion of diverse lineages or multiple such invasions. A denser sampling of taxa will be necessary to clarify habitat states for ancestral cochliopines and thereby enable evaluation of these and other hypotheses relating to the complex biogeographic history of the regional fauna.

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