

Phylogenetic Relationships within the Aquatic Snail Genus *Tryonia*: Implications for Biogeography of the North American Southwest

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We examined the phylogenetic relationships among 23 species of the North American aquatic snail genus *Tryonia* (Hydrobiidae), 10 additional representatives of the subfamily Cochliopinae, and two outgroups. Maximum parsimony analysis of a 601-base-pair sequence from the mitochondrial COI gene did not support monophyly of the genus nor its subgenus *Paupertryonia*. A clade composed of the type species of *Tryonia* and 16 congeners was strongly supported by the COI data and congruent with recently discovered variation in female genitalic morphology. This “true *Tryonia*” clade included two large western subclades having a sister-group relationship. The phylogenetic structure of one of these subclades is congruent with vicariant events associated with late Neogene history of the lower Colorado River drainage. The other subclade mirrors development of the modern Rio Grande rift and inception of modern topography in the southwestern Great Basin during the late Neogene. Both subclades are represented in the composite *Tryonia* fauna of the Amargosa River basin, whose assembly is attributed to the complex geological history of the Death Valley region. © 1999 Academic Press

INTRODUCTION

The North American Southwest (Lowe and Brown, 1982, Fig. 1) is an attractive region for biogeographic inquiry because of its complex landscape and drainage, which has been molded by a dynamic geologic and climatic history. Regional aquatic biota often live in restricted environments which are isolated by inhospitable deserts and mountain ranges and thus are ideal subjects for evaluating response to potential vicariant events. A rigorous synthesis of southwest aquatic biogeography

has been hindered by incomplete knowledge of both physical and biological aspects of this subject. Although the geological development of the Southwest is known in considerable detail (Burchfiel *et al.*, 1992; Sedlock *et al.*, 1993), the early history and interrelationships of regional drainages have not been well established (e.g., the Colorado River; Lucchitta, 1984; Elston and Young, 1991). Subsequent deposition, deformation, and erosion usually have obscured pertinent evidence. Additionally, there are few relevant phylogenetic studies for groups other than fishes. Finally, there has been a pervasive assumption that biogeography largely reflects Pleistocene events (e.g., Hubbs and Miller, 1948; Hubbs, 1974).

Minckley *et al.* (1986) proposed considerable antiquity (Oligocene–Miocene) for the western North American fish fauna. Their integrative treatment emphasized the complex role of geological events in effecting vicariance. They also suggested that fishes may have been introduced to and/or transferred within the region by rafting on allochthonous terranes, intracontinental microplates, and other tectonically displaced or extended crustal fragments (also see Hendrickson, 1986). They offered preliminary hypotheses for historical area relationships in western North America based on key geological events (Minckley *et al.*, 1986, Figs. 15.4 and 15.5), which were partly congruent with phylogenetic data then available for regional fishes (Minckley *et al.*, 1986, Figs. 15.10 and 15.11). This work set the stage for a new era in biogeographic study of western North American aquatic biota, and pertinent phylogenetic hypotheses have since been generated, although these have focused almost exclusively on fishes (e.g., Smith, 1992; Parker and Kornfield, 1995; Simons and Mayden, 1998; but also see Good and Wake, 1992; Tan and Wake, 1995).

We present a phylogenetic and biogeographic analysis of another component of southwestern aquatic ecosystems, snails of the family Hydrobiidae. Hydrobiids are the most diverse group of aquatic snails in North America, with about 35 genera and 285 described

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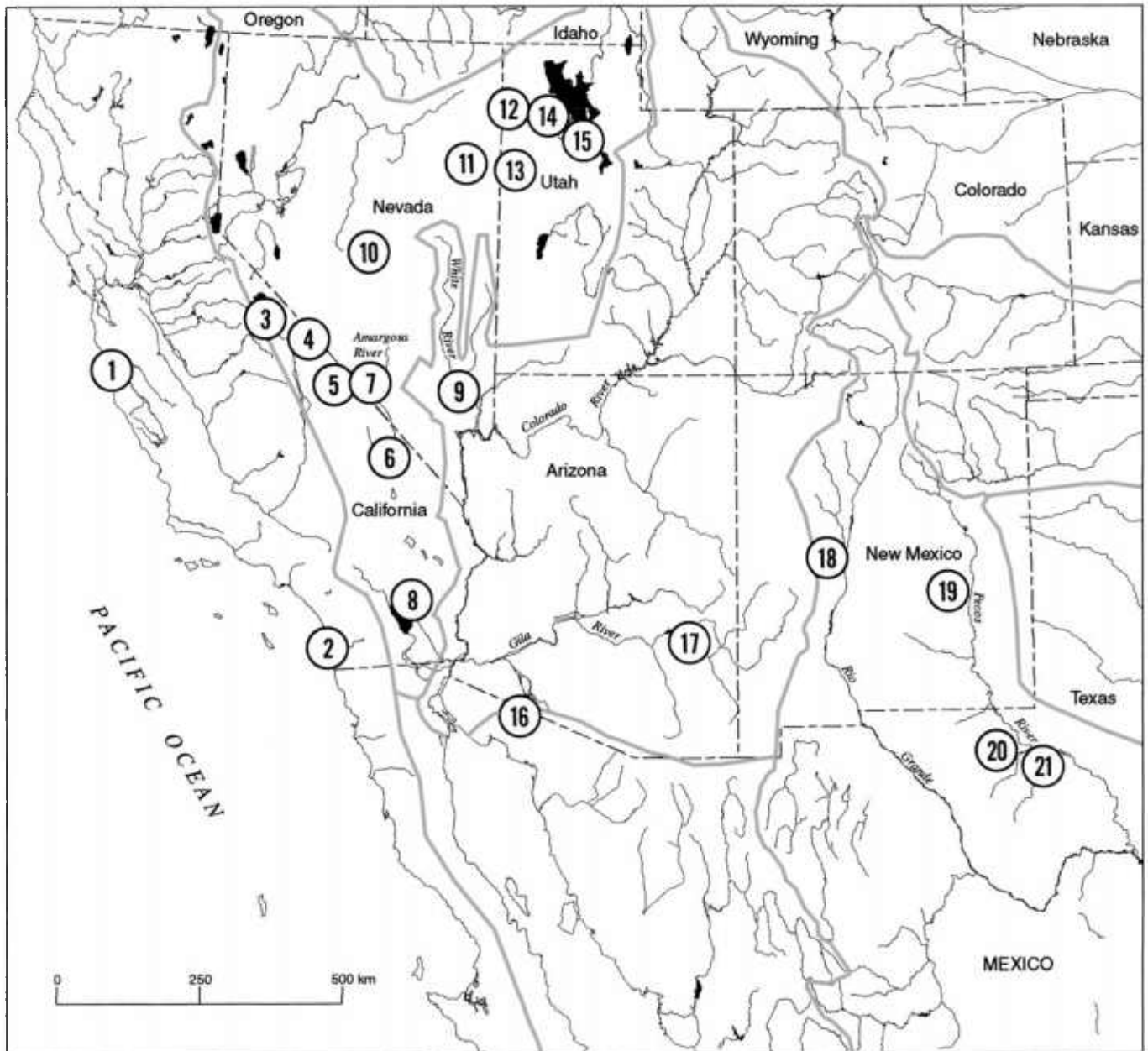


FIG. 1. Map showing location of sample localities for *Tryonia* species in the North American Southwest. Major drainage basin boundaries are indicated by thickened gray lines. 1, Moro Cojo Lagoon (*T. imitator*); 2, Penasquitos Lagoon (*T. imitator*); 3, Whitmore Hot Springs, Long Valley (*T. protea*); 4, Grapevine Springs, northern Death Valley (*T. margae*, *T. rowlandsi*); 5, Central Death Valley (*T. robusta*, *T. salina*); 6, Saratoga Spring, southern Death Valley (*T. variegata*); 7, Ash Meadows (*T. angulata*, *T. elata*, *T. ericae*, *T. variegata*); 8, "Oasis Spring," Salton Trough (*T. protea*); 9, Moapa National Wildlife Refuge (*T. clathrata*); 10, Potts Ranch, Monitor Valley (*T. n. sp. 1*); 11, southeast Steptoe Valley (*T. n. sp. 2*); 12, Blue Lake, Bonneville basin (*T. protea*); 13, Fish Springs National Wildlife Refuge, Bonneville basin (*T. protea*); 14, Skull Valley, Bonneville basin (*T. protea*); 15, Tooele Valley, Bonneville basin (*T. protea*); 16, Quitobaquito Spring, Rio Sonoyta drainage (*T. quitobaquiae*); 17, Tom Niece Spring, Gila River drainage (*T. gilae*); 18, Ojo Caliente, Rio Grande drainage (*T. alamosae*); 19, Lost River, Pecos River drainage (*T. kosteri*); 20, Phantom Lake, Pecos River drainage (*T. cheatumi*); 21, Fort Stockton area, Pecos River drainage (*T. adamantina*, *T. circumstriata*).

species (Turgeon *et al.*, 1998). Hydrobiids have figured prominently in the development of provocative, albeit nonphylogenetic hypotheses of western North American biogeography (e.g., Taylor, 1985).

The hydrobiid genus *Tryonia* is composed of 22

currently recognized extant species (Hershler and Thompson, 1992). Distribution and endemism of *Tryonia* parallel patterns documented for one of the better studied groups of southwestern fishes, pupfishes of the genus *Cyprinodon* (Miller, 1981; Minckley *et al.*, 1986).

As with most hydrobiids, *Tryonia* species are obligately aquatic, have direct development, and apparently disperse but slowly within their habitat, features which link them tightly with drainage history. Most species are locally endemic in major drainages of the southwest, where they inhabit thermal springs. Sympatry of congeners is rare, suggesting that the phylogeny of *Tryonia* may be informative with respect to regional historical biogeography. Eight congeners (*T. angulata*, *T. elata*, *T. ericae*, *T. margae*, *T. robusta*, *T. rowlandsi*, *T. salina*, and *T. variegata*) are unique to the Amargosa River drainage, a segment of the Death Valley hydrographic system (*vide* Miller, 1943) in the southwest Great Basin. These provide a potential source of additional data pertinent to the biogeographic history of this remarkable area (Miller, 1981; Taylor, 1985; Minckley *et al.*, 1986; Hershler and Pratt, 1990). Six species (*T. adamantina*, *T. alamosae*, *T. brunei*, *T. cheatumi*, *T. circumstriata*, and *T. kosteri*) are endemic to the Rio Grande basin. Two species (*T. clathrata* and *T. gilae*) are unique to the lower Colorado River basin (west of the Colorado Plateau) while *T. quitobaquitae* inhabits internal drainage in the vicinity of the Colorado delta. *Tryonia protea* lives in both the Great Basin and lower Colorado River basin. *Tryonia imitator* lives in Pacific coastal drainage. Some of these species are salt tolerant: *T. salina*, for instance, lives in Cottonball Marsh in Death Valley, where salinities range up to several times that of seawater (LaBounty and Deacon, 1972). *Tryonia imitator* lives in coastal strand habitats and tolerates a broad range of salinity regimes (Kellogg, 1985). *Tryonia aequicostata* and *T. brevissima*, which are profoundly disjunct from western congeners, live in springs and freshwater lakes in peninsular Florida (Thompson, 1968). Neogene fossils suggest that congeners early ranged into Central America and northern South America (Taylor, 1966; Wesselingh, 1996; Wesselingh *et al.*, 1996), although allocations of these to *Tryonia* are controversial (Nuttall, 1990).

In a recent review of the subfamily Cochliopinae (Hershler and Thompson, 1992), *Tryonia* was placed in the informal "*Littoridina* group" along with 12 other New World genera in which males have glandular papillae on the penis. *Mexipyrgus*, locally endemic in northeastern Mexico, was conjectured as the closest relative to *Tryonia*. *Tryonia* is defined by a few distinctive (but not demonstrably synapomorphic) shell and genitalic features (Taylor, 1987; Hershler and Thompson, 1992), and even these details have not been described for many of the species currently allocated to the genus. Nonphylogenetic hypotheses of congener relationships were proposed on the basis of patterns of penial ornament (Taylor, 1987; Hershler, 1989). Taylor (1987) erected the subgenus *Paupertryonia* for five species from the Rio Grande–Pecos River basin which lack basal papillae on the penis (*T. adamantina*, *T. alamosae*, *T. brunei*, *T. cheatumi*, and *T. kosteri*).

To provide a robust framework for biogeographical analysis of *Tryonia*, we examined the monophyly and evolutionary structure of the genus using mitochondrial DNA sequences. In another study, sequences from the mitochondrial cytochrome *c* oxidase subunit I (COI) gene were used to generate a phylogenetic hypothesis for species of the Death Valley system (Hershler *et al.*, 1998). Herein we analyze COI sequence variation for the remaining congeners. We evaluate monophyly of *Tryonia* and propose an hypothesis of phylogenetic relationships within the genus. We also evaluate congruence of *Tryonia* biogeography with area relationships implied by the geologic and hydrographic history of the Southwest.

MATERIALS AND METHODS

We analyzed extant species currently allocated to *Tryonia* and three undescribed species (two from the Great Basin and one from the coastal plain of Alabama) conforming to the genus in general features. Efforts to collect material proved unsuccessful only in the case of *T. brunei*, which we were unable to find at its single (type) locality in west Texas. Sequence data for species from the Death Valley region are from Hershler *et al.* (1998). To test monophyly of *Tryonia* within the Cochliopinae, we also analyzed other members of the *Littoridina* group (*Aphaostracon*, *Littoridinops*, *Mexipyrgus*, *Onobops*, and *Pyrgophorus*; Hershler and Thompson, 1992) and representatives of the presumably more distantly related "*Heleobia* group" (*Heleobia* and *Heleobops*; Hershler and Thompson, 1992). Australasian taxa (*Ascorhis* and *Phrantela*) considered among the more plesiomorphic hydrobiids (Ponder and Clark, 1988; Ponder *et al.*, 1993) were used as outgroups (trees were rooted with *Phrantela*). Multiple samples were analyzed for several species of *Tryonia* (including the more widespread congeners) in order to evaluate intrapopulation and intraspecific variation. Taxa and localities are listed in Table 1, and sampling localities for *Tryonia* of the North American southwest are in Fig. 1. All analyzed specimens were live-collected in the field and either placed directly into 70–90% ethanol or flash-frozen in a portable liquid nitrogen canister. Voucher material from these samples was repositied in the Recent mollusk collection of the National Museum of Natural History (USNM).

Laboratory Methods

Genomic DNA was extracted from whole frozen snails using the Chelex method of Walsh *et al.* (1991) and from ethanol-preserved specimens using the CTAB method (Bucklin, 1992). A 710-base-pair (bp) segment of COI was amplified via polymerase chain reaction (PCR) using primers COIL 1490 and COIH 2198 (Folmer *et al.*, 1994). Protocols for amplification, sequencing, and alignment are given in Hershler *et al.* (1999).

TABLE 1

List of Analyzed Taxa

Species	Locality	Drainage (<i>Tryonia</i> only)
<i>Tryonia (Paupertryonia) adamantina</i>	Diamond Y Spring, Pecos Co., TX	Pecos River drainage, Rio Grande basin
<i>Tryonia aequicostata</i>	Lake Eustis, Lake Co., FL (LE); Alexander Springs, Lake Co., FL (AS)	St. Johns River basin, Atlantic Coastal
<i>Tryonia (Paupertryonia) alamosae</i>	Spring 100 m west of Ojo Caliente, Socorro Co., NM	Rio Grande basin
<i>Tryonia angulata</i>	Big Spring, Ash Meadows, Nye Co., NV	Amargosa River basin (upper), Great Basin
<i>Tryonia brevissima</i>	Lake Panasoffkee, Sumter Co., FL	Withlacoochee River basin, Gulf Coastal
<i>Tryonia (Paupertryonia) cheatumi</i>	Phantom Lake spring, Jeff Davis Co., TX (PL1); Phantom Lake spring outflow (first lateral canal) (PL2)	Pecos River drainage, Rio Grande basin
<i>Tryonia circumstriata</i>	Diamond Y Spring, Pecos Co., TX (DY); Diamond Y Draw, Pecos Co., TX (DD)	Pecos River drainage, Rio Grande basin
<i>Tryonia clathrata</i>	Spring, Moapa National Wildlife Refuge, Clark Co., NV	White River drainage, Colorado River basin
<i>Tryonia elata</i>	Spring tributary to Kings Pool, Point of Rocks, Ash Meadows, Nye Co., NV	Amargosa River basin (upper), Great Basin
<i>Tryonia ericae</i>	Spring, north of Collins Ranch, Ash Meadows, Nye Co., NV	Amargosa River basin (upper), Great Basin
<i>Tryonia gilae</i>	Tom Niece Spring, Graham Co., AZ	Gila River drainage, Colorado River basin
<i>Tryonia imitator</i>	Penasquitos Lagoon, San Diego Co., CA (PE); Moro Cojo Lagoon, Moss Landing, Monterey Co., CA (MO)	Pacific Coastal
<i>Tryonia (Paupertryonia) kosteri</i>	Lost River, Chaves Co., NM	Pecos River drainage, Rio Grande basin
<i>Tryonia margae</i>	Grapevine Springs (upper warm spring), Death Valley, Inyo Co., CA	Amargosa River basin (lower), Great Basin
<i>Tryonia protea</i>	Whitmore Hot Springs, Long Valley, Mono Co., CA (WH); "Oasis Spring," Salt Creek, Salton Trough, Riverside Co., CA (OA); spring, south end of Fish Springs National Wildlife Refuge, Juab Co., UT (FS); Horseshoe Springs, Skull Valley, Tooele Co., UT (HS); Warm Springs, Tooele Valley, Tooele Co., UT (WS); spring, Blue Lake, Great Salt Lake Desert, Tooele Co., UT (BL)	Owens River basin, Great Basin (WH); Bonneville basin, Great Basin (FS, HS, WS, BL); Colorado River basin (OA)
<i>Tryonia quitobaquitae</i>	Quitobaquito Spring, Pima Co., AZ	Rio Sonoyta basin, internal drainage
<i>Tryonia robusta</i>	Travertine Springs, Death Valley, Inyo Co., CA	Amargosa River basin (lower), Great Basin
<i>Tryonia rowlandsi</i>	Grapevine Springs (lower warm spring), Death Valley, Inyo Co., CA	Amargosa River basin (lower), Great Basin
<i>Tryonia salina</i>	Spring, Cottonball Marsh, Death Valley, Inyo Co., CA	Amargosa River basin (lower), Great Basin
<i>Tryonia variegata</i>	Saratoga Spring, Death Valley, San Bernardino Co., CA (SA); Devils Hole, Ash Meadows, Nye Co., NV (DV)	Amargosa River basin (upper), Great Basin
<i>Tryonia</i> n. sp. 1	Spring, Potts Ranch, Monitor Valley, Nye Co., NV	Lahontan Basin, Great Basin
<i>Tryonia</i> n. sp. 2	Spring, southeast Steptoe Valley, north of Ely, White Pine Co., NV	Great Basin
<i>Tryonia</i> n. sp. 3	Salt Spring, Fred T. Simpson Wildlife Refuge, 22 km south-southeast of Jackson, Clarke Co., AL	Tombigbee River basin, Gulf Coastal
<i>Aphaostracon</i> sp.	Alexander Springs, Lake Co., FL (AS); Lake Panasoffkee, Sumter Co., FL (LP)	—
<i>Heleobia dalmatica</i>	Spring, Pirovac, Croatia	—
<i>Heleobops docimus</i>	Pond at Chisholm Point, Grand Cayman Island	—
<i>Littoridinops monroensis</i>	St. Johns River, Fort Gates Ferry, 4.8 km southwest of Welaka, St. Johns Co., FL (SJ); Simmons Bayou, Ocean Springs, Jackson Co., MS (SB)	—
<i>Littoridinops palustris</i>	Brackish marsh, 4 km southwest of Yankeetown, Levy Co., FL	—
<i>Mexipyrgus carranzae</i>	Mojarral West Laguna, Cuatro Ciénegas basin, Coahuila, México	—
<i>Onobops jacksoni</i>	Brackish marsh, 4 km southwest of Yankeetown, Levy Co., FL	—
<i>Pyrgophorus platyrachis</i>	Lithia Springs, Hillsborough Co., FL	—
<i>Ascorchis tasmanica</i>	Manly Lagoon, New South Wales, Australia (ML); Careel Bay, Pittwater, New South Wales, Australia (CB)	—
<i>Phrantela marginata</i>	Tributary of Thirteen Mile Creek, Tasmania, Australia	—

Note. If multiple samples were analyzed for a given species, locality abbreviations (in parentheses) are supplied for use in Figs. 2 and 3.

Data Analyses

We plotted the absolute number of transitions (TS) and transversions (TV) versus genetic distance for all pairwise comparisons in order to examine nucleotide substitution patterns among taxa. Cladistic analyses were performed using the maximum parsimony option of PAUP* 4.0 (Swofford, 1998). Based on the nucleotide substitution patterns and the possibility that saturation may affect our phylogenetic analysis, separate analyses were performed in which all substitutions were equally weighted, TS at the third position were downweighted 50%, and TS at the third position were dropped. Heuristic searches for shortest trees were performed because of the large number of taxa analyzed. An initial tree was obtained by stepwise addition and then subjected to trial rearrangements in an attempt to find shorter trees (branch swapping). One hundred replications of random stepwise additions were used to evaluate the effectiveness of this heuristic method. Uninformative characters were ignored and zero-length branches were collapsed. Bootstrapping (Felsenstein, 1985) with 500 iterations was used to estimate the reliability of branches on the shortest trees. Maximum likelihood scores for equally parsimonious trees were calculated using various models (Jukes and Cantor, 1969; Kimura, 1980; Felsenstein, 1981; Hasegawa *et al.*, 1985; Rodriguez *et al.*, 1990) to guide selection of a preferred topology.

RESULTS

DNA Sequence Variation

Alignments were unambiguous as COI is a protein-coding gene. Direct sequencing of PCR products yielded an aligned matrix of 601 base pairs. This sequence corresponds to positions 1566–2166 in the homologous *Drosophila yakuba* mtDNA sequence (Clary and Wolstenholme, 1985). The sequences were deposited in GenBank under Accession Nos. AF129300–AF129331. Of the 601-bp sequence, 247 sites were variable and 212 of these were phylogenetically informative. Most of the differences occurred in the third codon position, a pattern typical of mitochondrial protein-coding genes in other animals (Brown, 1985). Average base frequencies for the total data set were 25% A, 40% T, 17% C, and 18% G. Similar values were reported for another protein-coding mitochondrial gene, cytochrome *b*, in the marine gastropod genus *Nucella* (Collins *et al.*, 1996). Base composition bias was not evident among taxa.

Scatterplots of the absolute number of TS and TV against genetic distance for all three codon positions and for the first and third codon positions only are shown in Fig. 2. (There were very few TS and TV in the second codon position and thus this plot is not included.) Trends revealed by these plots conformed to

prior evolutionary findings for mitochondrial genes (Brown *et al.*, 1979, 1982; Collins *et al.*, 1996). The absolute number of both TS and TV increased linearly as genetic distance increased. TS outnumbered TV among closely related taxa. In the third codon position (Fig. 2C), as genetic distances increased, TS leveled off while TV continued to increase, suggesting that saturation of transitions occurred in comparisons of outgroups (*Ascorhis* and *Phrantela*) versus cochliopine snails.

No sequence differences were observed among two specimens of *T. cheatumi* from Phantom Lake spring nor for two *T. circumstriata* from Diamond Y Spring. Intraspecific sequence differences (uncorrected for multiple hits) ranged from 0 to 0.33% (*T. aequicostata*, $n = 2$; *T. cheatumi*, $n = 2$; *T. circumstriata*, $n = 3$; *T. imitator*; $n = 2$; *T. protea*; $n = 6$). For interspecific comparisons among in-group taxa, sequences differed by 1.3–14.8%. The two samples of *T. variegata* (from widely spaced populations within the Amargosa River drainage) differed by 5%, suggesting the presence of two distinct lineages and a need for revision of this species (also see Hershler *et al.*, 1999). Genetic distances between species of *Tryonia* and other analyzed taxa ranged from 16.1 to 22.5%.

Molecular Phylogenetic Analysis

When TS at the third position were downweighted 50%, and TS at the third position were dropped, 278 and 50 trees of shortest length were found, respectively. The resulting consensus trees were poorly resolved, suggesting loss of valuable phylogenetic information provided by TS and indicating that saturation is not a substantial problem within the cochliopine snails studied. When all characters were weighted equally, 8 trees of 863 steps were obtained (CI = 0.45) using maximum parsimony. Our preferred tree, that chosen from among the 8 equally parsimonious trees because it consistently had the lowest maximum likelihood score under the different models used, is shown in Fig. 3 (as a phylogram). Tree topology differed in the placement of the clade composed of *T. aequicostata* and *T. quitobaquitate*, which was positioned as in Fig. 3 or alternatively as sister to the clade composed of *T. cheatumi*, *T. circumstriata*, *T. salina*, *Tryonia* n. sp. 1, *T. margae*, and *T. imitator*. In addition, trees differed in relative positions of terminals within the subclades composed of *T. ericae*, *T. elata*, and *T. variegata* and *Littoridinops palustris* and *L. monroensis*.

Both Australasian taxa (*Ascorhis* and *Phrantela*) consistently occupied a basal position in the eight trees, providing support for monophyly of the Cochliopinae. An undescribed species from the central Great Basin resembling *Tryonia* ("*Tryonia*" n. sp. 2) occupied the most basal in-group position. Four main clades having high bootstrap support ($\geq 75\%$) were consistently resolved. Clade I is composed of four species currently

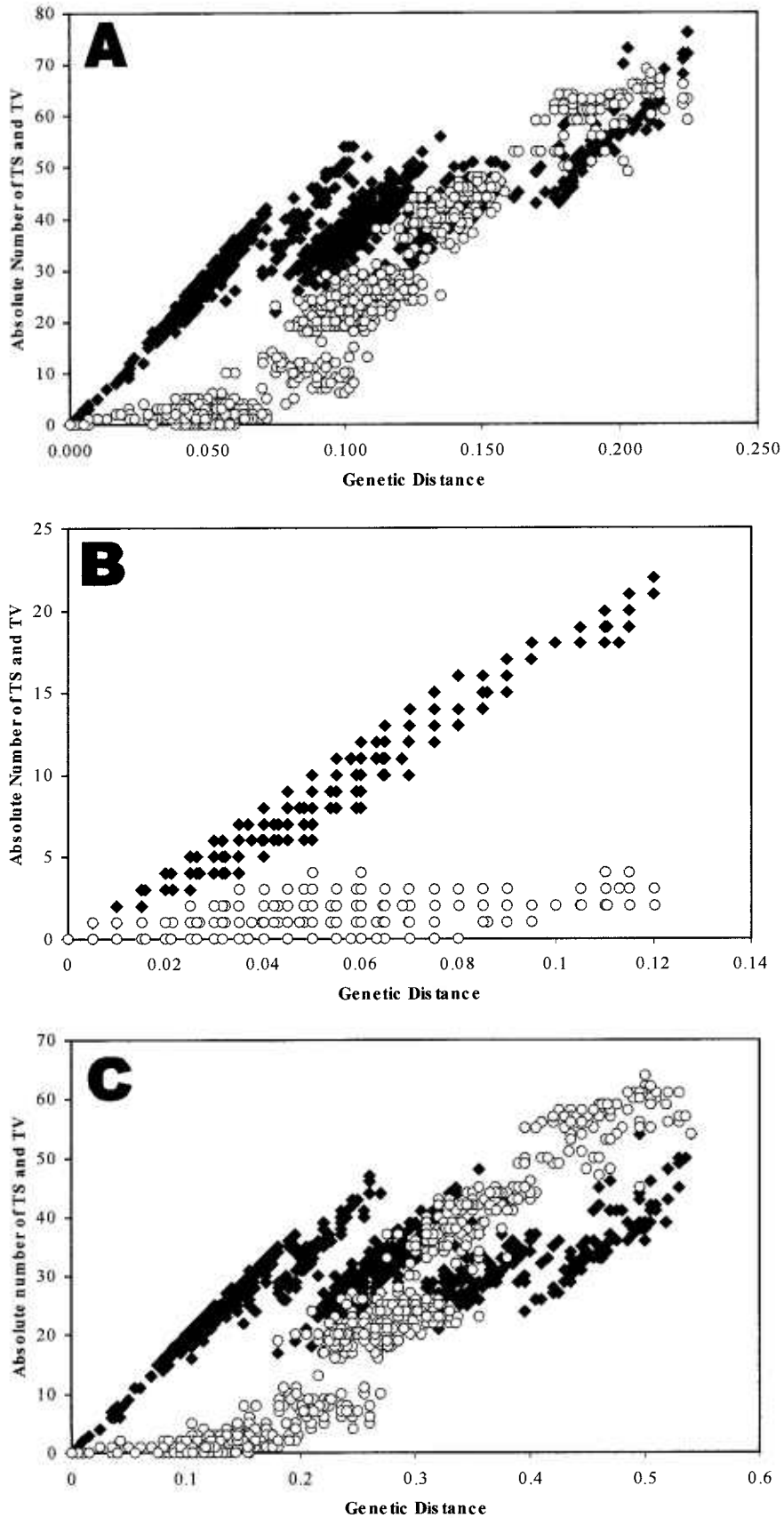


FIG. 2. Scatterplots of nucleotide substitutions (transitions, TS, ◆; transversions, TV, ○) versus genetic distance for all three codon positions (A) and for the first (B) and third (C) positions.

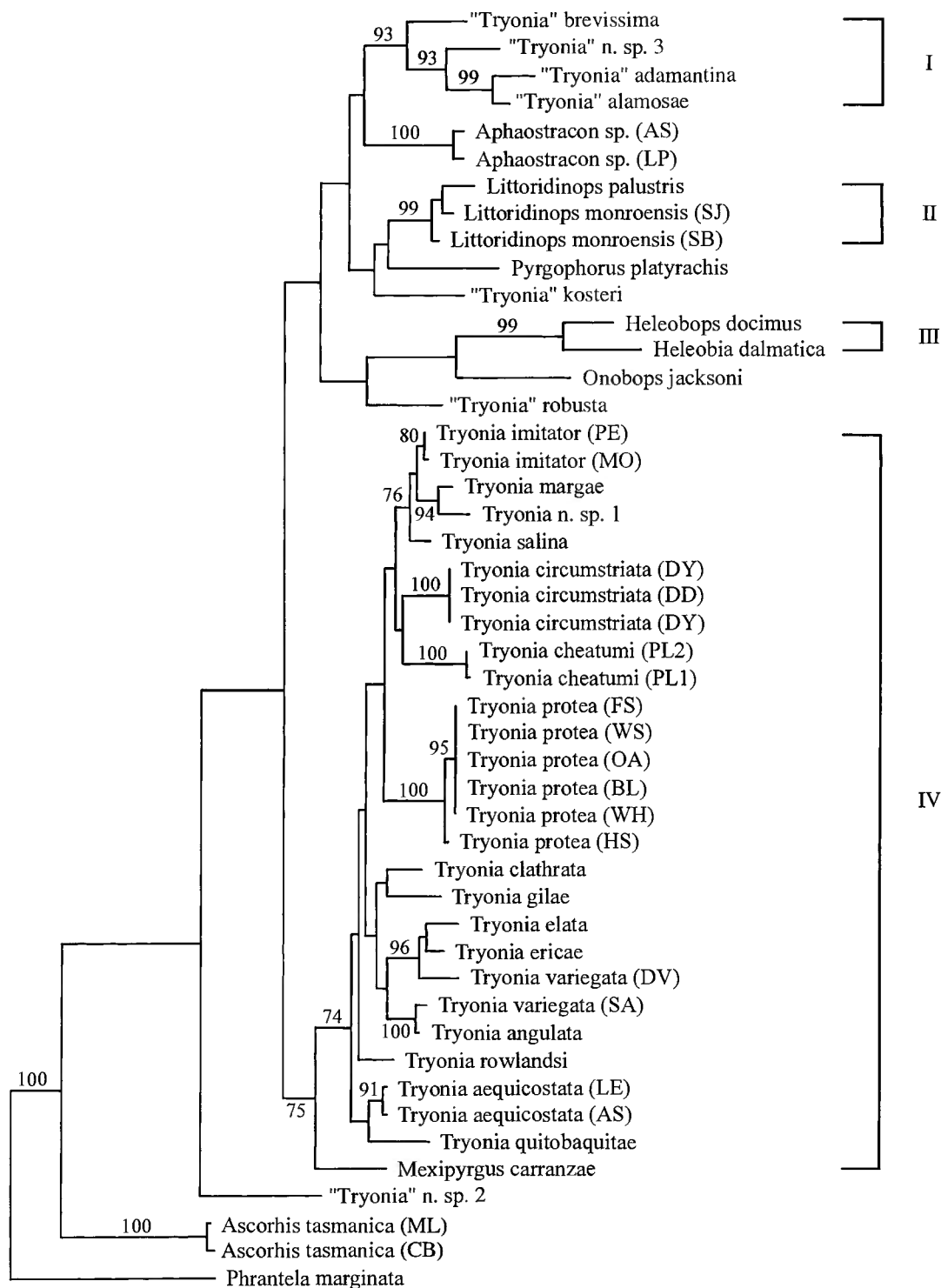


FIG. 3. One of eight phylograms of shortest length based on maximum parsimony analysis of mtCOI sequence data. CI, 0.45; HI, 0.55; TL, 863 steps. Numbers are bootstrap percentages for well-supported clades.

assigned to *Tryonia* (two from the Rio Grande basin and two from the southeastern United States). Clade II is composed of another member of the *Littoridina* group (*Littoridinops*). Clade III is composed of two members of the *Heleobia* group. Clade IV is composed of the type

species of *Tryonia* (*T. clathrata*), 15 other congeners, and the sister taxon to this group, *Mexipyrgus carranzae*. The subclade in clade IV consisting of "true" *Tryonia* was well supported with a bootstrap value of 74%.

All analyses indicated that *Tryonia*, as currently constituted, is polyphyletic. The subgenus *Paupertryonia*, which Taylor (1987) erected for five species from the Rio Grande basin (*T. adamantina*, *T. alamosae*, *T. brunei*, *T. cheatumi*, and *T. kosteri*), also is shown as polyphyletic.

DISCUSSION

Systematics

Placement of cochliopine snails having penial glandular papillae (*Littoridina* group) into clades which jointly do not constitute a monophyletic group and the associated polyphyly of *Tryonia* (as well as its subgenus *Paupertryonia*) are at odds with existing taxonomy. We suggest that this result reflects incomplete study of these taxa rather than a conflict between morphological and molecular data.

Most of the species allocated to *Tryonia* have not been thoroughly studied, particularly with respect to the female genitalia, which has been shown to be highly informative of relationships in hydrobiid and related snails (Ponder, 1988b). Ongoing morphological studies by the first author have revealed a potentially important difference in female groundplan among *Tryonia* species congruent with the mtCOI molecular-based cladogram. In true *Tryonia* and *Mexipyrgus* (clade IV) the sperm duct, which permits transfer of sperm from the seminal receptacle to the oviduct (Hershler and Ponder, 1998, Fig. 13), is coiled behind the pallial wall, whereas in *Tryonia* species forming clade I (and sister taxa belonging to *Aphaostracon*) and *T. kosteri* the duct is straight and extends into the pallial cavity. *Tryonia* n. sp. 2 has the alternative condition (coiled sperm duct) while *T. robusta* has a reductive condition in which the sperm duct is lost. These two species have distinct types of penial glands that only superficially resemble the glandular papillae shared by other snails assigned to *Tryonia*, suggesting a morphological basis for their highly divergent placements. As with *Tryonia*, a majority of the more than 400 hydrobiid genera currently in use (Kabat and Hershler, 1993) were not erected on the basis of well-studied synapomorphic characters, but instead represent "carryovers" from traditional taxonomy, and we predict that many will be identified as non-monophyletic upon further study.

Biogeography

The cosmopolitan distribution of the Cochliopinae suggests that the group arose during the late Mesozoic and main subgroups diverged prior to the late Triassic to early Jurassic break-up of Laurasia (Hershler and Thompson, 1992). [The chronostratigraphic time scale used herein is that of Palmer (1983).] If fossils from the upper member of the middle to late Miocene (11.6–10.1 mya) Mint Canyon Formation (date according to Terres and Luyendyk, 1985) of southwest California identified as *T. imitator* by Kew (1924) and Oakenshott (1958) are

true *Tryonia*, then a minimum age for the genus is established. The wide distribution of the genus also implies, in the absence of dispersal, that ancestral *Tryonia* was present prior to development of modern southwest basin and range topography beginning in the middle Miocene (21–14 mya; Christiansen and Yeats, 1992). The *Tryonia*–*Mexipyrgus* split (Fig. 3) cannot be precisely dated because of the uncertain hydrographic history of the Cuatro Ciénegas basin (to which *Mexipyrgus* is endemic) (Minckley, 1969).

A southern North American derivation and freshwater origin for *Tryonia* is implied by distributions and habitats of the sister group and basal in-group taxa. The Floridian distribution of *T. aequicostata* suggests that ancestral snails ranged along the northern Gulf of Mexico coastal plain eastward to the Atlantic margin. Vicariance of this species presumably was effected by marine transgressions or development of major deltaic regimes along the Gulf Coast during periods of the middle to late Tertiary (Winker, 1982; Salvador, 1991). Other monophyletic groups also are broadly disjunct across this region (e.g., poeciliid fishes, Rosen, 1978; various insects, Noonan, 1988). Our phylogenetic hypothesis (Fig. 3) suggests that this pattern is repeated in other cochliopine snails: *Tryonia brevissima* and *Tryonia* n. sp. 3 live along the eastern Gulf Coast, whereas more derived members of clade I live in the western United States.

The topology of clade IV (Fig. 4) implies early separation of an area composed of the lower Colorado River region and the upper segment of the Amargosa River drainage (inhabited by members of subclade B) from a surrounding region (subclade A). We have not identified a geologic event that may have been responsible for this separation, although we note partial congruence with the generalized position of the middle Tertiary continental divide, which included highlands extending along the eastern edge of the Mojave Desert and across southern Arizona (Christiansen and Yeats, 1992, Fig. 15). Our analyses are equivocal with respect to whether a southern area, defined by distributions of *T. aequicostata* and *T. quitobaquitae*, was separated prior (Fig. 4) or subsequent to (from within the region including subclade A) this divergence.

We interpret the phylogenetic structure of subclade B within the context of hydrographic history of the lower Colorado River region. Early workers assumed that Miocene–Pliocene deposits in this region recorded an arm of the proto-Gulf of California extending to near the edge of the Colorado Plateau, which precluded the existence of a lower Colorado River prior to recession of this embayment (e.g., Lucchitta, 1972, 1979; Blair, 1978; Busing, 1990). However, relevant stratigraphic units (Bouse Formation and possible equivalents) recently have been shown to be lacustrine (Spencer, 1996; Faulds *et al.*, 1997; Spencer and Patchett, 1997), thereby expanding the possibilities of an ancestral freshwater drainage in this region, although sedimentary evidence

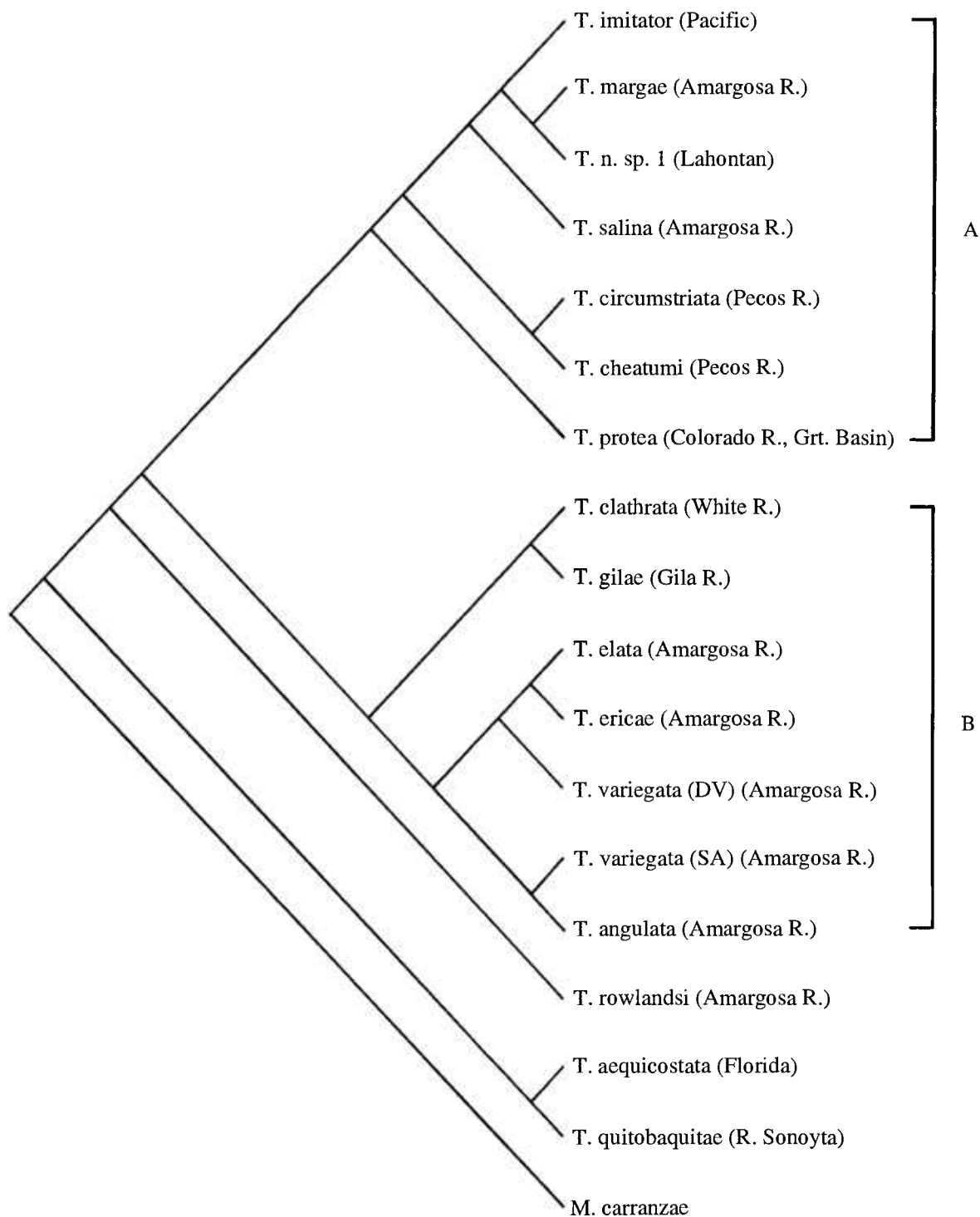


FIG. 4. Portion of preferred tree depicting the phylogenetic structure within clade IV. The tree is simplified (for the purpose of discussion) in that all species are represented by single samples, with the exception of *T. variegata* (*T. aequicostata*, LE; *T. cheatumi*, PL1; *T. circumstriata*, DY; *T. imitator*, PE; *T. protea*, WH).

indicates that a fully integrated, throughgoing Colorado River did not exist prior to ca. 4 mya (Buising, 1993). Howard (1996) presented sedimentary and geomorphic evidence that a lower Colorado paleodrainage, comprised of an ancestral Amargosa River coursing

south to integrate with the Gila River, drained to the California coast beginning in the late Paleocene. This is not to be confused with an oft-proposed Pleistocene connection between the Mojave and Colorado River drainages that is not well supported by geologic evi-

dence (Brown and Rosen, 1995; Hooke, 1998). The White River drainage (inhabited by *T. clathrata*) was captured by the Colorado River in the late Neogene (DiGiuseppi and Bartley, 1991; Williams, 1994). Earlier drainage relationships of the White River trough are uncertain, although this area was in close proximity to the Amargosa Desert prior to ca. 48 km of a post-15 mya lateral slip along the Las Vegas Shear Zone (Dubendorfer *et al.*, 1998). Phylogenetic relationships among *Tryonia* species imply that spring outflows from the White River area may have early integrated with the postulated lower Colorado paleodrainage (also see Taylor, 1983). Within the context of Howard's (1996) model, vicariance of the White-Gila River component of this paleodrainage may be attributed to diversion of the upper Amargosa River into Death Valley (also see Carr, 1984), a relatively youthful trough which formed only 6 mya (Serpa and Pavlis, 1996) by a "pull-apart" opening along major strike-slip faults (Burchfiel and Stewart, 1966). Divergence of species among subareas within the upper Amargosa River basin (Ash Meadows, Saratoga Spring) may be attributed to development of a topographic barrier which closed the intervening Tecopa subbasin from 3.0 to 0.2 mya (Hillhouse, 1987; Mackin, 1997; Anderson *et al.*, 1998).

The Sonoyta River (southernmost Arizona; *T. quitobaquita*) has been presumed to have emptied into the Gulf of California near the mouth of the Colorado River (Hubbs and Miller, 1948; Minckley *et al.*, 1986) prior to diversion of its outflow by Pinacate volcanics (Ives, 1936), which erupted 1.7–1.1 mya (Lynch, 1981). Interestingly, our cladogram suggests that this drainage had a closer historical relationship with Gulf Coastal drainage than with elements of the lower Colorado River drainage.

Subclade A is composed of taxa from the Great Basin, Colorado River, and California Coast drainages as well as snails from the broadly disjunct Pecos River drainage to the east. We conjecture that this clade is or was more continuously distributed through intervening northern Mexico. Although the single species described from northern Mexico (*T. hertleini*) became extinct in historic times, additional extant *Tryonia*-like snails have been collected from the region (e.g., Williams *et al.*, 1985; Minckley and Minckley, 1986) and evaluation of their relationships can provide a test of this hypothesis.

T. protea is uniquely parthenogenetic in the genus (Mulvey and Hershler, unpublished) and its broad distribution in the Southwest, which provides ambiguity with respect to the Colorado River basin, probably reflects increased dispersal ability associated with asexual reproduction (e.g., Ponder, 1988a) rather than biogeographic history. Sequence divergences among broadly disjunct populations of this species were less than 0.2%, which is congruent with recent dispersal-based origins.

Vicariance of the clade composed of Pecos River species (*T. circumstriata* and *T. cheatumi*) presumably reflects separation of this basin from areas to the west and may be attributed to uplift of the southernmost Rocky Mountains (Alvarado Ridge; most pronounced uplift phase 7–4 mya; Eaton, 1987) or associated development of the modern southern Rio Grande Rift in the late Miocene and Pliocene (9–3 mya; Seager *et al.*, 1984; Dickerson and Muehlberger, 1994). The Pecos River Valley developed later in the Pliocene as a result of solution collapse of this region (<3.5 mya; Gustavson and Finley, 1985).

Vicariance of *T. salina* may be attributed to the opening of central Death Valley 6 mya (Serpa and Pavlis, 1996). Subsequent vicariance within subclade A may be attributed to post-middle Miocene events effecting hydrographic closure of the Death Valley system from areas to the west and north. Evidence of early westward drainage from the Great Basin was summarized by Christiansen and Yeats (1992); hydrographic separation of western California and vicariance of *T. imitator* may be attributed to subsequent development of the Sierra Nevada divide. Although aspects of late Cenozoic uplift of the Sierra Nevada are controversial (Small and Anderson, 1995; Wernicke *et al.*, 1996), available evidence suggests that this range began to function as a divide during the late Miocene–Pliocene (9–3 mya; Chase and Wallace, 1986; Loomis and Burbank, 1988; Unruh, 1991). We attribute the broad historical distribution of *T. imitator*, from just north of San Francisco to Ensenada, Mexico (Kellogg, 1985), to dispersal among semicontinuous estuarine habitats along the Pacific coast. Modern topography in the western Great Basin developed as a result of tectonic breakup of regional erosional surfaces (e.g., Robinson and Stewart, 1984) in the Pliocene (<4 mya; Nitchman *et al.*, 1990). This presumably effected separation of the Lahontan and Death Valley systems (and vicariance of *Tryonia* n. sp. 1), although some form of drainage integration between these areas may have continued until disruption by Quaternary vulcanism (Russell, 1889).

Cladistic structure within *Tryonia* implies a composite Amargosa Basin fauna. However, on a local scale this drainage is divisible into two non-overlapping areas of snail endemism. Subclade A contains species living in the lower segment of this drainage (Death Valley) while subclade B contains species from the upper drainage segment (e.g., Ash Meadows, Saratoga Spring; above the abrupt "U-turn" that the river takes in southernmost Death Valley). These areas of endemism, having clearly different sister relationships, suggest that the river basin is not only a biotic, but also a geologic composite (*sensu* Platnick and Nelson, 1984).

As discussed above, final assembly of the Amargosa River basin can be attributed to late Miocene to Pliocene

tectonics that rerouted the upper segment of this drainage into Death Valley. However, how subclades A and B achieved close proximity in this region also requires discussion because there is no evidence of a persistent barrier which may have defined local vicariance. Taylor (1985) suggested that an arm of the proto-Gulf of California may have extended into the Death Valley area, thereby providing a barrier separating disparate molluscan elements to the east and west of this valley, but subsequent studies (cited above) have shown that such an embayment was not present in this region. Phylogenetic structure within *Tryonia* is congruent with an interpretation that progenitors of subclade A arrived from the south by tectonic transport along shear zones, as previously proposed for Death Valley *Cyprinodon*, which have been shown to be most closely related to fishes of northern Mexico based on mtDNA variation (Echelle and Dowling, 1992; Parker and Kornfield, 1995):

If the genus was not already present on land surfaces now comprising the Death Valley region, which were then located to the east and south, a parsimonious explanation for origin of *Cyprinodon* is provided by formation of near coastal and inland shear zones from Miocene to Recent. A long zone of right-lateral wrench-faulting developed in Mexico, extending northward into the Great Basin and northwest as the San Andreas Transform. Schollen ranging to blocks as large as the Transverse Range were displaced north-northwestward along this splintered alignment. Movements of more than 300 km are indicated for schollen along and across the Salton Sea region. Springs rising directly or indirectly along such fractures now support most fishes of the Death Valley region. Transport of fishes on schollen or in spring zones associated with migrating schollen seems reasonable, and potentials for passive or active dispersal through this mechanism have existed for longer than 20 My (Minckley *et al.*, 1986, p.605).

Upper and lower segments of the Amargosa River drainage are situated in the Walker Lane tectonic belt (in southeast California and southwest Nevada) on different structural blocks (Inyo-Mono, Goldfield, respectively; Stewart, 1988, Fig. 25–3) which, “for the most part, acted independently of adjacent blocks” (Stewart, 1988, p.686). These blocks are separated by the Furnace Creek Fault Zone, which extends >300 km and has accommodated ca. 80 km of the pre-Quaternary right-lateral slip (Stewart, 1988; Brogan *et al.*, 1991). On a more regional level, late Cenozoic dextral shear and associated strike-slip faulting characterize the Walker Lane belt (Carr, 1984a; Stewart, 1988, 1992), the Eastern California Shear Zone (Dokka and Travis, 1990a,b) in the Mohave Desert immediately to the south, and possibly western Sonora further to the south (Stewart, 1998). There is evidence of linkage of faulting between these zones (Dokka and Travis, 1990a,b; Savage *et al.*, 1990) and if these represented an early transform boundary (prior to development of the “Big Bend” of the San Andreas Fault System) and acted as a

continuous strike-slip system (as proposed by Stewart, 1998; also see Livaccari, 1979; Stewart, 1992), tectonic transport of snails into the Death Valley area from more southern locations in California could have been effected between 24 and 5.5 mya. Possible transport of snails into the region from even more southerly locations would require rafting on terrain west of the San Andreas Fault Zone, which has much more strike-slip displacement than that to the east (Dokka and Travis, 1990a), and may be less likely as only a single, highly derived species (*T. imitator*) lives in this western area.

CONCLUSIONS

Aside from an enigmatic early branching event, evolutionary structure within *Tryonia* is generally congruent with Miocene–Pleistocene geological events potentially contributing to vicariance. However, our interpretation of *Tryonia* biogeography is constrained in several ways and thus is largely speculative. The composite nature of *Tryonia sensu lato* renders fossil evidence equivocal as relevant clades cannot be distinguished on the basis of shell features. Whereas other regions have been molded by relatively few defining events of profound importance (e.g., Andean uplift in South America; Vari, 1988), vicariant patterns in the southwest usually can be attributed to alternative geological events of different ages: selection from among these in the absence of fossil evidence of branching times is decidedly arbitrary.

Our biogeographic hypothesis assumes that the distribution of Recent *Tryonia* reflects vicariance of an old, ancestral fauna. Alternatively one may conjecture that the group is much younger (and that early fossil *Tryonia*-like snails represent another clade) and achieved its broad distribution in the southwest principally by dispersal within and among late Pleistocene pluvial lakes. However, the distribution of *Tryonia* does not well match that of pluvial lakes (mapped by Williams and Bedinger, 1984) and there is, for instance, no evidence of late Pleistocene drainage integration between the Pecos River region and inhabited areas to the west. Given that the typical habitat of Recent *Tryonia* is thermal springs, the extent to which cold water pluvial lakes may have served as dispersal corridors is debatable, and one could alternatively argue that these habitats instead operated as barriers. The restriction of Recent *Tryonia* to lowlands also mitigates against the possibility that distributions have been achieved by moving over divides via montane headwater transfers.

Extant *Tryonia* species are concentrated in a few subregions of the West. This distribution is probably not attributable to sampling inadequacy, but instead to the fact that thermal springs are neither uniformly nor randomly distributed in the region (Waring, 1965).

Formation of thermal spring habitats is controlled by interaction between magmatic sources of heat, circulating groundwater, and faulting that results in vertical permeability (Curewitz and Karson, 1997). Further evaluation of *Tryonia* biogeography in relation to distribution in space and time of these physical features, as opposed to drainage patterns as traditionally viewed, may prove instructive.

Although there is some commonality of snail biogeographic pattern with that of pupfishes, there are also significant differences. For instance, the pupfish fauna of the Amargosa River basin is not composite (in contrast to *Tryonia*), but instead forms a monophyletic group (Echelle and Dowling, 1992). Additional studies of other groups are needed to generate a biogeographic synthesis of this area and the rest of the North American Southwest. We encourage more researchers to respond to the "call" for such studies which was issued by Minckley *et al.* (1986) in their seminal biogeographic synthesis.

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