A new species of *Praticolella* (Gastropoda: Polygyridae) from northeastern Mexico and revision of several species of this genus

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ABSTRACT

A new species of polygyrid land snail of the genus *Praticolella* from northeastern Mexico is described. This species has established invasive populations in the United States and Caribbean and has been confused with *P. griseola* and *P. berlandieriana*. The new *Praticolella* species is similar to *P. griseola*, but differs in being larger, having a more robust, depressed shell with white pigmentation, a flattened wide body whorl, and a more oval-shaped aperture. The range of these two species does not appear to overlap with *P. berlandieriana,* which is restricted to central, north, and east Texas. These two species are also circumscribed and their taxonomic history is reviewed. This new taxonomy was established using mitochondrial 16S rDNA and cytochrome c oxidase subunit-I sequences as well as geometric morphometric examination of the shells of each species.

Additional keywords: Mollusca, Invasive species, snail, mitochondrial DNA analysis, mitochondrial 16S rDNA, cytochrome c oxidase, geometric morphometric analysis

INTRODUCTION

Praticolella von Martens, 1892 is a genus of polygyrid land snails found throughout the southeastern United States (USA), Mexico, and South to Central America (Pilsbry, 1940). *Praticolella* is currently composed of 15 recognized species (Pilsbry, 1940; Hubricht, 1984), nine of which are species of conservation concern having global heritage ranks of G1, G2, or G3, indicating they are considered critically imperiled, imperiled, or vulnerable (Master, 1991; NatureServe, 2005). This paper aims to distinguish among several morphologically similar species of land snail in the genus *Praticolella*.

Species in *Praticolella* possess highly variable morphological characteristics often used in their taxonomy: the openness of the umbilicus; degree of depression of the spire; and the pattern of pigmented bands on the shells. This has led to disagreements about taxonomy of species in the genus (von Martens, 1890–1901; Singley, 1893; Pilsbry, 1940; Cheatum and Fullington, 1971; Neck, 1977; Hubricht, 1984). The last taxonomic revision of the United States species was by Pilsbry (1940) but excluded the five nominal Mexican taxa; these Mexican taxa were last revised by von Martens (1890-1901).

Praticolella griseola (Pfeiffer, 1841) is the only member of the genus currently considered to be introduced or invasive in the United States (USA) (Dundee, 1974; Robinson, 1999). Individuals identified as *P. griseola* have been recorded in the southeastern USA and the Caribbean since the 1920s. In addition, the United States Department of Agriculture (USDA) routinely intercepts *P. griseola* traveling with shipping trade.

This paper provides the means to distinguish several morphologically similar species of *Praticolella*, at least two of which regularly travel with shipments of fruit and greenhouse plants. The data presented here will make evident that other *Praticolella* species also need taxonomic attention, but this paper focuses on *P. griseola* and the species which must be considered to sort out the taxonomy of the invasive *Praticolella* species. These include: *P. griseola*, *P. berlandieriana* (Moricand, 1833), and *P. strebeliana* (Pilsbry, 1899). In this study, I use 16S rDNA (16S) and cytochrome c oxidase subunit I (COI) mitochondrial DNA and shell geometric morphometric analysis to provide the basic taxonomic and phylogenetic information necessary for taxonomy, conservation, and management of these invasive mollusks and native congeners.

MATERIALS AND METHODS

Table 1 lists specimens examined for DNA analysis, collection sites, latitude and longitude, and museum accession numbers of all specimens (also shown in Figure 1). Specimens examined in this study are deposited in the Academy of Natural Sciences of Philadelphia. Additional specimens for morphometric analysis (also listed in Table 1) were borrowed from the Florida Museum of Natural History, Gainesville; American Museum of Natural History, NewYork; Museum d'Histoire Naturelle, Geneva; and Field Museum of Natural History, Chicago.

Table 1. Locality information and museum number for specimens sequenced for DNA analysis followed by locality information and museum number for additional lots included in morphometric analysis. In these additional lots all adult, complete shells were photographed and included in morphometric analysis. ANSP numbers beginning with "A" represent lots preserved in alcohol. Latitude and Longitude presented in decimal degrees.

Species	Locality	Museum Number	Latitude	Longitude
Localities for DNA specimens				
Praticolella berlandieriana	9 km N New Braunfels, Comal Co. TX	ANSP A22076, ANSP 426024	29.7739	–98.1601
Praticolella berlandieriana	12.6 km SE of Blanco, Blanco Co. TX	ANSP A22079	30.0204	–98.3300
"Praticolella griseola" Cameron Co	Point Isabella high school, Port Isabel, Cameron Co. TX	ANSP A22074, ANSP 426021	26.077	–97.2271
Praticolella griseola	9.5 km N of Puente Arroyo Hondo, (N of Veracruz), VC, MEX	ANSP A22080	20.0883	–96.9106
Praticolella griseola	9 km N of Papantla, VC, MEX	ANSP A22082	20.46389	–97.34111
Praticolella griseola	Tula, NL, MEX	ANSP A22081	23	–99.7167
Praticolella griseola	San Rafael, VC, MEX	ANSP A22075, ANSP 426022	20.2	–96.85
Praticolella griseola	Veracruz, VC, MEX	ANSP A22078, ANSP 426029	19.2147	–96.16028
Praticolella griseola	La Mancha, VC, MEX	ANSP A22073, ANSP 426019	19.6061	–96.39889
Praticolella griseola	1.5 mi S of Jiménez, TMP, MEX	ANSP 426028	24.2167	–98.4667
Praticolella griseola	1 km E Howey Height, Lake Co. Fl	ANSP A22084	28.667676	–81.746159
Praticolella mexicana	Diente, ∼5 km S of Monterrey, NL, MEX	ANSP A22072 ANSP 426018	25.47728	–100.28673
Praticolella mexicana	Anahuac, NL, MEX	ANSP A22086	27.2519	–100.125
Praticolella mexicana	Puente San Rodrigo, COAH, MEX	ANSP A22089	28.6668	–100.9127
Praticolella mexicana	∼10 km W of Monterrey, NL, MEX	ANSP A22077, ANSP 426025	25.67861	–100.4481
Praticolella mexicana	3 km N Agua Buena, Rio Tamasopo, SLP, MEX	ANSP A22087	21.9419	–99.395
Praticolella mexicana	Key Largo FL	ANSP A22091	25.17202	–80.3666
Praticolella mexicana	2 km N Agua Buena, SLP, MEX	ANSP A22088	21.96426	–99.38899
Praticolella mexicana	Hidalgo, Hidalgo Co. TX	ANSP 426020	26.1	–98.263
Praticolella mexicana	15 km SW of Linares, where road to Caja Pinta runs along stream, NL, MEX	ANSP A22101, ANSP 426032 (Paratypes)	24.7573	–99.6581
Praticolella mexicana	∼5 km E Ciudad Victoria, TMP, MEX	ANSP A22085	23.7333	–99.1333
Praticolella mexicana	20 km N Mante, TMP, MEX	ANSP 426027	22.8833	–99.0167
Praticolella mexicana - int	USDA - JFK international airport interception from Dominican Republic	ANSP A22094	40.6501	–73.9496
Praticolella mexicana - int	USDA - Progresso from Mexico	ANSP A22093	26.0923	–97.9572
Praticolella mexicana	Hell, Grand Cayman	USDA-APHIS Collection	19.381774	–81.415936
Praticolella mexicana	Staniard Creek, Andros Island, Bahamas	ANSP A22090	24.844126	–77.892870
Morphometrics localities				
P. mexicana	15 km SW of Linares. In grass along fence at S end of park next basketball court, next to small stream. where Mx 58 to Caja Pinta runs along stream, NL, MEX	ANSP 426031 (Holotype), ANSP 426032, ANSP A22101 (Paratypes)	24.7573	–99.6581
	Canoas, SLP In park in town on road through town by stream.	ANSP 426026	21.94405	21.94405
P. berlandieriana	Milam County near Brazos River, 4.7 mi NE of Gause, USA, Texas	FMNH 259146	30.8289	–96.6706
	3.3 mi N New Braunfels, Comal Co.	ANSP 426023	29.7635	–98.1547
	20 M from Guadalupe River across from Guadalupe Canoeing 9 km N New Braunfels, Comal Co. TX	ANSP 426024 ANSP A22076	29.7739	–98.1601
	"Habite le Mexique, dans la province de Texas."	MHNG 37027		

(*Continued*)

Table 1. (Continued)

Species	Locality	Museum Number	Latitude	Longitude
"Praticolella griseola" Cameron Co	Cameron County, Port Brownsville, TX, USA	FMNH 259156	25.949904	–97.402715
	0.3 mi E Point Isabella high school, Port Isabel, Cameron Co. TX	ANSP 426021 ANSP A22074	26.077	–97.2271
Praticolella griseola	Nicaragua	FMNH 33486	12.865416	–85.207229

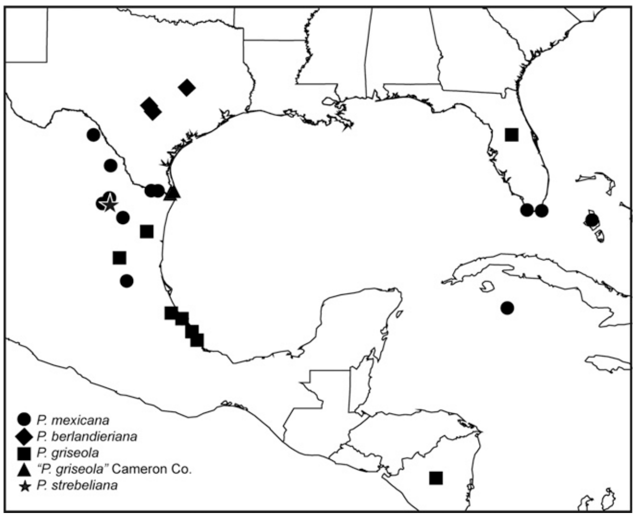

Figure 1. Map of specimens used for DNA analysis and additional localities of specimens used for morphometric analysis.

Individual sequences are available on Genbank, 16S: DQ085935-DQ086020, COI: DQ086021-DQ086095. Outgroups were included from other members of the Polygyrini (Emberton, 1995), specifically, *Polygyra cereolus* (Mühlfeld, 1816) and *Polygyra septemvolva* (Say, 1818).

Molecular Data Analysis: Total genomic DNA was extracted from several milligrams of tissue digested with CTAB lysis buffer and purified through standard phenol-chloroform procedures (Palumbi et al., 1991). Degenerate primers (5′-YRMCTGTTTAWCAAAAACAK-3′ and 5′-CCGGTCTGAATCCAGATCABGT-3′) were designed from the Palumbi et al. (1991) primer pair and Genbank sequences that amplified a ~450 bp fragment of the mitochondrial 16S gene. The Folmer et al. (1994) primers were used to amplify a ~600 bp fragment of the mitochondrial cytochrome oxidase c subunit I gene (COI) gene. Fragments were amplified by PCR, purified through gel extraction, and sequenced using BigDye 3.1 chemistry on an ABI 3100 automatic genetic analyzer. Specific protocols for amplification and sequencing can be found in Perez et al. (2005).

Sequences were assembled in Sequencher™ 4.0.5 (Gene Codes Corporation, Ann Arbor, MI) or Geneious Pro 3.5.6 (Drummond et al., 2006) and aligned in Muscle (Edgar, 2004). Garli 0.951 (Zwickl, 2006) was used to carry out maximum likelihood (ML) estimation of relationships. The ML analysis was carried out using Garli's default settings, as was an additional 100 replicate bootstrap analysis.

Shell Morphometric Analysis: In total, 237 specimens representing the following five species were examined: *P. berlandieriana* (46 specimens), *"P. griseola"* Cameron County (32), *P. griseola* (68), *Praticolella* new species (described below) (85), *P. strebeliana* (5) (Specimens used for DNA are listed in Table 1). We had difficulty in identifying to species specimens without living tissue for sequencing (shell-only specimens). Therefore, only a limited number of individuals from museum collections could be used for morphometric analysis, in addition to the individuals for which we gathered sequence data for morphometric analysis; this number mostly includes additional individuals or shell-only collections from the same locality as individuals with sequenced DNA. Color images were captured with a tripod-mounted, Canon PowerShot S3IS digital camera. Twenty-five landmarks (Figure 2) were digitized using tpsDig 1.31 (Rohlf, 2001).

Geometric morphometrics analyses were carried out using the Integrated Morphometrics Package, this includes the programs CoordGen, PCAGen, CVAGen, TwoGroup, and Regress 6 listed below (IMP software suite; Sheets, 2003) were used to examine shape variation through principal component analysis (PCA) and canonical variance analysis (CVA). PCA is a technique for simplifying descriptions of variation among individuals, while CVA simplifies descriptions of differences between pre-determined groups (Zelditch et al., 2004). In traditional morphometric analysis, PCA generally suffers from the overwhelming influence of size across the newly generated axes. However, geometric morphometric analysis eliminates size as a factor, yielding examinations of shape solely. In PCA, no *a priori* assumptions are needed to group individuals. In contrast, CVA determines the set of axes that best discriminates between groups; therefore an *a priori* assumption of group membership is necessary. For CVA analysis,

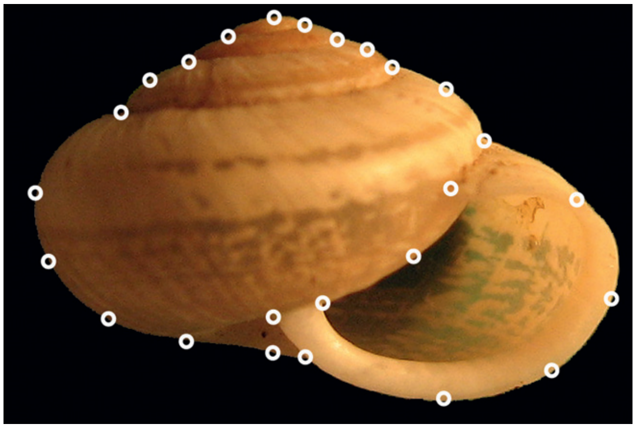

Figure 2. *Praticolella mexicana* individual (#436) from 15 km SW of Linares, Nuevo León, (ANSP 426031) Mexico showing landmarks used in the morphometric analysis. This individual used in both DNA and morphometric analyses.

individuals were grouped according to the clades identified by the molecular analysis.

Landmark coordinates were imported into CoordGen6f and converted to Procrustes distances using least squares Procrustes superimposition methods. A MANOVA carried out in SYSTAT 8.0 was used to examine differences in shape between species. Pairwise comparisons between all populations were performed in TwoGroup6c with Bonferroni correction to determine if there were significant shape differences. A PCA was performed with PCAGen6g on the data with *a posteriori* groups assigned by locality. A CVA was also performed using CVAGen6h with groups defined by the clades from the DNA analysis. The difference in shape between each species was examined directly using Regress6.

Abbreviations and Text Conventions: MHNG = Museum d'Histoire Naturelle, Geneva; FMNH = Field Museum of Natural History; ANSP = Academy of Natural Sciences of Philadelphia (ANSP numbers beginning with "A" represent lots preserved in alcohol); USDA = United States Department of Agriculture; GM = geometric morphometric analysis; PCA = principal component analysis; MANOVA= multivariate analysis of variance. Latitude and Longitude presented in decimal degrees.

RESULTS

Molecular Phylogeny: Maximum likelihood analysis of 417 bp of 16S and 493 bp of COI yielded a single tree (Figure 3). *Praticolella* new species (to be described below) comprised a well-supported monophyletic clade. Many individuals included in this clade were initially identified as *P. berlandieriana* due to their geographic location in northeastern Mexico. Some individuals in this clade were from invasive populations (Bahamas and Florida) or United States Department of Agriculture (USDA) interceptions and were initially identified as *P. griseola*, which is well known as invasive. The DNA tree also shows monophyletic lineages from both near Victoria, Tamaulipas, and near Mante, Tamaulipas. These are herein considered part of *Praticolella* new species , but further work is needed to examine population level versus species level differences among these lineages.

Individuals conforming to the morphology of *P. griseola*, including topotypic material, form a clade (100% bootstrap support; labeled *P. griseola* on Figure 3) that has deep subdivisions between different populations in the mitochondrial DNA and includes an individual from an invasive population in Lake County, Florida. The *P. griseola* clade is resolved as sister (75% bootstrap support) to a monophyletic group of individuals from Soto la Marina, Tamaulipas. Individuals from a small, morphologically unique, disjunct population of *P. griseola* were sampled in this study and are called here: "*P. griseola*" Cameron Co. (Pilsbry, 1940; Rehder, 1966). This population formed a distinct clade separate from *P. griseola*, but due to poor support in this portion of the tree, relationships remain uncertain.

Individuals from as close to the type locality of *P. berlandieriana* as could be determined (details below, within 30 km) form a clade sister to other Texas *Praticolella* species (84% bootstrap), including individuals of *P. trimatris* Hubricht, 1983, *P. pachyloma* (Menke in Pfeiffer, 1847) and *P. taeniata* Pilsbry, 1940.

Shell Morphometric Analysis: Differences in shell shape in *Praticolella* were assessed using GM (Figure 3). Shell variation is traditionally quantified through straight-line shell measurements and ratios and used to distinguish between individuals and populations at the species level (e.g., Heller et al., 2005; Tanaka and Maia, 2006). Recently, GM has been employed in examinations of snail shells, both to provide direct size-free analyses of shell shape and to answer broader evolutionary questions (Pfenninger and Magnin, 2001; Conde-Padin et al., 2007; Hayes et al., 2007).

The first PCA axis (PC1) explained 31.5% of the variation, the second (PC2) explained 15.3%, and the third (PC3), 13.1%. A MANOVA on the PCA scores found a significant difference among groups (Hotelling-Lawley Trace=2.012, F-Statistic=30.669, df=15, 686, $p<0.000$). Pair-wise comparisons of all species assessed by Goodall's F test showed that snails from each species had significantly different ($p<0.01$) shapes.

Each species was compared pairwise using TwoGroup to carry out Goodall's F-test. Pairwise comparisons were followed by a Bonferroni correction. This analysis found that each of the species' means are significantly different ($p<0.001$ in all cases). The lectotypes (ANSP 411457 and 77128) of *Praticolella strebeliana* are distinct on the first three PC axes (Figure 4) with the highest difference in mean value from the other species (Distance in mean value from *P. griseola*=0.0967; *P. berlandieriana*=0.0916;

Figure 3. Molecular phylogeny of *Praticolella*. Maximum likelihood phylogram based on 16S and COI mitochondrial DNA. The species discussed in this paper are marked by grey boxes. Numbers on branches are ML bootstrap values. Outgroups not shown.

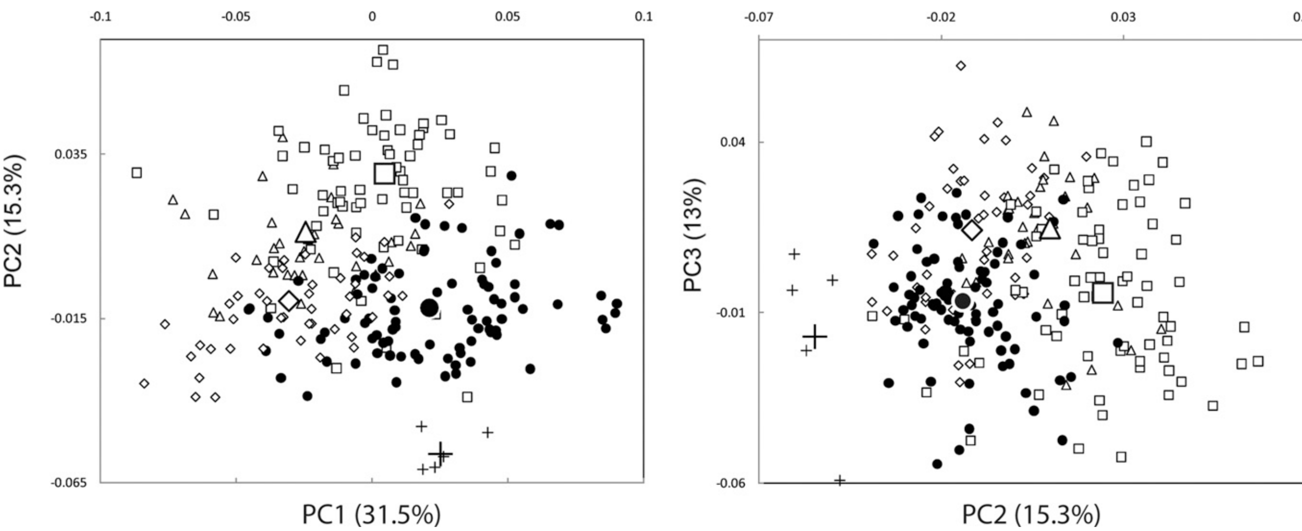

Figure 4. Principal component axes 1, 2, and 3. Percentages indicate the percent of the variance explained by each axis. Large symbols represent group means: *Praticolella mexicana* (•); *P. berlandieriana* (◊); *P. griseola* (□); "*P. griseola*" Cameron Co (Δ) *P. strebeliana* (+).

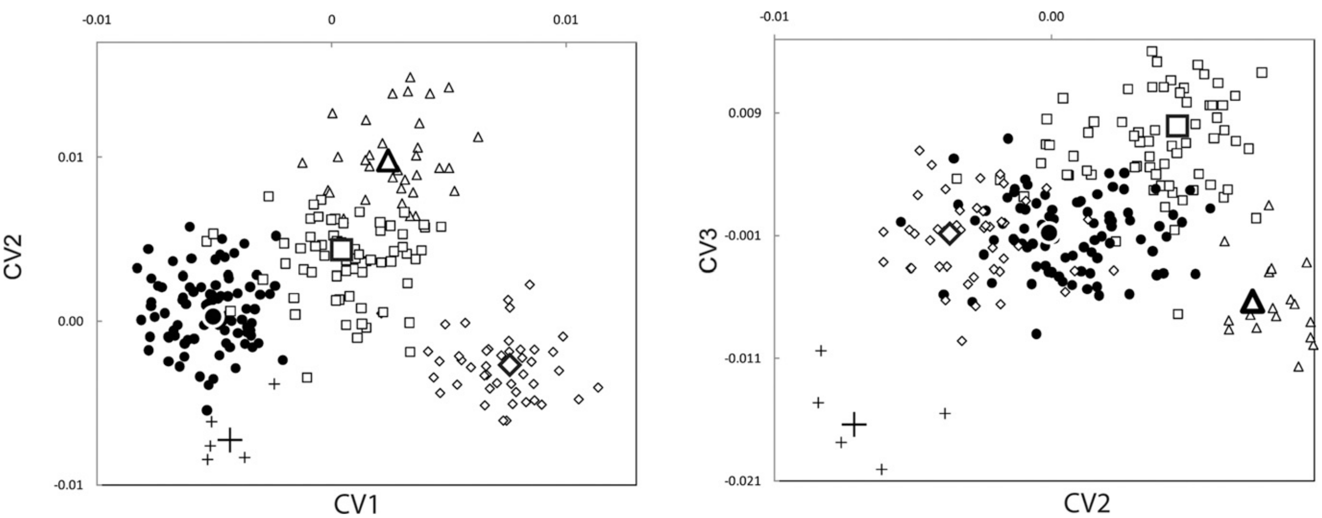

Figure 5. Canonical axes 1, 2, and 3. Discriminant scores calculated to maximally separate the five species. Left: the first and second canonical axes. Right: the second and third canonical axes. Large symbols represent group centroid. *Praticolella mexicana* (•); *P. berlandieriana* (◊); *P. griseola* (□); "*P. griseola*" Cameron Co (Δ) *P. strebeliana* (+).

Praticolella new species=0.0723). Although the species are significantly different, visual examination of Figure 4 shows there is a great deal of overlap in the shape variation present in each species. *Praticolella* new species is the most distinct in shape (Distance in mean value from *P. griseola*=0.0448; *P. berlandieriana*=0.0590; *P. strebeliana*=0.0723), but *Praticolella* new species, *P. griseola* and *P. berlandieriana* also have a great deal of overlap in shape (Figure 4; Distance in mean value=0.0518). CVA of each population yielded four distinct axes ($p < 0.05$) where all centroids were significantly different from each other (Figure 5). The resulting plot of CV 1 and CV 2 shows very little overlap among species, although a few individuals of *P. griseola* (three of 64) overlap into the new species' shape space. One individual of *Praticolella* new species grouped with *P. griseola*. The plot of CV2 and CV 3 widely separate *P. strebeliana* and *P. griseola* from the other species. Finally, "*P. griseola*" Cameron Co. is significantly different from the other species and distinct from *P. griseola* and *Praticolella* new species in all analyses. Figure 6 shows how shell shape differs from *Praticolella* new

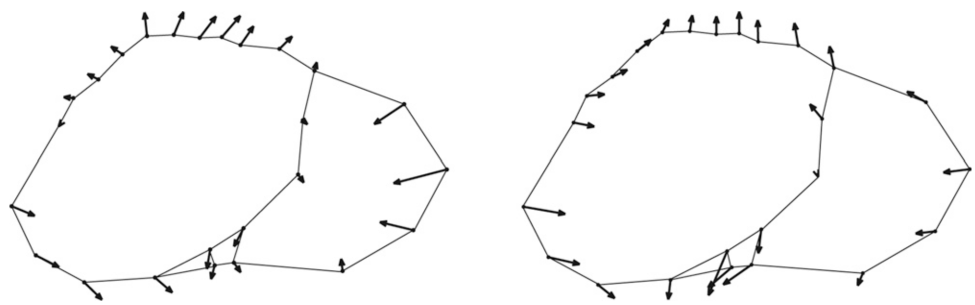

Figure 6. Change in shell shape between species. Left: Shape change to *P. berlandieriana* from *P. mexicana.* Right: shape change to *P. griseola* from *P. mexicana.* Shape change is exaggerated 3X by vector arrows to ease interpretation.

species to *P. berlandieriana* and (left) and from *Praticolella* new species to *P. griseola* (right).

SYSTEMATICS

Family Polygyridae Pilsbry, 1930

Genus ***Praticolella* von Martens, 1892**

Dorcasia Binney, 1878: 356.
Praticola Strebel and Pfeiffer, 1880: 38.
Praticolella von Martens, 1892: 138.

Type Species: *Praticolella ampla* (Pfeiffer, 1866), by original designation.

Diagnosis: Shell small, globose to slightly depressed with a conic spire of 4.5 to 5.75 whorls. Aperture either slightly or greatly reflected and without denticles. Narrowly umbilicate (Pilsbry, 1940). Penial diverticulum long and at least twice the volume of the penis (Emberton, 1995). Bifurcate or trifurcate penial retractor muscle (Emberton, 1995).

Distribution: United States: Florida, Georgia, Alabama, Mississippi, Louisiana, North Carolina, Texas, Mexico south to Panama, Caribbean islands.

***Praticolella mexicana* new species**
Figures (7–13)

Praticolella berlandieriana (Moricand, 1833): Fischer and Crosse, 1872: 256-257; Vanatta, 1915: 194, fig. 1 (genitalia); Pilsbry, 1940: 695, fig. 427a; Rehder, 1966: 290-291, fig. 20; Correa-Sandoval, 1993: 685; Correa-Sandoval, 1996: 137; Correa-Sandoval, 1999: 15; Correa-Sandoval, 2000: 493; Correa-Sandoval and Castro, 2002: 238.
Praticolella griseola Pfeiffer, 1841: Robinson, 1999: 415.

Description: Shell umbilicate, globose to somewhat depressed-globose. Lip thin, reflected to slightly cover umbilicus. Banding extremely variable, ranging from unbanded brown shell, unbanded white shell, to having nine complete and incomplete bands, radiating lines of white pigment, and streaks of white pigment on body whorl. Umbilical whorls with fine growth lines but no spiral striae and usually brown/gray colored with no white pigment, shiny. Average shell height=7.57, width=10.87, umbilicus width=0.69 mm, 5–5.6 whorls (Table 2).

Type Material: Holotype ANSP 426031, 27 May 1992, Ned E. Strenth (Figures 7–10). Paratypes ANSP 426032 and alcohol-preserved specimens ANSP A22101. Other material examined: Hidalgo, Hidalgo Co. TX, 21 Sept. 1991, Ned E. Strenth (Figure 11), ANSP 426020; College of the Bahamas Research Station, Staniard Creek, Andros Island, Bahamas, 20 May 2005, K. E. Perez, ANSP A22090 (Figure 12); Canoas, San Luis Potosí, Mexico, 23 July 2002, K.E. Perez, J.B. Pollock, ANSP 426026 (Figure 13).

Type Locality: 15 km SW of Linares, Nuevo León, Mexico, in grass next to small stream where MX 58 to Caja Pinta runs along stream, 24.757331 N, –99.658111 W.

Distribution and Habitat: Widely distributed in northeastern Mexico and south Texas on the eastern side of the Sierra Madre Oriental. There may be native populations in south Texas, though the collections examined were all from disturbed habitat or greenhouses. United States Department of Agriculture (USDA) often intercepts this species at the Texas/Mexico border. Introduced populations were found in Florida, Bahamas, Grand Cayman Island, Dominican Republic, Haiti, and Cuba. Several USDA interceptions were from Jamaica and Turkey. The native range of this species is most likely northeastern Mexico, north and east of the Sierra Madre Oriental. First, the basal lineages in this clade are all found in this region of Mexico. Second, collections from this region of Mexico predate the collection of this species in the Caribbean or Florida. This species was first reported as introductions collected in disturbed habitats of Florida in the early part of the 1900's.

The preferred diet of this species is unknown; however, it has been found on ornamental (greenhouse) plants and

Figures 7–13. Shells of *Praticolella mexicana* new species. **7–10.** Holotype, SW of Linares, Nuevo León, Mexico, 27 May 1992, Ned E. Strenth, ANSP 426031; side, top, and basal views of the shell and embryonic whorls, w=9.58 mm, h=6.59 mm, 5.25 whorls. **11.** ANSP 426020, Hidalgo, Hidalgo Co. Texas, w=10.59, h=7.46, 5.25 whorls, 21 Sept. 1991, Ned E. Strenth coll. **12.** ANSP A22090, College of the Bahamas Research Station, Staniard Creek, Andros Island, Bahamas, w=10.57, h=7.63, 5.25 whorls, 20 May 2005, K.E. Perez coll. **13.** ANSP 426026, Canoas, San Luis Potosí, Mexico, w=9.79 mm, h=7.18 mm, 5.25 whorls, 23 July 2002, K.E. Perez, J.B. Pollock colls.

Table 2. Shell measurements for the three species of *Praticolella*. Only adult shells with a full lip were measured: *P. berlandieriana* (n=24), *P. griseola* (n=36), *P. mexicana* (n=37). Values present, from top, range, mean and standard deviation. Abbreviations: h: shell height; w: shell width; aph: aperture height; apw: aperture width; umb: umbilicus width; # of whorls – number of whorls.

Species	h (mm)	w (mm)	aph (mm)	apw (mm)	umb (mm)	# of whorls
P. mexicana	6.3–9.19	9.38–12.27	4–6.77	4.85–6.92	0.4–1.08	5–5.6
	7.57±0.61	10.87±0.78	5.28±0.51	5.97±0.60	0.69±0.15	5.30±0.17
P. griseola	8.32–11.29	5.8–7.92	4.4–6.7	4.16–5.75	0.38–1.03	4.75–5.5
	9.65±0.78	6.91±0.51	5.34±0.47	4.88±0.39	0.71±0.16	5.12±0.16
P. berlandieriana	9.92–11.73	7.34–8.75	4.5–6.14	4.65–5.77	0.64–1.18	5–5.5
	10.49±0.49	8.16±0.40	5.52±0.42	5.19±0.29	0.85±0.13	5.35±0.22

is common in sugarcane, citrus, mango, banana, aloe, and papaya plantations (USDA interception records). The USDA has intercepted this species on shipments of mangos, papayas, ornamental plants, and furniture. These snails possess many of the typical characteristics of invasive snail species, such as living at high population densities in shrubs, tall grass, and under trash. This species is often found climbing walls and grass.

Etymology: Named in reference to the native distribution of this species in Mexico.

Taxonomic Remarks: *Praticolella mexicana* is similar to *P. griseola*, but differs in being larger, having a more robust, depressed shell with white pigmentation, a flattened wide body whorl, and a more oval-shaped aperture. Figure 6 (right) illustrates the difference in shape between *P. mexicana* and *P. griseola*. The body whorl of *Praticolella griseola* (Figure 14) is more rounded with a rounded aperture. The insertion of the peristome is much closer to vertical in *P. griseola* and horizontal in *P. mexicana*. *Praticolella berlandieriana* is distinguished from *P. mexicana* by having a taller, much thicker, heavier shell and widely expanded lip (Figure 6 left and 20).

Praticolella strebeliana was included in this study as it was described from Diente Mine near Monterrey, Nuevo León Mexico (Pilsbry, 1899) within the range of collections of *P. mexicana*. This species was described as completely brown with no bands; however, because occasionally *P. mexicana* individuals have no bands (populations from Hidalgo, Texas are all bandless with a brown base color), I thought it necessary to consider *P. strebeliana* as potentially having priority before naming this new taxon (*P. mexicana*). Therefore, to test whether *P. strebeliana* was an appropriate name, *Praticolella* specimens from Diente, the type locality of *P. strebeliana*, were collected for both DNA and morphometric analyses. Several collecting attempts at the type locality yielded no unbanded shells fitting the description of *P. strebeliana*. All individuals sequenced from this locality are within the *P. mexicana* clade. Therefore, I have no DNA evidence to distinguish *P. strebeliana*. However, morphometric analysis of the type specimens (ANSP 77128 and 411457) of *P. strebeliana* showed that they were very distinct from *P. mexicana*, *P. berlandieriana*, and *P. griseola* (Figures 4 and 5). *Praticolella strebeliana* has a frosted, corneous shell that is more globose than *P. mexicana*, as well as a downward tilted lip and greater degree of contraction behind the lip. Based on the differences in shell morphology and morphometric analysis I am considering *P. strebeliana* distinct from *P. mexicana*. In texture and coloration of the shell, *P. strebeliana* is more similar to *P. flavescens* than the other Texas or Mexican taxa.

Praticolella griseola (Pfeiffer, 1841)

Helix cicercula Férrusac in collection = *griseola* according to Pfeiffer 1848, 1: 337.
Bradybaena pisum Beck, 1837: 18 (*nomen nudum.)*
Helix griseola Pfeiffer, 1841: 41; Pfeiffer, 1848: 337.
Helix albocincta Binney, 1851: 109, 128.
Helix albo-zonata Binney, 1857: pl. 49, fig. 2.
Helix albolineata Gould in Binney, 1857: 34.
Helix splendidula Anton, 1839: 36. (*nomen nudum*).
Dorcasia griseola Pfeiffer, 1841; Binney, 1878: 348, fig. 231 (jaw), pl. vii, fig. v (teeth).
Helix berlandieriana var. *griseola* Pfeiffer, 1841; von Martens, 1892: 140, pl. 7, figs. 15–17.
Helix (*Praticola*) *griseola* (Pilsbry, 1891): 313.
Praticolella griseola Pilsbry, 1940: 690–692, fig. 425.

Description: *Praticolella* with a robust, umbilicate, depressed-globose shell. Number of pigmented bands on body whorl ranges from 1 to 8 with most shells having 2 or 3. Most individuals possess a complete cinnamon colored mid-body whorl band. Aperture lunate to round with a thin reflexed lip. Shell obliquely striate. Average shell height=9.65, width=6.91, umbilicus width=0.71 mm, 4.75–5.5 whorls (Table 2).

Type Material: Syntypes, 6 individuals, Mexico. Natural History Museum of London 20110179. Figures 14–19.

Distribution and Habitat: Pfeiffer (1841) gave the type locality of *P. griseola* as Veracruz. This species is native to Veracruz and southern Tamaulipas and has also been introduced to South Florida and New Orleans, Louisiana. Due to restriction of populations in the Yucatán and Guatemala to disturbed areas, it is considered invasive there as well (Harry, 1950). However, native populations in Guatemala have not been ruled out by this data. The complete range of this species will need further work to be fully circumscribed. Specimens labeled *P. griseola* in museum collections are often *P. mexicana*.

Taxonomic Remarks: *Praticolella griseola* was described by Pfeiffer (1841) in a short paragraph without illustration. The specimens are attributed to Hegewisch, referring to the physician and botanical collector Dr. Ernst Friedrich Adoph Hegewisch, who lived in Oaxaca, Mexico, around 1836–1840 (Pritzel, 1864). Pfeiffer's primary collection (collection 532) was lost with the destruction of the Stettin Museum (Dance, 1986). However, some Pfeiffer material resides in the Natural History Museum in London (NHMUK) including a lot of 6 specimens labeled "*H. griseola* Mexico Pfr" in Pfeiffer's handwriting (handwriting identified by Jonathan Ablett, Curator of Non-Marine Mollusca and Cephalopoda, NMHUK, pers. comm.). These specimens were also labeled "M.C." indicating they came from the Hugh Cuming collection. While it is not possible to conclude that these specimens were from the original type series, Pfeiffer's handwriting on the label indicates they are probable syntypes.

In the phylogenetic tree (Figure 3), topotypic specimens conforming to the original description of *P. griseola* formed a monophyletic lineage with individuals from an introduced population in Florida as well as specimens from the coastal plain of Veracruz and north into Tamaulipas.

Praticolella griseola has been the subject of much taxonomic contention. Von Martens (1890–1901) and Singley (1893) stated that *H. griseola* and *H. (Praticolella) berlandieriana* are connected by many intermediate forms and cannot be maintained as distinct species.

Figures 14–19. Shells of *Praticolella griseola*. **14–19.** Syntypes, Mexico, Pfeiffer material, H. Cuming Collection MNHUK 20110179. **14–17.** Side, top, and basal views of the shell and embryonic whorls. Scale bar = 1 mm (Figure 14). **18.** Side view of additional shell from same lot. **19.** Side view of additional shell from same lot.

However, Pilsbry (1940) found no connecting links between *P. griseola* and *P. berlandieriana* and further proposed that they formed an ecological pair with *P. griseola* living in warmer more humid regions, and *P. berlandieriana* living in cooler, semiarid country. However, Cheatum and Fullington (1971) stated, without presenting evidence, that, due to interbreeding, in a large assortment of shells representing all species (meaning all species present in south Texas) from the same geographic area it is difficult to determine where one species ends and another begins.

Praticolella griseola has been suggested to be made up of a number of well-characterized "races" living in a variety of habitats and climates (Rehder, 1966; Neck, 1977). Rehder's (1966) "races" of *P. griseola*, included the populations around Veracruz, Mexico and a second race comprised of a small, unique, disjunct population in Cameron County in south Texas. Individuals from this "race" were sampled in this study and are referenced herein as "*P. griseola*" Cameron Co. (Pilsbry, 1940; Rehder, 1966). These snails have a thinner lip and a dark-colored basal whorl. Taxonomic placement of this population is outside of the sampling and scope of this study, but the mitochondrial DNA results indicate that it is distinct from *P. griseola* and from other nearby *Praticolella* species and remains to be described.

Praticolella griseola has deep subdivisions between different populations in the mitochondrial DNA analysis. The individuals from Jiménez in particular are distinctive in morphology as well in that they have a slightly heavier lip and more solid shell. They also have more regular spiral striae on the embryonic whorl than typical *P. griseola*.

Praticolella berlandieriana (Moricand, 1833)

Helix (*Helicogena*) *berlandieriana* Moricand, 1833: 537, pl. 1, fig. 1.
Helix berlandieriana Moricand, 1833: Leidy in Binney, 1851: 255, pl. 8, fig. xi.
Dorcasia berlandieriana (Moricand, 1833): Binney, 1878: 347.
Praticolella berlandieriana (Moricand, 1833): Pilsbry & Ferriss, 1906: 125–126, figs. 1 and 2; Pilsbry, 1940: 694–697, fig 427b (shell); Webb, 1967: 133–136, figs. 12–17.

Description: Shell solid, narrowly umbilicate, globose-depressed with a low conic spire. Color white to gray to light buff, frequently with a gray band above the periphery; other bands or colored streaks common. Embryonic whorls glossy, sometimes gray to light brown, sometimes with fine spiral lines; later whorls weakly striate. Body whorl rounded at the periphery, somewhat contracted behind the lip. Lip white, widely expanded, strongly thickened within (Figures 20–23). Average shell height=10.49, width=8.16, umbilicus width=0.85 mm, 5–5.5 whorls (Table 2).

Type Material: Syntypes MHNG 37027, “Habite le Mexique, dans la province de Texas” (Moricand, 1833)

Distribution and Habitat: Edwards Plateau biotic province (Blair, 1950), central Texas, extending north to Arkansas. In mesquite or grassy areas, often found under trash and on roadsides.

Taxonomic Remarks: *Praticolella berlandieriana* was described by Moricand (1833) referring to specimens with the locality noted as “Texas” collected by Jean Louis Berlandier, a botanist from Geneva who collected botanical specimens in Mexico. Berlandier collected intensively in Bexar and Comal counties as well as along the road to Gonzales, Texas in the spring of 1828 (Geiser, 1948).While it is not possible to know exactly where within this region Berlandier collected these shells, I am treating specimens collected for DNA analysis from Texas, North of the Balcones Escarpment, NE of the San Antonio area (New Braunfels and Blanco River collections) as the best possible representatives of this species. This highway route follows the historical road

Figures 20–23. Shell of *Praticolella berlandieriana*, ANSP 426024, 9 km N of New Braunfels, along the Guadalupe River, Comal Co. TX; side, top, and basal views of the shell and embryonic whorls. w=10.06, h=8.28, 5.5 whorls, 1 July 2004, K. E. Perez coll.

between San Antonio and Gonzales. DNA sequence analysis resolves these individuals of *P. berlandieriana* as a separate unique lineage; other individuals from Mexico that have been treated as nominal *P. berlandieriana* have been herein assigned to other species in the genus.

Von Martens (1890–1901) treated *P. berlandieriana* as part of the Mexican fauna and identified its range as Texas and much of northern Mexico. He also considered this species to be synonymous with *P. griseola* as reflected in his extensive synonymy. Rehder (1966) attempted to distinguish *P. griseola* from *P. berlandieriana* and restricted *P. berlandieriana*'s range to central Texas through southern Tamaulipas, Mexico. Hubricht (1983) considered *P. berlandieriana* to have specific rank; however, he considered this species to be of ancient hybrid origin derived from a combination of lineages of *P. pachyloma* and *P. candida*. Mitochondrial DNA does not support this conclusion (Figure 3).

Praticolella berlandieriana has been considered to have a large range, from central Texas to central Mexico (Pilsbry, 1940; Rehder, 1966; Cheatum and Fullington, 1971). This species was then considered restricted to central Texas by Neck (1977) and Hubricht (1983); however, the name has continued to be applied to Mexican species with individuals identified as *P. berlandieriana* reported by Correa-Sandoval (1993; 1999) from Nuevo León, Tamaulipas, and San Luis Potosí. However, the lack of any individuals further south than central Texas forming a clade with *P. berlandieriana* indicates that these Mexican records most likely represent *P. mexicana* new species or other undescribed Mexican *Praticolella*. All the *Praticolella* in south Texas fall into other clades (Figure 3: south Texas Clade, "*P. griseola*" Cameron County, or *P. trimatris*) Therefore, it appears that the distribution of *P. berlandieriana* should be restricted to central, east, and north Texas.

The internal anatomy of an individual of *P. berlandieriana* from Comal County, Texas, near the type locality as described in this paper, was figured in Webb (1967). *Praticolella berlandieriana* is also figured (Vanatta, 1915) from a specimen from Victoria, Tamaulipas but this illustration does not represent true *P. berlandieriana*.

DISCUSSION

This study is the first to use molecular data to examine and delineate species boundaries in the family Polygyridae. DNA sequences for 16S and COI were used to estimate relationships within the genus *Praticolella* with emphasis on *Praticolella griseola* and the species taxonomically confused with it. This analysis provides an evolutionary framework for further inter- and intraspecific studies within *Praticolella* as well as providing some baseline for management efforts of the several invasive *Praticolella* species.

Accurate identification and the continuing deposition of species in natural history collections are of primary importance for management of invasive species. Predictions of how newly introduced organisms may be capable of surviving or altering habitats or ecosystems cannot be made unless the species in question has been identified accurately. Attempts to control spread or population growth of these species is hindered because information on ecology of the introduced species within its native range cannot be gathered or used without a correct identification. In the opposite case, data gathered in the newly introduced environment cannot be used by workers in areas where they have been introduced previously.

Molecular analyses found several exclusive lineages of snails that had previously been treated/identified as *P. griseola*. There are multiple invasive lineages of *Praticolella* in the USA, and the majority of individuals encountered both in established populations and intercepted by USDA are *P. mexicana* from trade goods shipped from the Caribbean. This result indicates most of the propagule pressure for *Praticolella mexicana* invasion is actually via secondary invasion through the Caribbean, not coastal Mexico as previously thought. This species also appears to be starting to establish populations worldwide with the first USDA interceptions from Turkey in 2009 (USDA Interception Number: APHTX062722570001).

Along with the discovery of multiple lineages of invasive species, this analysis also highlighted populations of *P. griseola* from south Texas, from a population disjunct from the rest of the species distribution by ~300 km. This population had long been regarded as a distinct "race" of *P. griseola* (Rehder, 1966; Neck, 1990); however, this study indicates this lineage is distinct and very limited in distribution.

In addition to the Cameron County, Texas lineage the molecular results of this study uncovered several very distinct lineages that cannot confidently have an available name applied. This includes the lineage sister to *P. griseola* from the Soto la Marina, Tamaulipas (TMP) area. Considered part of *P. mexicana* are two populations that form unique exclusive lineages, from near Ciudad Mante, TMP, and near Ciudad Victoria, TMP. Additional sampling will be required to determine the extent of the distribution of these lineages and their specific status. It is outside the scope of this paper and the available collection materials to circumscribe these species, but these molecular data suggests that there is much undescribed diversity within *Praticolella*.

The life-history characteristics of *Praticolella* lend this group of snails to an invasive life-style. They thrive in disturbed habitat, living at high population densities in shrubs, tall grass, and agricultural lands; consequently they frequently travel on citrus, vegetables, and ornamental plants. These species share a morphological type characterized by multiple color bands on the shell. These shell banding patterns have been proposed to be an adaptation for snails that climb up vegetation, thus providing camouflage from bird predators (Johnson, 1980), an alternative has been proposed that bands provide thermal control by reducing radiative energy absorption (Burla and Gosteli, 1993). This characteristic is therefore likely to be convergent and not taxonomically useful, although it has been used extensively in previous taxonomy of *Praticolella*.

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LITERATURE CITED

Anton, H.E. 1839. Verzeichniss der Conchylien. Welche sich in der Sammlung. Eduard Anton, Halle, 110 pp.

Beck, H.H. 1837. Index Molluscorum Praesentis Aevi Musei Principis Augustissimi Christiani Frederici. 127 pp.

Binney, A. 1851. The Terrestrial Air-breathing Mollusks of the United States and the Adjacent Territories of North America. Vol. 1. Charles C. Little and James C. Brown, Boston, 366 pp.

Binney, A. 1857. The Terrestrial Air-breathing Mollusks of the United States and the Adjacent Territories of North America. Vol. 2. Charles C. Little and James C. Brown, Boston, 362 pp.

Binney, W.G. 1878. Terrestrial Air-Breathing Mollusks of the United States and Adjacent Territories of North America. Vol. 5. Welsh, Bigelow & Co., Cambridge, 221 pp.

Blair, W.F. 1950. The biotic provinces of Texas. Texas Journal of Science 2: 93–117.

Burla, H. and M. Gosteli. 1993. Thermal advantage of pale coloured morphs of the snail *Arianta arbustorum* (Helicidae, Pulmonata) in alpine habitats. Ecography 16: 345–350.

Cheatum, E.P. and R.W. Fullington. 1971. The aquatic and land Mollusca of Texas. Bulletin of the Dallas Museum of Natural History 1, part 1: 1–74.

Conde-Padin, P., J.W. Grahame and E. Rolán-Alvarez. 2007. Detecting shape differences in species of the *Littorina saxatilis* complex by morphometric analysis. Journal of Molluscan Studies 73: 147–154.

Correa-Sandoval, A. 1993. Caracoles terrestres (Molluca: Gastropoda) de Santiago, Nuevo León, Mexico. Revista de Biologia Tropical 41: 683–687.

Correa-Sandoval, A. 1996. Caracoles terrestres (Mollusca: Gastropoda) de Iturbide, Nuevo León, Mexico. Revista Biologia Tropical 44: 137–142.

Correa-Sandoval, A. 1999. Zoogeografia de los gastropodos de la region oriental de San Luís Potosí. Revista de Biologia Tropical 47: 493–502.

Correa-Sandoval, A. 2000. Gastropodos terrestres del norte de Veracruz, Mexico. Acta Zoologica Mexicana 79: 1–9.

Correa-Sandoval, A. and R.R. Castro. 2002. Gastropodos terrestres del sur de Tamaulipas, Mexico. Acta Zoologica Mexicana 86: 225–238.

Dance, S.P. 1986. A history of shell collecting. E.J. Brill-Dr. W. Backhuys, Leiden, 265 pp.

Drummond, A.J., B. Ashton, J. Heled, M. Kearse, R. Moir, S. Stones-Havas, T. Thierer, and A. Wilson. 2006. Geneious v2.5.4. Available from http://www.geneious.com

Dundee, D.S. 1974. Catalog of introduced molluscs of eastern North America (North of Mexico). Sterkiana 55: 1–37.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Emberton, K.C. 1995. When shells do not tell: 145 million years of evolution in North America's Polygyrid land snails, with a revision and conservation priorities. Malacologia 37: 69–110.

Fischer, P. and H. Crosse. 1872. Mission Scientifique au Mexique et dans L'Amerique Centrale. Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. I. Part I. Imprimerie Nationale, Paris, pp. 153–304.

Folmer, O.M., W. Black, R. Hoeh, R.A. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology Biotechniques 3: 294–299.

Geiser, S.W. 1948. Naturalists of the Frontier. 2nd ed. Southern Methodist University, Dallas, 341 pp.

Harry, H.W. 1950. Studies on the nomarine Mollusca of the Yucatan. Occasional Papers of the Museum of Zollogy, No. 524. University of Michigan, Ann Arbor, 34 pp.

Hayes, D.M., R.L. Minton, and K.E. Perez. 2007. *Elimia comalensis* (Gastropoda: Pleuroceridae) from the Edwards Plateau, Texas: multiple unrecognized endemics or native exotic? The American Midland Naturalist 158: 97–112.

Heller, J., P. Mordan, F. Ben-Ami, and N. Sivan. 2005. Conchometrics, systematics and distribution of *Melanopsis* (Mollusca: Gastropoda) in the Levant. Zoological Journal of the Linnean Society 144: 229–260.

Hubricht, L. 1983. The genus *Praticolella* in Texas (Polygyridae: Pulmonata). The Veliger 25: 244–250.

Hubricht, L. 1984. Hybridization in the land snails of Eastern United States. Gastropodia 2(2), 20; 2(3), 21.

Johnson, M.S. 1980. Association of shell banding and habitat in a colony of the land snail *Theba pisana*. Heredity 45: 7–14.

Master, L.L. 1991. Assessing threats and setting priorities for conservation. Conservation Biology 5: 559–563.

Moricand, S. 1833. Note sur quelques espèces nouvelles de coquilles terrestres. Mémoires de la Societé Physique et d'Histoire Naturelle, Genève, 6: 537.

NatureServe. 2005. NatureServe Explorer: an online encyclopedia of life [web application]. Version 4.4. Available at http://www.natureserve.org/explorer.

Neck, R.W. 1977. Geographical range of *Praticolella griseola* (Polygyridae): correction and analysis. The Nautilus 91: 1–4.

Neck, R.W. 1990. Ecological analysis of the living mollusks of the Texas panhandle. American Malacological Bulletin 8: 9–18.

Palumbi, S.R., A.P. Martin, S. Romano, W.O. McMillan, L. Stice, and G. Grabowski. 1991. The Simple Fool's Guide to PCR. Special Publication of the Department of Zoology, University of Hawaii, Honolulu, 45 pp.

Perez, K.E., W.F. Ponder, D.J. Colgan, S.A. Clark and C. Lydeard. 2005. Molecular phylogeny and biogeography of spring-associated Hydrobiid snails of the Great Artesian Basin, Australia. Molecular Phylogenetics and Evolution 34: 545–556.

Pfeiffer, L. 1841. Symbolae ad Historiam Heliceorum. I. Casselis, 100 pp.

Pfeiffer, L. 1848. Monographia heliceorum viventium. I. E. A. Brockhaus, Leipzig, 484 pp.

Pfeiffer, L. 1866. Beschreibung neuer Landschnecken. Malakozoologische Blätter 13: 78.

Pfenninger, M. and F. Magnin. 2001. Phenotypic evolution and hidden speciation in *Candidula unifasciata* ssp. (Helicellinae, Gastropoda) inferred by 16S variation and quantitative shell traits. Molecular Ecology 10: 2541–2554.

Pilsbry, H.A. 1891. Land and Fresh-water Mollusks Collected in Yucatan and Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 43: 310–314.

Pilsbry, H.A. 1899. Descriptions of new species of Mexican land and freshwater mollusks. Proceedings of the Academy of Natural Science of Philadelphia 51: 391–402.

Pilsbry, H.A. and J.H. Ferriss. 1906. Mollusca of the southwestern states. Proceedings of the Academy of Natural Sciences of Philadelphia 58: 125–126.

Pilsbry, H.A. 1930. Anatomy and relationships of some American Helicidae and Polygyridae. Proceedings of the Academy of Natural Sciences of Philadelphia 82: 310–321.

Pilsbry, H.A. 1940. Land Mollusca of North America (north of Mexico). Vol I, Part 2. Academy of Natural Sciences of Philadelphia, 994 pp.

Pritzel, G. 1864. Einige Berichtigungen za den Materialien zu cinem Verzeichuiss der jetzt lebenden botanischen Schriftsteller. (Linnaea Bd. XIX. Heft 2. p. 146–192). Linnaea 19: 447–464.

Rehder, H.A. 1966. The non-marine mollusks of Quintana Roo, Mexico with the description of a new species of *Drymaeus* (Pulmonata: Bulimulidae). Proceedings of the Biological Society of Washington 79: 273–296.

Robinson, D.G. 1999. Alien invasions: the effects of the global economy on nonmarine gastropod introductions into the United States. Malacologia 41: 413–438.

Rohlf, F.J. 2001. Tps Dig 1.37. Department of Ecology and Evolution, State University of New York, Stony Brook, NY. Available from Stonybrook Morphometrics: http://life.bio.sunysb.edu/morph/.

Sheets, H.D. 2003. Integrated Morphometrics package (IMP). Software distributed by the author at www2.canisius.edu/∼sheets/morphsoft.html.

Singley, J.A. 1893. A preliminary list of the land, fresh-water, and marine Mollusca of Texas. Fourth Annual Report Geological Survey of Texas. Contributions to the Natural History of Texas. Part 1: 299–343.

Strebel, H. and G. Pfeiffer. 1880. Beitrag zur Kenntniss der Fauna mexikanischer Land- und Süsswasser-Conchylien. J. J. Kerbst, Hamburg, 144 pp.

Tanaka, M.O. and R.C. Maia. 2006. Shell morphological variation of *Littorina angulifera* among and within mangroves in NE Brazil. Hydrobiologia 559: 193–202.

Vanatta, E.G. 1915. A revision of the genus *Praticolella* von Martens 1892. Proceedings of the Academy of Natural Sciences of Philadelphia 67: 197–210.

von Martens, E. 1890–1901. Biologia Centrali-Americana. R.H. Porter, and Dulau and Co., London, 706 pp.

Webb, G.R. 1967. Erotology of three species of *Praticolella*, and of *Polygyra pustula*. The Nautilus 80: 133–140.

Zelditch, M.L., D.L. Swiderski, H.D. Sheets and W.L. Fink. 2004. Geometric morphometrics for biologists: a primer. Elsevier Academic Press, San Diego, 443 pp.

Zwickl, D.J. 2006. Garli: Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion, The University of Texas at Austin. Available from: http://garli.googlecode.com/.