LIFE HISTORY TRAITS OF THE PERFORATE DOME SNAIL, *VENTRIDENS DEMISSUS* (BINNEY, 1843) (GASTROPODA: ZONITIDAE), FROM SEABROOK, TEXAS

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Abstract.–*Ventridens demissus* is one of over 2,000 species of land snail in the United States and Canada. Like other zonitid snails, the species is small (10 mm in width) with a thin shell; its distribution ranges from the Appalachians to the southwestern Gulf Coast. Like many land snails, little is known about the biology of *V. demissus*, and its conservation status remains unstudied. Using a population from Seabrook, Texas, the morphology, reproductive behavior, and gut microbes of *V. demissus* were described in order to broaden the understanding of this land snail species' life history. Shell morphology data were consistent with those reported previously, while the mean shell required 4.6 N to crush. Reproductive behavior was witnessed between a single pair of individuals, who simultaneously probed one another with their dart apparatuses. In the laboratory, *V. demissus* laid over 300 small (1.5 mm) eggs, and the growth of twenty hatchlings was followed for at least ten weeks. Gut microbes were dominated by *Mycoplasma*, *Paenibacillus*, and enteric groups. These data fill in existing gaps regarding the biology of *V. demissus*. Future studies on the species should include additional populations from across its range, controlled breeding and rearing experiments, and finer-scaled microbial analysis to distinguish between natural gut flora and ingested microbes.

Keywords: terrestrial, life history, morphology, reproduction, land snail, microbiome

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Land snails represent a diverse and threatened fauna in the United States and Canada. Over 2,100 species are known to occur, and 48% of them have heritage ranks of GX-G3 (extinct through vulnerable; NatureServe 2018). The biology and natural history of land snails also remain under-studied, especially when compared to knowledge on their distribution. These data gaps are unfortunate given that land snails are ecological indicator species (Prezio et al. 1999), contribute to nutrient cycling and food webs (Mason 1970), and aid in floral dispersal (Gervais et al. 1998).

Recommended citation:
Medellin, A.A. & R.L. Minton. 2019. Life history traits of the perforate dome snail, *Ventridens demissus* (Binney, 1843) (Gastropoda: Zonitidae), from Seabrook, Texas. Texas J. Sci. 71: Article 1. https://doi.org/10.32011/txjsci_71_1_Article1.

One poorly understood land snail family is Zonitidae, comprising 13 genera and 198 species in the United States (NatureServe 2018). The genus *Ventridens* contains small, thin-shelled zonitid species. The perforate dome snail, *Ventridens demissus* (Binney 1843), is described as having a depressed convex shell, yellowish-brown in color, with an impressed suture and transverse (greatest diameter at a right angle to the spiral axis) aperture (Fig. 1). Binney also noted a white deposit within the shell, which Pilsbry (1946) later noted was limited to adults. Pilsbry also reported that *V. demissus* shells varied up to 10.4 mm in width, 6.8 mm in height, and with 7.5 whorls. Hubricht (1985) gave the range of *V. demissus* as the western half of the Appalachian slope from Pennsylvania to Alabama, and the Gulf Coast from western Florida to northeastern Texas (Fig. 2 inset). Like other *Ventridens* species, little is known about the biology of *V. demissus*. Egg laying was described by Ingram (1944) in the congeneric species *V. intertextus*; eggs were approximately 2 mm in diameter, and one egg laid in the laboratory did not contain an embryo. Bergey et al. (2014) encountered *V. demissus* as a non-native species transported through plant nurseries in Oklahoma, and Davis-Berg (2011) reported it as a possible prey species for *Euglandina rosea*. Stockdale Walden et al. (2017) reported it as a host for the parasitic nematode *Angiostrongylus cantonesis*, a common cause of eosinophilic meningitis (Murphy & Johnson 2013). In an effort to better understand the biology of *V. demissus*, a variety of physical and reproductive traits from a population in Seabrook, Texas were assessed in the laboratory.

MATERIALS & METHODS

Snails were collected from three urban parks in Seabrook, Texas (Fig. 2): Seabrook Wildlife Park (29.584736º N 95.0066871º W); Robinson Park (29.5875257º N 95.0003034º W); and Pine Gully Park (29.5914033º N 94.9960234º W). Although collected separately, all snails were treated as a single population due to proximity and

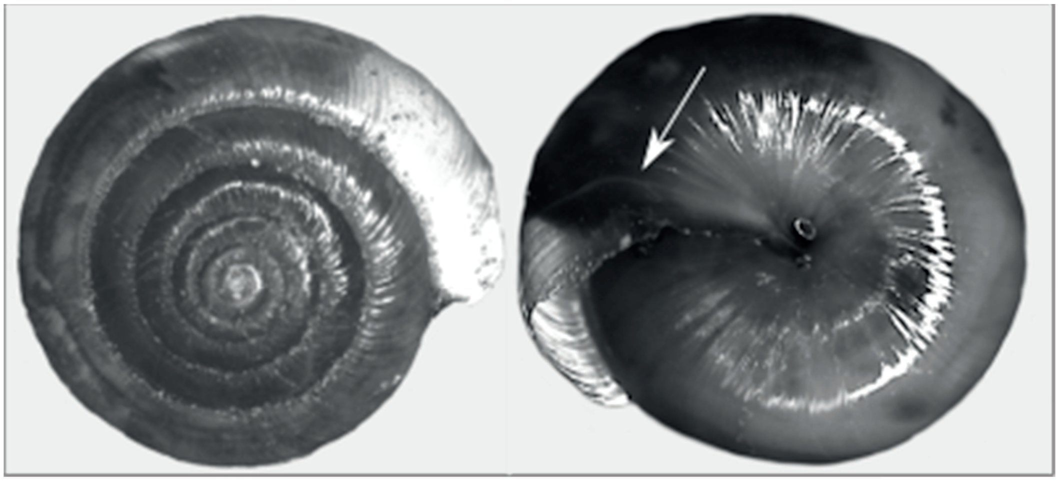


Figure 1. Shell of *V*. *demissus* from Seabrook, TX. The internal white deposit is indicated by the arrow.

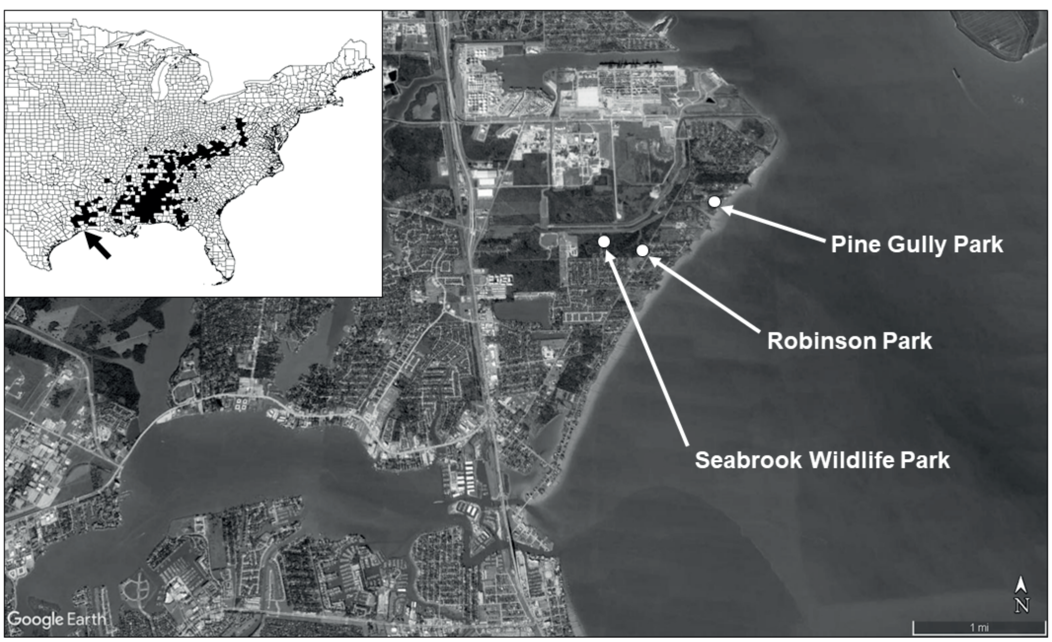


Figure 2. Map of the three collection sites in Seabrook. A distribution map for *V. demissus* based on Hubricht (1985; filled counties). The black arrow indicates the location of Seabrook.

because the parks are connected to one another by the Pine Gully floodplain. Dominant vegetation at the collection sites was post oak (*Quercus stellata*), loblolly pine (*Pinus taeda*), yaupon holly (*Ilex vomitoria*), cedar elm (*Ulmus crassifolia*), and winged elm (*U. alata*). Large trees shaded the collection site with an estimated 90-100% canopy cover, allowing very little light to the ground underneath. The average temperature in Seabrook was 21.7º C at time of morning collection in May 2017.

Shell height and shell width to the nearest 0.01 mm were recorded from 150 live *V. demissus* specimens using digital calipers. The straight-line distance from the edge of the aperture to the anterior edge of the white deposit in the shell was also recorded to the nearest 0.01 mm. Whorl count was determined following Burch (1962) under a dissection microscope. Height, width, and whorl count were tested for normality using a Shapiro-Wilk test (Shapiro & Wilk 1965) and unimodality using Hartigan's dip test (Hartigan & Hartigan 1985). Linear regression was used to correlate shell height and width, shell width and whorl count, and shell width and distance to the white deposit. All calculations were performed in PAST (Hammer et al. 2001), except Hartigan's dip test which was performed in the diptest package for R (Maechler 2016).

To determine shell strength, each of 20 empty *V. demissus* shells was placed umbilicus down on a metal plate, and a top plate was pressed on the shell apex. A Mark-10 series 5 force gauge mounted on an ESM303 motorized test stand was used to measure the force required to cause shell failure to the nearest 0.1 N. Force data were recorded every 0.1 sec until first shell failure. Linear regression was used to determine the relationship between shell width and strength.

Thirty live *V. demissus* were placed in each of six plastic aquaria filled with 5 cm of substrate (soil, twigs, leaves) from Pine Gully Park. Snails were fed commercially available salad mix with mushrooms and were misted daily to maintain moisture. One mating and one occurrence of egg-laying were observed while checking the aquaria for eggs. A total of 321 *V. demissus* eggs were collected across all aquaria, and the width of each egg was measured with digital calipers to the nearest 0.01 mm. Eggs that hatched were placed into a seventh aquarium and maintained as before. Hatchling growth was determined by measuring shell width using digital calipers over a 21-week period. Snails hatched within the same week were used a starting cohort and were measured every week.

Snail gut microbial content was assessed using five *V. demissus* collected live and immediately frozen at -20º C. Shells were gently cracked and the digestive tracts were dissected out from each snail. Genomic DNA was extracted from gut tissues using the MoBio PowerSoil kit and sent to MrDNALab (Shallowater, TX) for amplification and sequencing. The V4 region of the 16S rRNA gene was amplified by PCR with the 515/806 primer pair of Caporaso et al. (2011). Amplicons were sequenced on an Ion Torrent PGM following manufacturer's guidelines. Sequences were depleted of barcodes and primers, then sequences less than 150 bp were removed, as were chimeras and sequences with ambiguous base calls and with homopolymer runs exceeding 6 bp. The SILVAngs pipeline (http://www.arb-silva.de/ngs; Quast et al. 2013; Yilmaz et al. 2014; Glöckner et al. 2017) was used to generate operational taxonomic units (OTUs) at 97% similarity from the assembled reads and classify the OTUs taxonomically. Once dominant microbial taxa were identified, BLAST (Altschul et al. 1990) was used to identify sequences from close relatives and representative known organisms.

Results

Mean measurements for *V. demissus* shells were 5.66 mm ± 0.69 mm height, 8.19 mm ± 0.71 mm width, and 5.0 ± 0.5 whorls; distribution histograms for each measure are shown in Figure 3. None of the measures were normally distributed (Shapiro-Wilk test, $P<0.05$) nor unimodal (Hartigan's dip test, 10,000 replicates, $P<0.05$). Shell width was significantly positively correlated with shell height

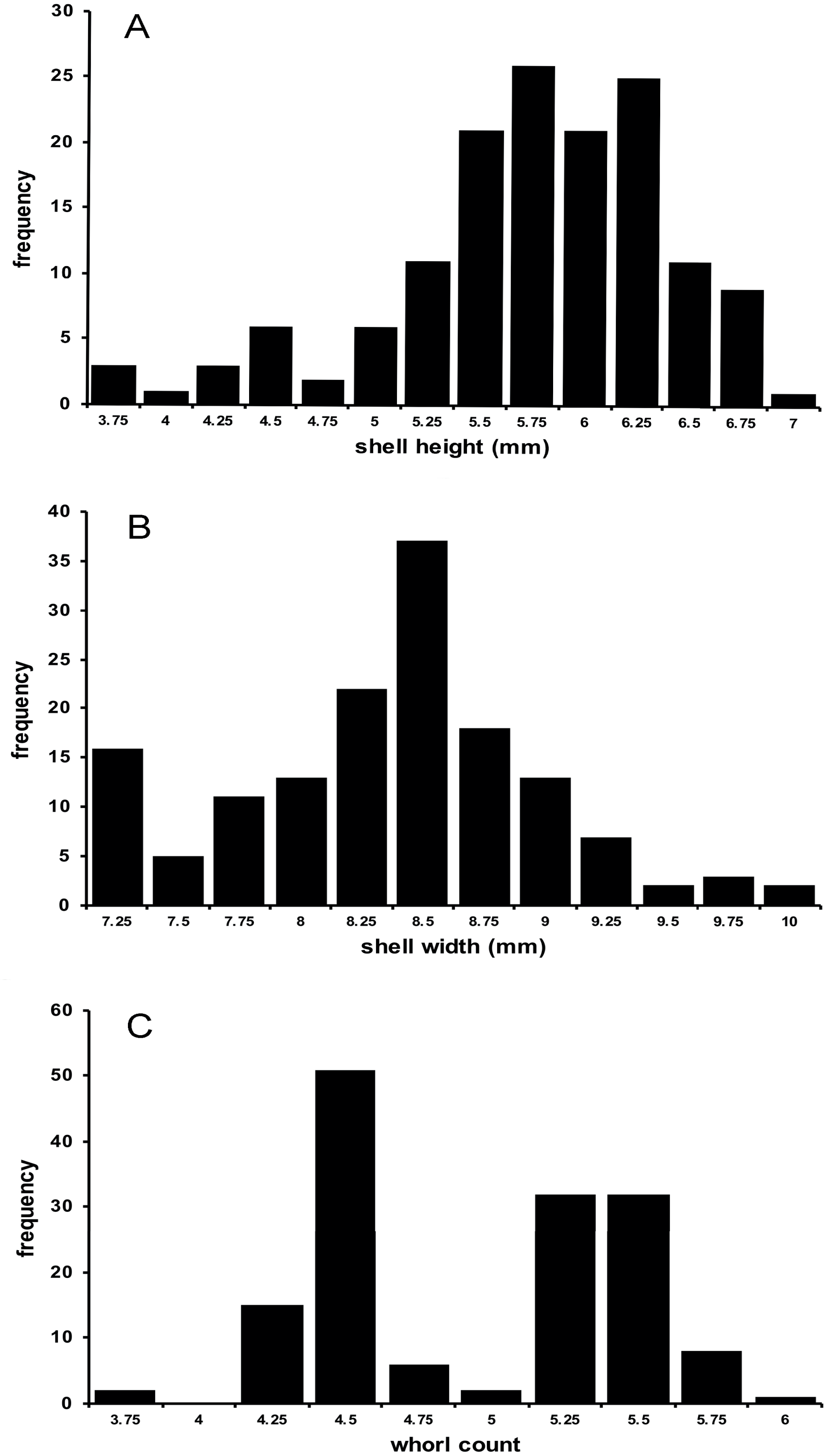


Figure 3. Histograms of shell heights (A), shell widths (B), and whorl counts (C) from 150 Seabrook *V. demissus*.

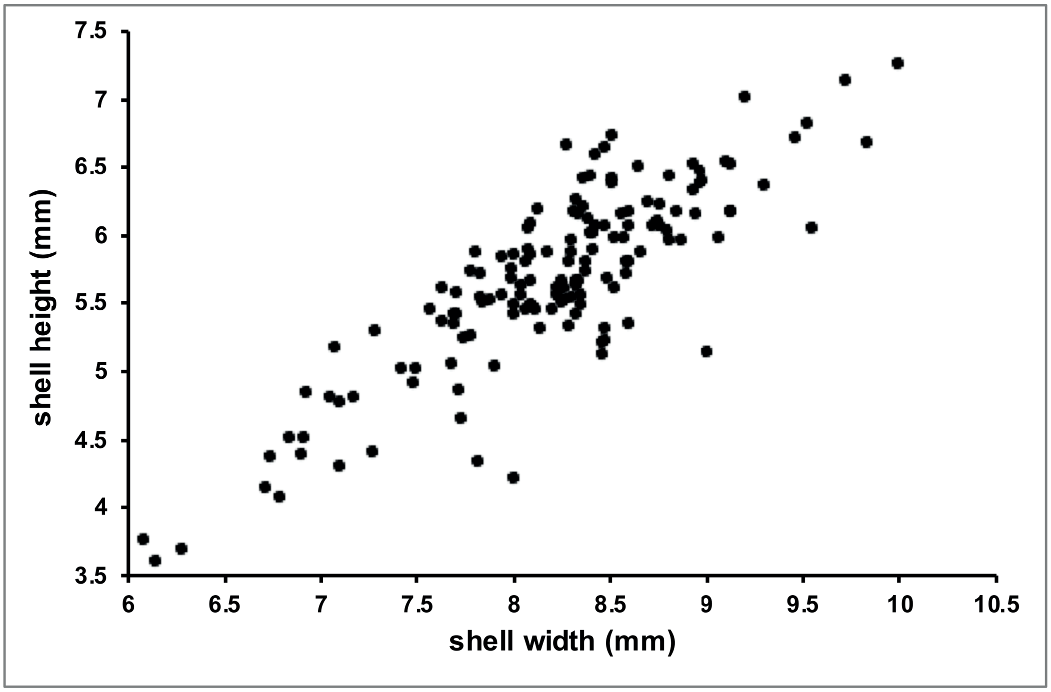
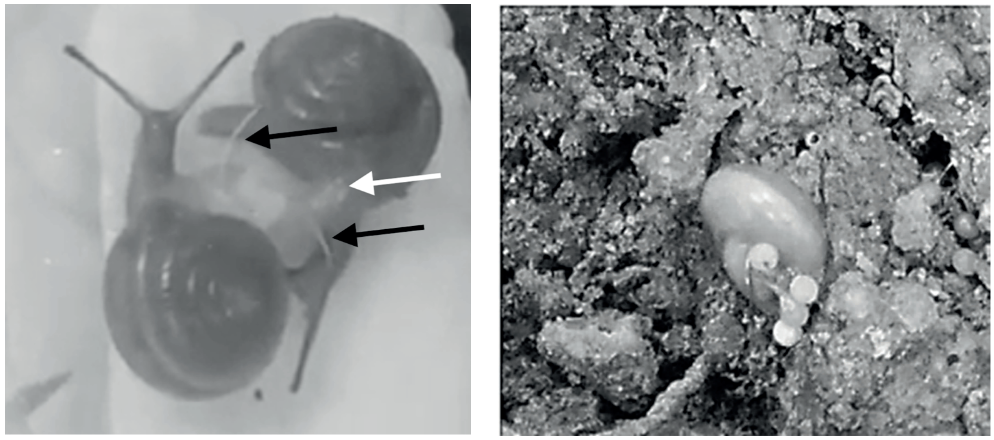


Figure 4. Scatterplot of shell heights versus shell widths from 150 Seabrook *V. demissus*.

(R^2 = 0.73, P<0.05; Fig. 4) and whorl count (R^2 = 0.18, P<0.05) but not significantly correlated with white deposit distance (P=0.53). Mean shell crushing strength was 4.6 N ± 2.5 N. Shell strength was not significantly correlated with shell width (P=0.32).

One incident of *V. demissus* mating in the laboratory was observed (posted on YouTube, https://youtu.be/cat3DNqtCd0). Two individuals were situated facing opposite directions with their feet touching. The dart apparatus of each individual appeared as a thin white structure that repeatedly retracted and extended; the apparatus of one snail (left in figure) made contact with the other (right in figure, Fig. 5a). Both snails utilized their dart apparatuses concurrently; the contacted snail (right in figure) may have extended its penis. This behavior continued for at least 15 minutes at which point we continued to gather other data. A single incidence of egg-laying was also observed in the aquaria (Fig. 5b). One individual was positioned aperture up, and four eggs were laid while we observed. Other eggs had been laid recently,



(A) (B)

Figure 5. (A) Still frame from the mating behavior video between two individuals *V. demissus*. The dart apparatuses can be seen as thin white structures (black arrows); the penis of the snail on the right may be also be visible (white arrow). (B) Egg-laying behavior in *V. demissus*. Other eggs are visible at the right.

but it could not be determined if they came from the individual being observed.

A total of 321 *V. demissus* eggs were laid in the aquaria; average egg width was 1.53 mm ± 0.12 mm (Fig. 6). Eggs were white and spherical with a slightly granular appearance. Twenty eggs ultimately hatched and the hatchlings had a mean shell width of 1.6 mm. All hatchlings survived six weeks; one each died in weeks seven, nine, and ten. In week eleven, 14 of the remaining 17 hatchlings died, with the remaining three hatchlings dying in week 15 (one) and week 21 (two). Growth rate of the hatchlings between weeks one and ten was (0.0185) (week number) + 1.61 mm. No snails reached adult size as defined by the presence of the white deposit inside the shell.

Rarefaction of OTU count versus number of reads suggested that the microbial diversity in *V. demissus* guts was not adequately sampled with five individuals (Fig. 7). Nine bacterial groups comprised 91.1% of all bacteria present in the gut samples (Table 1). *Mycoplasma* spp. were the most abundant microbial group at 52.1%

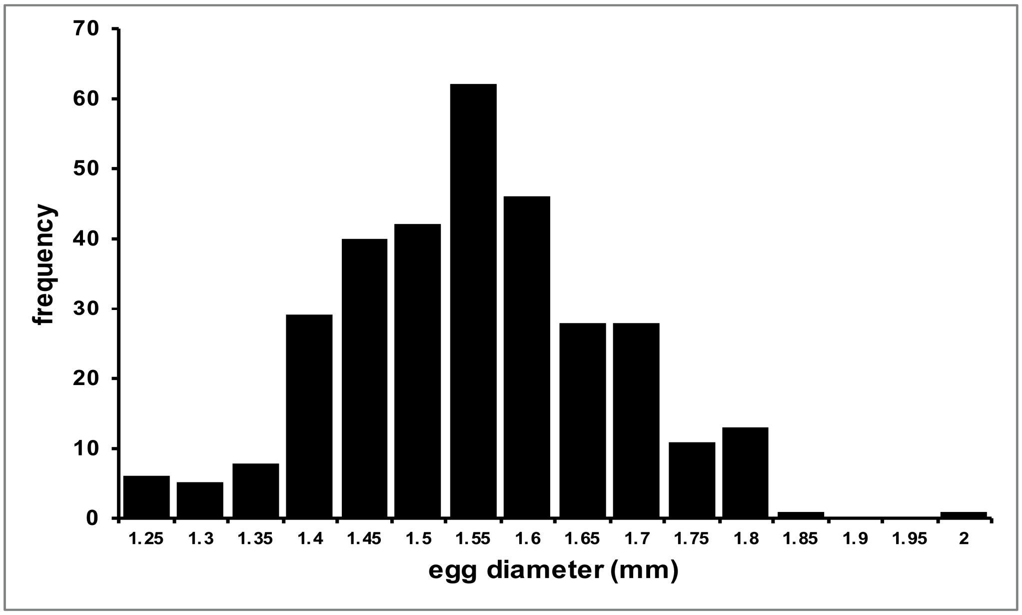


Figure 6. Histogram of egg diameters taken from 321 Seabrook *V. demissus* eggs.

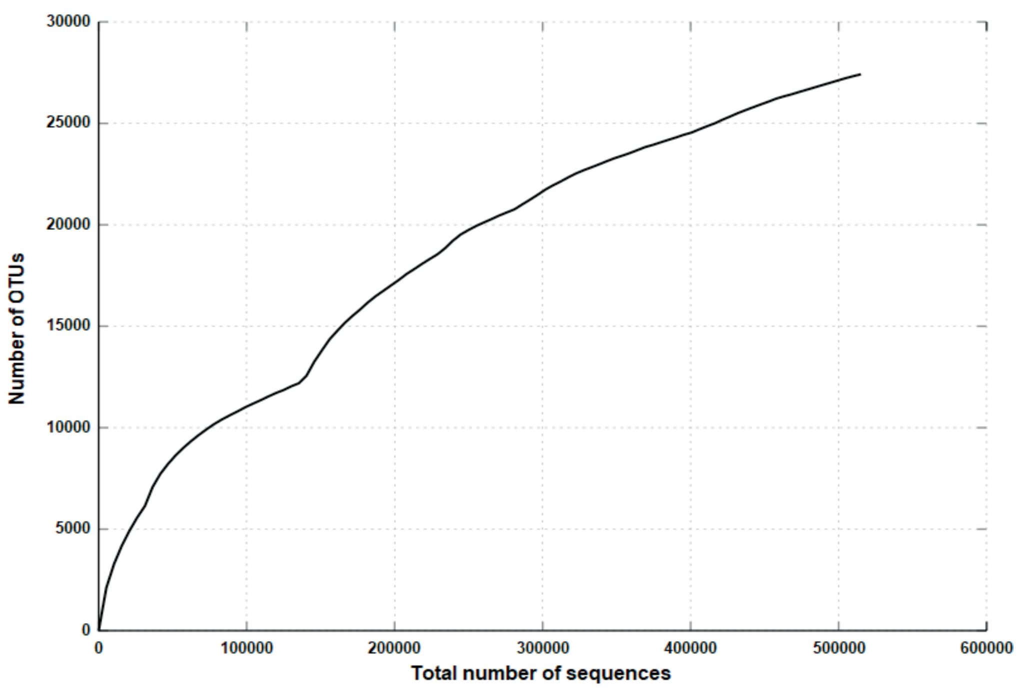


Figure 7. Microbial rarefaction curve of number of OTUs versus number of reads derived from five *V. demissus* gut samples.

Table 1. Bacterial groups present in *V. demissus* guts at abundances greater than 1%. Classification is based on SILVAngs results. BLAST results are comparisons to Genbank; asterisks (*) indicate equally best matches to ≥ 50 separate accessions.

Bacterial taxon	Total diversity (%)	Best BLAST match
Mycoplasma	52.1	FJ228920, uncultured OTU JN211307, uncultured OTU
Paenibacillus	10.7	JN530064, uncultured OTU
uncultured Simkaniaceae	10.4	AF364579, uncultured Chlamydiales
Enterobacter	8.9	*
Rosenbergiella	2.6	*
Klebsiella	2.3	*
Buttiauxela	1.6	*
Raoultella	1.4	KU724411, *Klebsiella pneumoniae* JQ407548, uncultured OTU
uncultured Spirochaetes	1.1	PopSet 253768011, uncultured OTUs
Other	8.9	n/a

of the total bacterial diversity. The best BLAST matches to the SILVAngs-identified OTUs present at ≥ 1% are also listed in Table 1.

Discussion

Ventridens demissus is a widespread zonitid species along the Appalachian slope and Gulf Coast of the United States (Hubricht 1985). To better understand the species, morphological, reproductive, and microbial data from populations at the extreme southwest edge of its distribution were gathered. Shell measurements of Seabrook *V. demissus* were consistent with those reported by Pilsbry (1946) from other states. No specimens with outer basal lamina were found, suggesting all of the shells used represented adults (Pilsbry 1946). Variation in land snail shell size and shape is a well-known phenomenon with a plethora of possible causes (see Goodfriend 1986 and references therein). Land snails are known to occupy and utilize microhabitats differently which can lead to distribution and morphological differences (Hazel & Johnson 1990; Chang & Emlen 1993), as can water and thermal regulation (Cowie & Jones 1985; Cook 2001; Pfenninger et al. 2005). The four measures assessed were neither normally distributed nor unimodal, suggesting intrapopulation variation or multiple age classes. Specific tests for factors known to affect shell variability were not performed.

Authors have long recognized the fragility of Zonitidae shells ("glass shells," Blanford & Godwin-Austen 1908; Cooke 1921). A shell crushing strength of 4.6 N was measured in *V. demissus*, at least one order of magnitude less than that observed in *Cepaea nemoralis* (Jordaens et al. 2006) and the genus *Cerion* (Quensen & Woodruff 1997). In land snails, predation is believed to strongly influence shell thickness and ornamentation (Woodruff 1978; Liew & Schilthuizen 2014). Zonitid snails like *V. demissus* are frequently preyed on by aperture-entering malacophagous snails, insects, and worms (Barker 2004 and references therein). This would lessen the utility of a crush-resistant shell (e.g., *Cerion*) and the investment of resources to construct one.

Reproductive behavior was documented in one mating pair of *V. demissus*. Two individuals were observed facing opposite directions, feet touching, utilizing their dart apparatuses. Body position during reproduction may vary between *Ventridens* species. Davison and Mordan (2007) reported that *Ventridens* mate face-to-face simultaneously. However, Webb (1948) noted that one individual mounted the shell of the other in *V. ligera*, while individuals followed one another head-to-tail in *V. suppressus.* These differences between *Ventridens* species may result from shell differences. For example, *V. ligera* is more globose than *V. demissus*, while *V. suppressus* frequently has apertural teeth (Pilsbry 1946). Both individuals of *V. demissus* extended their darts concurrently during observation. Webb (1948) described this behavior as part of courtship, but did not indicate whether it was reciprocal or not as he described the behavior of a single snail. The dart from one snail made contact with the other snail's body, and the penis of the contacted snail appeared to extend. These observations were consistent with those made by Webb (1948), who noted that dart probing in *Ventridens* species served to stimulate extension of the penial lobe. Neither penial contact nor spermatophore transfer was observed. Sperm exchange in *V. demissus* is expected to be similar to that seen in other *Ventridens* species (Webb 1948).

In the aquaria, *V. demissus* laid eggs that were approximately 1.5 mm in diameter. This was smaller than the 2–2.25 mm size Ingram (1944) reported for *V. intertextus*. Twenty of the 321 eggs discovered hatched, for a 6.2% hatching success rate. This was much lower than reported laboratory hatching success rates for other land snails including *Archachatina marginata* (30-82% success, Agbelusi & Adeparusi 1999), *Punctum pygmaeum* (66%, Baur 1989), and *Succinea putris* (53%, Dillen et al. 2009). Ingram (1944) reported that *V. intertextus* laid empty eggs in a lab setting. *Ventridens demissus* may also lay empty eggs, and it is unclear how many of the eggs laid in the aquaria were potentially viable. Hatchling growth was relatively constant for the ten weeks it was calculated for. Environmental variables including calcium availability (Beeby & Richmond 2007) and temperature (Benbellil-Tafoughalt & Koene 2015) can affect land snail shell growth rates. The week 10 die-off may have been natural, a result of laboratory rearing (e.g., wrong substrate, insufficient food quality), or a result of desiccation. Hurricane Harvey affected Houston during week 10, and the snails went without food or water during that time.

The diversity and abundance of gut microbes in *V. demissus* suggested that the most abundant bacterial group was *Mycoplasma* spp. This was noteworthy since *Mycoplasma* is rarely reported from non-vertebrates (Dupperon et al. 2013). Aronson et al. (2017) reported *Mycoplasma* as the dominant bacterial genus in a deep-sea snail, with close similarity to sequences derived from cultured abalone. The *Mycoplasma* sequences taken from *V. demissus* were most similar to uncultured taxa taken from freshwater (*Biomphalaria*, Genbank FJ228920) and terrestrial (*Achatina*, Genbank JN211307) snail gut samples and not similar to any human pathogens. Simkaniaceae, like *Mycoplasma*, are parasitic organisms, and *Paenibacillus* are common soil and plant bacteria and were likely ingested by the snails as opposed to being part of the normal gut flora (Everett et al. 1999;

Grady et al. 2016). Many members of Enterbacteriaceae that are common gut flora (*Enterobacter*, *Rosenbergiella*, *Klebsiella*, *Buttiauxela*) were also identified, though *Raoultella* was likely ingested (Dar et al. 2017).

While we provided descriptive data on the biology and life history of *V. demissus*, more work is needed to fully understand the species. Future investigations should include additional samples from across its distribution, as land snail populations frequently show localized adaptation (Baur & Raboud 1988). More thorough sampling will also show the frequency of shape and size variables in young and adult shells, and whether any geographical patterns exist. Growth series, studied from hatching through adulthood, will suggest when snail growth occurs and at what rate. More thorough dissection combined with refined next-generation sequencing methods may distinguish between enteric gut microbes and those which are ingested (Cardoso et al. 2012), giving insight into the diet of *V. demissus*.

Acknowledgments

We thank Phillip Harris, Cynthia Howard, and Kathryn Perez for constructive criticism on improving the manuscript. We also thank Taylor Perez for assistance in the lab, and Lea Fellman for providing specimens and locality information. The authors were supported in part by the Department of Biological and Environmental Sciences and the College of Science and Computer Engineering at UHCL.

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