THE ECOLOGICAL STATUS OF THE CARINATE PILLSNAIL

EUCHEMOTREMA HUBRICHTI

FINAL REPORT

A project funded in part by the Illinois Department of Natural Resources Wildlife Preservation Fund (Grant Number 01-042W)

Dr. Frank E. Anderson

Department of Zoology, Southern Illinois University, Carbondale, IL 62901

INTRODUCTION

The carinate pillsnail *Euchemotrema hubrichti* (Gastropoda: Polygyridae; slides) is a small, poorly known species of terrestrial snail known only from the limestone bluffs of the Larue-Pine Hills Ecological Area and southwestern Jackson County, Illinois. The species was listed as a Category 2 species by the United States Fish and Wildlife Service (USFWS) until the category was abolished. Category 2 status was used for taxa that the USFWS believed might be endangered or threatened, but for which persuasive data on biological vulnerability and threat were not available. The USFWS also used the Category 2 listing to encourage necessary research on vulnerability, taxonomy, and/or threats for the listed taxa.

The status of *Euchemotrema hubrichti* remains unresolved. The species was first described as a Pleistocene fossil and placed in the genus *Stenotrema* by Pilsbry (1939). At that time, no live *E. hubrichti* individuals had been found—only shells were known from the Pine Hills area. Pilsbry called the species a "spectacular find", as it was the only known carinate (keeled) member of the *monodon* group of polygyrid snails. Little work has been done on *E. hubrichti* since Pilsbry's initial description, although the species is figured in Burch (1962) and live snails have since been found by J. Slapcinsky (formerly at the Field Museum of Natural History) and M. Hutchison (formerly at the Nature Conservancy, Ullin, Illinois) (pers. comm.). Emberton (1995a), in his revision of polygyrid snail taxonomy and phylogeny, reclassified the species as *Euchemotrema hubrichti*. No detailed studies have been published on the distribution or ecology of the species, despite its possible threatened status.

This project has begun to address some of these issues. The initial phase of the project consisted of searches in the Larue-Pine Hills Ecological Area and nearby areas for both live *E. hubrichti* individuals and shells. Live snails were occasionally encountered at several sites along the large limestone bluff at Larue-Pine Hills, but neither live snails nor shells were found in other areas. Relatively high numbers of *E. hubrichti* were found in two areas at Larue-Pine Hills. Several snails were collected from these areas and returned to the laboratory for behavioral studies. Initial observations suggested that there might be differences in behavior between *E. hubrichti* and the other land snails found at these-sites. In particular, it appeared that *E. hubrichti* were more negatively geotactic, and may spend more time estivating. To address these questions, a behavioral experiment was begun and preliminary data have been collected suggesting that *E. hubrichti* may differ behaviorally from at least one other sympatric land snail. In the third phase of the study, a mark-recapture experiment was initiated to estimate *E. hubrichti* population sizes.

Project Objectives

1. To survey several habitats in southern Illinois (particularly the Larue-Pine Hills Ecological Area) for *E. hubrichti* shells and live individuals.

2. To maintain live *E. hubrichti* in the lab to study behavior and (if possible) mating and egg laying.

3. To perform laboratory-based comparative behavioral experiments between *E*. *hubrichti* and other land snail species that are sympatric with *E*. *hubrichti*.

4. To determine habitat preference and approximate abundance of *E. hubrichti* via surveys and mark-recapture experiments.

MATERIALS AND METHODS

All of the following experiments and surveys were carried out with the assistance of two undergraduate students and one graduate student in my laboratory.

Initial surveys: Several sites in southwestern Illinois were surveyed for live snails and shells. Sites with known limestone outcroppings were of particular interest. Most survey work was undertaken on the large limestone bluff face in the Larue-Pine Hills Ecological Area (see enclosed slides)—the only known habitat of *E*. *hubrichti* at present. Other sites surveyed included Chalk Bluff (just south of Little Grand Canyon) and Horseshoe Bluff (see attached maps). Average size at reproductive maturity for this species was estimated via examination of empty shells and shells from live specimens (reproductively mature snails possess a recurved, thickened lip at the aperture of the shell).

Laboratory cultures: Two mature and three immature *E. hubrichti* were brought to my laboratory at Southern Illinois University, Carbondale. Snails were kept in a small covered glass terrarium with approximately two inches of potting soil covered with fragments of moss and limestone rocks from Larue-Pine Hills. Snails were maintained in a cold room at 60° F on a 12-hour light/12-hour dark

photoperiod under a daylight-spectrum bulb. Snails were checked periodically (every two-three days) to see what the snails were eating, if eggs had been laid, etc.

Comparative behavioral experimental design: Eight ten-gallon glass aquaria were stood upright and partitioned lengthwise into two equal-volume chambers by fine plastic mesh. The initial round of experiments was performed at room temperature (about 70 $^{\circ}$ F) under a 12-hour light/12-hour dark photoperiod. In the first round of comparisons, eight E. hubrichti individuals were compared with eight individuals of another snail species from the same habitat, Anguispira alternata. One snail was placed into the bottom of each half-tank chamber so that each tank contained one snail from each species (snails were randomly placed within each tank—for example, *E. hubrichti* could be either on the right or left—to avoid experimental artifacts). Each chamber was supplied with a plastic petri dish full of water to maintain humidity. The tanks were covered with standard hinged aquarium covers held in place by binder clips. In the initial trial, the location of each snail and the snail's status (e.g., out and active or retracted within the shell) was recorded every six hours (12 midnight, 6 a.m., 12 noon and 6 p.m.) for one week. Two questions were addressed using this experimental design. First, does E. hubrichti spend more time higher in the tank than A. anguispira (i.e., does it exhibit greater negative geotaxis than other species, as suggested by field and lab observations)? Second, does E. hubrichti spend more time withdrawn inside the shell than A. anguispira?

Mark-recapture/dispersal experiments: Euchemotrema hubrichti individuals were found in relatively high abundances at two sites at the Larue-Pine Hills Ecological Area in March 2001 (see below). At these sites, a mark-recapture experiment was initiated in late May 2000. An ultra-fine point permanent marker was used to mark all captured snails with a number on the underside of the shell (slides). The reproductive status (immature or mature) and maximum shell diameter and height were recorded for each snail prior to release. In mid-July 2000, these two sites were resurveyed. Unmarked individuals were marked, and encounters with marked individuals were recorded. At this time, an attempt to estimate average dispersal over time was also initiated. After individuals had been marked and returned to the habitat, the snail's number was written on the rock substrate in permanent marker. The Petersen method (as described in Krebs, 1989) was used to estimate population sizes in the initial phase of the study via the following equation:

$$\widehat{N} = \frac{(M+1)(C+1)}{R+1}$$

where M = the number of snails marked in the first sample, C = the total number of snails captured in the second sample and R = the number of snails in the second sample that are marked. This rather crude method was used because (at this point) only a single round of recaptures has been performed.

RESULTS TO DATE

Initial observations and distribution of <u>E</u>. <u>hubrichti</u>: Despite extensive searches at several sites in the Larue-Pine Hills Ecological Area and two other areas (Chalk

Bluff and Horseshoe Bluff), very few live snails were found. No live *E. hubrichti* or shells were found at either Chalk Bluff or Horseshoe Bluff. The first live *E. hubrichti* found (a total of four) were found on the north and west faces of a small outcropping near McCann Springs less than 2 meters above the ground (see attached maps). Several empty shells were also found at the base of the west face of this outcropping. Other species were found on the east side of the outcropping (facing the parking area), but *E. hubrichti* was only found on the north and west sides. Extensive surveys along the base of the large bluff at Larue-Pine Hills, and near the top of the bluff in several places yielded a few live *E. hubrichti* (generally only on open bluff faces), but overall, numbers were very low.

Relatively large numbers of *E. hubrichti* were only found at two sites in close proximity to one another ("Slope 1" and "Slope 2"; Table 1 and slides), and it was the most common land snail species encountered at these two sites. *E. hubrichti* individuals were mostly found under ledges and back in crevices within the bluff, as opposed to the open face of the bluff (slides). Five animals were collected from these areas for laboratory observation (see below). Overall, a total of thirty-eight unique individuals were found—by far the largest concentration seen during the course of this study.

All shells (both empty and from live snails) of less than 9.0 mm maximum shell diameter were reproductively immature (lacked a recurved lip at the aperture of the shell; slides). All shells but one above this size were mature (one shell from a live snail at Slope 2 measured approximately 9.0 mm and was beginning to form the recurved lip at the aperture of the shell). Burch (1962) noted that the width of the shells of *Stenotrema* (now *Euchemotrema*) *hubrichti* was "8.9-9.7 mm" for mature snails, closely matching our findings (although we have found several individuals larger than 10 mm shell width). Burch's description of the shells as "whitish" is, of course, in error—workers at that time only had empty shells to work with (on live snails the shells are dark brown to almost black). Incidentally, during the course of the mark-recapture study, one snail appeared to form the lip in less than two months, suggesting that the maturation process can come to completion rather quickly.

Laboratory cultures: Several *E. hubrichti* individuals were successfully maintained in the lab for several months, but no mating or egg-laying was observed. The captive *E. hubrichti* seemed to spend a great deal of time withdrawn into the shell and affixed on the top cover of the terrarium (much more so than other land snails that we were also observing in the laboratory).

Comparative behavioral experiments: Data on the *E. hubrichti* and *A. anguispira* individuals used in the first round of the comparative behavior experiment are shown in Table 2, and the results of the first week-long experiment are shown in Table 4. *E. hubrichti* snails spent more time near the tops of the chambers than *A. anguispira* in five of the replicates (Tanks 1-4 and 6), with the opposite occurring in two replicates (Tanks 7 and 8), and only a slight difference observed in one replicate (Tank 5). Although there appears to be some support for the hypothesis that *E. hubrichti* is more negatively geotactic than *A. anguispira*, it is probable that the results are not statistically significant (no statistical tests have yet been performed, due to the small number of replicates).

Estimates of <u>E</u>. <u>hubrichti</u> abundance at two sites: The number of individuals captured and marked in the first round, and the number of marked individuals recaptured, are shown in Table 3. The corrected Petersen method produces a population size estimate of 65 snails at Slope 1 and 52 snails at Slope 2. There was no evidence that any migration of individuals had occurred between these two sites.

DISCUSSION

The initial phases of the research were a success: live Euchemotrema hubrichti individuals were found (along with a plethora of empty shells) at various sites in the Larue-Pine Hills Ecological Area. Furthermore, at two sites surveyed (herein referred to as "Slope 1" and "Slope 2"), E. hubrichti was by far the most common land snail present (Table 1). E. hubrichti was not, however, found at any other sites surveyed in southwestern Illinois, including Chalk Bluff and Horseshoe Bluff. Though other potential sites remain to be examined, including sites in southeastern Missouri, it seems unlikely that E. hubrichti will be found at these sites, for two reasons. First, it seems likely that E. hubrichti, should it exist outside of the Larue-Pine Hills Ecological Area, will be found only in areas of exposed limestone, due to the requirement of calcium carbonate for shell production. Land snail diversity is generally much lower in sandstone bluff habitats than limestone bluffs (Hutchison, unpublished report), but exposed sandstone is much more common in southern Illinois than exposed limestone. Second, other researchers (Hutchison and Slapcinsky) have only found E. hubrichti in the Larue-Pine Hills region. Our preliminary surveys of other

regions have produced no evidence that *E*. *hubrichti* has lived in these regions recently.

It seems likely that pockets of (relatively) high *E. hubrichti* abundance exist scattered throughout the Larue-Pine Hills area that were not uncovered by our initial surveys. For example, J. Slapcinsky noted that he found several individuals "at the top of the bluff" (pers. comm.), but he was unclear about specific localities. We hope that future surveys in these areas will reveal other subpopulations of this species.

Pockets of relatively large *E. hubrichti* groups may provide some insight into the habitat preferences of this species. The two areas of high *E. hubrichti* abundance found at Slope 1 and Slope 2 were of a very particular character. Like most bluff faces in the Larue-Pine Hills area, Slope 1 and Slope 2 are shaded by trees and are largely covered with moss and lichens (slides). Unlike most regions on this bluff, however, the tops of the bluff are accessible at Slope 1 and Slope 2 by steep dirt slopes that run along the face of the limestone outcroppings. This made it particularly easy to explore the top of the face of the outcroppings in these areas. At this point, it is impossible to determine whether *E. hubrichti* actually prefer such specific habitats, or if *E. hubrichti* is instead very common along the outer bluff face at the tops of most outcroppings in the Larue-Pine Hills area (where these areas are shadowed and moss-covered). Unfortunately, studying the tops of several bluffs via rappelling or rock-climbing is beyond the scope of the current study, but could be incorporated into future work (assuming permits could be obtained).

Laboratory cultures of *E. hubrichti* were very robust and have survived throughout the duration of the research thus far. Unfortunately, no evidence of

mating or egg-laying was seen. Environmental cues are critical for timing of developmental changes and reproductive behavior in many animals, including invertebrates. In this respect, the laboratory habitat certainly is not ideal for these animals—uniform temperatures and day lengths in the cold room where the snails were housed probably removed any environmental cues for mating that may exist for these snails. In the future, we may attempt to keep snails in captivity at temperatures and photoperiods closer to ambient to try to elicit reproductive behavior. Observations of the captive snails did provide some insight into the behavior of these animals. First, E. hubrichti showed a tendency to spend a great deal of time withdrawn inside the shells and attached to the sides or cover of the terrarium. Other snail species (A. alternata, Polygyra albolabris and Triodopsis fosteri) were also maintained in a similar terrarium under similar conditions, but individuals of these species generally spent far less time withdrawn into their shells, and also spent less time on the sides or on the cover of the terrarium. These observations lead directly to the comparative behavior experiments (see below).

Initial results of the mark-recapture experiments suggest that although concentrations of *E. hubrichti* appear to be restricted to a few areas in the Larue-Pine Hills Ecological Area, these areas may harbor relatively large numbers of individuals. Admittedly, the mark-recapture techniques are crude and have produced a population size estimate that should be taken with extreme caution (it is likely an overestimate; Krebs, 1989), but they do seem to provide evidence of a "hidden" reservoir of *E. hubrichti* in certain regions (e.g., Slope 1 and Slope 2). This should not be especially surprising. These snails appear to spend a great deal of time estivating under ledges or in cracks on the bluff face. On any given

sampling trip (particularly when snails are not active), it is likely that most snails are out of reach within the bluff. The flattened lens shape of the *E. hubrichti* shell makes this even more feasible.

The initial round of comparative behavior experiments suggested that *E*. *hubrichti* may differ in one respect (geotaxis) from at least one other sympatric land snail species of similar size, *A. alternata* (Table 4), possibly bearing out preliminary field and lab observations. Unfortunately, at this point, far too few replicates of this experiment have been performed to find significant differences in behavior among species, if such differences exist. An undergraduate in my lab will be continuing this experiment throughout fall semester 2001 under a variety of experimental conditions as part of an undergraduate research project.

Behavioral comparisons between *E. hubrichti* and other sympatric land snail species are important for a variety of reasons. Behavioral differences could explain observed differences in preferred habitats between *E. hubrichti* and other species, and knowledge of such differences could be critical for conservation decisions. At first, *E. hubrichti* seems to be in an ideal conservation situation—the only known population(s) exist in or near a National Natural Landmark under the jurisdiction of the United States Forest Service. Hence, it seems unlikely that this snail will be seriously impacted by human activities. Management policies in the Larue-Pine Hills Ecological Area should take possible impacts on the longterm survival of *E. hubrichti* into consideration. Controlled burns in areas of the Larue-Pine Hills Ecological Area, for example, may only minimally disrupt other animals (and in fact may be important to the continued health of the community), but they may be devastating to a rare, patchily distributed land snail that is unable to respond to such an immediate threat (M. Hutchison, pers.

comm.). Understanding the underlying basis for the habitat preferences of *E*. *hubrichti* could be important for decisions regarding locations where controlled burns and other management actions should (or should not) take place. We hope that our future comparative behavioral laboratory studies, as well as continued field work, will provide information that will allow *E. hubrichti* to be maintained in the wild into perpetuity.

SUMMARY

We have demonstrated that *E. hubrichti* are relatively abundant in highly localized areas of the Larue-Pine Hills Ecological Area, and that this species can be found in low numbers along the face of the large limestone bluff in this area. Behavioral differences among species may account for the apparent preference of *E. hubrichti* for habitats near the tops of limestone outcroppings in this region (habitats that, with few exceptions, are extremely difficult for humans to study). Mark-recapture experiments suggest that at least two areas harbor relatively large populations of *E. hubrichti*, but further work is necessary to refine these estimates of population size.

PROSPECTUS

Each of the phases of the study described above are ongoing. Additional surveys of potential habitats will be performed along other bluff lines in southern Illinois (and perhaps southern Missouri), although it seems unlikely (given the negative findings thus far) that *E. hubrichti* will be found at other sites.

The mark-recapture and dispersal estimation experiments will be continued with regular sampling throughout the fall in an attempt to refine estimates of population size at the two localities. Finally, further behavioral studies will be done to compare E. hubrichti with two other common local species-Triodopsis fosteri and Polygyra albolabris-as well as A. anguispira. In particular, different test conditions will be used (e.g., inclusion of limestone substrate and/or moss) and additional replicates performed. This work will be performed as part of an undergraduate research project during fall semester 2001. Finally, the highly restricted nature of this species, and the presumed low levels of dispersal, seem to present an ideal situation for studying gene flow and phylogeography on a relatively tiny scale. Research of this sort with other land snails has demonstrated an astonishing amount of cryptic genetic diversity over very small spatial scales (Emberton, 1995b; Thomaz et al., 1996; Douris et al., 1998; Chiba, 1999). It is highly likely that *E. hubrichti* (and other species in the area) harbors such diversity. I am interested in pursuing this avenue of research in the future. Insights from such work, as well as the research already in progress, could be very useful for the development of conservation plans.

EXPENDITURES

Supplies

Field work: Film and film developing; topographic maps of Larue-Pine Hills region and nearby areas; flashlights (all other incidental expenditures—e.g., GIS equipment, notepads, camera with tripod, markers, collecting equipment—funded through SIUC internal funds and lab start-up money). *Behavioral experiments*: ten ten-gallon aquaria with covers for behavioral experiments; plastic mesh for dividing aquaria into chambers.

Travel

Ten round trips by car to Larue-Pine Hills from Carbondale (approximately 60 miles total per trip; total of 600 miles at 32.5 cents/mile).

Per diem expenditures

Ten days of per diem (\$28/day) for one graduate student (Alonso J. Córdoba).

Site	GPS coordinates	Total number of live snails found
McCann Springs	(not recorded)	4
Slope 1	37 [°] 33.700N, 89 [°] 26.465W	20
Slope 2	37 [°] 33.687N, 89 [°] 26.449W	18

Table 1. Localities and numbers of all groups (>1 individual) of live

Euchemotrema hubrichti snails discovered during the course of this research.

	Species	Α	Species B					
	Shell Diameter	Mature?	Shell Diameter	Mature?				
Tank 1	9.5	Y	10.8	N				
Tank 2	9.1	Ν	9.1	N				
Tank 3	8.6	Ν	9.3	Ν				
Tank 4	8.3	Ν	9	Ν				
Tank 5	10.2	Y	8.1	Ν				
Tank 6	8.6	Ν	8.1	N				
Tank 7	7	Ν	7.9	N				
Tank 8	7.9	Ν	9.6	Ν				

Table 2. Size and reproductive stage data for all individuals used in the comparative behavior experiment. Sexual maturity was determined by the presence of a recurved lip at the shell aperture; shell diameters are in millimeters.

Site	Number of snails captured/marked initially (M)	Number of snails captured in second round (C)	Number of marked snails recaptured in second round (R)	Estimated population size	
Slope 1	12	9	1	65	
Slope 2	7	12	1	52	

Table 3. Results of the initial round of mark-recapture experiments.

		Tank 1		Tank 2		Tank 3		Tank 4		Tank 5		Tank 6		Tank 7		Tank 8	
		Α	В	A	В	A	В	A	В	A	В	Α	В	Α	В	Α	В
Day 1	6 p.m.	15s	2s	42s	0s	19s	0s	50s	5s	0s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	15s	2s	42s	0s	19s	0s	50s	5s	0s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	5s	0s	0s	50s	0s	0s	50s	0s	29s
	12 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2a	0s	50s	0s	0s	50s	0s	29s
Day 2	6 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2.s	0s	50s	0s	0s	50s	0s	29s
Day 3	6 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
Day 4	6 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	1 2 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
Day 5	6 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	2s	0s	50s	0s	0s	50s	0s	29s
	12 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
Day 6	6 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	Os	0s	50s	0s	0s	50s	0s	29s
	12 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
Day 7	6 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
	12 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
	6 a.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s
	12 p.m.	50s	2s	42s	0s	19s	0s	50s	1s	0s	0s	50s	0s	0s	50s	0s	29s

Table 4. Activity budget data from initial experimental trial comparing *Euchemotrema hubrichti* (A) and *Anguispira alternata* (B). Data entries are XY; the snail's height in cm above the chamber bottom and <u>a</u>ctive or in <u>shell</u>.

LITERATURE CITED

Burch, J. B. 1962. <u>How to know the eastern land snails; pictured-key for</u> <u>determining the land snails of the United States occurring east of the Rocky</u> <u>Mountain Divide</u>. W. C. Brown Co., Dubuque, Iowa.

Chiba, S. 1999. Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: evidence from mitochondrial DNA sequences. Evolution 53:460-471.

Douris, V., R. A. D. Cameron, G. C. Rodakis, and R. Lecanidou. 1998. Mitochondrial phylogeography of the land snail *Albinaria* in Crete: long-term geological and short-term vicariance effects. Evolution 52:116-125.

Emberton, K. C. 1995a. When shells do not tell - 145-million years of evolution in North-America polygyrid land snails, with a revision and conservation priorities. Malacologia 37:69-109.

Emberton, K. C. 1995b. Cryptic, genetically extremely divergent polytypic, convergent and polymorphic taxa in Madagascan Tropidophora (Gastropoda: Pomatiasidae). Biological Journal of the Linnean Society 55:183-208.

Krebs, C. J. 1989. <u>Ecological methodology</u>. Harper & Row, New York, New York.

Pilsbry, H. A. 1939. Land Mollusca of North America (north of Mexico). Printed by the George W. Carpenter Fund for the Encouragement of Original Scientific Research, Philadelphia.

...

• •

. •

Thomaz, D., A. Guiller, and B. Clarke. 1996. Extreme divergence of mitochondrial DNA within species of pulmonate land snails. Proceedings of the Royal Society of London, Series B 263:363-368.

. .

















