MORPHOMETRIC ANALYSIS OF *CARYCHIUM EXILE* AND *CARYCHIUM EXIGUUM* IN THE GREAT LAKES REGION OF NORTH AMERICA

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Abstract *Statistical analyses were conducted on shell heights and widths of 5177* Carychium exile *and 1178* Carychium exiguum *individuals from 141 locations across a 1300 x 1000 km region centered on the North American Great Lakes. Both within co-occurrence sites, and between all sampled populations, the shell dimensions of these taxa were bimodally-distributed and statistically distinct. Thus,* C. exile *and* C. exiguum *are clearly separated and represent different species. Continuous latitudinal variation was observed in the shell size of both species, with largest individuals occurring in the north. In* C. exile, *these larger forms have often been referred to as* C. e. canadense. *Scanning Electron Micrographs of individuals from eight populations ranging from southern Illinois to northern Michigan to southern Ontario demonstrate that internal lamellae shape is too variable both within and between populations to be taxonomically useful. Analysis of the within population proportion of* C. e. exile, C. e. canadense, *and intermediate size classes demonstrate that most support individuals representing all three classes. Thus, the division of* C. exile *into distinct subspecies does not appear warranted.*

Key words Carychium exiguum, Carychium exile, Carychium exile canadense, *morphometrics, North America, systematics.*

INTRODUCTION

The genus *Carychium* Müller, 1774 comprises a group of minute terrestrial snails with highly elongated shells that occur in North America, Eurasia, the Caribbean, Indonesia, and the Philippines (Pilsbry 1948). Currently eight taxa are reported from eastern North America (Burch & Van Devender 1980, Hubricht 1985): *Carychium clappi* Hubricht, 1959; *Carychium exiguum* (Say, 1822); *Carychium exile* H.C. Lea 1842; *Carychium exile canadense* Clapp, 1906; *Carychium mexicanum* Pilsbry, 1891; *Carychium nannodes* Clapp, 1905; *Carychium riparium* Hubricht, 1978; and *Carychium stygium* Call, 1897.

As these species tend to not possess unique soft-body anatomies, conchological features are most often used for classification (Harry 1951, Burch & Van Devender 1980). Eastern North American taxa are generally distinguished by the degree of shell striation and size. Shell striation is lacking or weak in *C. exiguum, C. mexicanum, C. nannodes, C. riparium, C. stygium,* while *C. clappi, C. exile, C. e. canadense* have strongly striate shells. Shell dimensions range from the short, narrow (1.3 x 0.4 mm) *C. nannodes* to the tall, narrow (2.1 x 0.7 mm) *C. e. canadense* and the tall, wide (2.5 x 0.9 mm) *C. stygium*. Other morphological features that have been used to identify these species include the thickness and width of the apertural lip, the shape, size and placement of the internal lamellae, and general shell form (Burch & Van Devender 1980).

Perhaps the most taxonomically contentious entities within this group are *Carychium exiguum, Carychium exile exile,* and *Carychium exile canadense* (Figure 1). *Carychium exiguum* has 1.6–2.0 mm long x 0.7–0.8 mm wide shells that are smooth or only weakly striate and of whitish or clear corneous color (Pilsbry 1894, 1948; Burch & Van Devender 1980). It is a common denizen of open and forested wetlands ranging from Kansas and South Dakota to Newfoundland, Nova Scotia, and the coastal plain of South Carolina (Hubricht 1985). *Carychium exile* has 1.6–2.2 mm long x 0.6–0.7 mm wide shells that are strongly striate and of whitish or clear corneous color (Pilsbry 1894, 1948; Burch & Van Devender 1980). It has been found throughout most of the eastern U.S. and southeastern

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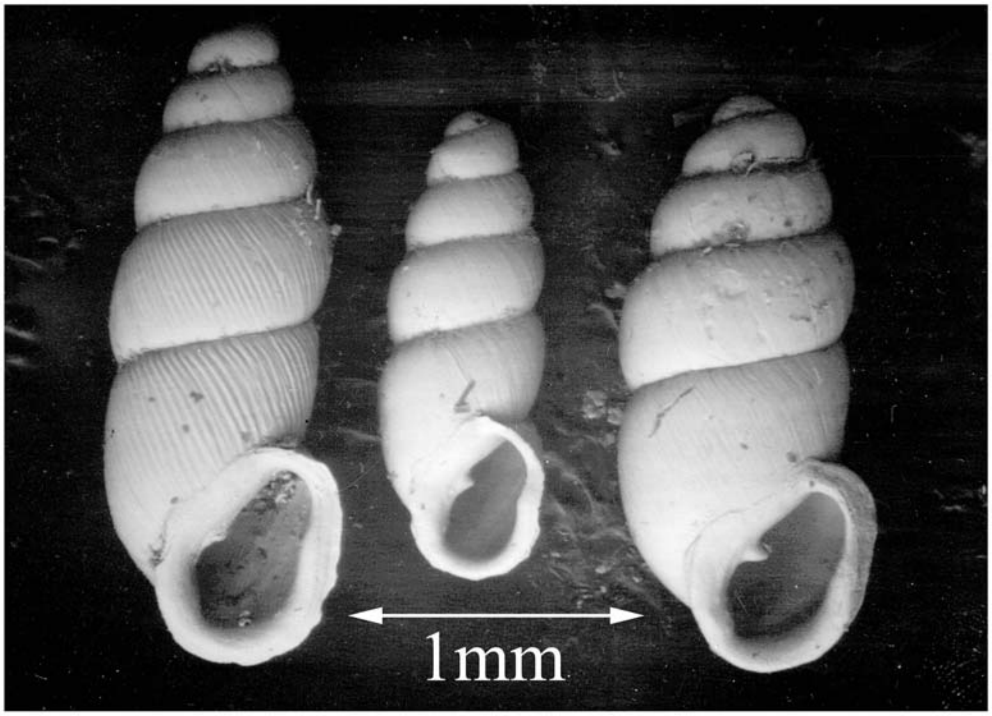


Figure 1 Scanning electron micrograph of *Carychium exile*, *Carychium nannodes* and *Carychium exiguum* from the western Great Lakes region of North America. From left to right: *C. exile*, UWGB 935, Buck Creek Tributary 1, Clayton County, Iowa, USA (91°10'55"W, 42°51'47"N); *C. nannodes*, UWGB 3866, Crawford Lake, Halton County, Ontario, Canada (79°56'27"W, 43°28'27"N); *C. exiguum*, UWGB 3676, Cedarburg Bog, Ozaukee County, Wisconsin, USA (88°1'4"W, 43°22'59"N).

Canada, and is most frequently encountered in decaying leaf litter of mesic upland woods, bedrock outcrops, and wooded swamps (Oughton 1948, Pilsbry 1948, Hubricht 1985). The nominate subspecies is reported to have shells <1.75 mm tall, a V-shaped internal lamellae, and be more southern in distribution. *Carychium exile canadense* is reported to have shells >1.75 mm tall, a flat internal lamellae, and be more northern in distribution (Clapp 1906, Winslow 1922, Burch & Van Devender 1980, Hubricht 1985).

Oughton (1948) reported considerable overlap in shell characteristics between some Ontario *Carychium exile* and *Carychium exiguum* populations. Harry (1951) stated that sufficient data did not exist to recognize more than one natural species in this group. Both Harry (1951) and Burch & Van Devender (1980) suggest that *C. exiguum* and *C. exile* canadense represent endpoints along a morphological range of continuous variation, with *C. e. exile* representing intermediate individuals. Based on these conclusions, some North American malacologists (Branson 1961, Baerris 1980, Burch & Van Devender 1980, Frest & Dickson 1986) have chosen to lump *C. exile* into *C. exiguum*.

However, Baker (1939), Pilsbry (1948), Oughton (1948), Robertson & Blakeslee (1948), Leonard (1959), Hubricht (1985), and Burch & Jung (1988) have all maintained these as separate taxa. Hubricht (1963) stated that *Carychium exiguum* and *Carychium exile* were always readily separable, even at sites of sympatric occurrence. In spite of such contrasting statements, hypotheses relating to the conchological distinctness of these taxa have never been subjected to potential falsification through objective, statistical tests. For instance, even though Harry (1951) measured the dimensions of over 2000 individuals from 38 sites in the Lower Peninsula of Michigan, he used no inferential statistical tests

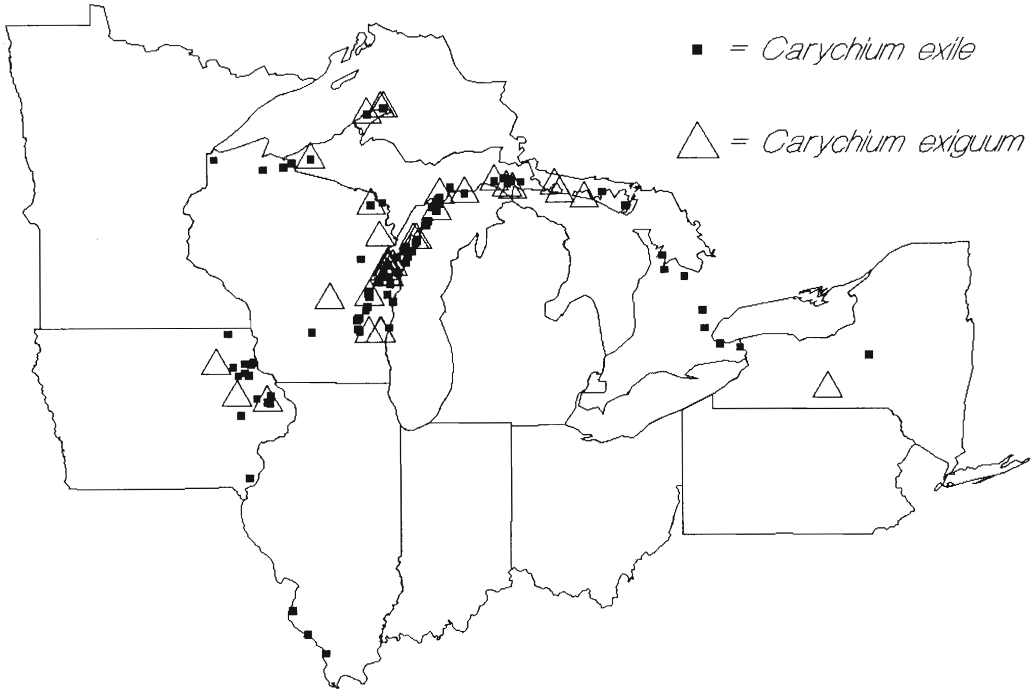


Figure 2 Map of study region, showing location of 116 measured *Carychium exile* and 35 measured *Carychium exiguum* populations.

to analyse these data.

To help resolve questions about appropriate taxonomic divisions within this group, we have conducted such analyses on *Carychium exiguum* and *Carychium exile* shells collected from Illinois, Iowa, Michigan, Minnesota, New York, Ontario, and Wisconsin. These populations span a considerable portion of the geographic range of *C. exiguum, C. exile exile* and *C. exile canadense*. Three main questions will be addressed: (1) How distinct are shell dimensions of *C. exiguum* and *C. exile* within the region and within sites of co-occurrence? (2) How strong is clinal variation in shell size for *C. exiguum* and *C. exile* across the region? (3) Do internal lamellae configuration and shell size patterns of *C. exile exile* and *C. exile canadense* confirm the presence of two subspecies?

METHODS

STUDY SITES

Populations of both *Carychium exiguum* and *Carychium exile* were collected during a regional survey of terrestrial gastropod faunas of over two dozen habitat types within a 1300 x 1000 km area centered on the Niagaran Escarpment in the Great Lakes region of North America (Nekola 1999). All *C. exile* populations, and approximately $^{2}/_{3}$ of all *C. exiguum* populations encountered by October 1998 were measured for a total of 116 *C. exile* and 35 *C. exiguum* stations (Figure 2). Analysed *C. exile* populations originated from 6 states or provinces, including Illinois (2 sites), Iowa (22), Michigan (20), New York (2), Ontario (9) and Wisconsin (60). Analysed *C. exiguum* populations originated from the states or provinces of Iowa (3 sites), Michigan (12 sites), New York (1 site), Ontario (1 site), and Wisconsin (18 sites). The single encountered population of *C. nannodes* (from

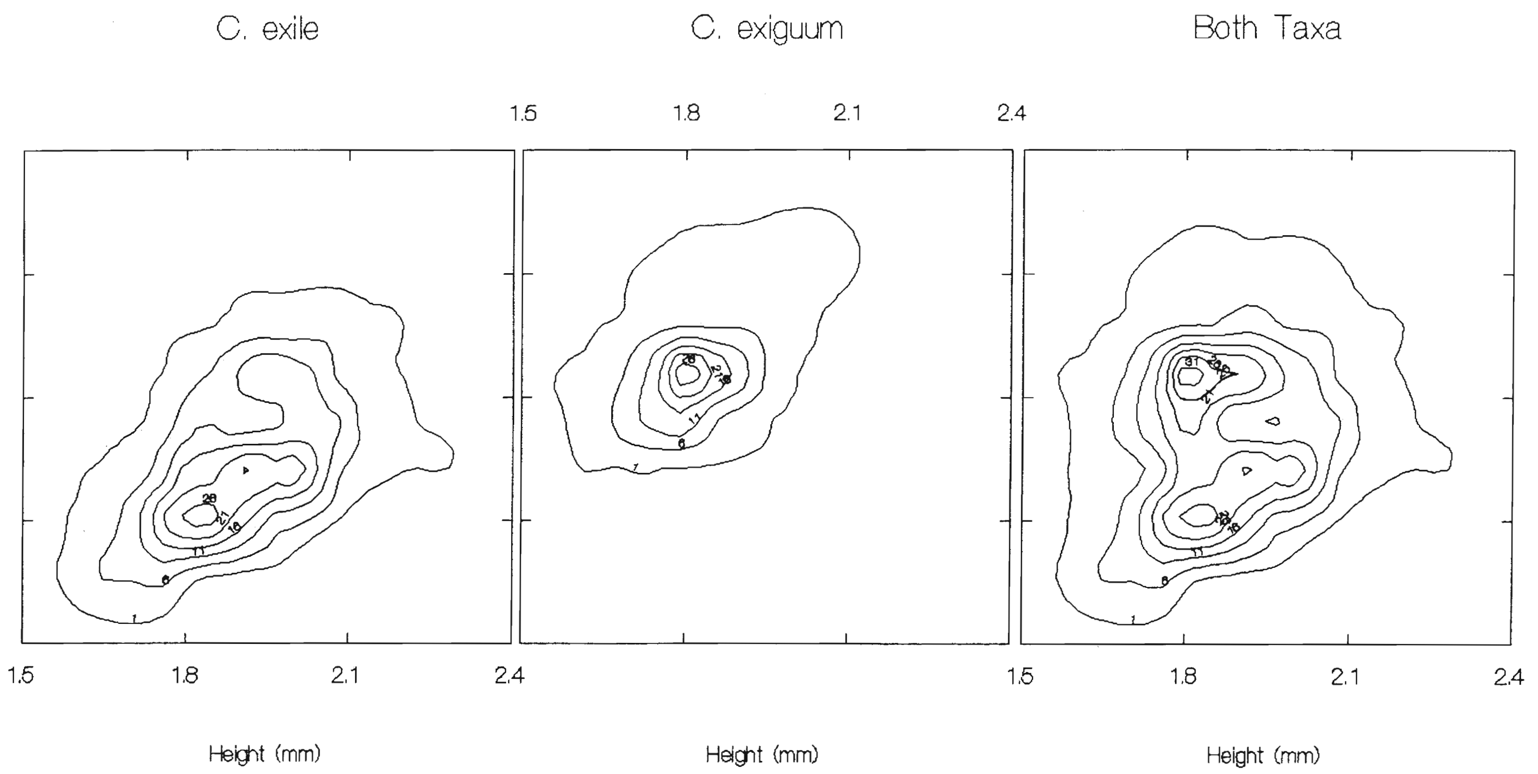


Figure 3 Contour diagram shell size frequency of *Carychium exile, Carychium exiguum* and all *Carychium* individuals from sites of co-occurrence. Contour intervals were drawn using distance weighted least squares smoothing.

Crawford Lake Park in Halton County, Ontario) was also measured.

FIELD AND LABORATORY PROCEDURES

The latitude-longitude coordinates for each population was determined through digitization of USGS (or equivalent) 7.5 minute topographic maps. To minimize statistical bias from use of polar coordinates, these locations were converted to Cartesian UTM Zone 16 coordinates using ARCINFO.

Soil litter samples were collected and slowly dried. These samples were then soaked in water and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8" (9.5 mm), #10 (2.0 mm), #20 (0.85), and #40 (0.425 mm) mesh screens). Sieved fractions were dried and hand picked against a neutral-brown background. All *Carychium* shells and shell fragments were removed.

Individuals were provisionally assigned to either *Carychium exiguum* or *Carychium exile* based upon the degree of shell striation. Like Hubricht (1963), we found this feature to demarcate two groups (Figure 1), with one being smooth to weakly and irregularly striate (*C. exiguum*) and the other being strongly and regularly striate (*C. exile*). *Carychium nannodes* individuals from Crawford Lake were identified by their smooth shell surface and size (height <1.5 mm).

In order to compare shell shapes of these forms, the height and width of all fully grown, undamaged *Carychium* shells from each site were measured in increments of 0.02 mm using a dissecting microscope with a calibrated ocular micrometer. Shells were measured with the aperture facing down. Height was calculated from the tip of the protoconch to the base of the body whorl, while width was measured at the widest section of the body whorl in back of the apertural lip. The apetural lip was not considered as its width varied with shell maturity and weathering, providing unstable estimates of maximum shell width. A total of 5177 *Carychium exile*, 1178 *Carychium exiguum*, and 25 *Carychium nannodes* individuals were measured. These data are available from the corresponding author upon request.

Lastly, variation in the shape of the internal lamellae within and between selected *Carychium exile* populations were documented using scanning electron micrographs taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and #2 Gamma Correction. Eight populations were chosen from across the study region. Within each, a segment of the penultimate whorl was removed from a dozen individuals to expose the internal lamellae. Three individuals were then selected from each population to illustrate the observed range of lamellae shapes.

STATISTICAL ANALYSES

Histograms of shell height and width were constructed for each population of more than 20 measured shells (52 *Carychium exile*, 20 *Carychium exiguum*), and visually inspected to ensure that none seriously violated assumptions of normality or included bimodal distributions.

1. How distinct are the shell dimensions of *Carychium exiguum* and *Carychium exile* within the region and within sites of co-occurrence?

As *Carychium* typically reproduces through self fertilization (Bulman 1990), it is highly likely that individuals within a population will be genetically uniform and lack statistical independence. To help minimize this form of pseudoreplication (Hurlbert 1984), two different analyses were employed for between vs. within population comparisons.

Canonical discriminant analysis (Kleinbaum *et al.* 1988) was used to determine if significant segregation existed in the height and width of shells between the 584 *Carychium exile* and 255 *Carychium exiguum* shells encountered at all 10 co-occurrence

TABLE 1
Summary statistics for canonical discriminant analysis of *Carychium* shell dimensions for sites of *Carychium exile* and *Carychium exiguum* co-occurrence.

Factor	Value
Canonical Correlation	0.761
Eigenvalue	1.378
Likelihood Ratio	0.421
Approximate F	575.8
Number df	2
Density df	836
p	0.0001

TABLE 2
Classification summary for canonical discriminate analysis of *Carychium exile* vs. *Carychium exiguum* shell dimensions from sites of co-occurrence.

Shell Surface			Size Cluster	
		Wide Group	Narrow Group	Total
Striate				
	Number	487	97	255
	Percent	83.39	16.61	
Smooth				
	Number	7	248	584
	Percent	2.75	97.25	
Total				
	Number	494	345	839
	Percent	58.88	41.12	
Total Error Count Estimate Percent			9.68%	

TABLE 3
Summary statistics for height vs. width regression for *Carychium exile* and *Carychium exiguum*, with width serving as the dependent variable.

Variable	C. exile	C. exiguum
Intercept	0.1950	0.5132
Intercept Std. Error	0.0381	0.0985
Intercept p	<0.0005	<0.0005
Slope	0.2310	0.1247
Slope Std. Error	0.0193	0.0538
Slope p	<0.0005	0.0268
r^2	0.5633	0.1400

p-value for difference between *C. exile* and *C. exiguum* intercepts:	<0.0005
p-value for difference between *C. exile* and *C. exiguum* slopes:	0.0547

sites. Shell height and width were used as dependent variables while species identity (based on level of shell striation) was used as the categorical predictor. A contour diagram showing the frequency of all *Carychium* shell sizes within these sites was drawn using distance weighted least squares smoothing (McLain 1974). Because the null hypothesis in this test assumes only a single taxa to be present, and because only sites of co-existence were considered, the potential lack of genetic independence between individuals within sites was controlled. As such, all individuals were considered independent observations.

Multiple least-squares linear regression was used to compare shell height vs. width relationships between all *Carychium exiguum* and *Carychium exile* populations. Because of the likely genetic uniformity within populations, combined with the fact that most of the sampled sites did not contain both taxa, individual shells could not be considered to represent independent observations. To control for this potential bias, mean height and width was calculated for each population (116 *Carychium exile* and 35 *Carychium exiguum*), and used for further analysis. While this greatly decreases sample size, it represents a more conservative statistical test as a greater degree of independence will exist between observational units. Testing for differences between the best-fit slopes and intercepts was accomplished by adding a binary variable (representing species identity) into the model following methods outlined by Kleinbaum *et al.* (1988). These data were displayed using a scatterplot in which 95% Gaussian confidence ellipses (Sokal & Rohlf 1981) were drawn around each species in graph space.

2. How strong is clinal variation in shell size for *Carychium exiguum* and *Carychium exile* across the region?

Least-squares linear regression was used to analyse the relationship between mean population shell width and height vs. UTM N and UTM E coordinates. Because only four measured *Carychium exile* populations exist south of UTM 4600 km N, and the potential that these sites might bias results, these analyses were also repeated following their exclusion. Mean shell height and width were plotted against UTM N and UTM E coordinates, with central tendencies being indicated through locally weighted scatterplot smoothing (Cleveland 1979).

3. Do internal lamellae configuration and shell size patterns of *C. exile exile* and *C. exile* canadense confirm the presence of two subspecies?

SEM images of internal lamellae from the 24 selected individuals (three each from eight populations) were arranged in a single plate to allow for easy comparison of variation within and between populations. Additionally, the frequency of *Carychium exile* (<1.8 mm tall), *C. e. canadense* (>2.0 mm tall), and intermediate (1.8–2.0 mm tall) individuals was calculated within each population. These frequencies were mapped using bar icons in which the percentage of black represents the frequency of that particular size class within each population. No icon was mapped if a given size class was absent.

RESULTS

Visual inspection of height and width histograms demonstrated that none of the 52 *Carychium exile* and 20 *Carychium exiguum* populations with 20 or more measured shells seriously violated assumptions of normality. The minor violations noted were in the form of skewing. None of the populations showed any tendency for biomodality.

1. How distinct are the shell dimensions of *Carychium exiguum* and *Carychium exile*

within the region and within sites of co-occurrence?

The contour plot of shell dimension frequencies from sites of *Carychium exiguum* and *Carychium exile* co-occurrence demonstrated a highly bimodal distribution, particularly in relation to shell width (Figure 3). The great majority of highly striate individuals *(C. exile)* were limited to the narrower cluster, while essentially all of the smooth individuals *(C. exiguum*) were limited to the wider group. Canonical discriminant analysis documented that these clusters were significantly differentiated (p=0.0001; Table 1). Use of shell striation as the sole discriminating factor lead to only a 9.68% error rate (Table 2). These errors were not symmetrically distributed, with 2.75% of non-striate individuals being members of the narrower cluster, and 16.61% of striate individuals being members of the wider cluster.

Similar patterns were found when mean shell height vs. width was compared between all populations. Highly significant (p<0.0005) differences were observed in the intercepts of the best-fit regression lines, being 2.5 times larger in *Carychium exiguum* as compared to *Carychium exile* (Table 3). Marginal differences (p=0.0538) were also present in the best-fit slopes, with *C. exiguum* populations tending to increase in width as a function of height at almost one-half the rate observed in *C. exile*. Comparison of the 95% Gaussian ellipsoids for both species demonstrates essentially no statistical overlap in height-width space (Figure 4). Within both species, continuous variation in average shell dimensions was noted between populations. Additionally, for both species at shell heights <1.8 mm, the correlation between shell width and height appeared to weaken or vanish.

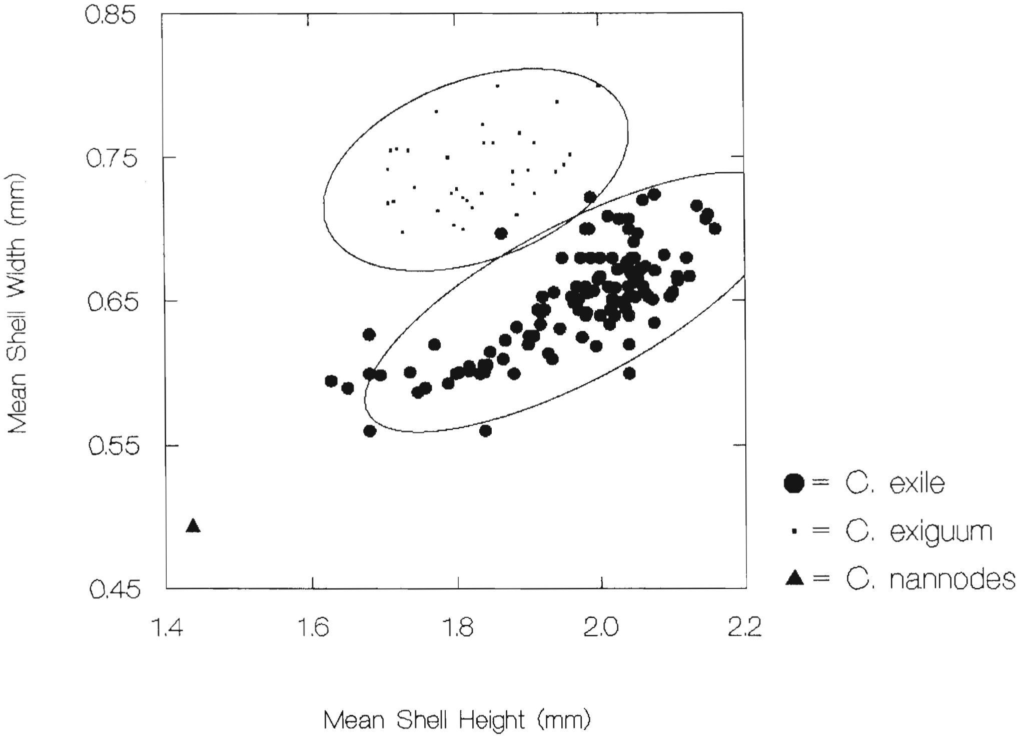


Figure 4 Scatterplot of mean shell width vs. mean shell height for all measured *Carychium* populations. 95% Gaussian ellipsoids have been drawn around the distributions of *Carychium exile* and *Carychium exiguum* in this graph space.

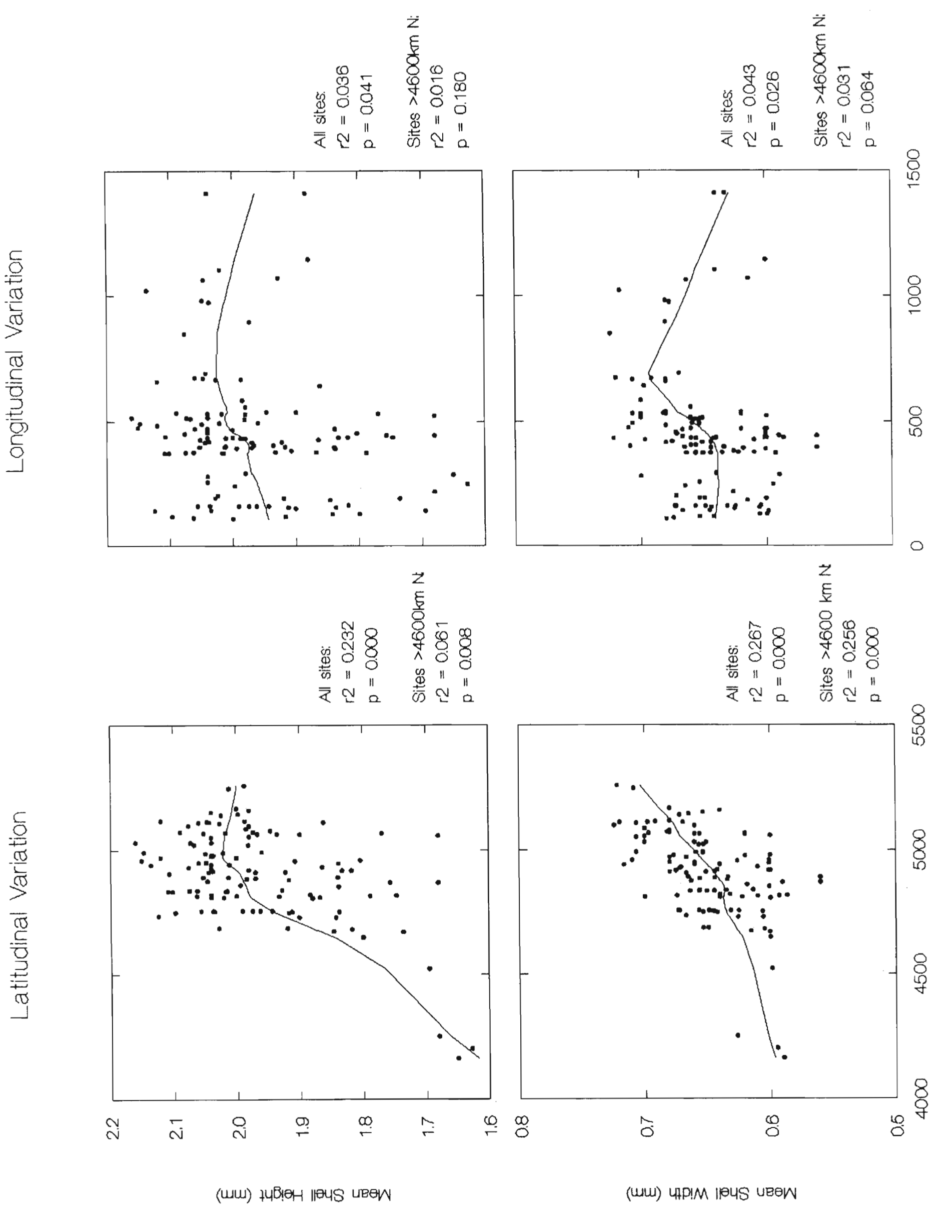


Figure 5 Scatterplots showing mean *Carychium exile* shell height and width vs. longitudinal and latitudinal position. Response lines in these graphs were fit using locally weighted scatterplot smoothing.

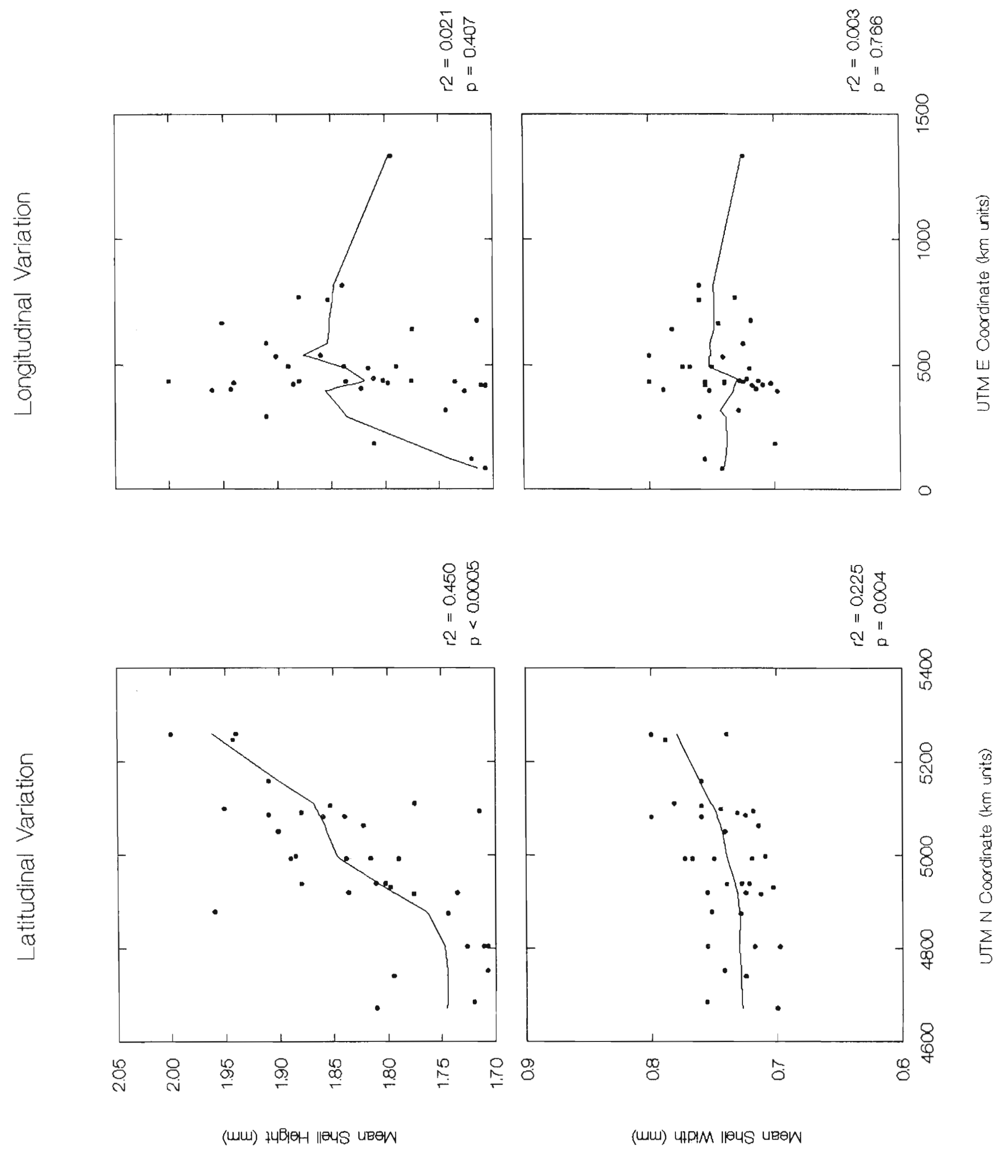
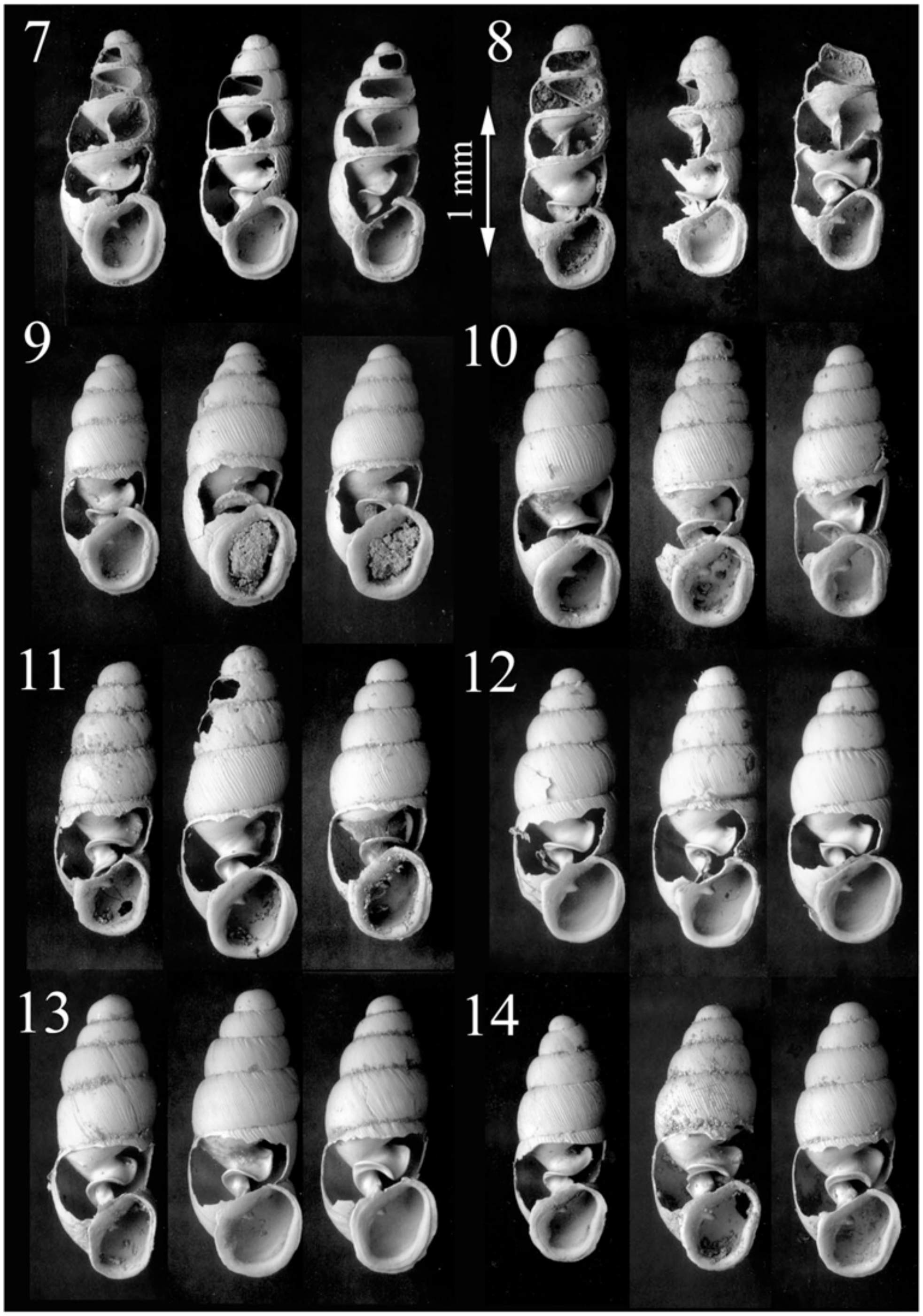


Figure 6 Scatterplots showing mean *Carychium exiguum* shell height and width vs. longitudinal and latitudinal position. Response lines in these graphs were fit using locally weighted scatterplot smoothing.

Figures 7–14 Scanning electron micrographs of internal lamellae shape and size from eight *Carychium exile* populations. Three shells from each are used to illustrate the range of variation. Populations are ordered based on their geographical location from the most southwestern through the most northern to the most southeastern. **7** UWGB 3862, Franklin Hill, Calhoun County, Illinois, USA (90° 36' 38" W, 39° 3' 57" N). **8** UWGB 39, Pine Creek, Jackson County, Iowa, USA (90° 50' 41" W, 42° 8' 27" N). **9** UWGB 5137, Williams Creek, Allamakee County, Iowa, USA (91° 28' 41" W, 43° 8' 14" N). **10** UWGB 1393, Oakfield Brickyard, Fond du Lac County, Wisconsin,



USA (88° 33' 10" W, 43° 40' 27" N). **11** UWGB 521, Ansels Point, Delta County, Michigan, USA (86° 34' 26" W, 45° 48' 12" N). **12** UWGB 3063, Copper Harbor Marina, Keewenaw County, Michigan, USA (87° 54' 14" W, 47° 28' 19" N). **13** UWGB 2249, Maple Hill, Chippewa County, Michigan, USA (84° 46' 55" W, 46° 9' 34" N). **14** UWGB 2472, Skinners Bluff, Grey County, Ontario, Canada (80° 59' 31" W, 44° 47' 36" N).

2. How strong is clinal variation in shell size for *Carychium exiguum* and *Carychium exile* across the region?

Regression of *Carychium exile* shell height (Figure 5) demonstrated a significant ($p<0.0005$) and moderately strong ($r^2=0.232$) positive correlation with latitude over the entire data set. Shell height ranged from less than 1.7 mm in the south to almost 2.2 mm in the north. While this relationship remained highly significant ($p=0.008$) after removal of the southernmost 4 sites, the strength of the relationship fell to almost 1/4 its previous level ($r^2=0.061$). Regression of height vs. longitude demonstrated only a marginally significant ($p=0.041$) trend, which vanished ($p=0.18$) when the southernmost sites were removed. This trend is not monotonic, with shells from central sites being taller than those to the east or west.

Regression of *Carychium exile* shell width (Figure 5) demonstrated a significant ($p<0.0005$) and moderately strong ($r^2=0.267$) positive correlation with latitude for the entire data set. Shell widths ranged from less than 0.56 mm in the south, to almost 0.72 mm in the north. This relationship remained highly significant ($p=0.008$) and moderately strong ($r^2=0.256$) following removal of the southernmost 4 sites. Regression of width vs. longitude demonstrated only a marginally significant ($p=0.026$) trend, which decreased in significance ($p=0.064$) when the southernmost sites were removed. This trend is not monotonic, with shells from central sites being wider than those to the east or west.

Regression of *Carychium exiguum* shell height (Figure 6) demonstrated a significant ($p<0.0005$) and strong ($r^2=0.45$) positive correlation with latitude. Shell heights ranged from less than 1.7 mm in the south to 2.0 mm in the north. Regression of height vs. longitude demonstrated no significant ($p=0.407$) trends.

Regression of *Carychium exiguum* shell width (Figure 6) demonstrated a significant ($p=0.004$) and moderately strong ($r^2=0.225$) positive correlation with latitude. Shell widths ranged from 0.7 mm in the south to 0.8 mm in the north. Regression of height vs. longitude demonstrated no significant ($p=0.766$) trends.

For both species, the rate of increase in shell height and width with latitude was not constant. In *Carychium exile,* little decrease in shell size was apparent south of UTM 4600 km N, and in *Carychium exiguum*, little decrease in shell size was noted south of UTM 4900 km N.

3. Do internal lamellae configuration and shell size patterns of *Carychium exile exile* and *Carychium exile canadense* confirm the presence of two subspecies?

SEM imaging of the internal lamellae of the 24 *Carychium exile* individuals from eight stations (Figures 7–14) demonstrates that considerable variation is present both within and between populations. Lamellae shape did not fall into clearly identifiable classes, with most individuals possessing intermediate shapes. All populations demonstrate at least some variation in this feature, with Franklin Hill (Illinois; Figure 7), Ansels Point (Michigan; Figure 11), and Copper Harbor Marina (Michigan; Figure 12) possessing the least. Populations with the flattest lamellae include Franklin Hill (Illinois; Figure 7) and Pine Creek (Iowa; Figure 8), while those with the most V-shaped include Copper Harbor Marina (Michigan; Figure 12) and Maple Hill (Michigan; Figure 13). No clear relationship between lamellae shape and shell size was noted: flat lamellae were present in both small (Figure 7) and large (Figure 10) shells while V-shaped lamellae were present in both small (Figure 9) and large (Figure 10) shells. However, flatter lamellae may be become somewhat more common as shell size decreases.

Mapping of the three *Carychium exile* size class frequencies within populations (Figure 15), demonstrated that while *C. e. exile* individuals are largely restricted to areas west of Lake Michigan, *C. e. canadense* and intermediate individuals are found in all but the most southern sites. Forty-five stations harbored individuals that fell into all three size

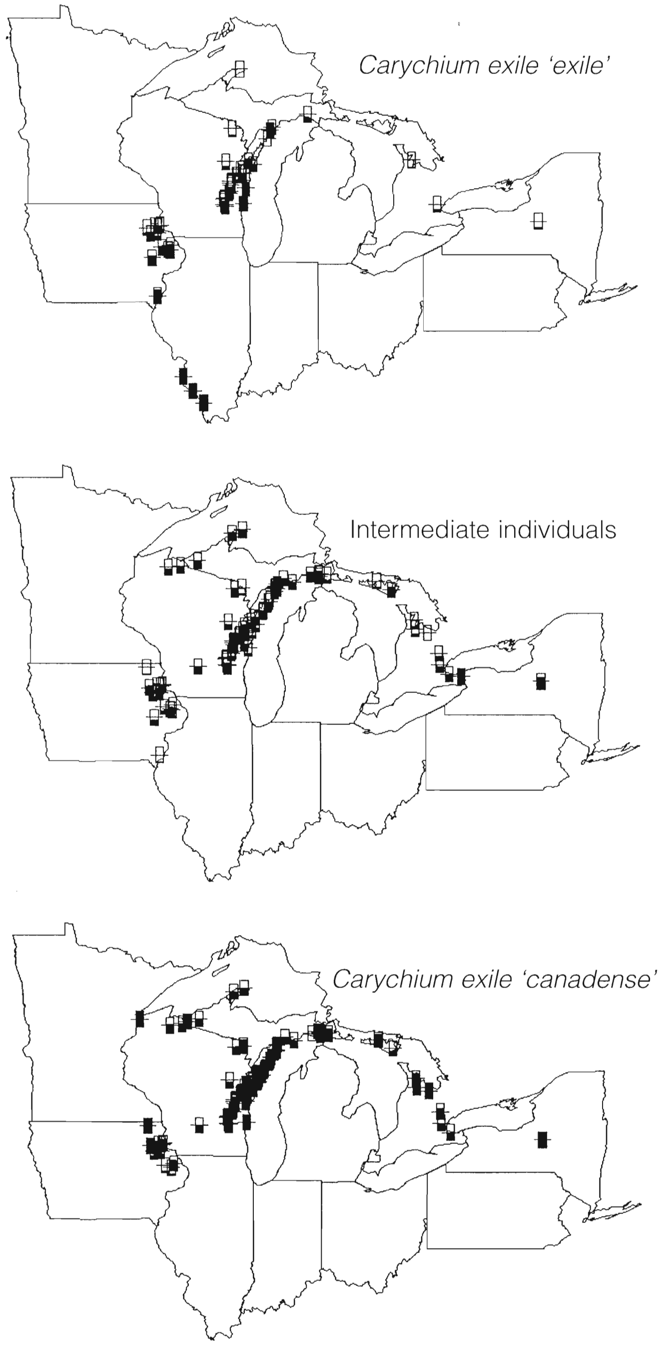


Figure 15 Distribution of *Carychium exile exile* (shell height <1.8 mm), *Carychium exile canadense* (shell height >2.0mm) and intermediate (shell height 1.8-2.0mm) within sampled *C. exile* populations. Box icons are printed if a site possessed individuals within the given size class. The amount of black fill in each box is equal to the proportion of individuals within that population which fall into the size class.

classes. Five sites were represented by *C. e. exile* and 18 by *C. e. canadense* individuals only. Only a single site (Buck Creek 4 in Clayton County, Iowa) was found to have *C. e. exile* and *C. e. canadense* individuals but no intermediates. However, only 5 measurable shells were recovered from this site.

DISCUSSION

DISTINCTNESS OF *CARYCHIUM EXILE* AND *CARYCHIUM EXIGUUM*

These analyses clearly document that *Carychium exile* and *Carychium exiguum* should be maintained as separate species. Within sites of co-occurrence, *Carychium* individuals exhibit a strongly ($p=0.0001$) bimodal distribution in shell height & width, with smooth shells (*C. exiguum*) being approximately 15% wider than striate shells (*C. exile*) of the same height. The degree of shell striation can be used with over 90% accuracy in assigning individuals into either of these two size classes.

The distinctness of these species was maintained when mean shell dimensions were compared for populations across the entire study region. Essentially no overlap was noted between the 95% Gaussian ellipsoids characterizing each species range of shell heights and widths. Accordingly, the best-fit height-width regression lines also had significantly ($p<0.0005$) different intercepts.

Given such obvious distinction between these two taxa at both local and regional scales, it is unclear why some have maintained them as a single, continuously varying species. The main source of this confusion can be traced to inadequacies in the analysis provided by Harry (1951). First, unlike the current study, the populations upon which his analyses were based were limited to only a portion of the Lower Peninsula of Michigan, and were sampled across only a few distinct habitat types. As such, it was not possible for him to document broad-scale morphological patterns.

Second, he only used shell measurement data in a descriptive sense and never subjected them to statistical tests. Because of this, obvious trends were ignored. This can be most clearly seen in his Plate 9, which was used to support the contention that continuous variation exists in the height and width of *Carychium exiguum* and *Carychium exile* shells. In fact, his data actually demonstrate a bimodal distribution of shell dimensions, with one mode occurring at 1.95 x 0.80 mm, and the other at 1.85 x 0.85 mm. These two modes correspond exactly to our analyses, with the first mode likely representing *C. exile* and the second *C. exiguum*. It is interesting to also note that these two groups also differed in their habitat affinities, with mode 1 individuals (*C. exile*) being primarily collected from upland woods, and mode 2 individuals (*C. exiguum*) from wetlands.

Another likely source for confusion between these two taxa is the fact that degree of shell striation is a more variable morphological feature than shell dimension. Even though very useful, shell striation alone is not sufficient to assign individuals unquestionably to one species or the other. This is especially true for *C. exiguum*, where almost 17% of individuals were assigned to *C. exile* even though they possessed shell widths characteristic of *C. exiguum*. Based upon accounts provided in Oughton (1948) and Harry (1951), it seems likely that such moderately-striate *C. exiguum* individuals were considered as intermediates. However, our analyses demonstrate that when the number of distinguishing features is extended to include shell width and height, these species are readily and easily sorted. Intermediate forms do not exist even within sites of co-occurrence.

CLINAL VARIATION IN *CARYCHIUM EXILE* AND *CARYCHIUM EXIGUUM*

Both *Carychium exile* and *Carychium exiguum* demonstrate significant clinal variation with larger individuals occurring in the north. This variation is continuous in both species. The magnitude of this change is 67% greater in *Carychium exile* as compared to *Carychium exiguum*. This may help explain why Clapp (1906) and Pilsbry (1948) chose to designate the northern and southern forms of *C. exile* as different subspecies, while at the same time keeping *C. exiguum* a single entity possessing a latitudinal 'zonal variation' in shell size. However, even though of smaller total magnitude, the strength of clinal variation in *C. exiguum* shell size is actually almost twice as great as that for *C. exile*.

The weak longitudinal relationships noted in *Carychium exile* shell size, however, appear to simply reflect a sampling artifact. As collections were focussed along the Niagaran Escarpment, populations from the center of the study area also tended to be more northern in location. This non-regular sampling pattern, combined with strong latitudinal changes in size, should be enough to explain the observed weak, non-monotonic longitudinal trends.

TAXONOMIC UTILITY OF *CARYCHIUM EXILE EXILE* AND *CARYCHIUM EXILE CANADENSE*

Subspecies are usually defined as taxonomically distinct aggregates of populations that are limited to a specific subdivision of a species range. Mayr (1963) emphasized that simply showing statistical distinctness between populations does not indicate the presence of subspecies: only when such populations are geographically isolated, leading to a minimal amount of introgression between forms, is the use of subspecies taxonomically useful. Sourakov (1995) suggests that subspecies are a valid taxonomic concept only when at least 95% of individuals and populations can be easily segregated.

Our data clearly shows that neither of these criteria is met for *Carychium exile exile* and *Carychium exile canadense*. Even though Winslow (1922), Harry (1951), Burch & Van Devender (1980), and Burch & Jung (1988) all state that *C. e. exile* possesses a V-shaped lamellae, while that of *C. e. canadense* is flat, we could find no evidence of this pattern. All possible intermediate forms were found, with considerable variation occurring within single populations. In particular, continual gradation between flat and V-shaped lamellae was observed in three of the eight selected populations (Figures 8, 9, 14).

We also saw little evidence to support the contention that smaller shells from more southern locations had more V-shaped lamellae, or that larger shells from more northern sites possessed flatter lamellae. The populations with the flattest lamellae actually occurred in the smallest shells originating from the most southern populations, while the populations with the most V-shaped lamellae actually tended to occur in large shells originating from the north and east. The depth of lamellae indentation did not even vary predictably with shell size within sites. As can be clearly seen in Figure 9, 6, and 8, the largest shells actually tend to have the most deep indentations. Our data support the contention of Brooks & Kutchka (1937) and Pilsbry (1948) that within *Carychium exile* this feature is too variable to be taxonomically useful.

The presence of continuous clinal variation in *Carychium exile* shell size also supports the view that there is little taxonomic utility in recognizing *Carychium exile exile* and *Carychium exile canadense*. The introgression zone between these two forms essentially covers the entire study region, with intermediate individuals being absent from only the far south. Fully 40% of all populations possess individuals referable to *C. e. exile*, *C. e. canadense*, and intermediate size classes. Only 20% of populations contain *C. e. exile* or *C. e. canadense* individuals but lack intermediate forms. None of the measured *C. exile* populations possess bimodal distributions in shell size, further indicating that segregation of small and large shells does not occur within populations.

As the assignment of individuals and populations into *Carychium exile exile* or *Carychium exile canadense* is impossible over much of the Great Lakes region, it would seem appropriate to treat *C. exile* as a single taxonomic entity that possesses a distinct north-south clinal variation in shell size. This seems especially appropriate given that

C. exiguum, which has always been considered a single taxonomic entity, actually possesses a stronger north-south clinal variation in shell dimension.

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