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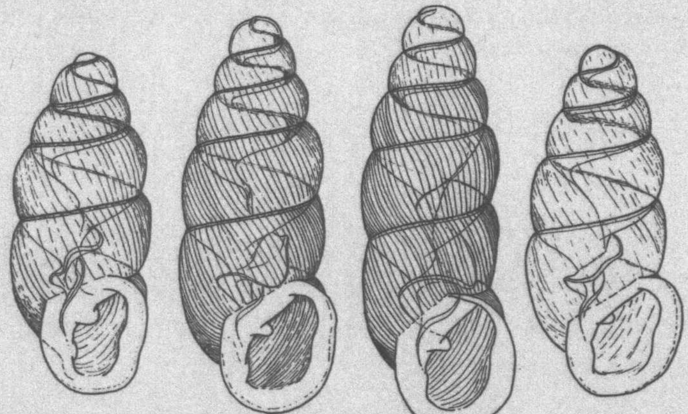
CARYCHIUM EXIGUUM (SAY) OF LOWER MICHIGAN

MORPHOLOGY, ECOLOGY, VARIATION AND LIFE HISTORY (GASTROPODA, PULMONATA)

Harold W. Harry



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PREFACE

The original aim of this investigation was a study of the morphology of *Carychium exiguum* (Say) for the purpose of expanding the knowledge of its systematic position. While that objective remained the primary goal during the study, there arose related problems which required at least preliminary investigation, and which have important bearing on morphology. The minute size and shy habits of this snail indicated a quantitative approach as desirable. It was necessary to gain knowledge of the occurrence of *Carychium* in the field, in order that material could be gathered in the desired quantities. Very early in the collecting, considerable variation in form and size of the shell was noted; as speciation in this genus has been based on such characters, it then became necessary to investigate the morphological difference between *C. exiguum* and the several very similar nominal species which have been attributed to Lower Michigan. The scarcity of immature snails in the field during the early summer, together with their sudden appearance and peculiar size groupings led to a quantitative study of the life history as demonstrated by the field work. While none of these problems have been pursued very far, and all suggest the need of intensive study for their own sake, it seems desirable to present such conclusions as could be drawn from the accumulated data.

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CARYCHIUM EXIGUUM (SAY) OF LOWER MICHIGAN; MORPHOLOGY, ECOLOGY, VARIATION AND LIFE HISTORY (GASTROPODA, PULMONATA)

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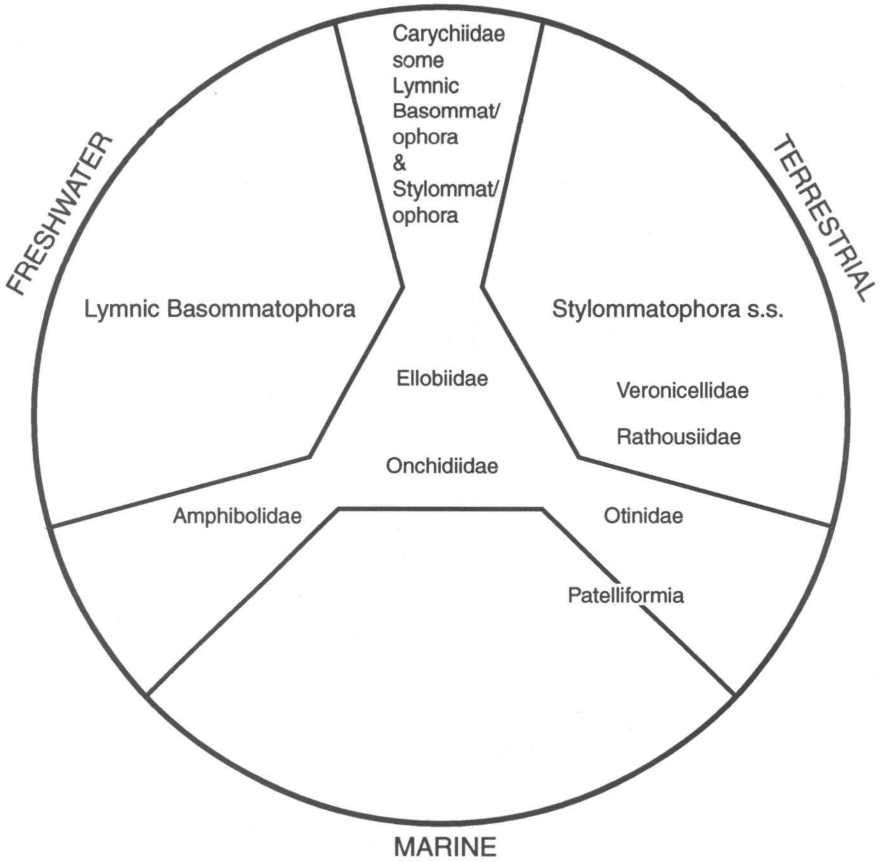
INTRODUCTION

The Gastropoda Pulmonata consist of a diversified assemblage of snail groups whose phylogenetic relationships remain obscure. The classifications proposed have about exhausted the creditable combinations, yet few solutions to the puzzle find more than limited agreement among biologists. The most important recent contributions are those of Thiele (1929-1935), Pilsbry (1948), Boettger (1944), and especially Hubendick (1945, 1947). The methods of classification differ chiefly in aspect and evaluation of limited evidence. It seems that a more profitable approach would be to gain new evidence, rather than attempt further systematic revision.

One part of the biology of the Pulmonata which has had little emphasis and yet which helps to define the problem of their classification, is their ecological relationships. The grosser aspects of pulmonate ecology are diagrammed in Plate I. Generally, the universe of ecology is divided into three realms, marine, freshwater and terrestrial. While many organisms can be referred to one or the other of these realms with little doubt, others can not. Many pulmonates are among the latter group. Thus, in systematic catalogues of a given geographical area and ecological realm, those animals about which there may be doubt as to their correct ecological allocation are treated arbitrarily. For example, Pilsbry (1948) includes *Carychium* among the land mollusks of North America but excludes the Ellobiidae *s.s.*, although the prosobranch family Truncatellidae, which inhabits the same situation as members of that family, is included by him. Truncatellidae and Ellobiidae are generally considered marine, though both contain distinctly terrestrial species in some regions. Walker (1918) considered the Ellobiidae as belonging to the freshwater realm. Plate (1897) thought all ellobiids were terrestrial, but Odhner (1925) emphatically states that *Marinula* is marine. The same situation exists in the case of *Carychium* in the American systematic literature, for it is sometimes included in the freshwater fauna, or again in the terrestrial. Fischer & Crosse (1900) resolved the dilemma by recognizing the various ellobiid genera as inhabiting different realms.

The incongruities arise from failure to realize that ecological realms are not simple entities, mutually exclusive, but result from the frequency of

PLATE I



Ecological distribution of the major Pulmonate groups.

combination of complex ecological factors. The exact statement of the quality and quantity of these effective factors (*e.g.*, temperature, moisture, substrate, biota, etc.) of a given habitat are seldom available, often impractical or impossible to take in the field; reports are more generally given of the ecological aspects which result from the combination of these interacting factors. This academic quandary can be resolved to a large extent by recognizing that the intermediate zones are as equally worthy of consideration as are the major realms themselves. Usually in nature the intermediate zones, or minor realms, are spatially marginal to two major ones as shown in Plate I. However, this is not essential, for occasionally a minor realm habitat will appear as an island in a major one without the presence of the other major realm which might adjoin it. One such example is the presence of salt flats in inland areas, far removed from the sea, yet containing biotic elements of the salt marshes on the coasts. Another example is the wet depressions in terrestrial situations, not marginal to surface water, yet of a high moisture content; such situations often contain *Carychium,* and will be dealt with below in considering the ecological occurrence of that snail in Michigan. Even the minor realms have their intermediate zone, represented in Plate I by the central area of the chart, and in nature by the salt marsh.

Placing the various pulmonate groups on the chart, we see that they inhabit all the major and minor realms, though very few characteristically extend into more than one. *Carychium* is often considered as a subfamily of the Ellobiidae (Thiele, 1935; Odhner, 1925), but sometimes removed to a special family of their own (Pilsbry, 1948; Boettger, 1944). This genus, and perhaps the others included in the Carychiidae by Pilsbry (1948), inhabit moist places far removed from the marine environment, while the Ellobiidae *s.s.* are, with few exceptions, narrowly limited to the intermediate realms bordering the sea.

Of the genera other than *Carychium* which Pilsbry includes in the Carychiidae, little more is known than descriptions of the shells in systematic literature. *Carychiopsis* Sandberger is known only as fossils in the European Tertiary; Wenz (1923) has compiled a species catalogue of them with extensive bibliography. *Zospeum* Bourguignat occurs only in caves of the Balkan peninsula; the most recent catalogue is that of Wolf (1938). Occasionally, in the literature the statement is made that *Zospeum* is blind. Whether this is an adaptation to a cavernicolous mode of life may remain a speculative question, since the surface-dwelling *Ellobium aurismidae* and *E. aurisjudae,* the largest members of the family, are also reputedly blind. *Carychium stygium* of Mammoth Cave, Kentucky, is by my own observations not blind. It is the only known pulmonate indigenous to caves of the

United States. Though Wolf lists it both in the genus *Carychium* and *Zospeum*, the latter combination is undoubtedly in error.

In originally describing the genus *Coilostele*, Benson (1864) dubiously included it in the Ellobiiacea (his Auriculacea) because it shows resorption of the internal partitions of the shell and bears a general resemblance in the external shell to some small ellobiid genera. In monographing the species, Pilsbry (1908) once placed them in the stylommatophoran Ferussaciidae which the shells also closely resemble externally, but later he (1948) removed the genus to the Carychiidae. Unlike other species in the latter family, *Coilostele* has the apertural lip sharp and straight, not reflected or thickened. On the other hand, *Blauneria* and some other small Ellobiidae show little terminal elaboration. *Coilostele* (as emended to *Coelostele*) was included in the Ferussaciidae by Thiele, to follow it with the genus *Caecilioides*. In the latter group resorption is not common, but has recently been reported in *Caecilioides consobrina prima* from Guatemala (Harry, 1950). What systematic evaluation should be given this character should rest on its correlation with other features of the anatomy when that is known. Internal resorption of the shell is indeed general in the Ellobiiacea but not universal; thus, Fischer and Crosse found resorption in the shell of *Marinula* but not in *Pedipes*. These two genera are very similar in characters of the external shell; indeed, Odhner thinks resorption is the best criterion for distinguishing the two.

As the nominal American species of *Carychium* have been recently summarized by Pilsbry (1948), a detailed review of them will be omitted here. What little is known of the external anatomy of the American species has usually been presented as drawings and a few brief notes in the systematic literature (*e.g.*, F.C. Baker, 1902). Morse (1864) investigated the radula and jaw, and Winslow (1922) reported on the internal lamellae of the shell. The anatomy of the European *Carychium minimum* has been described by Moquin-Tandon (1855) and Lehmann (1873) in some detail, and Odhner (1925) has recently redescribed the jaw and radula. Those few other scattered notes on the anatomy which have come to my attention are cited where relevant.

Statistical studies on the shell of *Carychium* have engaged the attention of at least four students. Clapp (1906) used mean height and mean width of the shell, correlated in a general way with distribution, to separate *Carychium exile canadense* as a distinct subspecies. Zimmermann (1925), Thorson & Tuxen (1930), and Boycott (1901) have studied the variation of shell dimensions of the European species of *Carychium*. These studies are reviewed below in the section on variation of the shell (p. 48-51).

Knowledge of the ecology of *Carychium* is also meager, being chiefly an occasional note in systematic literature to the effect that it lives in moist places, or rarely a listing in synecological studies. Nothing is known of the life history of American species. *Carychium minimum* is said by Lehmann (1873) to be oviparous.

The principal papers dealing with ellobiid anatomy are those of Fischer & Crosse (1900) who give a critical summary of previous work; Plate (1897) on *Pythia scarabaeus;* Pelseneer (1894) on *Phytia myosotis;* Koslovsky (1933) on *Melampus boholensis,* and Odhner (1925) on *Marinula juanensis.* Hubendick (1945) has recently revised and evaluated the knowledge of ellobiid anatomy.

MATERIALS AND METHODS

The material on which the present study is based was collected in the Lower Peninsula of Michigan during the period 1949-1951. A catalogue of the important localities and the specimens obtained from each is given in Tables 1, 3, 5 and 6. Methods of sampling and preservation depended on the field conditions and the use for which individual lots were intended, the following three methods were used.

(1) Hand picking in the field. Specimens were removed from leaf humus or decaying wood with the tip of a wet straw, and placed directly into 70% alcohol. Since immature specimens and empty shells are easily overlooked in the field, this method is of little value for population studies. It was used chiefly in the grassland habitats where light was sufficient and little leafmold was available. The yield of this method is small compared to the next.

(2) Dry leaf samples. Where organic mulch was plentiful, several handfuls of it were placed in a cloth bag to be examined in the laboratory. To obtain living specimens, it is best to sort the sample within a few hours after it is collected. The process of concentrating it requires from three to eight hours for a sample of one to two quart capacity. Frequently a number of samples were gathered from different localities before returning to the laboratory. This made it impossible to concentrate them for several days, or even weeks. Samples kept in field bags in the laboratory should be dried out as soon as possible if they are to be used for population counts. Under proper conditions of temperature and moisture, these samples continue as living microcosms, though probably at considerable variance with conditions in the field. There may be an increased production of juveniles (see Table 8); some animals which were alive when collected may die, and their shells be cleaned, thus altering the component classes of the population. But such soft forms as slugs are rarely found or are identifiable after drying.

(3) Alcoholic leaf samples. When field excursions of several days were made, facilities for the proper drying of leaf samples were not available; moreover, the dried samples furnish material of little use for anatomical studies except on the shell, jaw and radula. To overcome these difficulties, several samples were placed in half gallon glass jars and flooded with alcohol. In the laboratory the samples were drained and dried before sorting. This method proved unsatisfactory. The alcohol provided a liquid medium wherein the natural acids of the environment could act with great success in destroying all calcareous material. The number of mollusks recovered was much less than that indicated by inspection of the samples in the field. What shells were found were fragile, bleached, and of no value for the present study. These samples are not listed in Table 1; the method is cited chiefly because it indicates the effectiveness of the natural acids in the field, at moderate temperatures. The

matter is further discussed below in the section dealing with the life history.

To concentrate the dry leaf samples in the laboratory, the samples were placed in a shallow white enamel pan, and carefully examined under a strong light. A small sable hair brush (size 000 is preferable) was used to transfer *Carychium* and the smaller associated mollusks to concentration chambers. The latter consisted of Petri dishes in which a bit of moistened filter paper or a few leaf fragments were placed. They should be kept covered during the process of picking to prevent escape or desiccation of the snails. *Carychium* and the associated species were placed in separate containers. Observations on the living animal were best made on snails in the concentration chambers, fresh from the field, rather than on material which had been cultured for some time in the laboratory.

Several methods were tried to kill the animal in a relaxed, extended condition. Stylommatophora are most easily relaxed and extended by drowning. This method proved ineffective for *Carychium* because they frequently contract far into the shell. Menthol water has been found effective for expanding the lymnic Basommatophora. To this relaxing agent *Carychium* also reacted indifferently. Menthol water caused rapid disintegration of the tissues in some cases. The most successful method was found to be that of flooding the extended *Carychium* with a few drops of hot water or hot fixative. This kills and fixes the animal in a matter of seconds after which the container can be filled with cool water to prevent undue histological changes. The animal may be transferred immediately to the fixing fluid of choice.

Alcohol of 70% strength was found to be the most convenient and useful fluid for histological fixation in preparation for sectioning material. Bouin's solution has the advantage of removing the shell, but caused excessive contraction of the tissues. It has the peculiar quality of rendering the tissue more elastic than alcohol, which greatly facilitates gross dissection. Corrosive sublimate was used with success in a few cases but it has no advantages over alcohol.

After fixation, the shells are best removed by placing the specimens in acid alcohol (three drops of concentrated HCl per 50 cc of 30% alcohol) for about eight hours. Removing the shell by acids leaves a pliable sheath around the animal which should be teased off with fine needles as it frequently has adherent detritus which is detrimental to sectioning or gross anatomical dissection.

For histological sections, specimens were first stained *in toto* with carmine, or more frequently with Ehrlich's acid hematoxylin. This shortens the staining process in sectioned material, and greatly facilitates locating the minute specimens both for imbedding and in trimming the paraffin block. Dioxane was chiefly used in the imbedding and post-imbedding processes. Sections of 10 micra were found optimum.

The gross anatomy was most conveniently studied in deshelled specimens placed in various fluids, among which alcohols of moderate strength, xylol, glycerin, water and clove oil were tried. Each fluid has its own use according to the degree of hardness or transparency desired. Minutennadeln imbedded in short applicator sticks were used in dissection. Much of the internal anatomy can be observed in specimens which are stained and cleared. Methylene blue was found the most useful stain for this purpose. Whole mounts were prepared in balsam.

While the external characters of the empty shell may be studied from dried material, wet specimens have the added advantage of being easier to manipulate. Furthermore, the transparent qualities of the shell and refractive index of some common laboratory fluids renders the internal structure easily studied in shells filled and submerged in these liquids. This also obviates the tedious and often disastrous technique of opening the shells with small needles or forceps as has been the custom of previous students (Pilsbry, 1948; Winslow, 1922). The small aperture and labyrinthine interior of the shells of *Carychium* create a problem in filling the interior of the shell with liquid. This infiltration may be easily accomplished by placing the dry shells together with a few drops of alcohol or water in a small Pyrex test tube. The tube is heated over an alcohol lamp just to the boiling point and the bulb of the tube is then plunged into a beaker of cold water. If the shells do not become filled immediately the process may be repeated. Care should be taken that fluids used to store shells are not acid.

Shells for measuring were placed on a strip of wet cotton cloth on a microscope slide, and first oriented to desired position under a low-powered binocular microscope. Actual measurements were done with a compound microscope, using an ocular micrometer in a 10x ocular and 3.2x objective. This method is comparable to that used by Zimmermann as well as by Thorson and Tuxen. All adult shells of a sample were measured, excluding only those broken in a position which would render the reading invalid. Two measurements were taken, the height of the shell, being its maximum extent along the columellar axis, and the maximum diameter, taken at right angles to the height and including the reflected lip of the shell's aperture. The short method of calculation was used on ungrouped class intervals for obtaining the statistical parameters presented in Table 10. The formulae are those recommended by Simpson & Roe (1939); see also Boycott (1928).

Sorting juveniles into size-classes was done with the specimens in 70% alcohol, using a binocular microscope. In counting the number of whorls of the shell, the suture-whorl count was taken rather than the more conventional method of counting whorls of the primary cone. These two methods will be explained below in the section on the biconic concept of a snail's shell.

Under favorable conditions, *Carychium* can be cultured in the laboratory for extended periods. Isolating individuals with little leaf mold in a small container was tried with little success, probably due to manipulation of the individual and the difficulty of controlling moisture. The most satisfactory cultures proved to be the simplest. A quantity of the leaf humus containing *Carychium* was placed in a closed glass container of quart capacity or larger. Ordinary canning jars or small aquaria are suitable. Such cultures have been maintained for 13 months, and need only be placed in the dark and kept moist at moderate temperatures. The associated organisms, particularly annelids, rapidly reduce the leaf mold to a fine mulch, which does not seem advantageous to *Carychium* from the standpoint of the latter's photophobic habits and possibly also from the standpoint of food. Examination of the cultures caused disturbance which doubtlessly resulted in the death of some specimens. Moreover, laboratory specimens were more sluggish and sensitive to light and manipulation than material fresh from the field, possibly because the temperature of the laboratory was at least 10° C warmer than the usual (summer) temperatures of *Carychium* habitats in the field.

ECOLOGY OF *CARYCHIUM* IN LOWER MICHIGAN

During the present study, the ecology of *Carychium* was considered only for the purpose of locating sufficient material for other phases of the problem. The geographical distribution of these snails in Michigan, as determined by my own collecting, is given in Table 1. It will be seen that there are records in most of the counties north of the Saginaw and Grand River valleys, but south of this area only Washtenaw, Lapeer and Huron counties are represented. Very likely representatives of the genus occur in every county of the state as Walker (1906) believed. The geographical distributions of American Carychiidae are given by Pilsbry (1948). In Michigan, *C. exiguum* (Say), *C. exile* H.C. Lea and *C. exile canadense* Clapp have been generally recognized (Pilsbry, 1948; Winslow, 1926; Walker, 1906; Goodrich, 1932). In addition, Winslow (1922) describes shells of "*C. exiguum* var.?"

which she thought might be *C. nannodes* Clapp. Nothing similar was collected in Michigan during the present study, but the record is of interest since Oughton (1948) recorded *C. nannodes* from southern Ontario and thought that species was what Winslow studied in the record cited above. Analysis of the specimens collected during the present study will be deferred to the account of variation of the shell which follows.

In my experience, *Carychium* occurs in Michigan always in isolated microhabitats, areas of a few feet maximum dimension, surrounded by areas unsuited to the survival of these snails. These microhabitats seem to have three characteristics in common: the presence of decaying plant material providing (1) the direct source of food for *Carychium* and (2) shelter; (3) high moisture content of the leaf mold, approximately constant throughout the year. Most frequently the plant material consists of the annual leaf-fall, which is being converted by *Carychium* and its numerous cohabitants into the top layer of the soil. Boettger (1944) states that *C. minimum* is a humus feeder. The shelter which the leaf mold provides is primarily protection from light but also serves to hold moisture. The moisture content is chiefly provided by the seepage of ground water. While the small depression of the terrain which usually contains the *Carychium* microhabitat may hold some water of precipitation, it would never seem to be covered for more than a few hours after a heavy rain, except perhaps in winter when this moisture is solid and the temperature much reduced.

Occasionally the moisture is provided by capillarity from an adjacent body of water, as a small stream which may not overflow its banks for periods longer than a few hours, or a lake which likewise remains within its border. During the present study, *Carychium* was not found in areas which undergo frequent flooding such as the floodplains of major streams. Nor was it taken along the margins of temporary woods pools, which, except for the fluctuation of moisture content that might take place, would otherwise seem to be ideal habitats.

Carychium shells are abundant in stream drift, doubtlessly washed from the headwater areas of the watersheds by heavy rains. Many museum lots and records in the literature are based on stream-drift material, and therefore heterogeneous with regard to individual colonies. These shells have an unusual capacity for holding air, in contrast to some shells with larger apertures and rapid increment of the primary cone, as *Vitrina* or *Succinea,* and thus easily float (see above, in "Materials and Methods").

H.B. Baker (1911, p. 142) noted *Carychium* in washed-in plant detritus (decaying wood and sedges) on a sand beach at Saginaw Bay. He observed that such colonies were narrowly circumscribed, surrounded to a considerable extent by sand which would be unfavorable for the snails.

He also attributed an annual life to these colonies, the whole habitat (plant detritus) and its molluscan inhabitants being renewed in the spring after the thawing of the Bay.

The three requisites for an environment suitable to *Carychium* were strikingly demonstrated in the case of *C. stygium* Call, in Mammoth Cave, Kentucky. These snails were found near the Dead Sea, an isolated lake with subterranean connection with the River Styx which runs nearby. When the river is at flood stage it deposits on the inclined ledges of the Dead Sea Chamber much fine red silt and probably also organic matter. This silt is kept moist by general seepage in the chamber after the river has receded. It is on these ledges that *C. stygium* occurs, living in permanent darkness on a very wet surface which may contain organic matter. Call (1897) reported the snails on wood and fungi in the cave. However, I found the chips of wood were not more productive than the silted ledges, and I could find no specimens associated with fungus. Behind the columns of the Ruins of Karnak, in Mammoth Dome, similar conditions prevail. There is total darkness with plentiful seepage moisture, the latter evidently originating from the surface, for leaf fragments could be found in the trickles of water which wet the columns. *Carychium stygium* also occurred there, but searching in the dryer chambers of the cave, some of which contained old wood supporting a growth of fungus, failed to reveal any specimens.

In Michigan, microhabitats suitable for *Carychium* were located by searching for particular aspects of vegetation and topography which had been found to harbor them. These macrohabitats are of three general types, as outlined below. The locality records of Table 1 are grouped according to these types.

(1) ***Thuja forests.*** This macrohabitat type is characterized by a predominance of *Thuja* and spruce, and often contains white birch and other hardwoods. Very frequently these forests are marginal to lakes or streams, but they also occur in depressions of the terrain where surface water is absent. Small depressions in the forest floor are *Carychium* microhabitats par excellence. Fig. 1 of Plate II illustrates a *Thuja* forest from which most of the evergreens have been cut in preparation for building a house. It indicates the amount of birch which may be present in these woods. This macrohabitat type is preeminently characteristic of the boreal life zone (see Walker, 1906), and therefore found north of the Saginaw-Grand River dividing line, but it also occurs in Huron County on the Saginaw Peninsula, and possibly elsewhere in the southern part of the state. It is characterized by deep leaf mold, rotting stumps and logs, irregular pocketing of the forest floor, dense shade and little or no undergrowth. Some clumps of moss (as *Campylium stellatum, Brachythecium* and *Mnium*) in Reese's Bog,

TABLE 1. Catalogue of material.

Lot No.	County	Locality by Section, Township, Range	Date	Method of Collecting	Total No. Collected	Remarks
Macrohabitat predominantly of "*Thuja*" type:						
C1-C5	Emmett	NW 1/4 Sec 27 T39N R4W	1*)	Q	1*)	Cecil's Bay
E1	Emmett	Sec 3 T35N R4W	28 VII 49	H	16	
R1-R4	Cheboygan	Sec 4 T36N R3W	2*)	Q	2*)	Reese's Bog
B1	Cheboygan	Sec 4 T36N R3W	2 VII 49	H	36	
B2	Cheboygan	Sec 4 T36N R3W	2 VII 49	H	10	
B3	Cheboygan	Sec 4 T36N R3W	2 VII 49	H	32	
B4	Cheboygan	Sec 4 T36N R3W	20 VI 49	H	7	
B5	Cheboygan	Sec 4 T36N R3W	17 VII 49	H	3	
B6	Cheboygan	Sec 4 T36N R3W	17 VII 49	H	3	
B7	Cheboygan	Sec 4 T36N R3W	28 VII 49	Q	17	
B8	Cheboygan	Sec 4 T36N R3W	4 VIII 49	Q	42	
B9	Cheboygan	Sec 4 T36N R3W	1 VII 50	Q	13	
S5	Oceana	Sec 11 T13N R15W	22 VIII 49	Q	96	
S9	Oceana	Sec 36 T15N R17W	23 VIII 49	Q	10	
S20	Mason	Sec 23 T18N R16W	24 VIII 49	Q	109	
S32	Wexford	Sec 9 T24N R9W	25 VIII 49	Q	52	
S52	Clare	Sec 22 T18N R6W	29 VIII 49	H	4	
S58	Missaukee	Sec 7 T23N R7W	30 VIII 49	Q	271	
S71	Kalkaska	Sec 15 T28N R7W	30 VIII 49	Q	46	
S92	Benzie	Sec 4 T26N R13W	1 IX 49	Q	19	
S126	Leelanau	Sec 32-33 T30N R11W	8 IX 49	H	1	
S139	Antrim	Sec 13 T29N N9W	9 IX 49	H	1	
S149	Antrim	Sec 32-33 T30N R6W	9 IX 49	Q	28	
M34	Preque Isle	Sec 30 T35N R5E	30 VI 50	Q	28	
M36	Alcona	Sec 16 T28N R9E	29 VI 50	Q	16	
M45	Montmorency	Sec 25 T30N R1E	3 VII 50	Q	273	
M63	Alpena	Sec 11 T32N R8E	30 VI 50	Q	24	Plate 2 Fig. 1
M64	Oscoda	Sec 36 T26N R2E	3 VII 50	Q	217	
Macrohabitat predominantly of "grassland" type:						
K1	Cheboygan	Sec 19 T38N R3W	7 VII 49	H	11	Mud Creek
K2	Cheboygan	Sec 19 T38N R3W	30 VII 49	H	15	
K3	Cheboygan	Sec 19 T38N R3W	1 VII 50	H	—	
S8	Oceana	Sec 13 T15N R17W	23 VIII 49	H	17	
S10	Oceana	Sec 5 T14N R16W	23 VIII 49	H	2	
S17	Lake	Sec 7 T19N R12W	23 VIII 49	H	12	
S34	Wexford	Sec 31 T24N R11W	25 VIII 49	H	7	
S55	Missaukee	Sec 1 T21N R8W	29 VIII 49	H	7	
S66	Kalkaska	Sec 18 T28N R5W	30 VIII 49	H	9	
S74	Grand Traverse	Sec 8 T26N R9W	31 VIII 49	H	23	
S93	Benzie	Sec 6 T26N R13W	1 IX 49	H	37	
S134	Leelanau	Sec 14 T29N R13W	8 IX 49	H	22	
S147	Antrim	Sec 35 T31N R8W	9 IX 49	H	12	
S164	Emmett	Sec 17 T37N R5W	16 IX 49	H	47	
S170	Cheboygan	Sec 5 T37N R3W	17 IX 49	H	16	
S178	Cheboygan	Sec 10 T34N R1E	17 IX 49	H	6	
M33	Roscommon	Sec 16 T22N R1W	3 VII 50	Q	104	
M46	Bay	Sec 13 T15N R4E	29 VI 50	H	8	Plate 2 Fig. 2

TABLE 1. (Continued)

Lot No.	County	Locality by Section, Township, Range	Date	Method of Collecting	Total No. Collected	Remarks
Macrohabitat predominantly of "hardwood" types (mixed unless specified):						
Q1	Cheboygan	Sec 12 T36N R1W	3 VII 49	H	18	
T1	Cheboygan	Sec 12 T36N R1W	3 VII 49	H	14	Long Lake
T2	Cheboygan	Sec 12 T36N R1W	30 VI 49	Q	54	
G1-G16	Washtenaw	Sec 35 T2S R6E	3*)	Q	3*)	Plate 3
S53	Clare	Sec 7 T18N R6W	29 VIII 49	Q	29	
S110	Benzie	Sec 19 T25N R14W	7 IX 49	Q	148	
S131	Leelanau	Sec 13 T32N R11W	8 IX 49	Q	4	
M62	Iosco	Sec 23 T22N R8E	29 VI 50	Q	9	
M51	Otsego	Sec 9 T30N R2W	3 VII 50	Q	36	Maple
M50	Montmorency	Sec 30 T30N R1E	3 VII 50	Q	30	Maple
M66	Ogemaw	Sec 12 T22N R2E	3 VII 50	Q	18	Maple
M40	Huron	Sec 13 T18N R14W	4 VII 50	Q	3	Birch
M38	Lapeer	Sec 16 T7N R12E	5 VII 50	Q	8	*Populus*
M39	Lapeer	Sec 9 T7N R9E	5 VII 50	Q	6	*Populus*
M1	Bay	Sec 13 T15N R4E	29 VI 50	Q	11	Oak
M60	Arenac	Sec 17 T19N R7E	29 VI 50	Q	33	

1*) - C1-C5 Emmett County, periodically collected; see Table 5.
2*) - R1-R4 Reese's Bog, Cheboygan County, periodically collected; see Table 6.
3*) - G1-G16 Geddes Island, Washtenaw County, periodically collected; see Tables 3 and 4.
Q - quantitative leaf samples, concentrated in the laboratory.
H - material hand-picked and concentrated in the field.

Letters prefixing lot numbers indicate in a general way the correlation of material, thus: the C, R, T, K and G lots were taken by repeatedly collecting the same five microhabitats.

Each lot of the B series is from a different microhabitat in Reese's Bog, and distinct from the microhabitat which furnished the R series.

The S series represents distinct localities on the northwest side of the Lower Peninsula of Michigan collected during August and September of 1949, and the M series represents distinct localities on the east side of the Lower Peninsula collected during late June and early July of 1950.

Cheboygan County, were found harboring *Carychium* in their deeper, dying portions. This snail was never found associated with *Sphagnum*, however. Ferns, as well as mosses, may be abundant. Often there are seepage springs and small streams along the margins of which *Carychium* occurs. The Cecil's Bay station in Emmet County (lots C1-C5) is adjacent to a small *Typha*-filled swamp, and the major station of Reese's Bog, Cheboygan County (lots R1-R4) is marginal to a small stream.

(2) **Grasslands.** Under this heading are included open areas which are covered by low-growing annual vegetation, not shaded by trees. Besides grasses, several other plants may characterize the flora of this macrohabitat, among them may be mentioned *Iris, Typha, Solidago, Lobelia* and *Onoclea.* This habitat type is also usually marginal to small streams and lakes or marshes whose water level does not fluctuate appreciably throughout the year. However, come grasslands wetted only by subsurface seepage also

PLATE II

Habitats of *Carychium.* FIG. 1. *Thuja* habitat in Alpena County. Most of the *Thuja* has been cut. Station M63. FIG. 2. Grassland habitat (foreground) of station M46, and hardwood habitat (background) of station M1. Near Saginaw Bay, Bay County.

yielded *Carychium*. The several macrohabitats of this type investigated south of the Saginaw-Grand River dividing line produced no *Carychium*, though collecting was limited in that region.

In the northern part of the state the grassland macrohabitats were one of the most productive types investigated. While a few natural grassy areas were visited (*e.g.*, station M33, where sufficient decaying organic matter was present to take a quantitative sample), it soon became evident that most of them were much affected by human activity, as witness their occurrence along roadsides and in pastures. Indeed, they appear to be maintained as grassland areas by the agency of man, by his mowing the roadsides and introducing grazing animals into the pastures. Probably many of the grassland habitats were originally *Thuja* forests, evidence of which remains in old stumps and logs. If this hypothesis be correct, it is noteworthy that *Carychium* is not affected, at least under these conditions, by man's control of the environment.

In grassland habitats, collecting was most easily done by searching the underside of sticks and wood, or even large pieces of paper or discarded metal objects. From these the snails were picked by hand in the field. Returning to a given grassy habitat at a later date and examining the same object always revealed more *Carychium*, though the object had been picked free from all visible specimens on the first visit. Very likely the snails are distributed through the grass roots and thin layer of decaying organic matter about them from which they wander to the surface of the log or other objects.

The grassland habitat itself is dependent upon a greater amount of light than would be allowed by the foliage canopy in a *Thuja* or hardwood forest. Yet within the stratum of organic detritus and grass roots, very thin in comparison with the similar layer of other macrohabitat types, and under the logs, etc., which occur in these habitats, we may suppose there is sufficient darkness to encourage *Carychium*.

Fig. 2 of Plate II illustrates two habitats productive of *Carychium*. This area is in the marshes at the lower end of Saginaw Bay. Low, concentric ridges, evidently representing ancient beach dunes, parallel the shore of the bay and in close between them *Typha*-filled marshes, presumably of constant water level. A road has been built traversing the ridges at right angles. Along the road grow *Solidago, Iris, Onoclea, Carex* and various grasses. The roadside had been freshly mowed when the picture was taken. *Carychium* (lot 146) was picked here from under a large tin can lying in the seepage area of the roadbank close to the water's edge. The snails were also found in oak leaves in the ditch where the road crosses the ridge (background of picture; lot M1). H.B. Baker (1911: 143) described the ecology of similar dunes and marshes just inland from the southern shore of Saginaw Bay and notes the presence of *Carychium.*

(3) **Hardwood forests.** Under this large category a number of subdivisions are necessary. Most of the extensive upland forest types, such as pine, aspen-bracken association and oak above the Saginaw-Grand divide are almost if not devoid of conditions suitable for *Carychium.* Exceptions to this were noted; a small hollow filled with *Alnus,* ferns and grass, and surrounded by a narrow zone of mixed hardwood transitional to the oak flatlands of Roscommon County constituted station M33. Since the specimens were picked from a quantitative sample of decaying grass leaves this habitat should really be considered of the grassland type.

In general, in the upper part of the Lower Peninsula, a zone of mixed hardwood is to be found between the *Thuja* lowland acme and the aspen-bracken or other upland forest type. Here these mixed hardwood zones have extensive width, they often contain *Carychium* microhabitats. Lots T1 and T2 are from such a zone along the roadside near the south end of Long Lake, Cheboygan County; a narrow margin of grass, *Solidago* and *Onoclea* edged the road embankment. In this zone there was a substrate of leaf mold provided by the trees. Elm was one of the most prominent trees of this assemblage, which also contained hickory and a few isolated *Thuja* and birch.

There are some deciduous forests of limited extent but constituting almost pure stands of one type of tree, which may provide favorable *Carychium* microhabitats. Undisturbed maple forests contain a deep leaf mold layer on a pocketed forest floor with little undergrowth. In the deeper parts of the old stump holes *Carychium* is often present though never abundant in my experience. Moreover, the shells from such localities have a form included in the concept of *C. exile canadense,* and are among the largest specimens found during the present study (lots M50 and M51). This is discussed below (p. 39). An almost pure stand of birch was found at the northern end of Huron County, which contained *Carychium* (lot M40). The conditions of the forest floor were similar to that described for the maple forest.

The deciduous forests discussed thus far are those characteristic of the boreal life zone, which in Michigan occurs primarily north of the Saginaw-Grand River dividing line. South of that line, *Populus* is often an indicator of microhabitats containing *Carychium.* Such was the case of the Washtenaw County station (G series of samples), from which the major material was taken for anatomical study. This station is on an island in the Geddes impoundment of the Huron River. The summer appearance of this station is illustrated in Fig. 1 of Plate III, and its fall appearance is illustrated in Fig. 2 of the same plate. The small *Populus* in the center of the picture grows in the small depression which contains the rich *Carychium* colony. Also present are *Cornus* and *Alnus,* many annuals and perennials, the latter including blackberries and wild grapes. Adjacent to the *Populus* depression is a small pool (Fig. 1 of Plate III), and in line with these two is a larger pool not seen in the photograph. Both the pools and the *Populus* depression are in a large sink, possibly an artificial excavation, for the sink contains no trees of any size though all around it on the island there is a forest of oak. Neither of the pools are connected above the ground with Geddes Pond. However, when the water of the pond was lowered about two feet, by opening Geddes Dam in the summer of 1950, the water levels in the two pools likewise went down. It subsequently rose again as the level of Geddes Pond rose, after the dam was closed. The *Populus* depression is just deep enough to reach the level of the water table of the pond and pools, and presumably its moisture content likewise fluctuated.

In the course of this work isolated ecological factors were not consistently measured with exactness. However, several synecological studies which record *Carychium,* or associated biota found with it in the present study, have provided data on these factors. The few temperatures taken during the present study indicate the leaf mold layer in which *Carychium* lives is 5 to 10 degrees lower than the air temperatures from late spring to early fall. In mid-winter, the samples from the Washtenaw County station were frozen solid. These samples produced living specimens after they were thawed. Water seemed greatly in excess to that present during the parts of the year when the ground was not frozen.

In a deciduous forest on Mt. Katahdin[1] Maine, which contained *Carychium,* Blake (1926) noted that many organisms occurring in the leaf layer of the forest floor survive freezing for many weeks. He found temperatures of the soil 15 centimeters below the surface of the ground to range from 7° above to minus 2° C, and the range below the surface showed less weekly fluctuation than the air temperature 0.6 meters above the ground, which ranged from 2° above to minus 15° C during the period of November to March.

Evidently the hydrogen ion concentration plays an important and direct role as a factor affecting *Carychium* and other mollusks which are exposed to it. This has been touched on above in discussing the alcoholic leaf sampling method of collecting and will be considered again in discussing the evidence of mortality for colonies of these snails. Those few determinations of pH made during the present study were very crude but indicate a wide range within an area of a few feet. A few determinations

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[1] Spelled Mt. "Ktaadn" in his article.

PLATE III

Seasonal changes in habitat. FIG. 1. The *Carychium* station on Geddes Island, Washtenaw County. The microhabitat occurs in a depression from which grows the small *Populus* tree, slightly to the right of center. Summer aspect. FIG. 2. Autumn aspect of the same locality shown in Figure 1. The small pool (lower left) is covered with freshly fallen leaves.

were made in Reese's Bog, using a soil testing kit (colorimetric). The variation of pH encountered in a *Thuja* forest such as Reese's Bog is indicated by the pH ranges found for various mosses which inhabit such an environment as reported by Robinove & LaRue (1929). Atkins & Lebour (1923) thought the hydrogen ion concentration of the soil to be a limiting factor in the distribution of snails in Ireland although they admit there are probably other factors involved. They found *Carychium minimum* in soils of pH 6.5 to 7.0 but the animals were more common at the latter pH. However, their data are based on only two stations, each presumably sampled only once.

Strandine (1941) has given monthly variation in pH, organic content and moisture for a habitat of *Succinea ovalis* in Illinois. Each monthly sample contains data for the four strata of the forest floor which he recognized: leaves, leaf-mold, top-soil and sub-soil. The pH showed a general trend to be most acid in the leaf mold layer, which, however, ranged from 5.9 to 7.2 during the year. Organic matter varied from the greatest percentage in the leaf layer (always over 85%) to the least in the subsoil (always under 8%, usually much less) throughout the year. Moisture content showed least variation in the sub-soil, ranging from 11.3 to 24.4%, and most variation in the leaf-mold layer, ranging from 32.9 to 338.5%.

Generally, in treating the ecology of snails in a given region, there is an attempt to fit the mollusks to patterns of topography or plant habitats. An example is found in the introduction to Goodrich's "Mollusca of Michigan" (1932), and the literature is replete with others. Indeed, the outline of macrohabitat types given above borders on this procedure.

Boycott (1929) has proposed another method which promises great rewards in establishing a pattern of ecology for land snails. While some land snails may be obviously limited by a simple factor of the environment, most are not. In essence his thesis is that snails have a differential tolerance for the range of environmental factors considered as a complex entity. He would deny competition as an important relationship among humus feeding snails, and thus excluded the concept of associations in the sense that it is useful in plant ecology. Without recourse to exact measurement of the effective components it is possible to note the results of these factors by the assemblages of snails of a given habitat, he stated that: "The species which live in the worst places occur also in the best" and he, therefore, drew up a graded hierarchy of habitats characterized by the mollusk species which they contain. The categories of this series have one to five species, "each group being less particular about shelter and alkalinity than those below it" in the series.

This approach is similar to that of Raunkiaer's (1934) in grouping plants according to their morphological adaptations to the unfavorable season, and indexing a given area by the various percentages of each category or "life-form" which it contains. Raunkiaer's approach would be more difficult to apply to land snails because their morphological adaptations are less distinctive or varied than are those of plants; possibly it could be done if more life histories of snails were known and correlated with the seasons. However, Strandine asserted that *Succinea ovalis* is the commonest snail of its habitat in his study-area of Illinois, based on a Raunkaier's analysis. Findings during the present study (Table 2) do not support his conclusions, though perhaps he was dealing with habitats more favorable for *Succinea* and less favorable for some of its associated species, while the converse may be true of the present study.

Table 2 presents selected lists of mollusks found occurring with *Carychium* in Michigan. The lists were selected according to the more frequent assemblages and include almost all the associated species found. The number of specimens indicates total number of shells, living or dead, and all growth stages. Perfection of this method would require further analysis of those components. The lists are probably inaccurate in recording the number of slugs, which were seldom preserved by the methods used. Some of the larger snails, as *Anguispira, Haplotrema* and the polygyrids have a range of vagility and browsing interest greater than that of the smaller leaf mold inhabitants, and occur with fewer individuals in a unit area than the latter. Other members of the list, notably some of the freshwater species, are possibly strays which have gotten into the *Carychium* habitat because the latter are marginal to habitats more suited to the strays. This is true of *Aplexa* and *Helisoma,* possibly also of the other planorbids, but it does not seem to apply to *Sphaerium occidentale* and *Fossaria dalli* of the Washtenaw County station (series G). These species seem to live in conditions essentially similar to *Carychium,* though occurring at the lowest part of the *Populus* depression, and not extending as far up the slope as *Carychium.*

In the present instance, attention is focused on *Carychium* habitats. Further studies should also be directed to each of the other species to determine the habitat types in which they occur, but in which *Carychium* (or another associated species, respectively) is absent. Nor should the possibility of absence of a species due to isolation be overlooked. Several habitats were found during the present study which appeared ideal for *Carychium* but which proved negative. The conservative identifications of associated species given in Table 2 are also to be taken with reservation. On the relatively small numbers of specimens of the associated species nothing like the morphological variation or other phases of the biology noted in *Carychium* was found. Yet, it is probable that taxonomic concepts

TABLE 2. Lists of mollusks associated with *Carychium*, in selected stations in Michigan.

Species	Lot numbers, county, locality and macrohabitat type. (See below).											
	1	2	3	4	5	6	7	8	9	10	11	12
Carychium exiguum	1173	899		x104	54	11	33	18	3	6	1354	9
Stenotrema hirsutum											2	
Stenotrema leai		3				2	2		1	3	2	
Stenotrema fraternum	1	1							1			
Triodopsis albolabris	x	1										
Triodopsis multilineata					x						1	
Mesodon thyroidus										1		
Haplotrema concavum	1											
Euconulus fulvus	16	19	x	2	3		4	7	4			
Retinella electrina											77	
Retinella binneyana	60	113		6	7		5		1			6
Retinella indentata									2		36	
Paravitrea multidentata								11				
Hawaiia minuscula											3	
Zonitoides arboreus		1	x				10	13			2	7
Zonitoides nitidus						4						
Striatura exigua	38	17		2	20			19				5
Striatura milium	6				5			5				4
Striatura ferrea	1											
Vitrina limpida									4			
Deroceras laeve											23	
Deroceras reticulatum			x									
Anguispira alternata	1	2					1				4	
Discus cr. catskillensis	75	87	x	2	19		3	76	2			
Helicodiscus parallelus	x				25		65	1				
Punctum minutissimum	130	233			5		12	2	1		2	5
Pallifera dorsalis	x										x	
Oxyloma retusa						4				3		
Succinea ovalis		7			1		1	3	13		35	
Succinea avara		9										
Succinea cf. decampi						1						
Strobilops labyrinthica	15	80		7	31		13	4				
Gastrocopta contracta							16				1	
Gastrocopta tappaniana		67					11	3		1	1	
Vertigo ovata	23	25		1			1			2	1	3
Vallonia sp.			x									
Planogyra asteriscus	22				3							
Columella edentula	3	1			11		4					3
Cionella lubrica		16			1	1		2	2		23	
Planorbula armigera		4		2		1						x
Gyraulus circumstriatus	2	3										
Helisoma campanulatum												x
Fossaria dalli	2			1							2	1
Stagnicola palustris												x
Aplexa hypnorum	1	1				3				1		1
Sphaerium occidentale	7	83		11							100	1
Musculium transversum												1
Pisidium abditum												1

TABLE 2 (Continued)

Lot numbers, county, locality and macrohabitat type.

1: Reese's Bog, Cheboygan Co. R1, R2, R3. *Thuja*.
2: Emmet Co. C1, C2, C3, C4, C5. *Thuja*.
3: Mud Creek, Cheboygan Co. K3. Grassy.
4: Roscommon Co. M33. Grassy.
5: Long Lake, Cheboygan Co. T2. Intermediate.
6: Bay Co. M1. Deciduous (oak).
7: Arenac Co. M60. Deciduous (mixed).
8: Ogemaw Co. M66. Deciduous (maple).
9: Huron Co. M40. Deciduous (birch).
10: Lapeer Co. M39. Deciduous (*Populus*).
11: Washtenaw Co. G2, G5, G7, G8, G9. Deciduous (*Populus*).
12: Iosco Co. M62. Deciduous (mixed).

will be altered for several of the groups represented when more intensive studies of individual species are undertaken.

Besides the mollusks listed, a large number of other invertebrates were found but not counted or identified beyond major groups. These include spiders, mites, insects, earthworms and enchytraeids, pseudoscorpions and myriapods.

Occasional synecological studies mention *Carychium.* F.C. Baker (1910) lists *Carychium exile* and the associated mollusks of a station in Illinois. All the associated species are among those included in the present study. The station from which he listed *Carychium* is apparently of the grassland macrohabitat type proposed above and was produced by clearing a forest.

In his ecological study of a deciduous forest on Mt. Katahdin in Maine, Blake (1926) gives some interesting data on *Carychium.* He recognized *C. exiguum* and *C. exile,* both occurring in the leaf layers of the forest floor (in which he differentiated only leaf layer and top-soil layer). *Carychium exiguum* was reported as the third most common inhabitant of that layer, while *C. exile* occurred as the 17th most abundant of the 30 invertebrates listed. *Carychium exiguum* was "present in the largest numbers of any mollusk," and is graphed as reaching a peak of abundance (number per volume of stratum) in February, and *C. exile* in November (the only month from October through February in which it was found). He discusses the fluctuation of abundance (no exact figures are given) of *C. exiguum,* which remained at a moderate level from November through January but greatly increased in February. This increase he suspected was due to a rising moisture content (rising temperature was also noted) which was coincidental with that time. In his summary he considers the fluctuating abundance of the leaf and soil organisms as due to vertical migration during the fall and winter. But since he found *C. exile* limited to the leaf-layer, and in view of microhabitat concepts proposed above, it appears that insufficiency of sampling methods produced his results.

H.B. Baker (1911) discussed the molluscan habitats in the area of the south shore of Saginaw Bay. Some of his *Carychium* records have been cited above under the temporary decaying wood-sedge heaps washed upon the beach and the parallel dunes and marshes inland from the Bay. He also noted the presence of *Carychium* in "swampy meadows" (p. 148) and deciduous forests ("wooded flats" near the Pigeon and Pinnebog Rivers, also "swampy woods," p. 148). There is an implication in his report of spring flooding in some of these permanent habitats of *Carychium.* This discrepancy with our field observations may be a matter of perspective. The need of considering small areas a few feet in diameter as the limited habitat of land snails should be emphasized. To generalize the potentials of vagility, the habits of the snail, as well as the extent of tolerable factors of the environment, should all be considered in defining the habitat of a given snail. Baker's report is further of interest in that it often cites *C. exiguum* and *C. exile* from the same habitat, and in the close agreement of his lists of other mollusks associated with *Carychium* with those listed in Table 2 of the present study, even though his concepts of a habitat probably include a larger area.

LIFE HISTORY OF *CARYCHIUM* IN LOWER MICHIGAN

Field data on the life history of *Carychium exiguum* in Michigan indicates a very short reproductive period occurring in midsummer. No eggs have been observed in field samples or laboratory cultures, yet evidence from the anatomy of the genital tract (to be discussed in the section on the reproductive system) indicates this snail is oviparous and produces about three eggs. Growth of the juveniles continues through the summer. By mid-fall the young almost entirely disappear from the population, which winters as adults. Such immatures as occur at other times of the year than during the growth period probably are products of the normal reproductive season, much delayed in growth, rather than of eggs laid at other times of the year. The rare extra-seasonal juveniles found were usually more than half-grown and most often represented only by dead shells (compare Tables 3 and 4). There is dubious evidence that mortality for both juveniles and adults is higher during late summer and early fall than during other times of the year. The life span is at least one year, but there is little evidence of how much longer the individuals may average beyond that time.

TABLE 3. Actual numbers of *Carychium* collected from a living population at the Geddes Island (Washtenaw County) station.

		Juvenile whorl classes										
Lot Number	Date	Under 1	1 – 1 1/4	1 1/2 – 1 3/4	2 – 2 1/4	2 1/2 – 2 3/4	3 – 3 1/4	3 1/2 – 3 3/4	4 – 4 1/4	Total juv.	Adults	Total live population
G1	6.V.50				1		1	1		3	41	44
G2	11.VI.50								2	2	78	80
G3	18.VI.50									0	47	47
G4	28.VI.50		1							1	49	50
G5	9.VII.50	28	69	30	2					129	69	198
G6	16.VII.50	4	18	15	4					41	28	69
G7	17.VII.50	1	18	28	18	2				67	37	104
G8	25.VII.50	6	98	109	97	25	5	2		342	40	382
G9	3.VIII.50	9	71	103	122	70	23	8		406	31	437
G10	14.VIII.50		8	18	39	11	8	1		85	5	90
G11	27.VIII.50		4	6	20	19	14	9	2	74	22	96
G12	22.IX.50			4	5	14	18	14	4	59	45	104
G13	26.X.50					5	5	5	4	19	42	61
G14	6.XII.50									0	17	17
G15	3.I.51						1			1	20	21
G16	25.II.51									0	21	21

TABLE 4. Actual numbers of dead *Carychium* shells taken at the Geddes Island (Washtenaw County) station.

		Juvenile whorl classes										
Lot Number	Date	Under 1	1 – 1 1/4	1 1/2 – 1 3/4	2 – 2 1/4	2 1/2 – 2 3/4	3 – 3 1/4	3 1/2 – 3 3/4	4 – 4 1/4	Total juv.	Adults	Total dead shells
G1	6.V.50							1		1	4	5
G2	11.VI.50						1	1		2	11	13
G3	18.VI.50				1	1				2	9	11
G4	28.VI.50							1		1	10	11
G5	9.VII.50			1	1	2	1	1	1	7	18	25
G6	16.VII.50									0	4	4
G7	17.VII.50						1		2	3	13	16
G8	25.VII.50		5	3	5	1	3	2	1	20	48	68
G9	3.VIII.50		5	4	2	1				12	10	22
G10	14.VIII.50			3		1	2	1		7	12	19
G11	27.VIII.50		1	2	2	3	2			10	19	29
G12	22.IX.50		2	5	27	20	36	5	6	101	24	125
G13	26.X.50			1	2	9	18	13	6	49	37	86
G14	6.XII.50		1	1	12	35	29	23	12	113	56	169
G15	3.I.51				3		1	5	2	11	17	28
G16	25.II.51				2	10	10	7	2	31	29	60

The life history is best presented from the data of the colony studied in Washtenaw County which were collected repeatedly from May, 1950, to February, 1951. Actual numbers of living individuals taken at each date are listed in Table 3 and those of the dead shells in Table 4. Since the quantity of material collected each time was only approximately the same for different samples (one to two quarts of leaf mold), and not measured exactly, the size groups are not absolutely comparable. Comparison on a percentage basis is presented graphically in Plate IV. The determinate growth of the shell of *Carychium* allows exact differentiation of a mature, or ephebic, shell-stage from the immature stages. This difference is discussed below (p. 31).

Through May and June or 1950, the adults constituted over 90% of the total population. Between 28 June and 9 July there was a sudden appearance of juveniles in such numbers that the adults then formed only one-third of the total population. All immature specimens of the 9 July sample are less than half grown, and predominantly grouped near the minimum size-range. Samples taken during the next three months indicate a gradual shifting of the mean juvenile size toward the adult limit. The curve of immature size-array was nearly flattened by late October and probably disappeared in early November. About a month after its first appearance, the minimum size-group is no longer evident in the field. But some of the juveniles have already reached the range of adult size (3H - 4H suture whorls) while the minimum size-class is still present. No criterion was discovered whereby the adults of one season could be distinguished from those of the previous season or seasons.

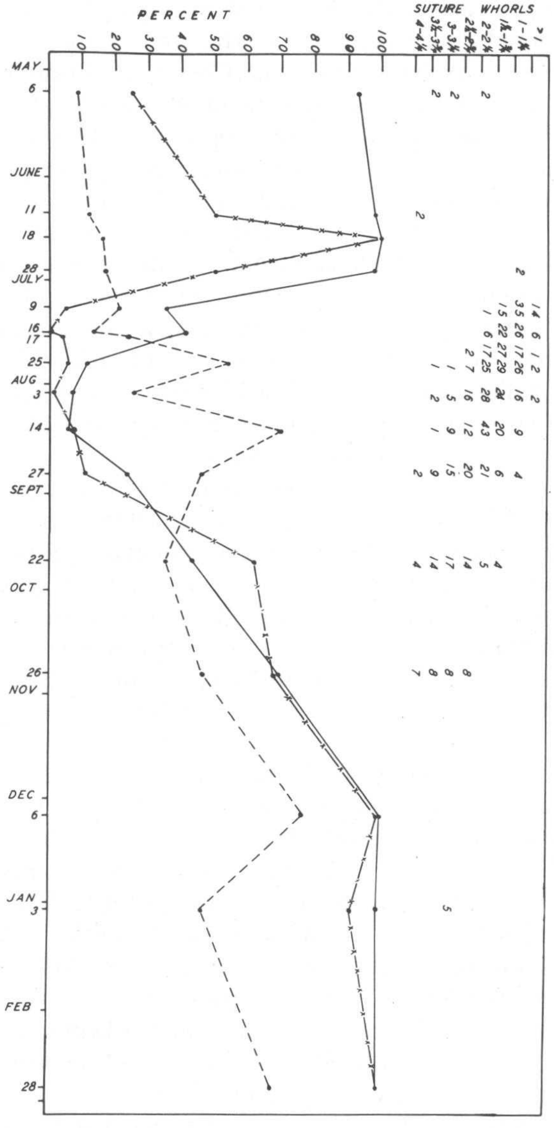
Unless totally consumed by predators, or for any reason whereby the individual is removed from the habitat, the shelled snails on dying leave a record of their existence by the shell itself. In a given sample, empty shells are in varying state of deterioration from at least two causes. (1) Chemical erosion of the shell may be reasonably assumed in such an acid medium as moist leaf mold. Translucent shells become opaque and white, and are more fragile than those containing the living animal. The effect of natural acids on destroying shells was strikingly demonstrated in the alcoholic leaf sampling method described above in the section on Materials and Methods. (2) Several biological agents which destroy the shells may be detected by inspection; plant rootlets often invade the shell, and living snails often rasp at other shells for a convenient, concentrated source of calcium. In studying a population of *Succinea ovalis*, Strandine assumed that an increase in the number of dead shells relative to the number of live snails indicated an increase of mortality. This hypothesis would have more justification if the effect of physiochemical and biological deteriorating agents was constant throughout the year. In all likelihood the shells deteriorate more rapidly with increased temperature and moisture and decreased pH. The situation becomes further complicated on considering the seasonal variation of the rate at which the biological agents act to consume empty shells. The effect of all destructive agents would seem to be much less in winter, particularly when the leaf mold layer is frozen, than at other times of the year.

It is notable that the dead shell index of adult *Carychium,* as shown by the broken line in Plate IV, follows the general density pattern of that presented by Strandine for *Succinea,* except that a marked decrease in dead shells is noted for *Succinea* from October to December. During the earlier half of the growing season, the percent of the dead juvenile shells of *Carychium* dropped to less than 10, while during the latter half of that period they greatly increased in numbers, rising to and maintaining a maximum through the winter. At the same time the adult shells are increasing, rising from a steady 10% during the spring to over 40% in mid-July, and maintaining a high frequency during the rest off the year. This may indicate an elevated mortality rate for both juveniles and adults during the late summer and fall. Many juveniles do not reach maturity; a comparison of Tables 3 and 4 indicates that the death rate is about the same for all stages of juveniles. The dead adult shells increase in number somewhat earlier than the dead juveniles, beginning at about the time of the egg-laying season. This mortality may indicate that the adults die after oviposition.

That the numerical data resulting from the methods employed should not be interpreted too exactly needs little emphasis. As a check on validity, two samples were collected on subsequent days (16 and 17 July). The discrepancies between them do not disrupt the general trend of the pattern to any appreciable extent. The juvenile shell sizes were counted by using a binocular microscope with the shells in 70% alcohol. While this procedure allows them to be oriented with more facility than when the shells are dry, the center of gravity of the shells is such that those class-sizes ending in 1 whorl are difficult to count, and in the last analysis it was found that those sizes had invariably been slighted. Hence the grouping of the classes shown in Tables 3 through 6.

There is some evidence for presuming the pattern outlined for the life history of *Carychium* on the basis of the Washtenaw County material may be valid with slight modifications for the rest of the Lower Peninsula of Michigan. Early collecting in Cheboygan and Emmet counties was done by hand picking the samples in the field in June and July, 1949. It was noted that juveniles were almost absent and that what few occurred were

PLATE IV



Graphic analysis of the population components of the Washtenaw County station, based on the data of Tables 3 and 4. Numbers at the top of the graph indicate percentages of whorl classes of the juveniles. The adult whorl class is from 3 1/2 to 4 1/2, but shells without at least columellar reflection of the lip were included as juveniles. The solid line indicates percent of adults in the living population. The broken line indicates percent of dead adult shells (living and dead adult shells constituting 100%). The broken line with crosses indicates percent of dead juvenile shells (living and dead shells constituting 100%).

usually over half-grown and often only dead shells. But more juveniles than adults could be detected in the field at the first collecting of the Cecil's Bay station, Emmet County, on 23 July. This station, and a similar one in Reese's Bog at the north end of Burt Lake, Cheboygan County, were thereafter sampled quantitatively at intervals of several days for a period of about one month. The absolute numbers of shells collected are presented in Tables 5 and 6, from which the percentage analyses presented graphically in Plate V are derived. Though the segment of the life history presented by this data is very limited, it approximates the pattern of population composition of the Washtenaw County colony for the same season. The essential difference may be that the two northern colonies seen to have a slightly later reproductive season than the latter. If such a difference is real, it may be due to differences in the latitude or season, or both. Both northern stations were revisited early in July, 1950, and found to contain less than 10% juveniles in the living population (the data are included in the graphs and tables of the 1949 collections).

The results of regional collecting of the northwest counties of the Lower Peninsula of Michigan, done in August and September of 1949, is presented in Table 7. Most of the populations contain a large number of living juveniles. Assuming all stations followed the pattern outlined for the Washtenaw County station, some of the juveniles would already have reached the adult limit by the time of collection. The chief discrepancies (*i.e.*, no juveniles, or 100% adults in the living population) are those small lots, hand picked in the field. Possibly juveniles were overlooked in collecting.

Table 8 presents the data of the regional collecting on the east side of the Lower Peninsula of Michigan from 29 June to 5 July, 1950 (*i.e.*, just prior to the expected phenological period). Half of the lots contain only adults in the population. In the other half a variable but rather large number of juveniles were found. This discrepancy might be due to differences in the time of the phenological period according to the localities. A large technical error may also be responsible for the discrepancies. The work involved in concentrating and analyzing the samples extended over a period of several months during which time the material was kept in cotton bags in the laboratory. Possibly insufficient drying allowed the samples to continue as cultures simulating conditions of the field.

In laboratory cultures general evidence in support of the life history as outlined above was obtained. Occasional juveniles may be found at any time of the year, but high percentages of juveniles were found only in cultures during the middle of the summer. The habits of *Carychium* are such that it would be difficult to examine cultures of quart or gallon ca-

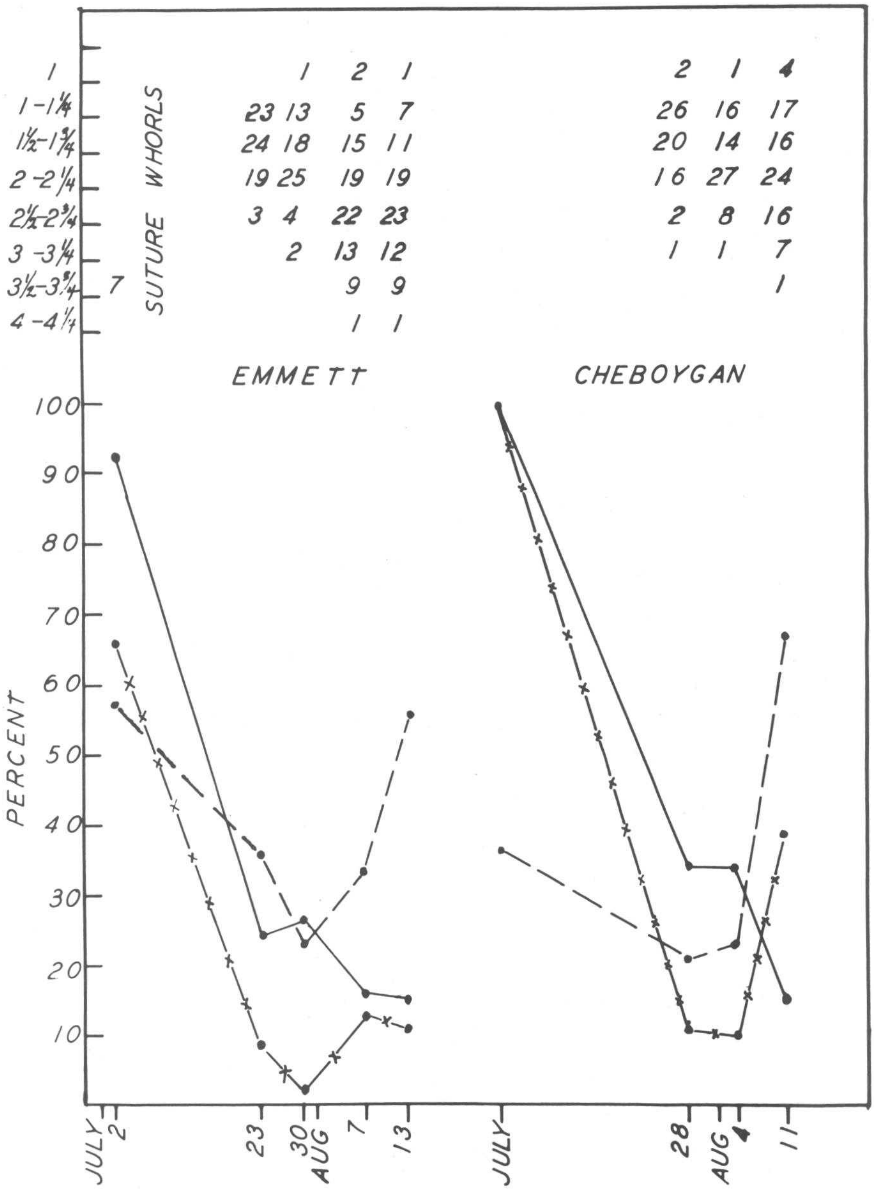
TABLE 5. Actual numbers of living *Carychium* and dead shells collected at the Cecil's Bay, Emmett County, station.

		Living animals Juvenile whorl classes										
Lot Number	Date	Under 1	1 – 1 1/4	1 1/2 – 1 3/4	2 – 2 1/4	2 1/2 – 2 3/4	3 – 3 1/4	3 1/2 – 3 3/4	4 – 4 1/4	Total juv.	Adults	Total adults and juv.
C1	23.VII.49		40	42	26	5				113	64	177
C2	30.VII.49	1	13	19	26	15	2			76	28	104
C3	7.VIII.49	4	12	33	41	49	30	11	2	182	35	217
C4	13.VIII.49	1	10	15	26	32	17	12	2	115	21	136
C5	2.VII.50						1			1	13	14
		Dead shells										
C1	23.VII.49		2	5	1		1	2		11	36	47
C2	30.VII.49				1	1				2	8	10
C3	7.VIII.49		3	2	2	3	2	1		13	18	31
C4	13.VIII.49		4	1	5		2	1	1	14	26	40
C5	2.VII.50						1	1		2	17	19

TABLE 6. Actual numbers of living *Carychium* and dead shells collected at the Reese's Bog (Cheboygan County) station.

		Living animals Juvenile whorl classes										
Lot Number	Date	Under 1	1 – 1 1/4	1 1/2 – 1 3/4	2 – 2 1/4	2 1/2 – 2 3/4	3 – 3 1/4	3 1/2 – 3 3/4	4 – 4 1/4	Total juv.	Adults	Total adults and juv.
R1	28.VII.49	7	94	73	59	8				241	122	363
R2	4.VIII.49	3	47	42	82	23	2			199	102	301
R3	11.VIII.49	8	37	35	51	35	16	2		184	32	216
R4	1.VII.50									0	33	33
		Dead shells										
R1	28.VII.49		6	3	3	4	4	4	5	29	32	61
R2	4.VIII.49		6		2	3	3	5	2	21	30	51
R3	11.VIII.49		21	18	28	19	9	11	9	115	66	181
R4	1.VII.50				1	1	3	3	1	9	18	27

PLATE V



Graphic representation of the Cecil's Bay, Emmett County, and Reese's Bog, Cheboygan County, stations, based on the data of Tables 5 and 6. Symbols as on Plate IV.

TABLE 7. Regional collections of late August and early September, 1949, in the western part of the Lower Peninsula of Michigan, analyzed for age (size) and viability groups. H: hand picked in the field; Q: quantitative leaf mold sample taken. The percentages in "Adults alive" column are based on total living population.

Lot Number	Date (all 1949)	County	Collecting method	Juveniles alive	Juveniles dead	Adults alive	Adults dead	Total living population	Percentage adults alive	Total shells alive and dead	Macrohabitat type
S5	22.VIII	Oceana	Q	30	4	57	5	87	65	96	*Thuja*
S8	23.VIII	Oceana	H	6	0	10	1	16	63	17	Grassland
S9	23.VIII	Oceana	Q	1	1	2	6	3	67	10	*Thuja*
S10	23.VIII	Oceana	H	1	1	0	0	1	0	2	Grassland
S17	23.VIII	Lake	H	1	0	10	1	11	99	12	Grassland
S20	24.VIII	Mason	Q	16	17	29	47	45	64	109	*Thuja*
S32	25.VIII	Wexford	Q	15	10	14	13	29	48	52	*Thuja*
S34	25.VIII	Wexford	H	5	0	1	1	6	17	7	Grassland
S52	29.VIII	Clare	H	0	0	4	0	4	100	4	*Thuja*
S53	29.VIII	Clare	Q	4	6	18	11	22	50	29	Hardwood
S55	29.VIII	Missaukee	H	1	0	6	0	7	86	7	Grassland
S58	30.VIII	Missaukee	Q	183	29	32	27	215	15	271	*Thuja*
S62	30.VIII	Kalkaska	H	0	0	1	0	1	100	1	Hardwood
S66	30.VIII	Kalkaska	H	0	0	8	1	8	100	9	Grassland
S71	30.VIII	Kalkaska	Q	4	1	36	5	40	90	46	*Thuja*
S74	31.VIII	Grand Trav.	H	2	0	21	0	23	92	23	Grassland
S92	1.IX	Benzie	Q	5	3	7	4	12	58	19	*Thuja*
S93	1.IX	Benzie	H	2	0	33	2	35	60	37	Grassland
S110	7.IX	Benzie	Q	52	8	59	29	88	53	148	Hardwood
S126	8.IX	Leelanau	H	0	0	1	0	1	100	1	*Thuja*
S131	8.IX	Leelanau	Q	0	0	0	4	0	0	4	Hardwood
S134	8.IX	Leelanau	H	6	0	13	3	16	59	22	Grassland
S139	9.IX	Antrim	H	0	0	1	0	1	100	1	*Thuja*
S147	9.IX	Antrim	H	4	1	7	0	7	70	12	Grassland
S149	9.IX	Antrim	Q	9	1	10	8	18	53	28	*Thuja*
S164	16.IX	Emmett	H	9	0	38	0	38	81	47	Grassland
S168	16.IX	Emmett	H	0	0	1	0	1	100	1	Hardwood
S170	17.IX	Cheboygan	H	3	0	12	1	13	80	16	Grassland
S178	17.IX	Cheboygan	H	1	0	5	0	5	83	6	Grassland
S179	17.IX	Cheboygan	H	2	0	3	0	3	60	5	Hardwood

pacity at frequent intervals for exact data without excessively disturbing the snails.

There is a prevailing notion in some malacological literature that many mollusks are fecund whenever the temperature of the environment is within optimum range and throughout that period. Whitney (1938) found this true in *Vallonia*, and it may indeed be the true situation in some snails. Lovett & Black (1920) report the occurrence in Oregon of the eggs of *Ariolimax agrestis* (*Deroceras reticulatum*) at all seasons of the year, but most abundantly in the spring and early summer. They do not say whether or not a single individual is found for the whole of this period.

A variety of life history patterns in snails have been revealed by the more critical studies in the subject, of which only a few will be cited here. In the region of Pittsburgh, Pennsylvania, *Vitrina* is reported almost absent in the warmer parts of the year. Yet it is very common and active

TABLE 8. Regional collections of late June and early July, 1949, in the eastern part of the Lower Peninsula of Michigan, analyzed for age and viability groups. H: hand picked in the field; Q: quantitative leaf mold sample taken. The percentages in "Adults alive" column are based on total living population.

Lot Number	Date (all 1949)	County	Collecting method	Juveniles alive	Juveniles dead	Adults alive	Adults dead	Total living population	Percentage adults alive	Total shells alive and dead	Macrohabitat type
M46	29.VI	Bay	H	0	0	8	0	8	100	8	Grassland
M1	29.VI	Bay	Q	0	0	11	0	11	100	11	Oak
M60	29.VI	Arenac	Q	3	2	8	20	11	73	33	Hardwood
M62	29.VI	Iosco	Q	0	0	1	8	1	100	9	Hardwood
M36	29.VI	Alcona	Q	0	5	24	12	24	100	41	*Thuja*
M63	30.VI	Alpena	Q	0	1	12	11	12	100	24	*Thuja*
M34	30.VI	Presque Is.	Q	3	1	3	9	6	50	16	*Thuja*
M51	3.VII	Otsego	Q	7	1	26	2	33	79	36	Maple
M50	3.VII	Montmorency	Q	12	4	8	6	20	40	30	Maple
M45	3.VII	Montmorency	Q	20	39	101	102	121	83	242	*Thuja*
M64	3.VII	Oscoda	Q	8	31	52	126	60	86	217	*Thuja*
M66	3.VII	Ogemaw	Q	0	6	7	5	7	100	18	Maple
M33	3.VII	Roscommon	Q	4	0	77	18	81	95	99	Grassland
M40	4.VII	Huron	Q	0	0	3	0	3	100	3	Birch
M38	5.VII	Lapeer	Q	3	0	5	0	8	63	8	*Populus*
M39	5.VII	Lapeer	Q	0	0	4	2	4	100	6	*Populus*

during the colder seasons. Oviposition was noted in November, when the air temperature was a few degrees above freezing (Clapp, in Pilsbry, 1948, p. 503).

Hoff (1937) reports a phenological period of one month (April) for *Fossaria parva* in Illinois. The eggs hatch in May and June, and the adults of the previous year die during the latter month. He stated "Growth is confined to definite seasons of the year, is influenced by climatic conditions, and ceases only with the death of the individual."

For another snail of the same genus, *Fossaria modicella,* Van Cleave (1935) reported two generations a year in Illinois. A generation hatched in late July or early August lives through the winter, producing another generation in March, and then dies. The generation of March grows to maturity and produces another generation in the late summer. He thinks most of the spring brood also dies soon after oviposition. He also emphasized continuous growth throughout life in *F. modicella.*

Boettger (1944: 424) stated that Basommatophora hatched in the spring become sexually mature in the fall of the same year, and he cited spring broods of *Lymnaea stagnalis* as laying eggs in August, though they have not yet reached maximum size. Egg production is absent during the colder months, but begins in the spring, rises to a peak in May, and gradually decreases but persists through the summer. He emphasized the discrepancies between life histories in the field and laboratory cultures. Fresh cultures tend to maintain the normal field pattern, but after a time develop a different timing due to the more uniform conditions of the environment.

THE SHELL

Concepts of Two Cones

Certain concepts of the form of a snail's shell which are extensively used in the later portions of the present paper need a word of explanation. The primary cone of a coiled snail's shell is that geometric form approached by the portion of the shell which has its apex at the apex of the shell, and its base approximated by the shell's aperture. The axis of this cone is imaginary, not represented by any part of the shell itself.

The primary cone is coiled about another axis and approaches thereby a geometric form which is termed the secondary cone. This is defined as having its apex at the apex of the shell, its base approximated by the base of the shell, and its axis represented by the columella. Of the numerous modifications which the theoretical biconic form is capable, only a few concern us in the present study.

Heterostrophy consists of a sharp angle near the apical end of the secondary axis. It is more marked in those forms which have several whorls of the primary cone apical to the point of flexure (some Pyramidellidae). However, most of the cases of heterostrophy have one whorl or less of the primary cone above that point (reduced heterostrophy), and frequently in these cases the phenomenon has not been noticed. Thus, in the very early growth stages of the shell of *Pedipes*, a reduced heterostrophy is evidenced but completely occluded by later stages of growth (unpublished data). Reduced heterostrophy is also present in *Otina* where it is easily demonstrated by removing the shell with acid alcohol and examining the visceral mass to determine the position of the axis of the secondary cone. Although the shell has scarcely one whorl, and a very rapid increment leading to a large aperture, heterostrophy usually causes rupture of the visceral mass when it is withdrawn from the shell in preserved specimens, this phenomenon led to the supposition of heterostrophy, later confirmed by the method noted.

Heterostrophy is usually accompanied by a reversal of the direction of coiling of the primary cone at the point of flexure of the secondary axis. Most frequently the initial portion of the shell is sinistral (coiled counter clockwise when viewed apically) and post-flexural coiling is dextral. This sinistro-dextral heterostrophy is exemplified by many Ellobiidae and Pyramidellidae. But the ellobiid *Blauneria heteroclita* constitutes a prominent exception in which the direction of coiling is sinistral both above and below the flexure (sinistro-sinistral heterostrophy). Theoretically dextro-dextral and dextro-sinistral heterostrophy are possible but no examples are known. The causes and phylogenetic significance of heterostrophy are completely unknown. Morrison (1950) suggested that the systrophic (synonymous with heterostrophic?) apex of the ellobiids may indicate a pelagic veliger larva.

As the primary cone is coiled about the columella to form the secondary cone of the shell, a certain radial sector of the primary cone's periphery is hidden, by being included inside the secondary cone. This sector constitutes the internal partition between the subsequent whorls of the shell. In some snails the occluded sector is resorbed to a varying extent (Fischer & Crosse, 1890). In *Carychium* a narrow subsutural shelf remains, but in *Melampus* the shelf is completely lacking. The significance of resorption is also unknown. It seems invariably accompanied by a fusion of the whorls of the visceral mass, corresponding to the degree to which resorption is active.

The usual method of counting the whorls of a snail's shell consists of counting the actual whorls of the primary cone. The method is extensively outlined in many places (Diver, 1931; Brooks & Kutchka, 1937) and need not be repeated here. Another method, and one which the writer prefers in his own work, is that of counting the number of whorls of the suture rather than those of the primary cone. The writer has found this method admits of less subjective error, may be as easily applied to a high-spired as to a low-spired shell. H.B. Baker (1938: 6) pointed out that neither method is very exact. The number of suture whorls obtained differs from the number of whorls of the primary cone by a half whorl. If the suture is counted just to the aperture of the shell, as was done in the present study, the suture whorls are a half less than the whorls of the primary cone. If the projection of the suture along the periphery of the shell is counted, the number of suture-periphery whorls is a half greater than the number of whorls of the primary cone.

Though growth of the snail's shell proceeds in a gnomonic fashion, certain indications of structure, sculpture and the relation of the primary cone to the secondary one allow various stages of growth to be recognized. Woodward (1909) reviews and defines these terms, which were originally applied by Hyatt. Whether the concepts involved in the series really allow interpretation of phylogeny in the completed shell is a speculative question. Correlation of particular stages is sometimes difficult. One phase of this problem which concerns us in the present study is the matter of determinant and indeterminant growth. Snails having determinant growth of the shell are those in which the shell shows at some final stage a condition beyond which there is no more shell increment. This is usually manifest by special elaboration of the aperture such as the production of denticles or lamellae or an expanded lip. After this stage, termed the ephebic stage in the terminology of Hyatt, no more shell is normally produced. Such is the case in *Carychium.* In *Pythia* the ephebic stage is sometimes accompanied by additional shell growth, producing thus the gerontic stage (Harry, 1951). Absence of any terminal elaboration of the aperture or any other indication in the shell of periodic growth is exemplified by some snails, and many examples are found in the lymnic Basommatophora. Hoff (1937) and Van Cleave (1935) both considered the growth of the respective species of *Fossaria* which they studied to persist throughout the life of the snail; it is therefore indeterminant growth. H.B. Baker (1938) expressed a similar opinion about the growth of many Pacific Zonitidae.

F.C. Baker (1902) speaks of the shells of *Physa* as "annuan," "biannuan," etc., according to whether they show one or two or more transverse white streaks, which are probably nothing more than labial calluses produced at different parts of the life history. At the time each callus was produced there would be terminal elaboration of the aperture which would simulate determinate growth of the shell. Yet, in some cases at least, the shell showed increment beyond that stage repeating the process later. Such an intermediate condition may be termed periodic growth. In *Physa* and some others it seems to be irregular but in *Pythia* there is regular periodicy of growth, at least morphologically if not temporally (Harry, 1951).

The importance of noting these types of growth have been under-emphasized in the past in studying shell architecture. In some shells which have indeterminant growth, occasionally measurements of the shell's dimensions are given without any indication of the number of whorls which accompany them or notation concerning the type of growth manifest.

In describing positional relationships of structures of the cephalopedal mass, those terms ordinarily applied to a bilaterally symmetrical animal are acceptable. But coiling of the visceral mass produces positional distortion to such a degree that these terms are often confusing when applied to that portion of the body. In the present paper, they have been avoided, except where standardized by established usage (*e.g.*, left pallial vein). Positional relationships of the visceral mass are described in terms relative to the primary and secondary cones: **apically** indicates toward the apex, of either cone; **basally** indicates toward the base of the secondary cone; **aperturally** indicates toward the base of the primary cone, and implies that a structure conforms to the coiling of that cone; **peripherally** indicates toward the periphery of the secondary cone; **columellarly** indicates toward the columella of the shell.

Growth Changes in the Shell of *Carychium exiguum*

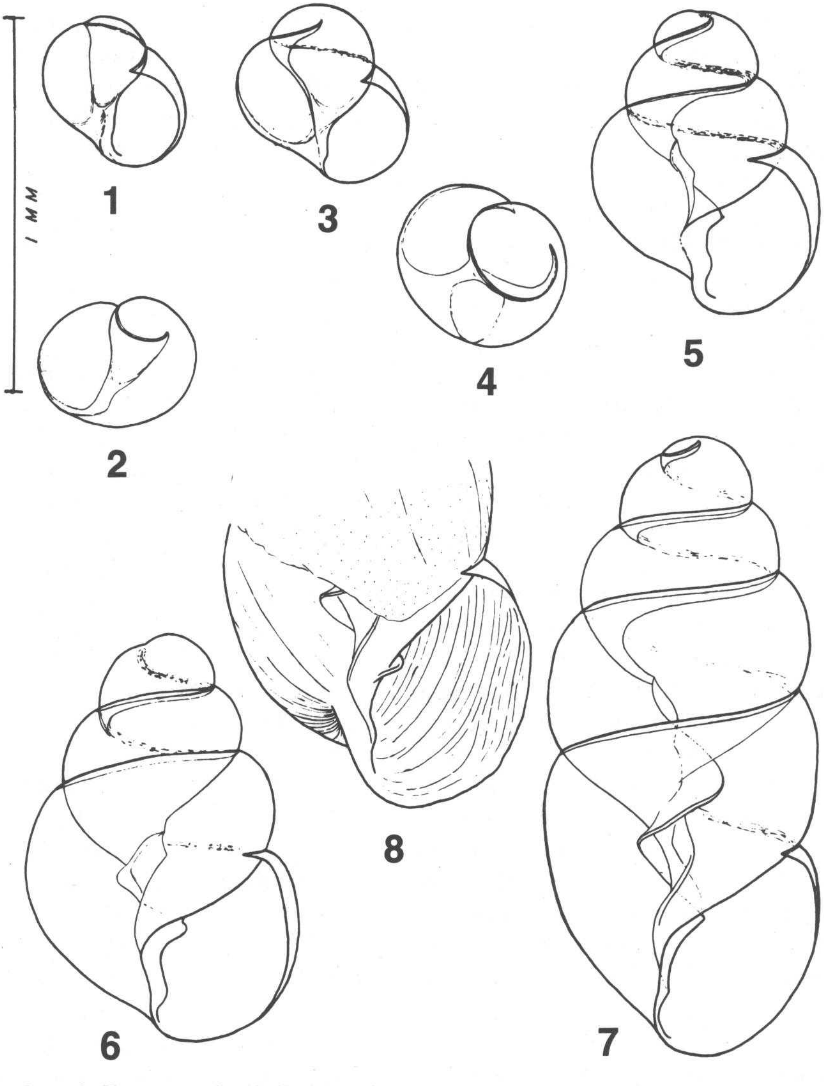
Shells of the most juvenile post-embryonic stage of *Carychium* (Plate VI, Figs. 1 and 2) have slightly less than one suture whorl. The internal partition is complete and parallels the columellar axis. The shell is dextral, without umbilicus; the columellar lip is thickened and slightly projecting in the mid-region of its length.

Resorption of the internal partition begins with post-embryonic growth (Plate VI, Figs. 3 and 4). At slightly over one whorl there is a prominent concavity of the internal margin of the shell leaving only a lamellar remnant of the original internal partition. This sutural shelf projects basally as a continuation of the curvature of the whorl which originally composed it. In *Pythia,* the sutural shelf resulting from resorption extends toward the columella, standing thus in the diametrical plane of the secondary cone. It is composed of peripheral and columellar parts, the latter of which broadens out as it approaches the apex, and sometimes recreates the columella (Harry, 1951). No such medial portion is evident in any stage of *Carychium. Pythia* shows an internal reconstruction not evident in this genus.

After post-embryonic growth is begun the protoconch is demarked from the later shell by a linear, hyaline mark (Plate VI, Figs. 3 and 4). Using transmitted light and higher magnifications this can be noted only in shells of slightly over one whorl. It is a phenomenon of differential refraction which is not easily seen in the older shell. The protoconch is smooth, as are the earlier post-embryonic whorls, showing no sculpture at any magnification used during the present study.

The two lamellae become better defined as the shells grow. The lower lamella, which is truly on the columella, is represented by the bulge of the columella of the protoconch (Plate VI, Fig. 1). The bulge becomes slightly more pronounced in shells of one suture whorl, at which stage the upper lamella has not yet appeared. By the second whorl stage, both lamellae are plainly evident, in the position and relationship with the internal partition of the shell which they maintain throughout later stages of growth. The upper lamella is distinctly blade-like, having a uniform thickness greatly exceeding its vertical dimension (in cross-section). It extends from its attachment at right angles, and its lower end is situated just at the ill-defined junction of the columellar and parietal parts of the aperture. According to its position it should be termed the columello-parietal lamella. The height of the lower lamella does not exceed the width of its transverse section except in the most mature aspects of the shell (see below). The

PLATE VI



Growth Changes in the Shell of *Carychium exiguum*. FIG. 1. Apertural view of a shell of the minimum free-living size observed. Less than one suture whorl. FIG. 2. Same shell as Fig. 1, in normal crawling position, as seen from above. FIG. 3. A shell of one suture whorl, apertural view. FIG. 4. Same shell as Fig. 3, in normal crawling position, seen from above. FIG. 5. Shell of slightly over two suture whorls. FIG. 6. Shell of 2 3/4 suture whorls. FIG. 7. Shell of four suture whorls. FIG. 8. Maturing lip, showing columellar expansion which produces a pseudoumbilicus. The contracted animal is indicated by stippling.

columellar lamella has a much narrower diameter to its whorl, in proportion to its total length, than does the upper lamella. Indeed, the lower lamella blends into the line of the columellar part of the aperture, producing merely a notch at its lower end and at its upper extremity is almost in line with the free margin of the internal partition. At its upper terminus the upper lamella meets the line of the absorbed partition at almost a right angle and produces there a slight point. A similar point may be seen at the upper terminus of the lower lamella.

In all pre-ephebic stages the apertural columella is thickened and cylindrical, recalling the columellar plate in *Pedipes,* though being much less expanded than the latter. As this columellar pillar is not evident in *Carychium* above the aperture, a considerable amount of shell revision must have occurred during the growth of the shell in this region.

Throughout the first two whorls of growth, resorption of the internal partition of *Carychium* extends to within half a whorl of the aperture. During the third whorl of growth the resorptive process slows and the free margin remains in the third whorl. There is slight variation in the position in which it remains (cf. Figs. 7 and 8 of Plate VII); in the *"exile"* form it is about a half whorl farther from the aperture than in the *"exiguum"* form. At from 3 1/2 to 4 1/4 (rarely five or slightly more) suture whorls the aperture is completed. The first indication of the maturing aperture is the formation of a free columellar lip, thus producing a pseudoumbilicus (Plate VI, Fig. 8). It is accompanied by a narrow expansion of the basal and outer lip. The middle area of the outer lip often has a depression just behind the margin. The depression is shallow, broad and ill-defined, and is most evident in the mature shell. The expansion of the maturing lip quickly extends to its maximum, after which there is no further terminal growth around its margins, but additional layers are deposited on its inner surface, forming an opaque, flattened and ill-defined marginal lip callus. At the level of the preapertural fossa the thickening process continues, producing a projection which extends into the aperture toward the columella. While it is evident enough in American *Carychium* shells, it has chiefly attracted the attention of European students who have applied the trivial name *"tridentata"* to one of their nominal species. The concavity of the inner surface of the outer lip between the apertural angle and the "tooth" just described accommodates the pneumostome; it may be termed the pneumostomal sinus of the lip. A homologous sinus is present in many ellobiids, *e.g., Pythia* and *Ellobium.*

The body whorl of the one and two whorl stages is evenly rounded from suture to columella. During later stages there is a tendency for flattening of the peripheral part of the whorl. This results in a rounded shoulder near the suture and a somewhat sharper angle at the periphery which is basal to the area of flattening (Plate VI, Fig. 7). The more intense flattening of the body whorl in later growth leads to the "*exile*" extreme of form.

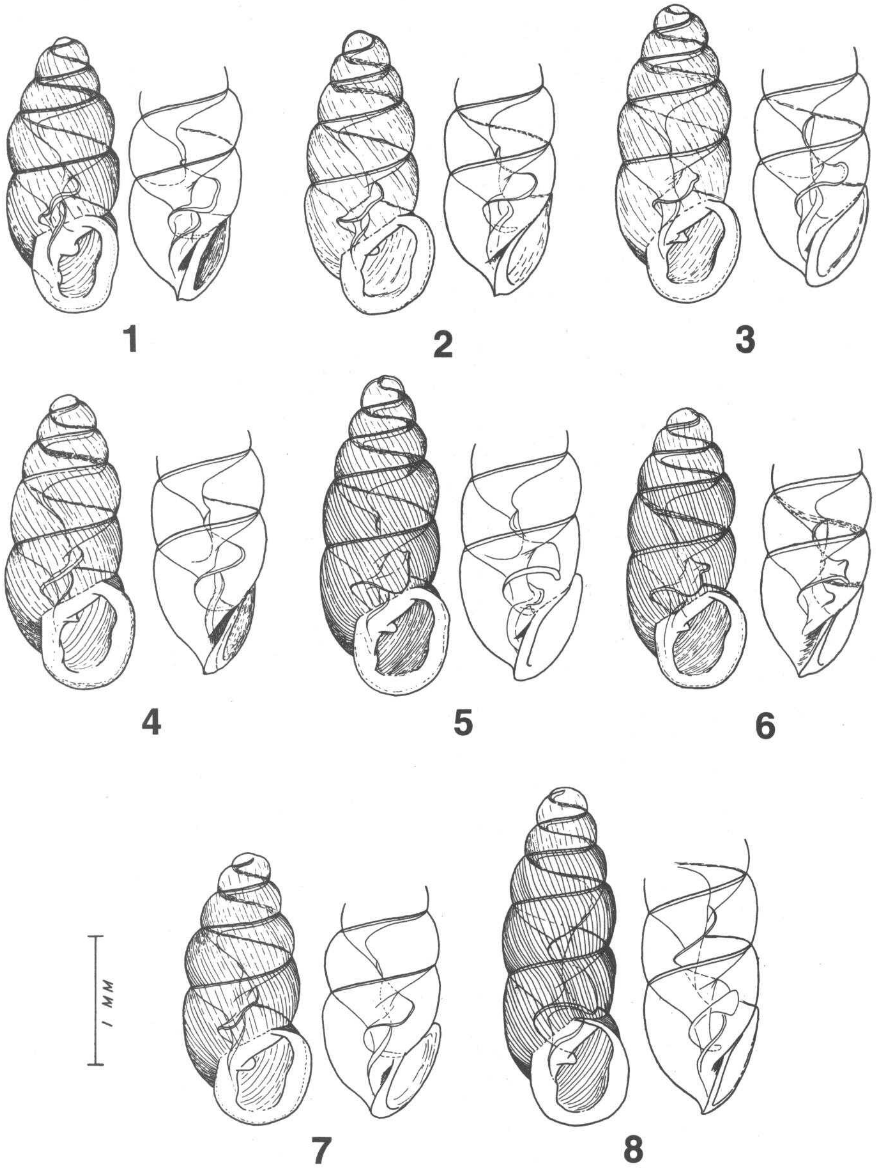
Something of the texture of the external shell of *Carychium* in Michigan is indicated by Plate VII. The more regularly, heavily striate shells are of the "*exile*" or "*exile canadense*" type, while the "*exiguum*" type may be nearly smooth. Such striae as are present on the latter are usually weak, vague and irregular, and discontinuous.

The lamellae of the mature shell vary considerable. The upper lamella of the "*exiguum*" type is slightly expanded in the body whorl and its margin S-sinuate, the portion nearest the aperture dipping down, *i.e.*, toward the base of the shell; the sinuosity occurs at about three-fourths whorls inward from the aperture (Plate VII, Fig. 7). In the "*exile canadense*" extreme the upper lamella is expanded until it almost reaches the periphery of the body whorl and dips prominently toward the base to form a large V (Plate VII, Fig. 8). This V is probably to be correlated with the downward flexure of the S-sinuosity of the lamella of the "*exiguum*" type. The V-lamella of "*exile canadense*" has its greatest downward flexure somewhat more than one whorl inward from the aperture, but the position is often closer to the aperture. The lamella of "*C. exile s.s.*" as shown by Winslow (1922) is somewhat intermediate to these two extremes in form and position and is approached by Fig. 5 of Plate VII.

The lower lamella of the ephebic shell is relatively simple, though it shows a broadening at the position of the greatest width of the upper lamella. In the "*exiguum*" type, this amounts to little more than a poorly defined nodule but in the "*exile canadense*" extreme it is a distinctly quadrate expansion somewhat longer than wide.

According to my observations, *Carychium exiguum* shows no heterostrophy at any stage of growth. Nor have I been able to detect it in any of the other species of shells which I have examined from this country and Europe. Perhaps the absence of this phenomenon could be included among the family characters separating Carychiidae from the Ellobiidae *s.s.* Indeed, Dall (1886) early recognized the "reversed apex" as a family character of the Ellobiidae but did not apply the term heterostrophy to it. He even thought it present in *Carychium* (l.c. p. 275, footnote): "*Carychium exiguum* Say ... The nucleus of this species is so little advanced toward a whorl when the regular spire begins that it at first seems as if this genus formed an exception to the family rule of having a sinistral nucleus. It is however, only superficially so. In *C. minimum* the version is often very recognizable, and some specimens of our species show it better than

PLATE VII



Variation in the mature shells of *Carychium exiguum* from Michigan. FIGS. 1-6. Specimens from the station sampled repeatedly in Reese's Bog, Cheboygan County (the R series). FIG. 7. A shell from the Washtenaw County station (G series). FIG. 8. A shell from station M51.

others."

Little attention has been given to the structure of the shell in the present study. It was found, however, that the cuticle (epiconch or periostracum) consists of two layers. This was repeatedly demonstrated in those shells dissolved away by acid alcohol. The outside layer is easily removed by teasing with fine needles, but there often remains remnants of the inner layer closely adherent to the surface of the animal which is easily demonstrated in sections. Translucent shells free from the animal when collected were subjected to the acid treatment and show the inner layer subtending the outer layer throughout the extent of the latter. The internal lamellae are outlined throughout their length by the periostracum, but whether one or both layers of the latter are involved was not determined. The reflection, but not the thickening, of the lip is evident in the cuticle. Both layers were attacked by weak KOH, and after being exposed to such a solution for several hours were reduced to a pulpy, sticky mass. I have seen both layers of the periostracum in *Otina* (where the inner layer is dark brown, opaque and brittle), *Physa, Succinea* and *Stenotrema.* Boettger (1944: 245) noted that the periostracum (of Basommatophora in general) may consist of several layers. Fresh *Carychium* shells of all stages are light straw-colored and transparent.

Variation of the Mature Shell

Previous concepts of speciation of American *Carychium* are based entirely on characters of the mature shell. Chiefly these pertain to size, sculpture, shell proportions and form.

As noted above (p. 7), three nominal species and subspecies of *Carychium* have been reported from Michigan. A review of the systematic history of these will indicate the doubt that has prevailed regarding their validity. For a more complete synonymy see Pilsbry (1948). *Pupa exigua* Say was described in 1822. In 1842 H.C. Lea described *Carychium exile.* Gould (1842) soon declared Lea's "*Carychium exile* is a common variety of *C. exigua,* Say." For the next 50 years those authors who made a critical decision on the matter considered the two forms synonymous (for example, W.G. Binney, 1865). Pilsbry (1891a) thought *C. exile* worthy of varietal rank under *C. exiguum.* In the same year (1891b) he again presented his views on the differential characters of the shell but noted: "Only the collection of specimens from points geographically intermediate between the extremes of the range of this genus, and the examination of such material by a competent person, can finally decide the question of the number of naturally defined species, and which, if any of them, must be considered geographic races or subspecies."

About a decade later F.C. Baker (1902) noted that *C. exile* always occurred with *C. exiguum* in the Chicago area, but that *C. exiguum* was about three times as common, and he stated: "In view of this fact it may be possible that one is a variety of the other, instead of a distinct species, as the two forms may interbreed."

For the last 50 years the two species have been regarded as distinct. While not known as completely as might be desired, their ranges in eastern North America seem to be almost, if not entirely, identical. In 1906 Clapp recognized a new variety of *C. exile* which he termed *C. exile canadense* because it seemed limited to the Canadian life zone. His subspecies was morphologically separated on its larger size.

Winslow (1922) attempted to separate these species on the basis of the internal lamellae. Although she indicated that variation does occur in the characters which she associated with each nominal species, nothing is given as to the number of specimens examined or the range of variation which might be encountered in each microhabitat. Her paper has been widely quoted by later authors including Pilsbry (1948), Brooks & Kutchka (1937), and Oughton (1948). The latter recognized only *Carychium exiguum* and *C. exile canadense* of this complex in Ontario. His account of their distribution and variation implies much doubt as to their specific distinctness as do the remarks of Brooks and Kutchka on shells from West Virginia.

In the present study, nothing was noted in the soft anatomy which seems to be of value in separating the species of this complex, but the shells show an amount of variation which required investigation. Shell characters which have been deemed of value for separating species fall into two groups, those which may be exactly measured, such as the dimensions of the shell and number of whorls, and those which may not, as amount of sculpturing or form of the lamellae.

Considering first those characters which permit little exactness in measurement, the general impression was obtained that there are two extremes of variation among *Carychium* shells in Michigan. These extremes are based on a combination of characters and fit rather closely the concepts of *C. exiguum* and *C. exile canadense* as now generally accepted. *Carychium exile* falls into this graded series somewhere near the *C. exile canadense* extreme. These two extremes are contrasted in Table 9; the characters which distinguish them are mostly relative. They do not seem to segregate independently. We may suppose that the characters of *C. exile canadense* are merely distortions of the corresponding characters of the *C. exiguum* type. This hypothesis should have as much validity as the presumption that the extremes represent distinct biological species. If the view that *Carychium* in

TABLE 9. Contrasting characters between *Carychium exiguum* and *C. exile canadense.*

C. exiguum	*C. exile canadense*
Shell Form	
Ovate-conic, the diameter being broader in proportion to the height.	Cylindric, the diameter being narrower in proportion to the height.
Whorls	
Rounded.	Flattened.
Sculpture	
Transverse striae indefinite, weak, discontinuous, sparse.	Transverse striae strong, regular, closely spaced.
Upper Lamella	
Upper lamella S-sinuate, curving first down (near the aperture) then up.	Upper lamella V-sinuate, which seems to be an overemphasis of the downward flexure of the S-sinuate lamella of the other extreme.
Sinuosity occurs about 3/4 whorl inward from the aperture.	Sinuosity occurs closer to one whorl inward from the aperture.
Lower Lamella	
Slightly expanded at about the position of maximum flexure of the upper lamella; expansion tending to an equidimensional node.	Expanded also at the position of maximum flexure of the upper lamella, but distinctly quadrate, longer than broad.
Resorption	
Resorption of internal whorls begins about 1 3/4 whorls from the aperture.	Resorption of internal whorls begins about 2 1/4 whorls from the aperture.
Number of Whorls	
About 4 suture whorls.	About 4 1/2 to 5 suture whorls.
Size	
Smaller.	Larger.

Michigan occurs as isolated colonies in small microhabitats is correct, we may then suppose that each colony has a gene-pool which may differ from that of another colony in some respects. Possibly few, if any, colonies have a complete complement of genetic factors to be found in all colonies of the area. The variation of effective environmental factors may further complicate the situation by evoking different phenotypes from similar genotypic potentialities.

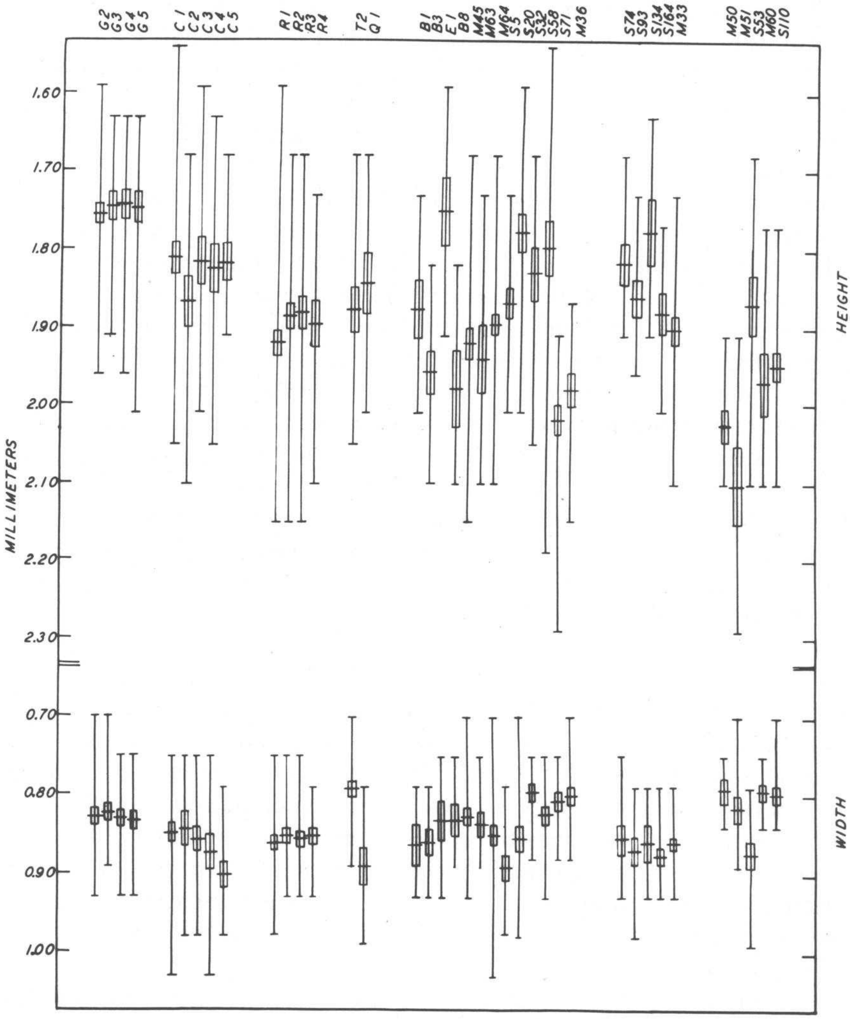
Fig. 7 of Plate VII illustrates a shell from the Washtenaw County colony (G series). It represents a typical *C. exiguum.* The shell illustrated in Fig. 8 is typically that of *C. exile canadense* from lot M51. Neither of these lots showed much variation of sculpturing or in the characters of form and internal lamellae. While this homogeneity is true of some lots, it does not hold for all. Figures 1 to 6 are selected examples from the repeatedly sampled station at Reese's Bog (R series), and they illustrate the amount of variation of the characters listed in Table 9. It is notable that none of these shells quite approach the extreme of form of either Fig. 7 or 8.

Table 10 shows the range and array of the number of whorls in mature shells of various lots. There is a general modality at about four suture whorls. On the limited observations made no tendency toward grouping

TABLE 10. The distribution of suture whorls among various lots of ephebic *Carychium exiguum* shells.

Lot No.	Suture Whorls						
	3 1/2	3 3/4	4	4 1/4	4 1/2	4 3/4	5
K1		3	6	1			
T2		1	8	14	8	1	2
Q1		6	9	3			
S71		1			12	2	
S58	2	4	6	16	8	1	
C3	5	14	20	9	3		
C2		9	10	8	8		
C1	9	26	46	14	5		
C4	5	6	22	3	1		
G3		1	19	15	2		
G2		1	4	5			
R4		4	17	10	11		
R1		1	9	9	5	1	

PLATE VIII



The graphic representation of the height and width relationship in *Carychium* shells from Michigan as derived from figures in Table 11.

Each line represents the range of size for the respective variant of each sample. The rectangles near the middle of the line indicate two standard errors of the mean on either side of the mean, the latter being indicated by the cross-line bisecting them.

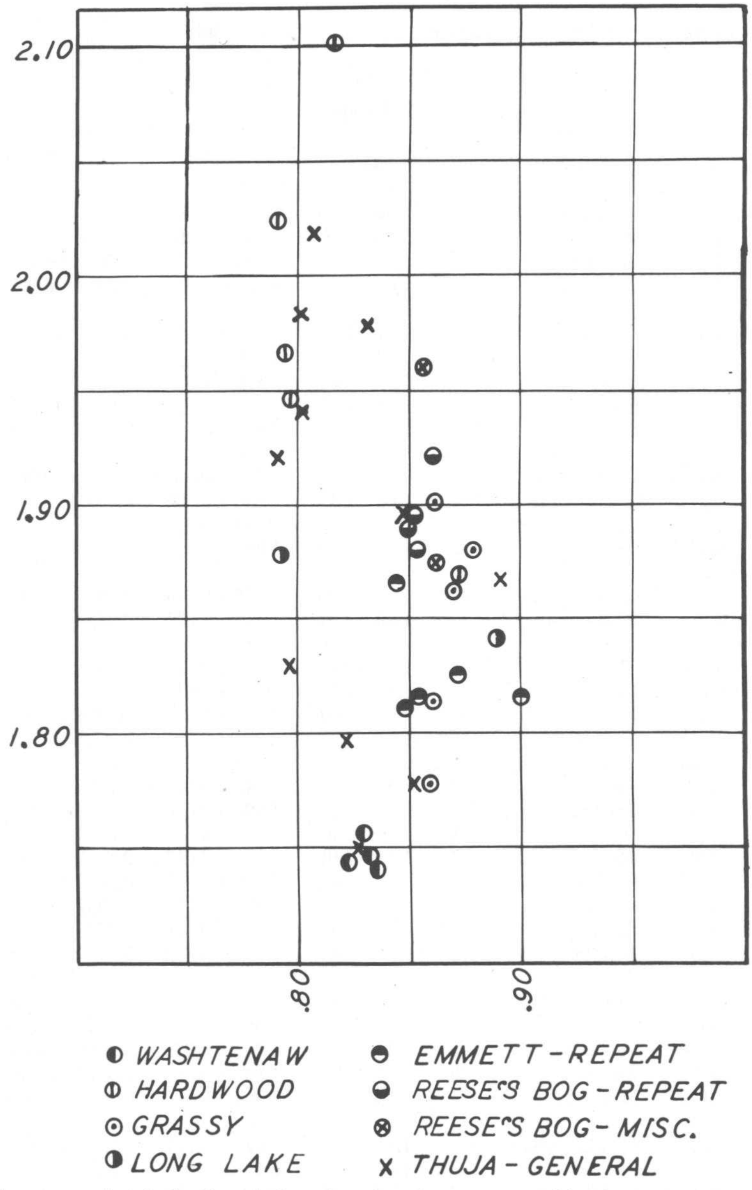
was recognized which might indicate that the number of whorls is distinct for each of two or more species. Again, no particular lot covers the range of variation of the group as a whole.

Measurements were made of the height of the shell and the major diameter at right angles to it in order to determine if any differences in the ratio of these characters would show grouping which might indicate a valid basis for speciation. The fundamental parameters of these measurements are presented in Table 11. The graphic representation of these data is given in Plates VIII and IX.

In Plate VIII, the three major stations which were repeatedly collected are grouped to the left (G, C and R series). Two neighboring colonies in Cheboygan County (T1 and Q1) are separated by a dirt road, which presumably forms an isolation barrier. These colonies are represented together in Plate VIII for ease of comparison. The three assemblages to the right of the chart are based on macrohabitat types: *Thuja* (toward the center), grasslands, and hardwood (on the right). The B3, B1 and B8 lots are of interest in that each represents an isolated colony, and distinct from that of the R series in Reese's Bog, Cheboygan County. The overlap of the rectangles representing the standard error of the mean can be used as a rough criterion for assuming two samples are or are not significantly different on the basis of the continuous variate being studied (Simpson & Roe, 1939). If the rectangles just touch or overlap the differences of the means are not significant. Those which do not touch probably represent significant differences. Just what taxonomic, genetic or physiological value should be attached to these mathematically significant differences seems to be an arbitrary matter. Such interpretation should be based on additional information about the organism being studied. Note that two very distinct samples such as S71 and S74 may not overlap even in their observed range (although they do if we use the criterion involving the theoretical range of three times the standard deviation on either side of the mean). But they can be joined by overlap in standard errors of the mean or ranges of other samples. However, no grouping of the various lots into two or more definite, exclusive classes which might be interpreted as representing distinct species is evident.

There is little indication that the samples from one macrohabitat type show ranges or means distinct from those of another. In the literature the statement is occasionally made that *Carychium exile* occurs in dryer situations than *C. exiguum* (Clapp, quoted in Pilsbry, 1948: 1059). This may be true. Two lots, M50 and M51, from maple forests are distinctly of the *C. exile canadense* extreme. Their occurrence in the field (in a deep, leaf-filled stump hole in a maple forest) also seemed to indicate a dryer situation

PLATE IX



The average height (ordinate) plotted against the average width (abscissa) of *Carychium* shells from Michigan. Data from Table 11.

The different lots are grouped as in Plate V by using contrasting symbols.

TABLE 11. Statistical parameters of height and width of individual lots of *Carychium exiguum* from Michigan.

Lot No.	County	Number	Height		
			Range	Mean	Standard Deviation
G2	Washtenaw	85	1.59 – 1.96	1.755 ± 0.007	0.0615 ± 0.005
G3	Washtenaw	54	1.63 – 1.91	1.745 ± 0.009	0.0626 ± 0.006
G4	Washtenaw	55	1.63 – 1.96	1.744 ± 0.010	0.0757± 0.007
G5	Washtenaw	78	1.63 – 2.01	1.746 ± 0.010	0.0844 ± 0.007
C1	Emmett	100	1.54 – 2.05	1.812 ± 0.011	0.1072 ± 0.008
C2	Emmett	36	1.68 – 2.10	1.868 ± 0.017	0.1017 ± 0.012
C3	Emmett	52	1.59 – 2.01	1.816 ± 0.016	0.1140 ± 0.011
C4	Emmett	41	1.63 – 2.05	1.826 ± 0.015	0.0960 ± 0.011
C5	Emmett	29	1.68 – 1.91	1.817 ± 0.012	0.0670 ± 0.009
R1	Cheboygan	154	1.59 – 2.15	1.922 ± 0.008	0.1002 ± 0.006
R2	Cheboygan	132	1.68 – 2.15	1.886 ± 0.008	0.0930 ± 0.006
R3	Cheboygan	85	1.68 – 2.15	1.881 ± 0.011	0.0986 ± 0.008
R4	Cheboygan	42	1.73 – 2.10	1.895 ± 0.015	0.0970 ± 0.011
T1	Cheboygan	40	1.68 – 2.05	1.878 ± 0.014	0.0907 ± 0.010
Q1	Cheboygan	18	1.68 – 2.01	1.842 ± 0.020	0.0742 ± 0.014
B1	Cheboygan	20	1.73 – 2.01	1.875 ± 0.019	0.0838 ± 0.013
B3	Cheboygan	32	1.82 – 2.10	1.961 ± 0.013	0.0760 ± 0.010
E1	Emmett	15	1.59 – 1.91	1.751 ± 0.022	0.0858 ± 0.016
B8	Cheboygan	17	1.82 – 2.10	1.979 ± 0.025	0.1025 ± 0.018
M45	Montmorency	89	1.68 – 2.15	1.920 ± 0.010	0.0982 ± 0.001
M63	Alpena	23	1.73 – 2.10	1.941 ± 0.023	0.1098 ± 0.016
M64	Oscoda	163	1.68 – 2.10	1.896 ± 0.006	0.0800 ± 0.004
S5	Oceana	58	1.73 – 2.01	1.869 ± 0.009	0.0734 ± 0.007
S20	Mason	69	1.59 – 2.01	1.779 ± 0.012	0.1032 ± 0.009
S32	Wexford	23	1.68 – 2.05	1.830 ± 0.017	0.0825 ± 0.012
S58	Missaukee	57	1.54 – 2.19	1.798 ± 0.018	0.1337 ± 0.013
S71	Kalkaska	35	1.91 – 2.15	2.020 ± 0.009	0.0542 ± 0.007
M36	Alcona	36	1.87 – 2.15	1.984 ± 0.012	0.0716 ± 0.008
S74	Grand Traverse	20	1.68 – 1.96	1.817 ± 0.013	0.0561 ± 0.009
S93	Benzie	31	1.73 – 1.96	1.863 ± 0.012	0.0648 ± 0.008
S134	Leelanau	16	1.63 – 1.91	1.778 ± 0.022	0.0886 ± 0.016
S164	Emmett	35	1.77 – 2.01	1.882 ± 0.013	0.0772 ± 0.009
M33	Roscommon	91	1.73 – 2.10	1.901 ± 0.009	0.0876 ± 0.007
M50	Montmorency	19	1.91 – 2.10	2.026 ± 0.011	0.0499 ± 0.008
M51	Otsego	27	1.91 – 2.29	2.101 ± 0.025	0.1304 ± 0.018
S53	Clare	27	1.68 – 2.10	1.870 ± 0.019	0.1036 ± 0.015
M60	Arenac	25	1.77 – 2.10	1.967 ± 0.021	0.1036 ± 0.015
S110	Benzie	85	1.77 – 2.10	1.948 ± 0.010	0.0888 ± 0.007

TABLE 11. (Continued)

Lot No.	Coef. of Correlat.	Width		
		Range	Mean	Standard Deviation
G2	+ 0.56	0.70 – 0.93	0.830 ± 0.005	0.0443 ± 0.003
G3	+ 0.34	0.70 – 0.89	0.824 ± 0.006	0.0430 ± 0.004
G4	+ 0.36	0.75 – 0.93	0.831 ± 0.005	0.0448 ± 0.004
G5	+ 0.60	0.75 – 0.93	0.834 ± 0.005	0.0388 ± 0.004
C1	+ 0.26	0.75 – 1.03	0.849 ± 0.007	0.0653 ± 0.005
C2	+ 0.20	0.75 – 0.98	0.843 ± 0.010	0.0612 ± 0.007
C3	+ 0.53	0.75 – 0.98	0.857 ± 0.009	0.0614 ± 0.006
C4	+ 0.38	0.75 – 1.03	0.873 ± 0.011	0.0705 ± 0.008
C5	+ 0.56	0.79 – 0.98	0.901 ± 0.009	0.0476 ± 0.006
R1	+ 0.17	0.75 – 0.98	0.861 ± 0.004	0.0521 ± 0.003
R2	+ 0.15	0.75 – 0.93	0.852 ± 0.004	0.0397 ± 0.003
R3	+ 0.27	0.75 – 0.93	0.855 ± 0.005	0.0432 ± 0.003
R4	+ 0.07	0.79 – 0.93	0.852 ± 0.006	0.0382 ± 0.004
T1	– 0.19	0.70 – 0.89	0.793 ± 0.008	0.0488 ± 0.005
Q1	+ 0.33	0.79 – 0.98	0.908 ± 0.011	0.0478 ± 0.008
B1	+ 0.08	0.79 – 0.93	0.862 ± 0.013	0.0580 ± 0.009
B3	+ 0.10	0.79 – 0.93	0.859 ± 0.007	0.0418 ± 0.005
E1	+ 0.61	0.75 – 0.93	0.831 ± 0.012	0.0457 ± 0.008
B8	+ 0.31	0.75 – 0.89	0.832 ± 0.010	0.0399 ± 0.007
M45	+ 0.56	0.70 – 0.93	0.793 ± 0.005	0.0425 ± 0.003
M63	+ 0.09	0.75 – 0.89	0.803 ± 0.008	0.0388 ± 0.006
M64	+ 0.25	0.70 – 1.03	0.849 ± 0.005	0.0672 ± 0.004
S5	+ 0.28	0.79 – 0.98	0.892 ± 0.006	0.0433 ± 0.004
S20	+ 0.86	0.70 – 0.98	0.853 ± 0.008	0.0624 ± 0.005
S32	+ 0.23	0.75 – 0.89	0.797 ± 0.008	0.0362 ± 0.005
S58	– 0.76	0.75 – 0.93	0.823 ± 0.006	0.0464 ± 0.004
S71	+ 0.24	0.75 – 0.89	0.808 ± 0.006	0.0349 ± 0.004
M36	+ 0.20	0.70 – 0.89	0.801 ± 0.007	0.0404 ± 0.005
S74	+ 0.70	0.75 – 0.93	0.856 ± 0.010	0.0424 ± 0.007
S93	+ 0.37	0.79 – 0.98	0.871 ± 0.009	0.0494 ± 0.006
S134	+ 0.74	0.79 – 0.93	0.860 ± 0.012	0.0466 ± 0.008
S164	+ 0.48	0.79 – 0.93	0.877 ± 0.006	0.0367 ± 0.004
M33	+ 0.46	0.79 – 0.93	0.861 ± 0.004	0.0405 ± 0.003
M50	+ 0.47	0.75 – 0.84	0.793 ± 0.008	0.0339 ± 0.006
M51	+ 0.51	0.70 – 0.89	0.817 ± 0.009	0.0464 ± 0.006
S53	+ 0.39	0.79 – 0.98	0.873 ± 0.009	0.0454 ± 0.006
M60	+ 0.53	0.75 – 0.84	0.795 ± 0.006	0.0309 ± 0.004
S110	+ 0.12	0.70 – 0.84	0.799 ± 0.004	0.0374 ± 0.003

than those colonies in the *Thuja* forests. No cline effect, that is, the gradation of a particular variable correlated with geography, seems apparent although the material is limited in this respect.

Besides technical and personal errors of measurement which might be involved, several objections may be brought against the methods presently used. That the three repeated stations (C, G and A series) show close agreement among their respective ranges gives some confidence in the method of measuring and sampling. Analysis of the data from some other point of view might provide evidence for the recognition of distinct species. The one other analysis tried is presented in Plate IX, in which the mean height of each sample is plotted against the mean width. Yet, the same generalities obtain as those previously presented. The coefficient of correlation between height and width is given for each sample in Table 11. In many instances this is too low to be significant. In general, shells of greatest height are not necessarily those of greatest or least width. Of the two instances in which the coefficient of correlation was negative, one (T1) is too close to zero to be significant. No distinct bimodality was detected in any array of heights or widths (data not presented), and, as previously pointed out, it was not possible to separate distinct morphological types in a given lot before measuring. There is very little skewness or kurtosis evident by inspection in the array of these dimensions.

The only study of a statistical nature on American *Carychium* is that of Clapp (1906), who gave a series of average height and width for *C. exiguum* and *C. exile canadense.* But he did not state the number of specimens in each lot, nor did he give any indication of dispersion. He concluded that *C. exile canadense* averages over 2.0 mm. in height and seems limited to the Canadian life zone (boreal life zone). He found that *C. exiguum* also becomes somewhat larger in the north (considering the whole of the United States), and one lot from Marquette County, Michigan, averaged 2.15 mm high.

In Europe a similar problem of doubtful species distinction in *Carychium* exists. Boycott (1901) reported the measurements of 200 shells of *C. minimum* Müller collected from flood-drift of the Thames River. He noted considerable variation in the height and in characters not easily measured, and concluded: "... on the whole, the species seems to offer a good field for anyone who cares to describe and name a number of fresh varieties." No mention was made of *C. tridentatum* Risso, the other species sometimes recognized in Europe. Kennard & Woodward (1926) list *C. tridentatum* as a synonym of *C. minimum.*

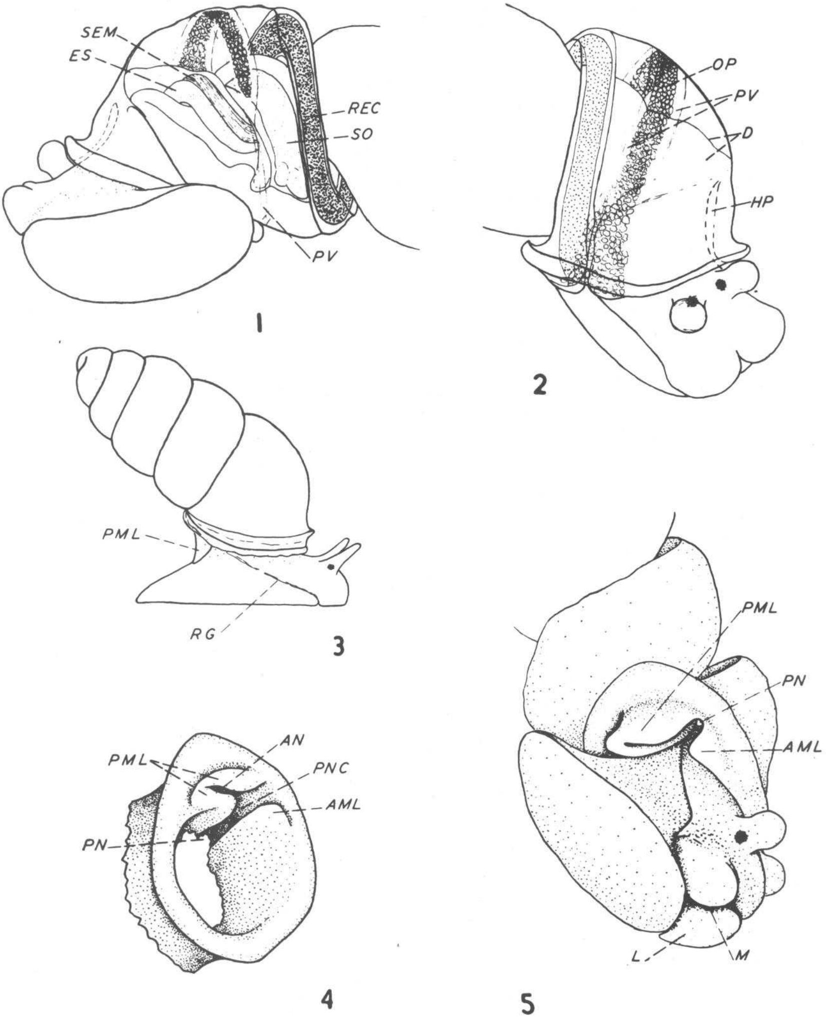
In 1925, Zimmermann reported an extensive study on 44 lots of *Carychium* from as many places in Europe. His material was mostly museum series and the possibility that his lots were not each from an isolated colony, though from a restricted geographical area, may not be significant when considered in terms of the scale of the area he was considering. In general, his lots are larger than those used in this study. Certain of his procedures are questionable. In some cases he split seemingly unimodal curves which showed slight platykurtosis, concluding that these curves were composed of two distinct but broadly overlapping species, and that these species lived together in the same habitat. Simpson and Roe apparently disagree with such a procedure both statistically and biologically and they (1939: 199) stated: "The easiest and only conclusive method of splitting heterogeneous samples is by frequency distributions that are plainly multiple and that do not overlap." They (l.c.: 200) add further: "Really separable taxonomic groups of animals such that all their variates have extensively overlapping distributions are very rarely found together in nature. Such completely intergrading groups, usually contiguous geographic races or successive geologic subspecies, do occur, but not normally in full association with each other." The question is further discussed by Diver (1940), Boycott (1929), and Atkins (1928), as well as in many other statistical studies on mollusk shells. The opinions and conclusions of those investigators are varied and often not in agreement with one another. The criteria for interpreting the taxonomic value of statistical conclusions are just as unstandardized as those for defining the limits of specific categories.

Zimmermann (1925) compared height of shell with the height/width ratio. This procedure is not uncommon in conchological statistics (see Atkins, 1928). Though apparently nowhere stated, it is perhaps an attempt to correlate size (*i.e.,* major dimension) with form (*i.e.,* the ratio).

Possibly such a procedure is statistically valid and it may be accepted as another attempt at detecting differences of variables which are of value for recognizing species. The less involved procedure of obtaining the coefficient of correlation (or, if preferred, the "z" of Fischer: see Simpson & Roe) between two dimensions would seem equally adequate for this purpose. Zimmermann concluded that C. *minimum* was limited to Europe north of the Alps, and that C. *tridentatum* occurred only south of the range of the former. At the junction of the ranges mixed colonies occur.

Thorson & Tuxen (1930), using the methods of Zimmermann, measured and analyzed 11 lots of *Carychium* shells from Denmark, the presumed area from which C. *minimum* was originally described. They found that figures of average height plotted against average width filled in the gaps in a scatter diagram between the position of a lot from Sweden and several from Central Europe. This gap had been the basis for Zimmermann's postulating a distinct race in Sweden. Thorson and Tuxen also showed

PLATE X



External morphology of *Carychium exiguum*. FIG. 1. Left side of a cleared specimen with the shell removed. FIG. 2. Anterior dorsal view of same specimen. FIG. 3. Normal crawling position of *Carychium*. From life. FIG. 4. Mantle collar from an opaque, preserved specimen. FIG. 5. Anterior ventral view of an opaque, preserved specimen with the shell removed.

Abbreviations. AML - anterior mantle lappet; AN - anus; D - diaphragm; ES - esophagus; HP - hypopeplar chamber; L - labial palp; M - mouth; OP - organ of Plate; PML - posterior mantle lappet; PN - pneumostome; PNC - pneumostomal canal; PV - pulmonary vein; REC - rectum; RG - reproductive groove; SEM - subesophageal columellar retractor muscle; SO - spermoviduct.

that the material from Denmark encroached considerably into the region of the diagram reserved for *C. tridentatum.*

Recently, Mr. Hugh Watson kindly supplied me with two lots of *Carychium* from England containing 30 specimens in each. These series show a distinct homogeneity within themselves as to form and size, and contrast markedly between each other. One lot is labeled "*C. minimum,*" the other "*C. tridentatum.*" Also, very recently, Mandahl-Barth (1950) has recognized both *C. minimum* and *C. tridentatum* from Denmark, giving figures of the shells.

Because of insufficient material, improper methods of analysis, different evaluations given to results, or for some other reasons, there has been no general agreement reached about speciation in *Carychium* of Europe or America. Few will doubt that shells which fit the previous concepts of *C. exiguum* and *C. exile* and its subspecies exist in Michigan; nor that shells which fit the concepts of *C. minimum* and *C. tridentatum* also exist in England and Denmark. Whether these species are only nominal or represent valid genetic distinctions, and thus are biological, is the significant problem. Its ultimate solution seems to require an investigation of the dynamic aspects of *Carychium* biology beyond those touched upon in this and previous studies.

EXTERNAL MORPHOLOGY AND BEHAVIOR

Except as noted, the following description is based on the living animal of *C. exiguum* (Plate X, Fig. 3). Other than the eye, true pigmentation is completely lacking in *Carychium.* The fasting animal is of a dull white color, translucent to transparent except in the more compacted pedal and upper visceral masses, which are opaque. When the animal is fed the digestive tract can be traced easily from the stomach to the anus due to its dark brown contents. The liver assumes a light golden color and there appear in it minute, hyaline, refractile granules of a darker brown shade. These granules persist for some time after the digestive tract is cleared of food and while the golden color of the liver is fading to the dull white of the fasting state. Similar granules can be seen in some Stylommatophora, *e.g., Cionella* and *Succinea.* Possibly due to methods used in fixing and staining the sectioned material, I was unable to detect granules of the liver which could be referred to those just cited in the serial sections.

The sole of the foot is oval, about three times as long as broad, with the sides parallel and straight. The posterior end is evenly rounded without a median notch. The anterior end is truncate by a transverse groove separating the sole from the labial palps. There are no grooves on the sole, nor marginal differentiation due to intensity of coloration, as may be seen in some helicids and other groups.

The ventral surface of the labial palps is appressed to the substrate and thus forms what superficially appears to be an anterior segment of the foot, being about as wide as the sole and one-third as long. A longitudinal mid-ventral cleft between the palps harbors the mouth.

No marginal or supramarginal pedal grooves are present. The posterior dorsal part of the foot is roundly flattened without medial keel or groove. From the right end of the pedo-palpal groove the reproductive groove (Plate X) extends in a straight line along the right lateral body surface to the pneumostome. There is nothing comparable on the left side. Other than the groove just mentioned, all dorsal parts of the cephalopedal mass are entirely smooth, without furrows, nodules or ridges. The smooth body surface is generally considered characteristic of the lymnic Basommatophora, in contrast to the Stylommatophora, which often have a definite, permanent pattern of ridges and grooves. Occasionally the tegument of the Ellobiidae is described as rugose. Tegumentary nodules and tentacular annuli of the living Ellobiidae which I have examined all seem to be phenomena of contraction, indefinite and transitional in character, and not comparable to the pattern of the Stylommatophora. However, Hedley (1916) described the external animal of *Phytia ornata* as having the "facial area covered with finer tubercles than the rest of the animal."

On the anterior dorsal aspect of the head a single pair of tentacles arises which are circular in cross-section. When fully extended the tentacles are about three times as long as their basal diameter. Separated by a distance about equal to their basal diameter at their attachments, the tentacles diverge at about right angles.

The single pair of tentacles of the Basommatophora is generally considered homologous to the ommatophores of the Stylommatophora (Simroth & Hoffmann, 1910: 91). By their round transverse section and relative short length in comparison with their diameter, the tentacles of the Ellobiidae approach the form of the ommatophore more closely than do the tentacles of the lymnic Basommatophora. In the latter group they are variously formed in different families, being, for example, flattened and triangular in the Lymnaeidae, or round and filiform in the Physidae and Planorbidae (see Hubendick, 1947).

In the lymnic Basommatophora there seems to be no homologue to the anterior tentacles of the Stylommatophora. In some Ellobiidae, however, small oval, supramarginal pads on the labial palps have been considered anterior tentacular rudiments. Hedley mentions their presence in *Phytia* *ornata;* Pelseneer (1894) noted them in *Phytia myosotis;* Plate (1897) denied their presence in *Pythia scarabaeus,* but my own investigations reveal their presence in that species. Although Lehmann (1873) describes similar structures in *Carychium minimum,* I have been unable to find anything comparable on the external animal of English examples of that species, nor in living or opaque, preserved specimens of *C. exiguum.* However, in both species of *Carychium* cleared whole mounts and sectioned material reveal unique differentiation of the epithelium in this area which may be comparable to the anterior tentacular pads. Unfortunately, the histology of these pads in the Ellobiidae *s.s.* is not known. Since this tissue in *Carychium* is apparently sensory, a detailed description of it is included in the section on the nervous system (p. 87).

Together with the body stalk, the expanded mantle margin completely fills the aperture of the shell and occludes the hypopeplar cavity (that part of the mantle chamber external to the pulmonary cavity). The pulmonary opening is at the posterior part of the mantle on the right side, and is close to the anus. However, the details of the anal-pneumostomal complex are best studied in preserved specimens (Plate X, Figs. 4 and 5). In a restricted sense the pneumostome is merely a circular opening between the pulmonary and hypopeplar cavities. Leading from the pneumostome to the mantle margin is a passage, the pneumostomal canal (Plate X), whose anterior and posterior walls are formed by mantle lappets of corresponding position. Their free margins are approximated to form the medial wall, and the lateral wall is formed by the mantle proper. The anterior mantle lappet bulges but slightly below the mantle margin as an elongated ridge. The posterior lappet at times extends prominently down the body stalk (Plate X, Fig. 3); on its anterior and ventral aspect is a prominent cleft which is the anus. The occluded hypopeplar chamber, the opening of the anus into the pneumostomal canal, and the character of the mantle lappets, – all suggest the condition in the Stylommatophora. In the lymnic Basommatophora, the hypopeplar cavity is spacious and the anus opens at some distance from the pneumostomal apparatus (Hubendick, 1947). In preserved specimens of *Carychium* the upper end of the reproductive groove is seen to extend high into the hypopeplar cavity in a region near the pneumostome. The external reproductive groove is a consistent character in the Carychiidae and Ellobiidae. It is not found in the lymnic Basommatophora or Stylommatophora.

In crawling, the adult snail carries the shell well elevated, with the columellar axis at about 45 degrees to the horizontal and in a plane with the longitudinal axis of the foot. Consequently, the head emerges from the base of the aperture; the posterior extent of the foot is below the suture of the body whorl. The shell is moved slightly from side to side, being continuously moved forward. The anterior end of the foot progresses uniformly but the tip of the tail is advanced in jerks which may indicate the presence of pedal waves. No waves were found by direct observation, although this examination was made with the animal extended and lying on its side with the sole free. In some Stylommatophora the waves are evident when the snail is in that position. In his interesting comparison of the rates of crawling of land snails, Oughton (1948) found the rate of *C. exile* to be 0.2 centimeters per minute.

Though the heart is actually located just below the periphery of the penultimate whorl and about an eighth whorl apical to the expanded lip, the heart beat can be detected in the living animal.

In the process of concentrating fresh leaf samples in the laboratory (p. 5), the negatively phototactic habits of *Carychium* are strikingly demonstrated. If the animals are placed on several bits of leaves in the moist concentration chamber most of them will be found after several hours underneath the leaf fragments, provided the latter retain sufficient curvature to remain partially elevated from the bottom of the dish. The light-shunning character is also consistent with field observations. Not all specimens in the concentration chamber flee from light, however. Some remain stationary and far contracted within the shell. This retraction may be due to manipulation. Even a slight jar of the concentration chamber was often sufficient to cause the contraction of the animal. Consequently, observations on the behavior of isolated individuals was difficult and bulk cultures were generally used.

The above observations were made on animals in moist air. A different behavior is noted when the animal is covered with a drop of water. Surface tension and the relatively more resistant medium now offer impediments. The shell droops and is dragged along the substrate in jerks. Although the animal is extended and moving the tentacles are contracted to form small knobs no longer than their width (as shown in all the figures of the tentacles except Plate X, Fig. 3). Locomotion also seems slower. Thus a distinct discomfort is evidenced when the animal is under water at room temperatures.

INTERNAL MORPHOLOGY

General Topographical Morphology

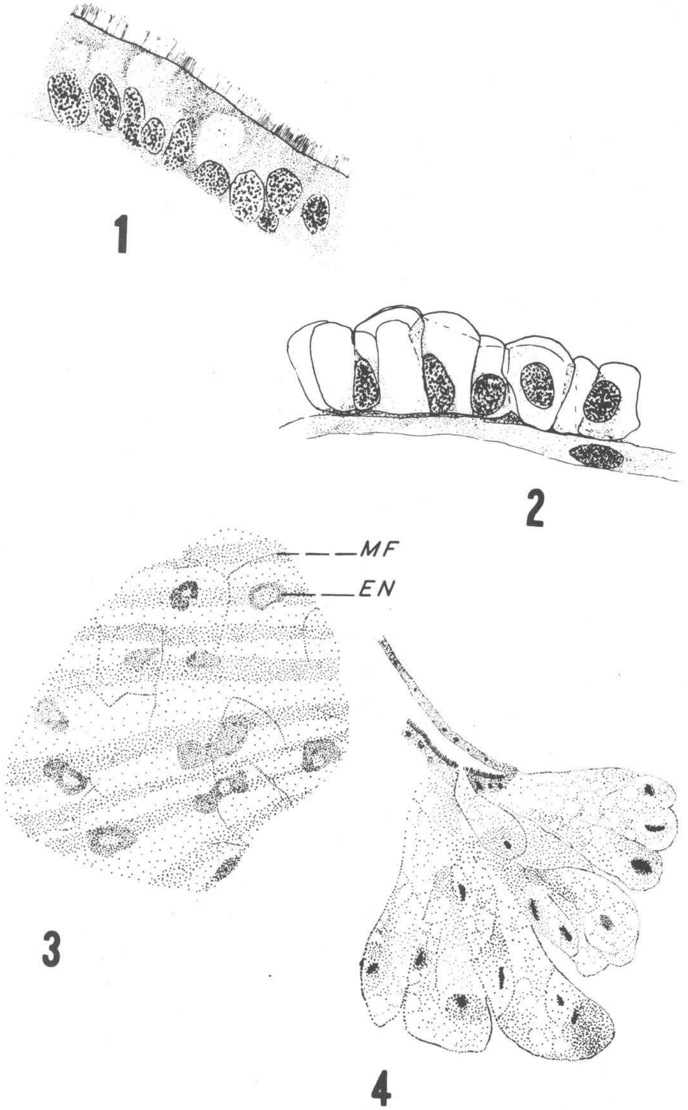
The tegument of *Carychium* is a single-layered epithelial sac reinforced within by a layer of muscular and connective tissue. The character of the epithelial cells, amount and arrangement of muscular tissue, and type and amount of connective tissue subtending the epithelium all provide tegumentary differentiation in different parts of the body.

The hemocoelic cavity is broadly invaded around the lower parts of the visceral mass by an infolding of the tegument thus forming the mantle cavity. The latter has two parts, a lower portion, extending completely around the body stalk (here termed the *hypopeplar* chamber, from the Greek meaning "below the skirt," to distinguish this part of the mantle cavity) and the upper, pulmonary chamber. Both chambers are completely lined by epithelium continuous with that which covers the exterior of the body.

The invasion of the hemocoel by the hypopeplar chamber is of negligible extent in the direction of the axis of the primary cone, occupying only a small fraction of the last part of the body whorl. By contrast, the pulmonary chamber in *Carychium* and most pupiform shells extends apically for about one whorl above the hypopeplar chamber, and in this region occupies most (about three-fourths) of the volume of the primary cone. The pulmonary chamber subtends the shell on the parietal and peripheral parts. In the region of the pulmonary chamber, the columellar portion of the shell is subtended by a restricted portion of the hemocoelic space, here termed the isthmian hemocoel. The part of the hemocoel apical to the isthmian portion, together with the structures it contains and the tegument bounding it, is the upper visceral complex (Plates XII and XIII). Below the pulmonary cavity, in the body stalk of the animal, the isthmian hemocoel is continuous with that of the cephalopedal mass. Because of several characteristics which the cephalopedal and isthmian hemocoels have in common, these two spaces, together with the structures which they contain and the tegument which bounds them, are termed collectively the lower visceral complex. The pulmonary cavity and its bounding membranes, together with the organs contained in its parietal and peripheral wall, constitute the pulmonary complex.

1. **The Pulmonary Complex.** The epithelial membrane of the pulmonary cavity subtending the parietal and peripheral portions of the primary cone of the shell is closely approximated to the epithelium covering the visceral mass (*i.e.*, the mantle); this approximation is so close in *Carychium* that the two membranes are usually not distinguishable except where they part to accommodate organs and vascular hemocoelic spaces between them (Plates XV and XVI). In other Stylommatophora and lymnic Basommatophora they are often separated by a considerable layer of connective tissue, which is recessed in tubular fashion, producing the pattern of blood sinuses known as the pulmonary network of blood vessels. Nothing comparable is detectable in *Carychium.*

PLATE XI



Internal morphology of *Carychium exiguum*. FIG. 1. Epithelium from the sole of the foot. FIG. 2. Epithelium lining the kidney resting on the epithelium of the pulmonary chamber. FIG. 3. Surface view of the mantle membrane as seen from the upper part of the upper visceral complex. FIG. 4. Posterior end of the pedal gland.

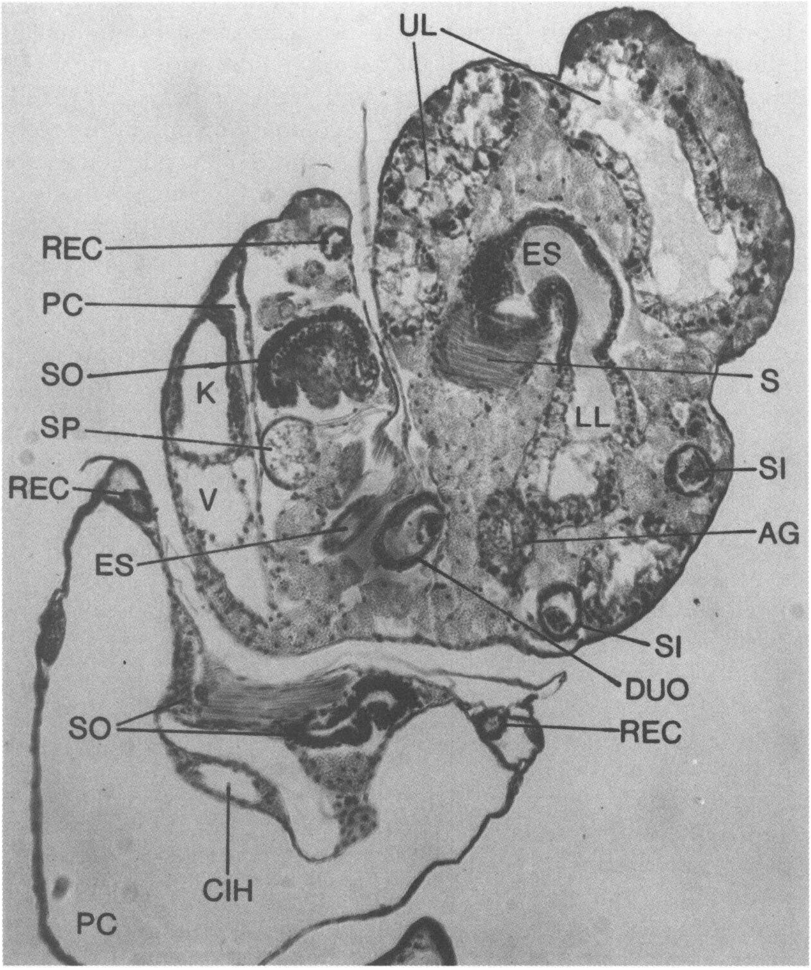
Abbreviations. EN - nucleus of the epithelium; MF - muscle fiber.

In *Carychium* four organs lie between these two membranes: (1) the pericardium, situated at the upper end of the pulmonary cavity and on the side opposite the suture of the whorl in which it lies (Plate XX, Fig. 2); (2) the kidney, situated at the same level as the heart and between the latter and the suture; (3) the last part of the digestive tube, termed the rectum, which is on the opposite side of the kidney from the heart and parallels the suture of the shell throughout the pulmonary complex (the rectum thus separates the peripheral and parietal portions of the pulmonary complex); (4) the organ of Plate (Plate X, Figs. 1 and 2), which consists of a group of glandular cells forming a band extending from the pneumostome apically for about half a whorl; it thus parallels the rectum and is adjacent to the pulmonary vein which courses along its side. This structure has the same position and a similar extent of an organ described by Plate in *Pythia.* A detailed discussion of Plate's organ is presented under the reproductive system (p. 88-91). Nothing comparable to an osphradium, or any remnant which might be interpreted as an osphradial ganglion, was detected in *Carychium.*

The separation of the pulmonary epithelium from the mantle epithelium is merely sufficient to accommodate the pericardium and kidney in the region of these two organs, but at the rectum the separation is more extensive forming a large space, triangular in cross section, and here designated the rectal wedge. Besides the rectum it contains a mass of connective tissue which is greatly recessed to form a tubular blood space, the rectal sinus. In sigmurethrous Stylommatophora the last half of the ureter is included in the rectal wedge, but no such structure is present in *Carychium.* Besides the rectal sinus there are two other separations of the pulmonary and mantle epithelia, which contain only tubular blood spaces; these are the pulmonary vein (Plate X, Figs. 1 and 2), extending from the pneumostome to the apertural end of the pericardium obliquely across the peripheral pulmonary wall, and the left pallial vein (Plates XIII and XVI) extending from the mantle margin to the apertural end of the pericardium along the junction between the peripheral pulmonary wall and the diaphragm. It parallels the columellar lamella of the shell, on the basal side of the latter. These vascular recessions are considered in more detail under circulatory system (p. 79).

The diaphragm (Plates XII and XIV; Plate X, Fig. 2) is that epithelial layer separating the pulmonary cavity from the isthmian hemocoel. This epithelium is continuous with the epithelium of the parietal and peripheral pulmonary wall and with them completes the lining of the pulmonary cavity. In many Stylommatophora the diaphragm is subtended in the isthmian hemocoel by a complex system of muscles (see Trappmann, 1916,

PLATE XII



Photomicrograph of the upper visceral complex of *Carychium exiguum*. Note the large mass of eosinophilic granulocytes which form a matrix about the organs. The spermathecal sac and entrance of the lower liver tube into the esophagus are shown. The muscular strands passing to the spermathecal sac probably insert on the pulmonary epithelium beyond, rather than on, the sac as is apparent in this photograph.

Abbreviations. AG - albumen gland; CIH - columellar isthmian hemocoel; D - diaphragm; DUO - duodenum; ES - esophagus; K - kidney; LL - lower liver tube; PC - pulmonary cavity; PLS - parietal lamella of shell; REC - rectum; S - stomach; SI - sigmoid intestine; SO - spermoviduct; SP - spermathecal sac; UL - upper liver tube; V - ventricle of heart.

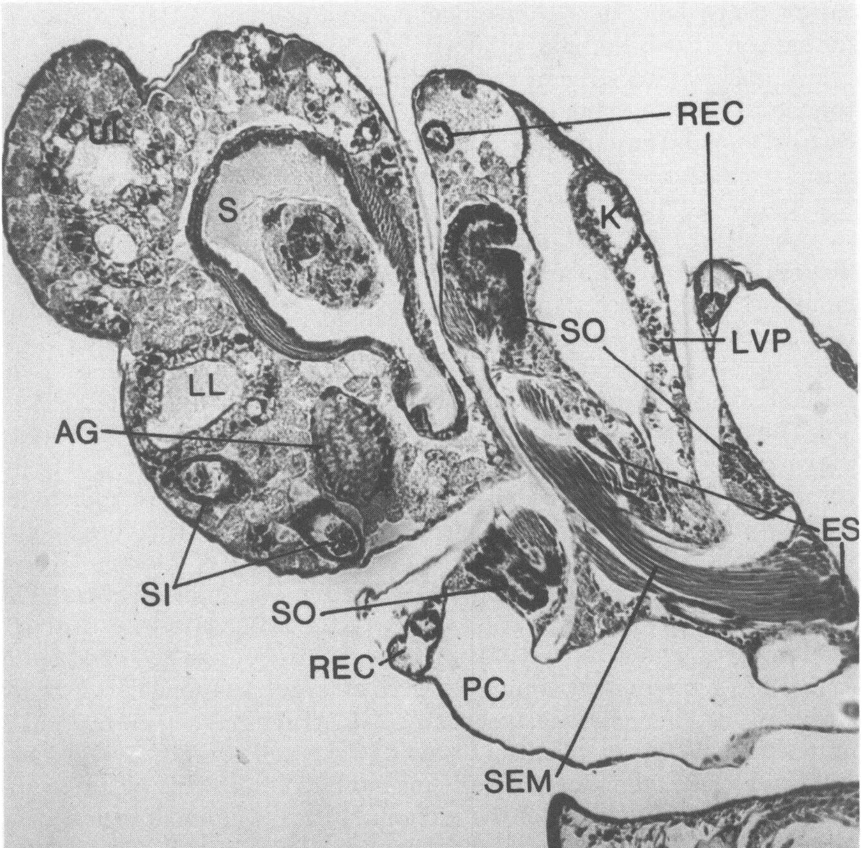
on *Helix)* and connective tissue adnate to the hemocoelic side of that membrane. Because of its position and muscular nature the diaphragm may be assumed to change the volume of the pulmonary cavity by the contraction of its subtending muscles and thereby facilitate gaseous exchange with the exterior when the pneumostome is open (Boettger, 1944: 317, implies the same for the Basommatophora).

In *Carychium* the structure of the diaphragm does not indicate such a function. Muscle fibers underlying the membrane are few and in their distribution and amount resemble the muscle fibers of the mantle epithelium (p. 63). An exception is noted in the case of phallate specimens (p. 93). Moreover, the reflection of the columellar mantle membrane over the two lamellae of the shell closely approaches the diaphragm along the free margins of the lamellae. At these lines the epithelium covering the lamellae's margins and the diaphragm are connected by a line of connective tissue which thus restricts the diaphragm into longitudinal units. These units would not seem as effective for regulating the volume of the pulmonary cavity as would a diaphragm not so restricted (Plate XVI).

2. **The upper visceral complex.** The apical end of the pulmonary cavity, the resorption of the internal partitions of the shell, and the origin of the columellar retractor muscle, all coincide in their position in relation to the primary cone of the shell, or, coiling of the visceral mass. This correspondence has considerable significance to the morphology of the snail. Apical to this point the hemocoel, though of large extent, is completely filled with the organs it contains and the connective tissue which forms a matrix around them (Plates XII and XIII). The organs are mutually imbedded in each other, a phenomenon more evident in larger pulmonates where the ovotestis and liver are extensively branched. In keeping with the resorption of the shell partitions there is a fusion of the whorls of the visceral mass. As seen by sectioning juveniles of one and two whorls this fusion is progressive with the growth of the animal. However, no histological basis was found to account for this phenomenon. The sutural position is still evident in the fused spire corresponding to the sutural-shelf remnant of the shell partition. Observations on *Pythia* show the upper visceral complex has the same partially fused condition of the primary cone, but here again the condition is only partial and not immediately evident when viewing the exterior of the visceral mass with the shell removed. This may account for Plate's conclusion that the whorls of the visceral mass are not fused. In *Melampus* the fusion is so complete that no trace of coiling is evident in the visceral mass of the adult (Koslowsky, 1933).

Robson (1915) stated that in *Marinula tristanensis* "portions of the resorbed shell septa are found in a superficial position in various parts of the body

PLATE XIII



Photomicrograph of the upper visceral complex of *Carychium exiguum*. Another section from the same individual shown on the previous plate. The gastric muscle is evident here, as well as the beginning of the duodenum and the typhlosole. Note the large cells in the left marginal vein which are apparently amoebocytes. The bubble-like cells on the free surface of the rectal wedge near the kidney are kidney cells outside of the kidney proper.

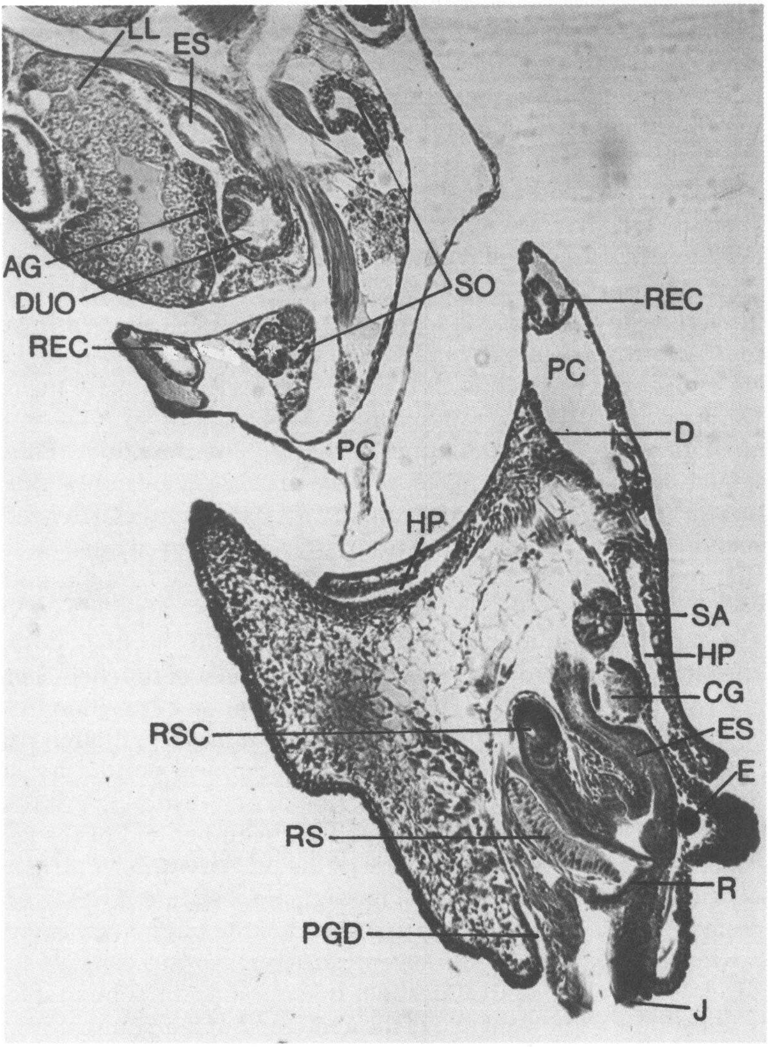
Abbreviations. AG - albumen gland; ES - esophagus; K - kidney; LL - lower liver tube; LVP - left pallial vein; PC - pulmonary cavity; REC - rectum; S - stomach; SEM - subesophageal columellar retractor muscle; SI - sigmoid intestine; SO - spermoviduct; UL - upper liver tube.

enclosed in epithelial pockets." This may indicate that resorption is not progressive with the growth of the snail but occurs in that species after the individual is nearing maturity.

Forming a matrix around the orbs of the upper visceral complex are large connective tissue cells whose cytoplasm is packed with large eosinophilic granules (Plate XIX, Fig. 2). Since these granules vary in size and number in different individuals, it is possible that they serve as storage for metabolic products. The granular eosinophilic cells of the upper visceral mass may extend for a short way into the isthmian hemocoel and rectal sinus, but they are not prominent in the lower visceral complex. Other connective tissue cell types are inconspicuous in the upper visceral complex.

Although renovation of the mantle membrane has occurred in such a way as to destroy the coiling of the visceral mass whorls to a large degree, certain of the structures contained in those whorls still follow the coil of the primary cone. That arrangement holds for the liver tubes and the albumen gland as well as the upper part of the spermoviduct. Other organs, such as the duodenum, esophagus and hermaphroditic duct, no longer coil about the axis of the secondary cone but parallel it in a rectilinear fashion. In snails which do not resorb shell partitions it must be admitted that these organs are coiled or straight according to the number of whorls and tightness of coiling of the visceral mass. Also, the coiling of these organs in those mollusks may vary according to their position - whether they are toward the periphery or columella of the shell. Perhaps the most striking example in *Carychium* of alteration of position in keeping with the fusion of the spire is the duodenum which, though peripheral, parallels the columella. Another topographical peculiarity of this part of the intestine in *Carychium* is notable. In non-resorbing pulmonates the duodenum passes from the stomach to the upper end of the pulmonary cavity where, on the sutural side of the primary cone, it turns transversely, becoming the lower loop of the sigmoid intestine. The lower loop of the sigmoid intestine abuts the apical end of the pulmonary cavity, the pericardium and kidney. These several structures form a concave surface conforming to the loop of the intestine. In *Carychium* the comparable loop of the intestine is somewhat above the apical end of the pulmonary cavity and the conformity of the latter is not evident. Indeed, certain portions of the reproductive system are intruded between the lower loop of the sigmoid intestine and apical end of the pulmonary complex. The relationship of these structures may be a peculiarity of *Carychium* not correlated with fusion of the whorls, for Odhner (1925) illustrates the apical end of the pulmonary complex as having a relationship with the sigmoid intes-

PLATE XIV



Oblique sagittal section through the cephalopedal mass to show a cross section of the buccal mass.

Abbreviations. AG - albumen gland; CG - cerebral ganglion; D - diaphragm; DUO - duodenum; E - eye; ES - esophagus; HP - hypopeplar chamber; J - jaw; LL - lower liver tube; PC - pulmonary cavity; PGD - duct of pedal gland; R - radula; REC - rectum; RS - radular support; RSC - radular sac; SA - salivary gland; SO - spermoviduct.

tine characteristic of the other pulmonates.

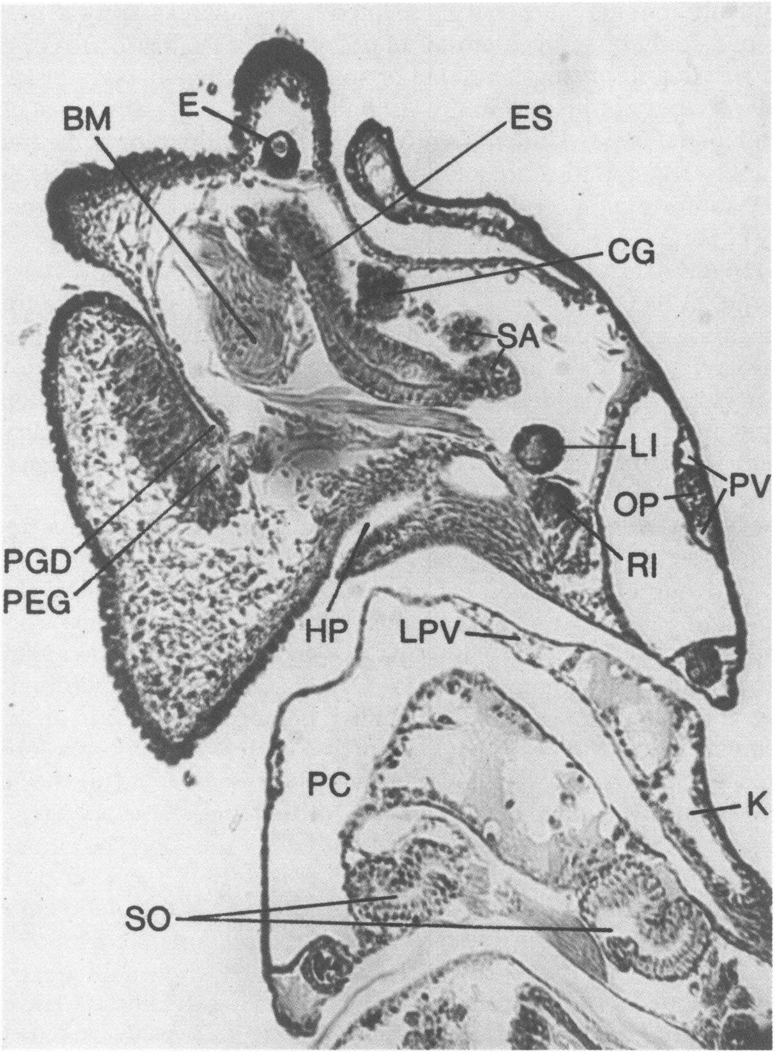
The mantle epithelium is illustrated in Plate XI, Fig. 3. Occasionally the cell membranes are more sharply defined than shown and they set off the flattened epithelium into a mosaic of polygonal units. The nuclei of these cells are irregular being lobulated or sometimes ring-shaped. Nuclei of similar shapes are present in the epithelium on the dorsal surface of the cephalopedal mass. Underlying the squamous epithelium of the mantle in the visceral complex are a few muscle fibers. These are widely separated, not forming a continuous sheet and all parallel the axis of the primary cone.

3. **Lower visceral complex.** In the lower visceral complex (Plates XIV through XVII) the hemocoel is much more spacious than in the upper, constituting a single large space around the visceral organs which lie free in the cavity and have a greater freedom of movement than those of the upper visceral hemocoel. The organs of the lower visceral complex are the buccal mass and esophagus, the spermoviduct, the central nervous system and pedal gland, and, in phallate specimens, the vas deferens and penis.

The isthmian hemocoel is divided longitudinally into two compartments by the approximation of the diaphragm and lamellae of the shell (Plate XVI). The parietal isthmian hemocoel is that part on the sutural side of the parieto-columellar or upper lamella. It contains the lower portion of the spermoviduct, the spermathecal duct, and the suboviducal moiety of the columellar retractor muscle (Plate XXV, Fig. 3). Since the spermoviduct opens at the apertural end of the isthmian hemocoel, there is in aphallate specimens no portion of the reproductive system in the cephalopedal hemocoel. The columellar isthmian hemocoel is included in the space between the two lamellae of the shell. It includes the esophagus and subesophageal moiety of the columellar retractor muscle. The amount of connective tissue in the isthmian hemocoel is very little, never packing the space. This reduction may imply free passage of the blood through these spaces, between the upper visceral and cephalopedal hemocoels.

The epithelium of the cephalopedal mass is everywhere subtended by a layer of connective and muscular tissue of varying thickness. The chief element in the connective tissue of this region seems to be the stellate type of small nuclei surrounded by a small area of cytoplasm from which radiate cytoplasmic strands. These structures provide a spongy pattern which presumably allows free passage of the body fluid. Such tissue completely fills the tail and forms a thick layer on the sole of the foot (Plates XIV and XV). Connective tissue is sparse in the central part of the cephalopedal hemocoel (Plates XVI and XVII), although it very likely plays a part in

PLATE XV



Oblique sagittal section through the cephalopedal mass showing the pedal gland and the innominate visceral ganglia.

Abbreviations. BM - buccal mass; CG - cerebral ganglion; E - eye; ES - esophagus; HP - hypopeplar chamber; K - kidney; LI - left innominate ganglion; LPV - left pallial vein; OP - organ of Plate; PC - pulmonary cavity; PEG - pedal gland; PGD - duct of pedal gland; PV - pulmonary vein; RI - right innominate ganglion; SA - salivary gland; SO - spermoviduct.

maintaining the positional relationships of the organs in that space. Except for the tentacular membrane supporting the eye, no definite membranes were recognized such as Kisker (1923) defined in *Helix.* Similar membranal arrangements of the connective tissue have been noted by Carriker (1947) in *Lymnaea* and Hoff (1940) in *Ferrissia.*

Besides the stellate cells, at least three other types of connective tissue cells are recognizable in the cephalopedal hemocoel of *Carychium.*

(l) Microgranulocytes containing lobate cytoplasm with a small elliptical nucleus centrally placed. The nucleus stains very darkly and the cytoplasm contains many small basophilic granules. These cells are much smaller than the eosinophilic granulocytes of the upper visceral mass.

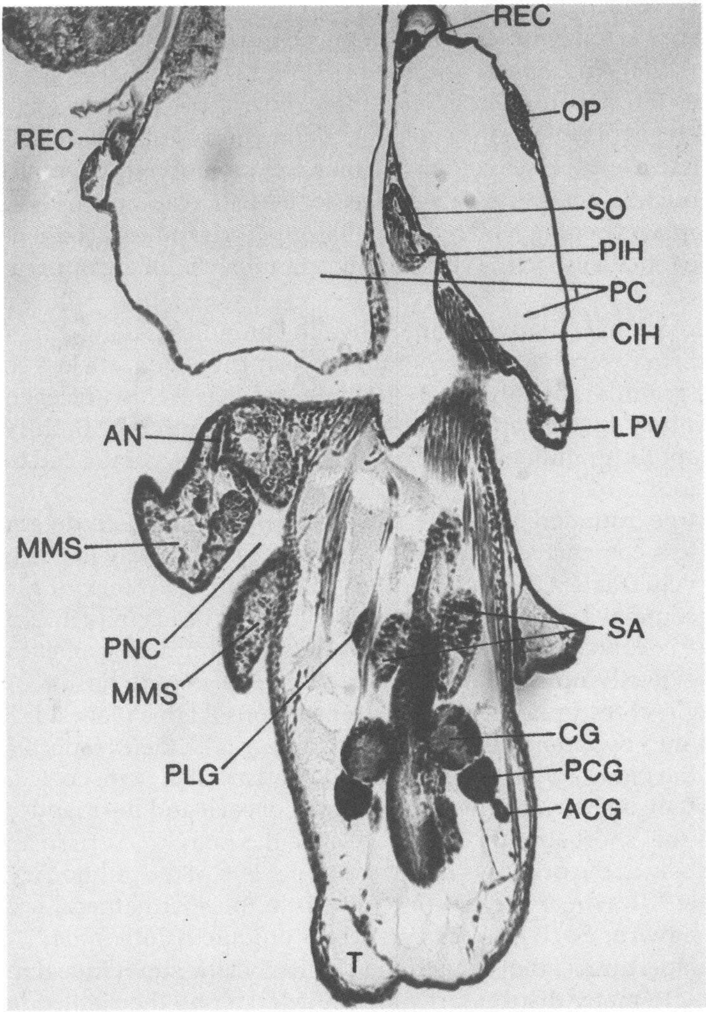
(2) Occasional clumps of larger, hyaline granules, taking a faint basic stain, may represent macrogranulocytes. These, too, are less compact and granular than the eosinophilic granulocytes. No nuclei could be definitely associated with these clumps of granules. Both types of basophilic granulocytes are best seen in the more compacted tissue of the foot.

(3) Large, rounded cells with small oval nuclei are often detectable in the less compacted parts of the hemocoel particularly in the left pallial vein (Plate XIII) and marginal mantle sinus. Their cytoplasm often contains large irregularly shaped bodies which may indicate that these cells are phagocytic. Possibly these are wandering ameboid cells.

As previously noted, the columellar retractor muscle has its origin at the margin of resorption of the shell's partition. At this place it is already divided into two moieties which immediately take their respective positions in the paraparietal and paracolumellar isthmian hemocoel. In those cavities they lie between the tubular organ of each and the mantle epithelium. A few short strands of muscle leave the margin of origin and pass transversely in the primary cone to the upper end of the pulmonary chamber (Plate XII, where they seem to attach to the spermathecal sac in the section shown). Such musculature seems unique to *Carychium.*

At the apertural end of the isthmian hemocoel the subooviducal retractor divides into many distributaries which insert along the right side of the cephalopedal mass. The subesophageal moiety similarly divides at the apertural end of the isthmian hemocoel, supplying the left side of the body with distributaries and, in addition, sending a large branch to the buccal mass, constituting the buccal mass retractor; it lies free in the cephalopedal hemocoel. Muscle strands from the two major moieties pass along the integument to the base of the tentacles, but do not seem to traverse the tentacular cavity as free muscles (see below); they form an integral part of the

PLATE XVI



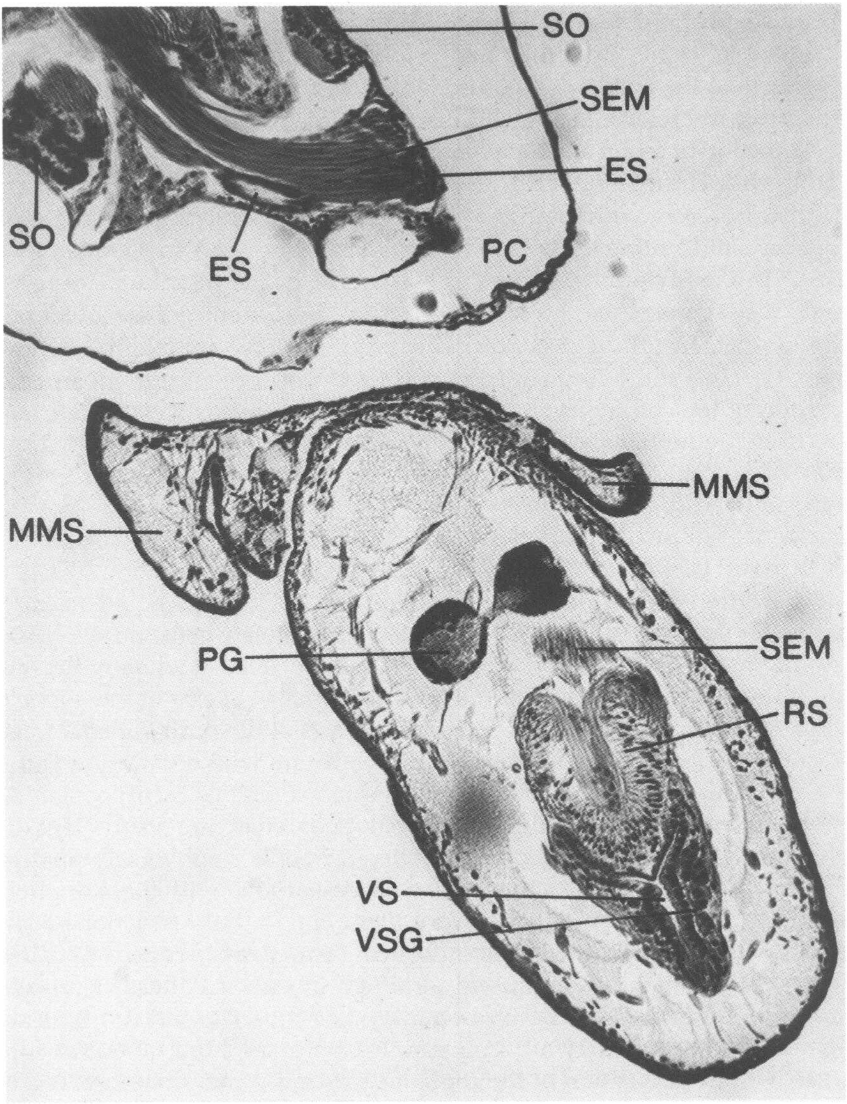
Frontal section through the cephalopedal mass at the level of the cerebral ganglia. Note the large marginal mantle sinus, the division of the isthmian hemocoel into parietal and columellar moieties, and the large left marginal vein of the pulmonary complex.

Abbreviations. ACG - anterior accessory cerebral ganglion; AN - anus; CG - cerebral ganglion; CIH - columellar isthmian hemocoel; LPV - left pallial vein; MMS - sinus of mantle margin; OP - organ of Plate; PC - pulmonary cavity; PCG - posterior accessory cerebral ganglion; PIH - parietal isthmian hemocoel; PLG - pleural ganglion; PNC - pneumostomal canal; REC - rectum; SA - salivary gland; SO - spermoviduct; T - tentacle.

musculature of the cephalopedal tegument. In the well-coiled pulmonates the columellar retractor muscle may be adnate to the tegumentary wall (presumably held there by connective tissue throughout its length) and it is thus *incorporate.* By contrast, the muscle may not be bound throughout its length to the body wall but lies loosely in the hemocoel so as to constitute a free retractor muscle. This distinction may have significance to both the direction of action and the point of fulcrum of these muscles. As Simroth (Simroth & Hoffmann, 1910) has pointed out, the columellar retractor and its distributaries, with the exception of the buccal retractor, are extensively incorporated among the lymnic Basommatophora (see also Boettger, 1944: 279). In the Stylommatophora at least some of the distributaries to the body wall, tentacles and sole of the foot are free for at least the lower portion of their length. The condition varies in the Stylommatophora, however, because some forms (*Helix* and *Achatina*) have a large incorporate portion of the columellar muscle supplying the tail, as well as an extensive free columellar muscle, closely paralleling the incorporate part. There may be no conspicuous part of this muscle incorporate in some forms, as *Trochomorpha* (personal observation). The presence or absence of a free part of the columellar retractor determines the ability of the snail to retract or to invert the cephalopedal mass as do the Stylommatophora. The situation is often compared to the inversion of a rubber glove, beginning at the finger tips. Basommatophora, lacking a free moiety of the muscle which inserts on the tegument of the body wall, only contract when withdrawing into the shell; inversion of the body wall, if any, begins at the region of the body stalk rather than at the anterior parts of the cephalopedal mass.

In *Carychium* it was not possible to determine with certainty whether the distributaries of the columellar muscle are free or incorporate. Although some portions within the cephalopedal mass are a sufficient distance from the body wall to be considered free, it is conversely possible that the thinly dispersed connective tissue associated with them might be sufficient to incorporate them. Very likely the spatial restrictions of the two isthmian hemocoels would serve in a similar way to restrict the direction of contraction of the muscle, although in these cavities the muscles are rounded in cross section, resembling free muscles, and not flattened against the wall as they are in lymnic Basommatophora. *Carychium* retracts without inversion of the cephalopedal mass and, therefore, resembles the Basommatophora in this respect. The epithelium of the cephalopedal mass is varied, usually cuboidal, occasionally columnar, and rarely squamous. Columnar epithelium is distributed chiefly in the region of the mantle margin around the pneumostome. The epithelium of the sole of the foot is cuboidal and uniformly ciliated, but no cilia could be

PLATE XVII



Frontal section through the cephalopedal mass at the level of the pedal ganglia and radular support.

Abbreviations. ES - esophagus; MMS - sinus of the mantle margin; PC - pulmonary cavity; PG - pedal ganglion; RS - radular support; SEM - subesophageal columellar retractor muscle; SO - spermoviduct; VS - vestibule (of the digestive tract); VSG - vestibular gland.

detected on the upper parts of the cephalopedal mass except in the pneumostomal canal. Present in the epithelium are unicellular glands (Plate XI, Fig. l). Some of these cells seem to extend into the connective tissue layer and are accordingly several times as long as their diameter. These structures were difficult to follow in sections and have not been studied in detail.

Along the groove which separates the foot from the labial palps the pedal gland opens (Plate X1, Fig. 4; PlateXIV). It has a large central lumen slightly flattened and circular in cross section, extending from the groove inward into the hemocoel and ending at about the posterior extent of the buccal mass. It lies between the buccal mass and the musculo-connective tissue layer of the sole where it is partly imbedded in the latter. The floor of the lumen is a ciliated, cuboidal epithelium while the cells of the roof are flattened and lack cilia. Throughout the floor of this lumen open prominent, globular gland cells. They are arranged in groups of several cells each, but form pseudoacini, for the gland cells open separately and directly into the central lumen. The nuclei of the pedal gland cells are small, oval, darkly staining, and are located near the expanded end of the cell. The cytoplasm shows a vague tendency to vacuolation and is basophilic. Koslowsky (1933) described a well-developed pedal gland in *Melampus boholensis* which differs chiefly in having small lateral canals receiving the secretion of the gland cells and opening into the central lumen. Plate (1897) reported a well developed pedal gland in *Pythia.* In the Ellobiidae and Carychiidae the pedal glands are well developed and comparable to those of the Stylommatophora. The lymnic Basommatophora by contrast have only concentrations of gland cells opening along the anterior margin of the foot.

The tentacles are merely caeca-like appendages to the general body wall and show a similar structure to the latter. The cavity they enclose is extensive because the musculo-connective layer beneath the epithelium is thin. In favorable sections the muscular tissue is seen to form two layers, a circular one on the outside and a longitudinal one within. Across the zone of juncture of a tentacle with the body wall there extends a thin sheet of connective tissue (Plates XV and XVI), seemingly irregular and discontinuous, although uniformly present in all specimens examined. This tissue supports the eye capsule. The shape of the tentacle in the living animal is described above (p. 52); in preserved specimens it is slightly contracted, the terminal half being bulbiform. The epithelium of the bulbous portion is differentiated from that of the stalk, the latter resembling that of the general body surface. Judging from its histology the epithelium of the tentacle tip seems to be sensory. Moreover, there is a large nerve supplying it from the cerebral ganglion.

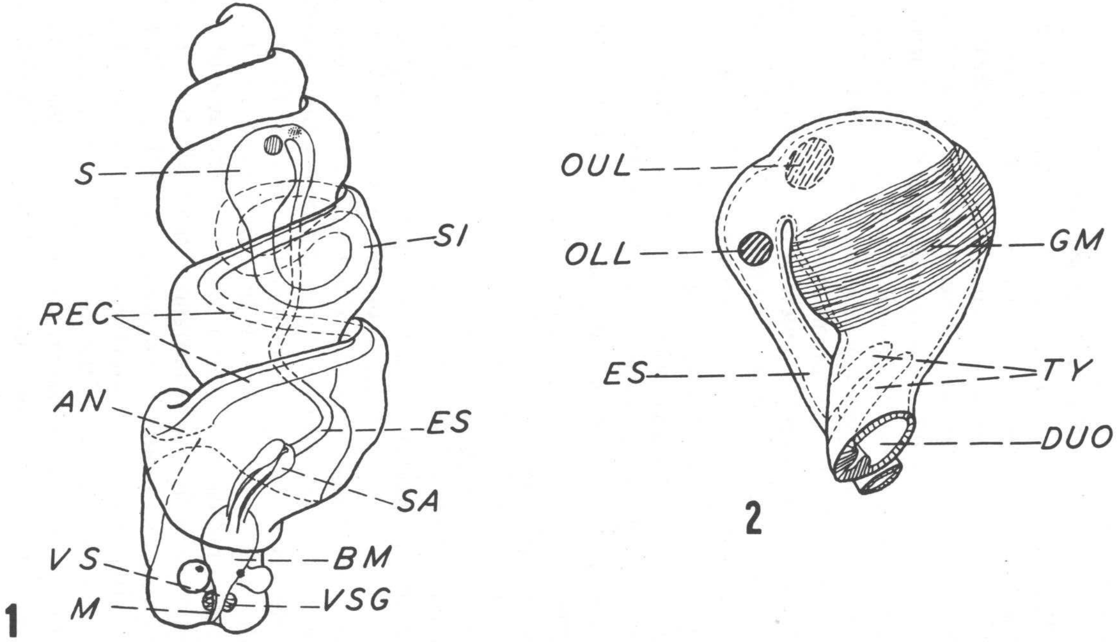
A narrow, crescent-shaped strip of epithelium borders the anterior edge of each labial palp. It agrees entirely in its histology with that of the tentacle tip. Both regions are covered with a prominent cuticle which is limited to the sensory areas. These zones are described in more detail under the nervous system (p. 87). Possibly the sensory areas of the labial palps are homologous to the labial pads noted in many Ellobiidae (p. 52). However, the histology of these pads is unknown, and the position of the sensory areas of *Carychium* is not strictly comparable to the labial pads.

Digestive System

Simplicity is the keynote of the digestive tract (Plate XVIII, Fig. 1), as noted in many other aspects of the form and structure of *Carychium exiguum*. Essentially the tract consists of a circular tube the walls of which are formed of a single layer of epithelial cells. The central digestive tract is ciliated from the dorsal portion of the buccal cavity to the anus, but not in the interior of the buccal cavity or vestibule or in the tubular glands (liver and salivary) evaginated from the central tube. In the buccal mass and stomach a muscular sheath plays a prominent role. Elsewhere along the digestive tube musculature is absent. The branching of the liver is minimal, consisting chiefly of large, shallow outpocketings of the spacious tubes which compose this organ. There is no branching of the salivary glands.

The mouth is a midventral, longitudinal slit between the labial palps and provides entrance into the vestibule (Plates XIV and XVII). The latter is a circular tube which proceeds dorsally for a short distance and then turns posterior to become incorporated in the musculature of the buccal mass. The buccal mass is a slightly elongate-oval structure, the length of which is about that of the vestibule. The jaw is situated at the point where the vestibule turns posterior. It is a crescentic, cuticular plate extending across the top of the vestibular lumen with its concave border projecting freely into that passage. No sculpture was detected on the free margin or surface of the jaw. Moreover, it was not possible to detect a fibrillar structure of this cuticular plate. In *C. minimum* Moquin-Tandon (1855) and Lehmann (1873) report a simple jaw without toothed margin or sculptured surface. They make no mention of a possible fibrous structure. However, Odhner (1925) describes and figures the jaw of that species as having such a structure. The vestibular lumen behind the jaw is lined with a thin cuticle, apparently continuous with the jaw; this extends to the expansion of the vestibule into the buccal mass, progressively thinning posteriorly. The post-gnathal cuticular structure of *Carychium* seems homologous to the

PLATE XVIII



Anatomical aspects of the digestive system. FIG. 1. Positional relationship of the digestive tract. The liver tubes are not shown. FIG. 2. The stomach from its columellar aspect.

Abbreviations. AN - anus; BM - buccal mass; DUO - duodenum; ES - esophagus; GM - gastric muscle; M - mouth; OLL - opening of lower liver tube; OUL - opening of upper liver tube; REC - rectum; S - stomach; SA - salivary gland; SI - sigmoid intestine; TY - typhlosole; VS - vestibule (of the digestive tract); VSG - vestibular gland.

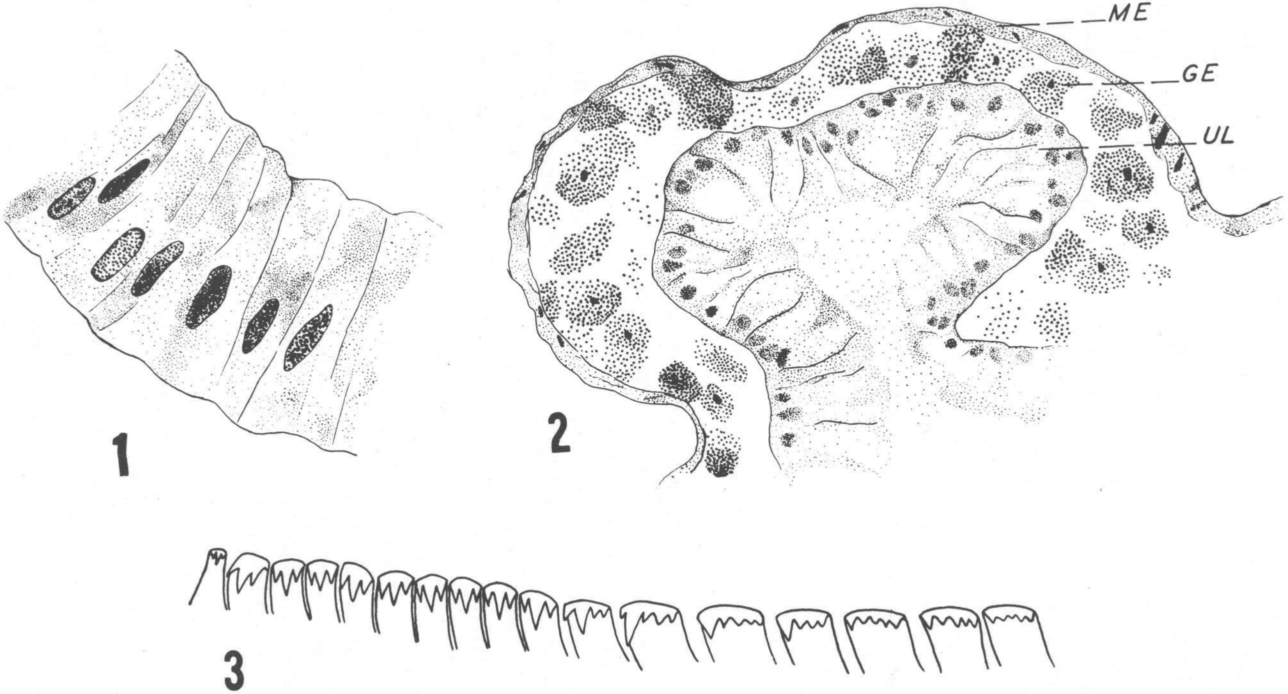
lateral cuticular appendages of some other Basommatophora, possibly modified by being restricted in extent in different families. The paragnathal plates of *Lymnaea* (Carriker's Fig. 6) occur in a relatively shorter vestibule than that present in *Carychium.*

On either side of the horizontal portion of the vestibule there is a group of gland cells (Plate XVIII, Fig. 1; Plate XVII). These appear to open into the vestibule at its expansion into the buccal mass. The cells do not project externally to the muscular investment. They show a close histological similarity to those of the pedal gland in being strongly basophilic and vaguely vacuolated flask-shaped cells with small basal nuclei Each opens separately into the digestive tract. The cells of one side form a discrete mass and are not arranged into pseudoacini as are those of the pedal gland. Possibly these cells constitute the "organ of Semper" of some authors. Adam (1933) has given an extensive review of the various structures so designated in different snails and concluded they are sufficiently variable in character in different snails to suppress the name "organ of Semper." It is notable that Carriker (1947) made no mention of such glands in his detailed study of *Lymnaea stagnalis appressa,* but did note diffuse, unicellular glands distributed throughout the buccal mass epithelium and anterior part of the esophagus; these may be homologous to the vestibular glands in *Carychium.*

In the region of the buccal mass the digestive tube expands ventrally into an anterior and posterior medial pocket; these are arranged around the radular support, a U-shaped structure lying in the frontal plane of the animal with the arch directed forward (Plates XIV and XVII). The two rami of the radular support are connected ventrally, thus forming a trough, the posterior margin of which is slightly concave. The form of the radular support agrees closely with that described in *Lymnaea* by Carriker. Both in that genus and *Carychium* the two lateral rami are continuous anterior and ventrally, thus contrasting with the condition in *Helix* (Trappmann, 1916) where the rami are connected only by a muscular band. Carriker advocated the term radular cartilage for this support because of its general use in the literature, though he recognized the distinctive type of tissue which composes this organ as not being typical cartilage. There is no extra-cellular matrix produced around the cells (Plate XIX, Fig. l).

The anterior buccal evagination of the digestive tract is patterned in conformity with the outer shape of the radular support against which it is closely pressed. It thus consists of a lateral trough on either side, joined medially by a transverse portion. Immediately behind the anterior evagination is the posterior tubular outpocketing, the radular sac (Plate XIV). This is arched longitudinally so that its posterior extremity curves up-

PLATE XIX



Histological details of the digestive system. FIG. 1. Histology of structures supporting the radula. FIG. 2. Histology of the upper liver tube showing eosinophilic granulocytes and mantle membrane near the apex of the visceral mass. FIG. 3. Dentition in one-half of a transverse series of the radula.

Abbreviations. GE - epithelium of gonad wall; ME - mantle; UL - upper liver tube.

ward. It lies in the trough between the two rami of the radular support and posteriorly extends slightly beyond it. In cross section this tubular structure is symmetrically circular in *Carychium*, while in *Lymnaea* Carriker described a longitudinal dorsal infolding of its wall which produces a groove in which resides another supportive structure, termed by him the collophore. Nothing comparable could be detected in *Carychium*. Lining the ventral half of the radular sac is the radula, consisting of a thin cuticular membrane, the odontophore, and the denticles which it bears. The epithelium of the radular sac is cuboidal in the dorsal region, somewhat flattened in the area underlying the radula and columnar in the posterior end. The odontoblasts, which by analogy with other snails (Boettger, 1944: 297) should occur at this end, could not be distinguished in detail.

The radular membrane bears about 100 transverse rows of teeth; each row consists of a median tooth with 16 teeth on either side. The base of the median tooth has concave margins while those of the lateral are quadrate becoming increasingly broad in proportion to the height toward the marginals (Plate XIX, Fig. 3). The central tooth bears a pointed mesocone and smaller denticles on either side. The first nine lateral teeth have a similar denticulate margin. In the marginal series, the ectocone and mesocone become progressively smaller while additional denticles are added as ectocones. Toward the outer marginals the denticulations are subequal in size and about five in number.

The above description of the radula agrees essentially with the report and figure of it as given by Morse (1864). The discrepancies probably result from his use of insufficient magnification. He reports the central and first four laterals as unidentate, the next six laterals bidentate and the remainder to be edentate. However, his report agrees with the present one in finding only 16 laterals on either side of the central. The denticulation of *Carychium minimum* as reported by Odhner (1925) differs chiefly from that of *C. exiguum* in having 19 instead of 16 teeth on either side of the central. Lehmann's report of the radula of *C. minimum* agrees essentially with Odhner's, except that he reports 20 teeth on either side of the central and 120 rows. He evidently did not distinguish the denticulations as clearly as did Odhner.

Surrounding the two ventral evaginations from the digestive tract and the radular support is a mass of muscular tissue which, together with the structures it encloses, constitutes the buccal mass. In some larger pulmonates the musculature of the buccal mass has been described at length with names given to the individual muscles. Carriker, for example, has described *Lymnaea stagnalis appressa*, correlating it with previous work, chiefly that of Trappmann on *Helix*. It has not been possible to give such detail in the present study, but certain of the major muscles can be detected, and allow the conclusion that the musculature of the buccal mass is essentially similar in structure and function to that of larger snails. Many of the smaller muscles are represented by single fibers or are absent.

Extrinsic musculature of the buccal mass consists of

(l) The subesophageal moiety of the columellar retractor which lies free in the cephalopedal hemocoel. It inserts on the posterior margin of the radular support (Plate XVII) and serves as a retractor of the buccal mass. Possibly it is separated from the portion of the columellar retractor supplying the body wall rather high in the columellar isthmian hemocoel.

(2) Protractors of the buccal mass. These muscles are mostly ventral, originating on the posterior margin of the radular support and inserting on the cephalopedal integument and vestibular wall around the mouth.

Primary intrinsic muscles also have their origin on the posterior part of the radular support. The radular retractor could be detected, lying in the trough between the radular support, dorsal to the ventral connective of the latter but ventral to the radular sac. It attaches along the posterior half of the radular sac. Opposing this muscle in function is the radular protractor, originating on the posterior margin of the radular support but passing entirely ventral to it and inserting on the anterior half of the radula (or subradular epithelium?), along the portion of the latter which bends ventrally over the anterior margin of the radular support. An anterior jugalis can also be recognized. This is a broad muscle having its origin on one posterior end of the radular support, passing upward along the side of the radular mass, across the anterior and dorsal aspects of the same and down the opposite side to insert on the opposite posterior end of the support.

At a middorsal point of the buccal mass the digestive epithelium again narrows to form a small tube, the esophagus. This organ passes posterior and upward to enter the columellar isthmian hemocoel. Inside the buccal mass, running transversely across the roof of the cavity and just anterior to the esophageal opening, is a ridge of tissue produced by columnar modification of the epithelium of the wall of the digestive tract (Plate XIV).

At the junction of the esophagus and buccal mass there opens into the latter on either side a salivary gland (Plate XVIII, Fig. 1; Plates XIV, XV and XVI). Each gland is composed of a single tube which passes posteriorly along the dorso-lateral parts of the esophagus to end blindly just before the esophagus enters the isthmian hemocoel. Throughout most of its length each salivary gland is a thin tube circular in cross section; at the hind end each expands to form a spherical mass superficially resembling the large ganglia of the nervous system in external appearance. The glands are composed of large cuboidal epithelial cells with vaguely vacuolated, moderately basophilic cytoplasm. Occasionally the vacuoles are expanded and have a homogeneous eosinophilic content. The histology of the cylindrical anterior portion and bulbous posterior part seems to be the same. At their posterior termini the glands are connected across the dorsal surface of the esophagus by a narrow strand of tissue which somewhat resembles the tissue of the gland but lacks a lumen.

Apical to its entrance into the upper visceral complex the esophagus courses in a rectilinear fashion and continues near the columella until it reaches the apical part of the antepenultimate whorl where it turns sharply toward the periphery and expands into the stomach. Just basal to this flexure the lower liver tube (Plate XII) opens into it.

The stomach consists of a simple spherical expansion of the digestive tube. The downward flexure of the digestive tube in *Carychium* seems to occur where the esophagus enters it (Plate XVIII, Fig. 2). Completely encircling the stomach is a broad band of circular muscle extending obliquely with its highest point on the side opposite the entrance of the esophagus. All portions of this muscle seem to be the same; there is no tendonous connection separating it into two half circles as in *Lymnaea* (Carriker). The epithelium which composes the wall of the stomach consists of small cuboidal cells prominently ciliated throughout. These form a smooth internal surface without folds or grooves. Unlike other Basommatophora, the stomach is undivided unless a slight constriction of the wall, corresponding to the position of the gastric muscle, be construed as such. No cuticular lining is evident in any portion. A large circular opening in the stomach above the gastric muscle connects the stomach with the upper liver tube.

In *Carychium* the liver (Plates XII and XIII) consists of two large tubes, with spacious central lumen and large glandular epithelial cells composing the wall. The upper liver tube originates on the upper part of the stomach and passes apically in keeping with the coil of the primary cone. This is comparable to the upper lobe of the liver of other snails. The lower liver tube joins the esophagus just before its entrance into the stomach and, in keeping with the coil of the primary cone, passes almost to the lower extent of the upper visceral complex. Both tubes are slightly constricted at intervals and thus appear segmented (Plate XX, Fig. 2, not labeled) into a series of linear swellings. In the lower tube (but apparently not in the upper) there are broad shallow outpocketings from the main tube to fill the space between the upper and lower loops of the sigmoid intestine. These evaginations represent branching of a vestigial sort. The wall of the hepatic tubes is entirely glandular with no differentiation into a non-glandular portion near their attachment which might serve as a special duct to the main part of the digestive tract (Plate XII).

At the base of the stomach the digestive tube again constricts to cylindrical proportions and passes in a line paralleling the columella but near the periphery of the visceral mass, to the basal side of the penultimate whorl a slight distance apical to the upper end of the pulmonary cavity. This portion of the digestive tract is the duodenal intestine. It is differentiated not only by its position but by being the widest portion of the intestine and having a unique internal structure. In its wall are two longitudinal bands of columnar epithelium forming ridges projecting into the intestinal lumen. These bands begin at the entrance to the duodenum and fade out at its lower extent, lying slightly spiraled around the axis of the tube. They may be termed the typhlosole, although their homology to that structure as described in *Lymnaea* by Carriker (1947) is dubious. In *Lymnaea* the typhlosole is described as an infolding of the muscular wall. Perhaps the typhlosole in *Carychium* is more nearly comparable to the raphe of *Lymnaea,* which has a similar structure but differs in position and pattern. No sphincter muscle such as Carriker found in *Lymnaea* and to which he attributes the formation of fecal pellets is present in *Carychium.* The feces in the latter genus are extruded in continuous ropes, circular in cross section; they resemble the Stylommatophora in this respect.

Having reached the basal side of the penultimate whorl the duodenum curves toward the suture of that whorl proceeding at the same time apically in relation to the primary cone. This curvature constitutes the lower loop of the sigmoid intestine. After extending nearly to the sutural side of the primary cone's penultimate whorl, being separated from the suture only by the pre-rectal portion of its later length, the sigmoid intestine again swings basally, then transversely, and finally takes its position paralleling the suture extending again toward the aperture. If this portion of the intestine were flattened out in one plane it would have the shape of an S, whence the name sigmoid intestine. That portion of it which runs parallel to the suture in the upper visceral complex may be termed the pre-rectal intestine for it continues into the pulmonary complex maintaining the same position.

The anus is a longitudinal slit in the anterior and ventral surface of the posterior mantle lappet and thus the anus opens into the pneumostomal canal (Plate I, Fig. 5). No rectal glands such as Koslowsky (1933) described in *Melampus* could be found in *Carychium.*

The digestive tract of *Carychium* shows a striking similarity to that of *Phytia* as shown by Pelseneer (1894). *Carychium* differs chiefly in lacking an expansion of the esophagus to form a crop, and in the muscle layer of the stomach being a continuous ring, not divided into semicircular parts. The division of the gastric muscle of *Phytia* is reminiscent of the condition in the lymnic Basommatophora. The opening of the liver ducts in the two genera are approximately the same; neither have a digestive caecum as do the lymnic Basommatophora.

Circulatory System

The pericardium and heart (Plate XX) show little difference from the "tube within a tube" which these structures form in well coiled pulmonates. The outer tube is represented by the pericardium, the inner by the two-chambered heart. Both membranes are composed of very thin, flattened epithelium, although nuclei and cell boundaries are difficult to detect. The apertural half of the heart is expanded to form a pear-shaped auricle with its constricted end toward the junction with the pericardium. The ventricle is similarly shaped, and its constricted end is directed toward the apical junction with the pericardium. Both chambers contain a few muscle fibers traversing their interiors. These fibers are slightly more numerous in the ventricle. A bivalved opening connects the two chambers with the free margins of the flaps directed into the ventricle.

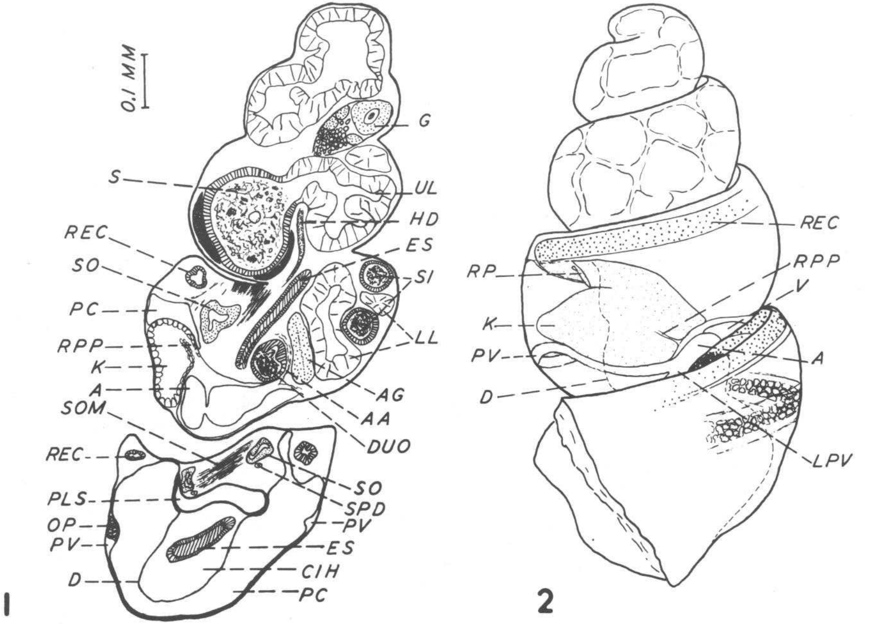
Of the arterial system in *Carychium* only the aorta and the rudiments of its two major branches could be detected (Plate XX, Fig. 1). The aorta leaves the ventricle at the point where the ventricular epithelium becomes reflexed to form the pericardium. It divides almost at its origin into two branches. One of them swings apically around the lower part of the duodenum (at about the transition of the latter into the lower loop of the sigmoid intestine) and is thus directed aperturally (Plate XX, Fig. 1, AA). It is possibly comparable to the anterior or cephalic artery of other pulmonates. The other branch proceeds apically along the periphery of the whorl for a short distance. It is perhaps homologous with the posterior artery of other pulmonates judging from its direction, *i.e.*, toward the upper visceral complex. Neither vessel could be traced very far. They seem to be nothing more than a slight concentration of connective tissue about a tubular lumen. Whether or not these arteries have a more extensive distribution than noted or really extend no farther than seen in this material remains for future study. It is interesting to note that Hoff (1940) could trace them no farther in *Ferrissia* than described here in *Carychium*. Possibly both snails have merely a rudiment of the extensive arterial pattern of other pulmonates. If the arteries open near their terminal extent, the blood would flow freely into the visceral hemocoel.

The venous system of *Carychium* is more complex than the arterial and presents certain features which greatly contrast with the general pattern of other pulmonates. Most of the volume of the mantle margin (constituting the outer wall of the hypopeplar chamber) is composed of a large blood sinus (Plates XIV through XVII). It extends as a complete circle around the mantle margin having an extensive communication with the cephalopedal hemocoel at the apertural end of the diaphragm. Presumably blood enters this marginal mantle sinus from the lower hemocoel. Blood also may return directly from the upper visceral complex via the rectal sinus, which likewise opens at its lower end into the marginal sinus. Draining this sinus are two vessels:

(1) The pulmonary vein arises near the pneumostome and extends obliquely across the peripheral wall of the pulmonary cavity to enter the auricle. At its apertural end the pulmonary vein consists of two moieties, one along each longitudinal margin of the organ of Plate (Plate XXIII, Fig. 1). They unite at the upper end of the organ to form a single vein. There is no observable increase in diameter of the pulmonary vein throughout its length although the branch along the basal margin of the organ of Plate seems a little smaller than its collateral member. No branches are received or given off throughout the entire length of the pulmonary vein.

(2) At the extreme basal margin of the pulmonary complex a large vessel extends from the marginal mantle sinus to the upper end of the pulmonary complex where it joins the pulmonary vein just before the entrance of the latter into the auricle (Plate XX, Fig. 2). This vessel is the left pallial vein of other pulmonates (Schmidt, 1916, on *Helix*). It is in *Carychium* a very short vessel situated on the basal side of the columellar lamella of the shell. In transverse diameter the left marginal vein is comparable in size to the rectal sinus, though lacking any such impediment as the rectum in its lumen (Plate XVI). It is several times the diameter of the pulmonary vein. The latter fact allows the conclusion that the left pallial vein is the chief route of return of blood from the marginal mantle sinus to the heart. The absence of a dendritic drainage pattern in the roof of the pulmonary cavity also leads to the conclusion that the marginal mantle sinus, and not the pulmonary chamber, is the chief site of external respiration in *Carychium*. Another peculiarity is that in most pulmonates the left marginal vein allows passage of blood from the upper visceral complex to the mantle margin (Deschamps, 1898; Schmidt, 1916).

PLATE XX



Anatomical aspects of the kidney and circulatory system. FIG. 1. Diagram of the visceral mass in section. FIG. 2. Details of the upper part of the pulmonary complex as seen in a stained and cleared contracted specimen.

Abbreviations. A - auricle of heart; AA - anterior artery; AG - albumen gland; CIH - columellar isthmian hemocoel; D - diaphragm; DUO - duodenum; ES - esophagus; G - gonad; HD - hermaphroditic duct; K - kidney; LL - lower liver tube; LPV - left pallial vein; OP - organ of Plate; PC - pulmonary cavity; PLS - parietal lamella of shell; PV - pulmonary vein; REC - rectum; RP - renopore; RPP - renopericardial passage; S - stomach; SI - sigmoid intestine; SO - spermoviduct; SOM - subviducal columellar retractor muscle; SPD - spermathecal duct; UL - upper liver tube; V - ventricle of heart.

Kidney

In *Carychium exiguum* the kidney (Plate XX) consists of a simple sac, the wall of which is one cell-layer thick. The sac is flattened parallel to the periphery of the primary cone, thus presenting a peripheral and columellar surface and a single margin. In peripheral profile the kidney is elongate oval, roundly pointed at both ends with its longitudinal axis parallel to the primary cone. There are no infoldings of the wall to produce renal lamellae as found in other snails. However, there are two radial incisions which extend into the lumen. One is on the basal margin near the apical end. It provides a passage between the pericardium and kidney. The renopericardial passage does not appear to be ciliated, but very little could be determined of its histology. The other constriction is near the apertural end of the kidney and toward the suture of the shell. This structure separates a narrow segment from the main cavity of the sac, which opens at the apertural end as a large renal pore. There is no tube or groove running from this pore.

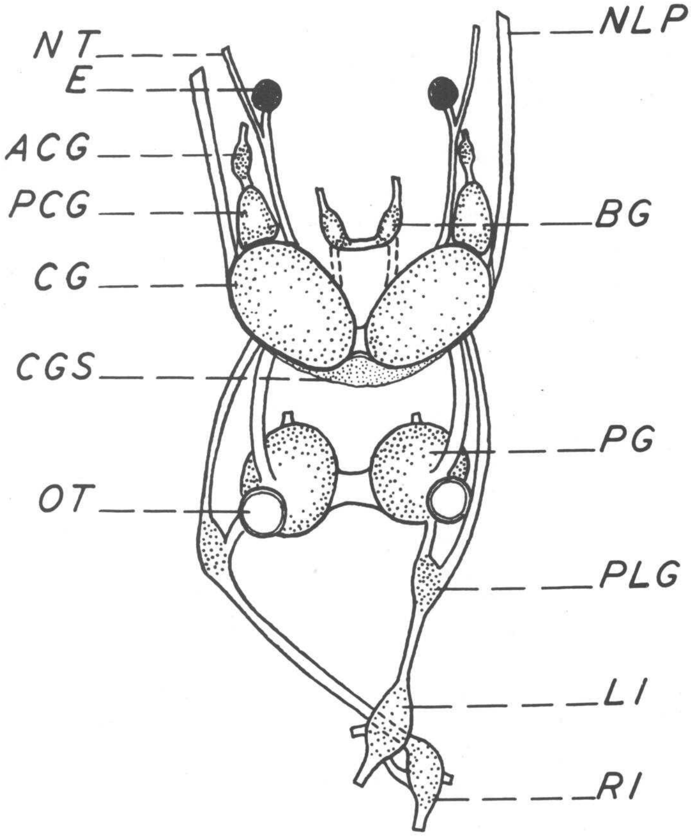
The large cells of the kidney wall (Plate XI, Fig. 2) have distinct cell boundaries and are cuboidal in form. The free surface of each cell is expanded producing a botryoidal effect. The nuclei are basal and lateral and there is a small amount of cytoplasm around them leaving a single large space constituting most of the cell volume. Nothing was detected in these large vacuoles although this failing may be a matter of technique. At any rate, their secretory nature was not confirmed. No cilia could be detected in any part of the kidney nor in the pulmonary cavity near its opening. The large kidney cells continue outside the kidney sac and are chiefly distributed over the free surface of the rectal wedge where they extend for about half a whorl. They are visible in the photograph of Plate XIII.

Pelseneer (1894) noted lamellae in the kidney of *Phytia,* and Plate (1897) noted them in *Pythia scarabaeus.* The latter's report I have been able to confirm by observation. Koslowsky (1933) reported the renal lamellae in *Melampus* to be transverse to the length of the kidney. In none of these forms is a ureteral groove or tube reported.

Nervous System and Sensory Organs

Bargmann (1930) has given a critical review of the central nervous system in pulmonates and its significance in tracing phylogeny. Hubendick (1945: 137) summarized this system in certain pulmonates of dubious re-

PLATE XXI



Reconstruction of the central nervous system.

Abbreviations. ACG - anterior accessory cerebral ganglion; BG - buccal ganglion; CG - cerebral ganglion; CGS - cerebral ganglion sheath; E - eye; LI - left innominate ganglion; NLP - nerve to labial palp; NT - nerve to tip of tentacle; OT - otocyst; PCG - posterior accessory cerebral ganglion; PG - pedal ganglion; PLG - pleural ganglion; RI - right innominate ganglion.

lationships including the Ellobiidae *s.s.* Simroth (in Simroth & Hoffmann, 1910) and Moquin-Tandon (1855) both picture the central nervous system of *Carychium minimum.* Their figures show certain discrepancies between them as well as with my findings in *C. exiguum.*

In gross dissection the ganglia of the nervous system have a granular, opaque appearance. The commissures, connectives and nerves are hyaline, cylindrical strands showing no structure or sheath. In sectioned material the nerves, commissures and connectives are eosinophilic and closely resemble single muscle fibers. This resemblance makes them difficult to trace. There is apparently no sheath of connective tissue surrounding any part of the nervous system as is the case in some other pulmonates. However, occasionally, a stellate connective tissue cell is seen adhering to a nerve. The ganglia have a homogeneous medullary portion in which long, fine strands are sometimes prominent and these are directed in line with the nerves, etc., which arise from the ganglia. The cortical portion of the ganglia consists of numerous spherical basophilic bodies which have a granular appearance and possibly constitute the nuclei of nerve cells. Techniques used in this work did not show these nuclei associated with particular cells. The layer of nuclei is absent where nerves and similar structures attach to ganglia. It has in no instance been possible to determine fusion of ganglia in sections of them.

The esophagus, buccal retractor muscle and salivary glands pass through the anterior nerve ring which is made up of the cerebral and pedal ganglia and their respective commissures and connectives. In expanded specimens the cerebral ganglia are situated behind the origin of the esophagus from the buccal mass, but in contracted specimens the latter is pulled through the anterior nerve ring so that the cerebral ganglia come to lie in front of it.

The cerebral ganglia (Plate XXI) are the largest of the central nervous system and they are approached in size only by the pedal ganglia. They are elongate, oval bodies, closely approximated but not touching. At the ventral part of this posterior approximation is the cerebral commissure. Dorsal to it and slightly more posterior is a peculiar inter-cerebral sheath. This casing extends from the extreme tips of the ganglia and intrudes partly between them, thus appearing triangular in cross section. A very thin sheet of this sheath may extend around the outer surface of the ganglia and to the lateral aspect of the posterior accessory cerebral ganglia (see below). The intercerebral ganglion sheath has spherical nuclei resembling those of the ganglia themselves. They are not as tightly packed as those of the cortical layer of the ganglia and the matrix in which they are imbedded takes a lighter stain and shows no fibrous structure. There is no recession of the nuclei of the ganglia adjacent to any part of the sheath, which might indicate the sheath as a commissure or accessory lobe of the ganglia.

In front of each cerebral ganglion and forming a line with it, there are two accessory ganglia (Plate XXI, Plate XVI). The posterior is the larger of these and it is closely appressed to the cerebral ganglion. In sections they are seen to be joined by a short connective so that the two are not actually fused. The anterior accessory ganglia are very small and separated from the posterior accessories by a distance about equal their length. They are joined to their respective posterior accessory ganglia by a connective. From the anterior accessories there arises a small nerve whose path could not be traced. By their position and relation to the cerebral ganglia the two accessory ganglia do not seem homologous to the tripartite ganglia of *Helix* (Schmalz, 1914) or *Lymnaea* (Pelseneer, 1901).

At the anterior end of each cerebral ganglion a large nerve arises from the ventral, lateral aspect and passes to the labial palps. At the anterior end, seen in the dorso-lateral aspect, there arises a nerve which passes to the eye and has a branch to the tip of the tentacle.

The buccal ganglia are elongate, oval, and joined by a commissure of moderate length; each shows a prominent nerve from the anterior end which seems to sink into the buccal musculature. The junction of these ganglia with the anterior nerve ring could not be positively ascertained, but in a few instances there appeared to be a connective from each ganglion to the posterior medial face of the cerebral ganglia.

The spherical pedal ganglia are separated by a distance about equal to their diameter. Only a single large commissure could be detected, joining their medial faces ventrally. Pelseneer (1901: 43) cited a second, smaller pedal commissure as characteristic of pulmonates, and noted its presence in *Phytia* and *Pythia*. Moquin-Tandon's figure of the central nervous system of *Carychium minimum* seems to indicate a double commissure of the pedal ganglia.

From the anterior ventral aspect of each pedal ganglion there arises a large nerve which sinks into the spongy connective tissue of the sole. On the posterior dorsal aspect of each ganglion, and slightly lateral, is situated a small spherical sac, the otocyst. This has a wall of flattened epithelium one cell-layer thick. Its innervation could not be determined nor could cilia or granules be detected in its interior.

The cerebro-pedal connectives arise from the ventro-lateral face of the cerebral ganglia and enter the pedal ganglia dorsally near the otocysts.

The posterior, or visceral, nerve ring contains only four ganglia. The two anterior of these are asymmetrical in relation to their distance from the pedal and cerebral ganglia to each of which they are joined on their respective sides by connectives. While some smaller nerves of the cephalic and pedal centers may have been overlooked it is possible to state with reasonable assurance that no nerves arise from the anterior ganglia of the visceral ring; they are, therefore, probably homologous with the pleural ganglia of other snails. The cerebropleural and pleuropedal connectives have their origins on the cerebral and pedal ganglia near the origin and insertion of the cerebropedal connectives.

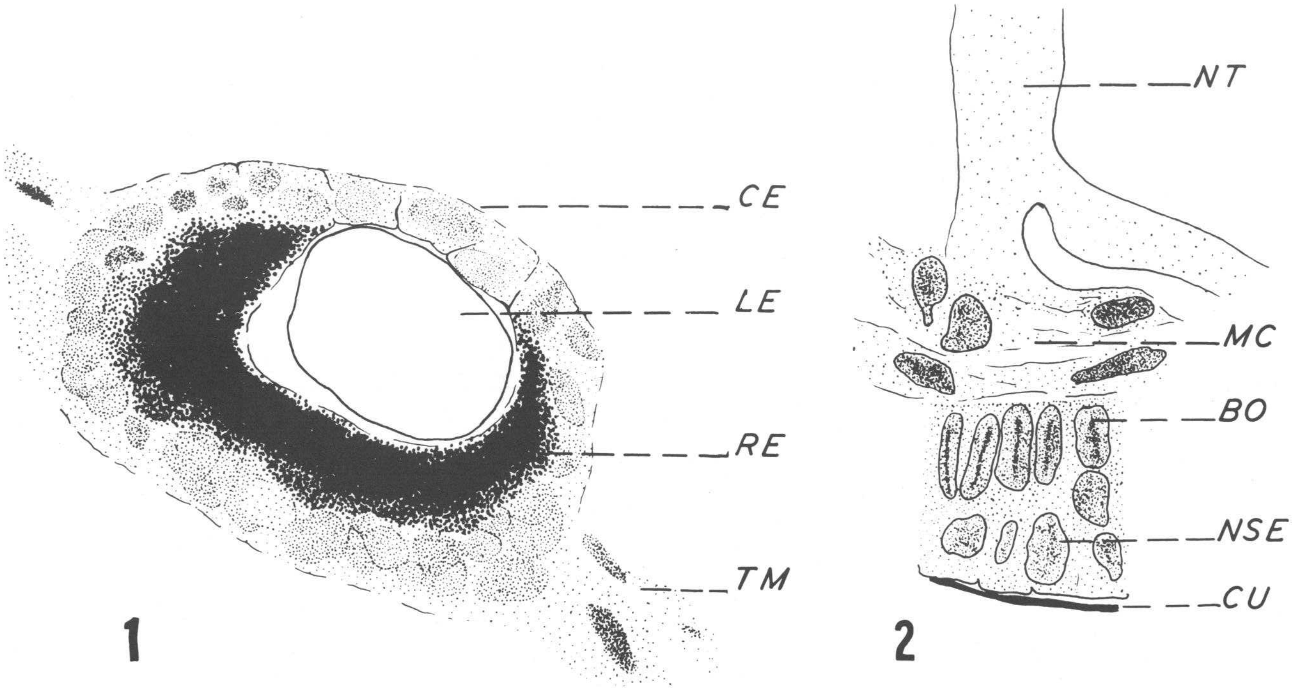
Behind the pleural ganglia on the visceral nerve ring are two other ganglia which lie close together in the cephalic hemocoel immediately below the opening of the oviduct. They are about equal in size and similar in their elongate, oval shape. Each gives off a large nerve at its posterior end. The one from the left ganglion apparently is directed toward the columellar isthmian hemocoel, while the one from the right innominate ganglion goes toward the parietal moiety of the isthmian hemocoel. From the middle of their lateral aspects each ganglion also gives off a small nerve. None of these four nerves could be traced for more than a short distance beyond their origins. The posterior ends of these ganglia are joined by a short commissure. Since the insertion of the nerves from these ganglia could not be determined, it is not possible to correlate them with other ganglia of the visceral nerve ring in pulmonates. We shall call these the right and left innominate ganglia to avoid adding further confusion to the literature on the point of homologies of the ganglia of this nerve ring.

From the anterior end of the right innominate ganglion there extends a long commissure to the posterior end of the left pleural ganglion. It passes ventrad to a similar commissure from the anterior end of the left innominate ganglion to the posterior end of the right pleural ganglion. The right pleuro-innominate connective is about twice as long as the left. Thus, chiastoneury (the twisting of the visceral nerve ring to form a figure 8) is distinctly shown in *Carychium exiguum.*

The most distinctive features of the central nervous system of *Carychium exiguum* are the diffuse array of ganglia, the twisted visceral nerve ring, and the accessory cerebral ganglia. In the matter of concentration of the ganglia it seems to present the most diffuse, and therefore primitive, pattern of any of the Ellobiacea yet studied (see Hubendick, 1945: 140). Hubendick (*l.c.*) has denied true chiastoneury which earlier authors had seen in *Chilina* although he noted that this phenomenon is suggested in both *Chilina* and *Amphibola* by the asymmetrical location of the ganglia of the visceral nerve ring.

The difficulties of determining fusion of ganglia of the visceral nerve ring in *Carychium,* a popular field of study for some writers, motivates caution in suggesting what the visceral ganglia might represent in other

PLATE XXII



Histological details of sensory structures. FIG. 1. Section of the eye. FIG. 2. Section of the sensory epithelium from the tip of a tentacle. Abbreviations. BO - basal organelle of sensory epithelium; CE - corneal epithelium; CU - cuticle; LE - lens; MC - musculo-connective tissue of tegument; NSE - nucleus of sensory epithelium; RE - retinal epithelium; TM - tentacular membrane.

snails. But, if we consider the parietal ganglia as absent (rather than fused with some other ganglia), then again *Carychium* has one of the most primitive central nervous systems yet reported in the pulmonates.

In *Carychium exiguum* there seems nothing comparable to the left parietal ganglion which is figured by Simroth (Simroth & Hoffmann, 1910: 255). The homologues in C. *exiguum* of the ganglia he labels right parietal and abdominal are differently shaped and arranged. Only a single anterior appendage of the cerebral ganglion is indicated by him, although judging by the shape of the latter ganglia in his drawing, perhaps he included the closely approximated posterior accessory cerebral ganglia as part of the main ganglia. Moquin-Tandon's figure of the central nervous system in C. *minimum* can scarcely be correct. He figures only two ganglia on the visceral nerve ring, the anterior attachment of which is not clear. An accessory ganglion on the right side, seemingly attached by only a single connective to the right pedal, is also difficult to interpret.

The position of the eye in *Carychium exiguum* has been noted above in the section on general morphology. The eye (Plate XXII, Fig. 1) is a hollow vesicle slightly wider than deep. The bottom of the vesicle is much thicker than the top and only one type of cell could be recognized. A thin, nonpigmented layer of cells extends over the top of the eye; these cells constitute the corneal epithelium. The lower portion of the vesicle is several times as thick and contains many large black pigment granules toward the lens space. No special nervous elements could be detected in the vesicle. The cavity of the cup is almost filled by a large, hyaline lens.

The epithelium of the tentacular tip and anterior margin of the labial palps is illustrated in Fig. 2 of Plate XXII. In this region the columnar cells appear to have two rows of nuclei, the more peripheral of which are oval, finely granular, and in general resemble the nuclei of the cuboidal epithelia near the tentacular tip. Those of the basal row are elongate oval with granules clustered about a central axis. The basal row may represent special sensory organelles rather than true nuclei. The location of sensory epithelia at the anterior base of the tentacles in some Basommatophora has been noted by Simroth (in Simroth & Hoffmann, 1910: 210), and Boettger (1944: 367), but whether the sensory epithelium of *Carychium* is to be correlated with those tentacular epithelia or with the labial pads of the Ellobiidae, or both, remains an open question. The prominent cuticle accompanying this area of cells in *Carychium* seems not to have been noted in the other cases.

Reproductive System

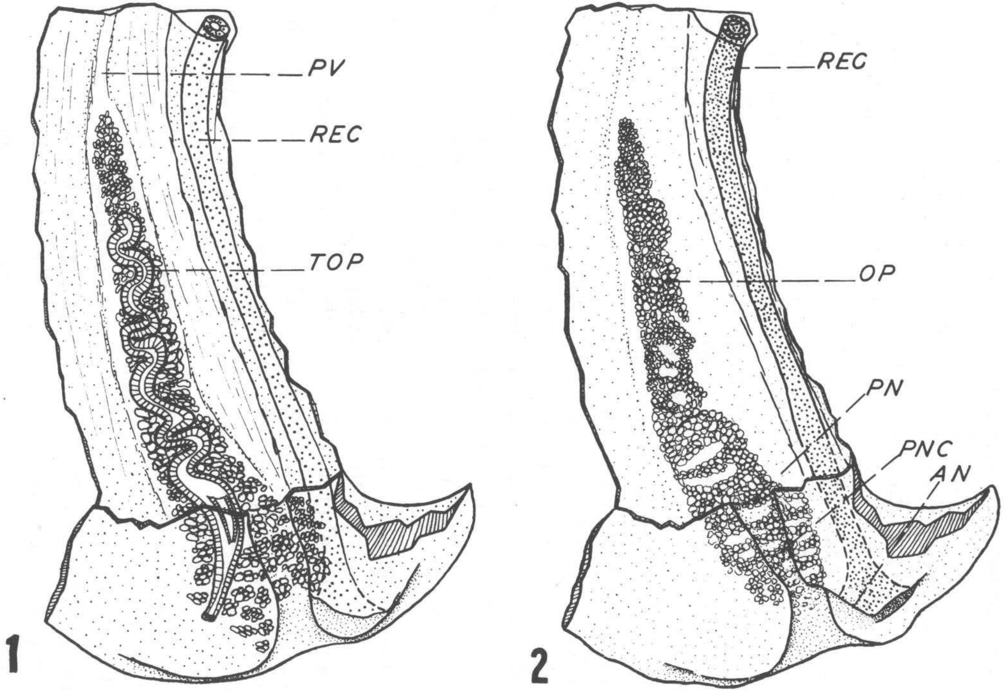
The anatomical accounts of *Carychium minimum* by Moquin-Tandon (1855) and Lehmann (1873) both indicate the male organs, vas deferens and penis, as present in that species. During the preliminary anatomical investigations in the study of C. *exiguum* it was, therefore, with some surprise that these organs were not discovered. Subsequent work indicated that two sexual types of this species exist in Michigan. These types are characterized by marked anatomical differences in several structures. Since both types produce sperm and ova, the designation of them as male and female is not suitable, but the presence of penis and vas deferens in one and its absence in the other permits the use of the terms phallate and aphallate for these types.

Unfortunately, the phallate type was encountered in only a few sectioned individuals and all of them are contracted. From the data of Table 12 it seems evident that the phallate type exists in varying percentages of the population among different colonies. Thus, of 42 specimens examined from the Washtenaw County station, only one phallate specimen was found, whereas a third of the population may be phallate in other colonies, although fewer individuals were examined. Because the length of life of *Carychium* under field conditions is not certainly known we can not be sure that the two types do not represent merely sexual phases through which a single individual passes. Such a phenomenon of alteration of the sex in an essentially hermaphroditic species is the rule in some mollusks and among the pulmonates it is found in *Deroceras.* Aphallate and phallate types within the same region have also been noted in several other pulmonates, but not previously in any of the Ellobiidae or Carychiidae. As this condition is most frequently reported in Pupillidae, Valloniidae and some small Zonitidae, it is sometimes attributed to economy of structure correlated with the small size of the individual (Watson, 1920; 1923). Few species showing this phenomenon have been discovered in the Basommatophora. In his extensive review of autofecundation and aphally in this suborder, Larambergue (1939) lists only *Physa subopaca, Lymnaea peregra* and *Bulinus contortus.* His experiments with the latter species indicate the condition is hereditary and probably controlled by several genetic factors. No intermediate specimens showing vestiges of the structures present in the phallate type have been encountered in aphallate *Carychium.*

One of the most striking differences in the two sexual types of *Carychium* is to be found in the organ of Plate, the position of which was noted above in the section on general morphology. Although this organ has no structural connection with the reproductive apparatus as usually understood, it nevertheless shows anatomical differences in the two sexual types which lead to the conclusion that it is associated in some way with reproduction.

A similar organ has been described by Plate (1897) in *Pythia* and seems

PLATE XXIII



The organ of Plate. FIG. 1. The organ of Plate reconstructed from sectioned phallate specimens and based on Figure 2. FIG. 2. The organ of Plate of an aphallate specimen.

Abbreviations. AN - anus; OP - organ of Plate; PN - pneumostome; PNC - pneumostomal canal; PV - pulmonary vein; REC - rectum; TOP - tube of the organ of Plate.

not to have been mentioned since. He described it as a long slim pouch, the narrow lumen of which is circumscribed by a single layer of columnar epithelial cells. Around the pouch there is a thick, felt-like sheath presumably of connective tissue. The sheath is supplied by several nerves, though these are so scarce and delicate that the organ was not considered sensory. The sac opens on the mantle collar's outer surface behind and somewhat dorsal to the female genital opening. The epithelial cells do not appear glandular, but Plate thought it possible that they secrete something in relation to the sex function. In *Pythia* the pouch courses from the opening parallel with the rectum up to the vicinity of the kidney opening, then turns sharply and, gradually decreasing in thickness, forms a second arm paralleling the first and ending blindly. The two arms are about the same length and each is accompanied on its outer margin by a pulmonary vessel. These two vessels unite above to form the pulmonary vein.

In *Carychium* the narrow, elongate organ of Plate (Plate XXIII, Figs. 1 and 2) is located in the peripheral wall of the pulmonary cavity, extending apically from the region of the pneumostome for about half a whorl (Plate X, Figs. 1 and 2). A blood vessel extends along each margin; these unite at the organ's apical end to form a single pulmonary vein. The organ consists of large cells, each with a small lateral nucleus and glandular cytoplasm. The latter presents various aspects which may indicate different stages of the secretory cycle. In some cells the cytoplasm is diffusely cloudy and basophilic. In others there are three to ten large vacuoles containing an homogeneous eosinophilic substance. In still others the vacuoles are empty. These gland cells extend into both mantle lappets and the external wall of the hypopeplar chamber which, with the mantle lappets, forms the pneumostomal canal. Probably the products of secretion empty directly into the pulmonary cavity and into the pneumostomal canal. In the lower part of the pulmonary cavity the epithelium covering the gland is very flat and shows short cilia.

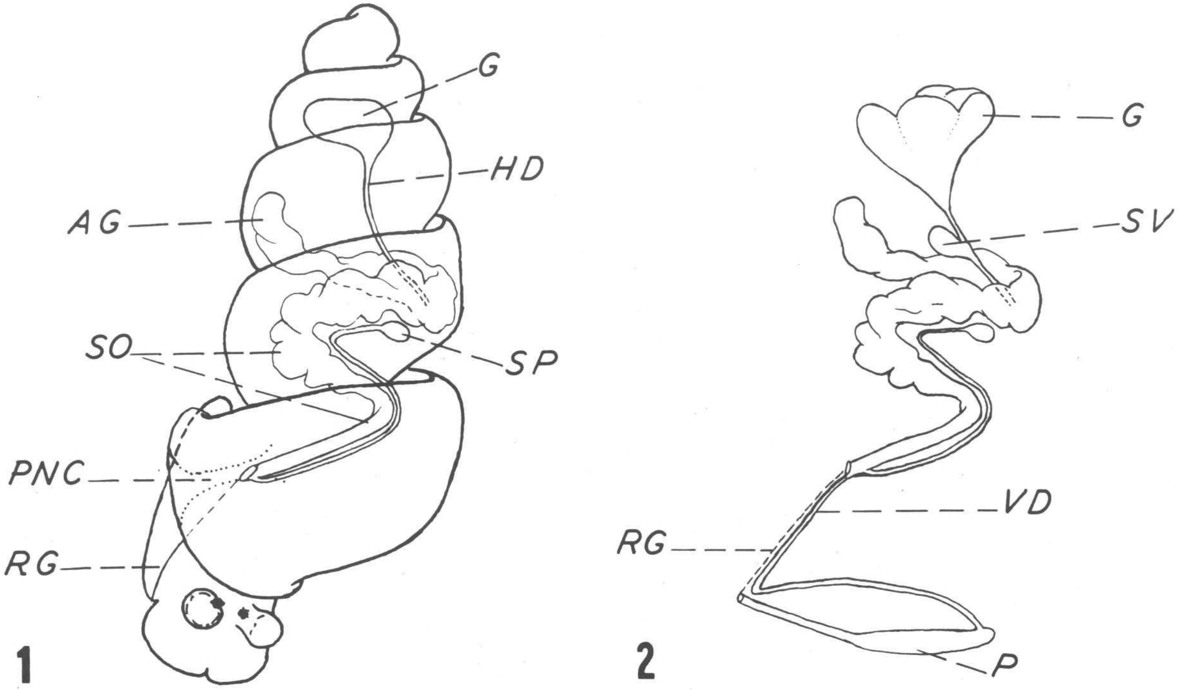
The above description applies to the gland as it is invariably found in the aphallate specimen. In phallate individuals there is imbedded in the organ a tubular sac (Plate XXIII, Fig. 1) whose wall is composed of a single layer of non-ciliated, non-glandular, cuboidal epithelium. This tube opens into the hypopeplar chamber on the anterior aspect of the anterior mantle lappet. Apically the tube ends blindly a short distance below the upper end of the glandular part of the organ. The lower half of the tube is straight and expanded, containing internally an elongate papilla, attached above and directed toward the opening of the tube. The papilla is itself luminate, opening at its free end. The contorted appearance of the upper half of the tube, as shown in Fig. 1 of Plate XXIII, may be due to the fact that all specimens examined were contracted. The rectum often shows similar contortions in specimens withdrawn into the shell. The glandular portion of the organ is of the same appearance as in the aphallate specimens except that the cells have been displaced by the tube (Plate XXV, Fig. 3). No visible connection between the gland cells and the tube were detected. Around the tube there is a thin sheath evidently of connective and muscular tissue, the latter being particularly prominent around the apertural, expanded portion.

Thus, in both position and structure the organ of Plate in the phallate specimens of *Carychium* bears a striking resemblance to that described in *Pythia.* The fact that the tubular portion is present only in phallate individuals lends further support to Plate's views that this organ is in some way connected with reproduction.

The organ of Plate is not to be confused with the mantle organ which Pelseneer (1894) first described in *Phytia* and which lies in the basal margin of the pulmonary cavity. Plate noted a similar organ in *Pythia,* and Koslowsky (1933) again cited it in *Melampus boholensis.* This structure, which may be termed the organ of Pelseneer, is not represented in any species of *Carychium* which I have examined (Table 12). My investigations of the anatomy of *Pythia scarabaeus* and *Melampus coffea* reveal that the organ of Pelseneer of these two species, while in the same position, have fundamentally different internal structures; histological data are regrettably lacking. The situation is further complicated by the so-called "hypobranchial gland" of *Amphibola.* This structure occurs at the apertural end of the kidney and extends to the lower part of the pallial complex (Hubendick, 1945: 107 and 155). It is, therefore, in a position comparable to the organ of Plate in *Carychium* and *Pythia.* Moreover, Odhner has described in *Marinula juanensis* an hypobranchial gland which he would homologize with that of *Amphibola;* but the gland in *Marinula* extends for a considerable distance along the rectum and between it and the kidney in the upper part of the pulmonary complex. Therefore, in its position it seems not strictly comparable to any of the structures just mentioned. Hubendick (1947) called attention to a large mantle organ in *Physa* which he suggests is homologous to the hypobranchial organ of *Amphibola.* Apparently there is no similar structure in other lymnic Basommatophora.

Another structural difference between the two sexual types in *Carychium* which is not a part of the reproductive system proper is found in the segment of the diaphragm over the parietal isthmian hemocoel of phallate specimens. In the aphallate specimens this region of the diaphragm presents no structural differentiation from the rest of the membrane. But in the phallate type the epithelial cells of this region are greatly swollen,

PLATE XXIV



Gross aspects of the reproductive system. FIG. 1. Gross aspects of the reproductive system in an aphallate specimen. FIG. 2. Gross aspects of the reproductive system in a phallate specimen based on a reconstruction from sections.

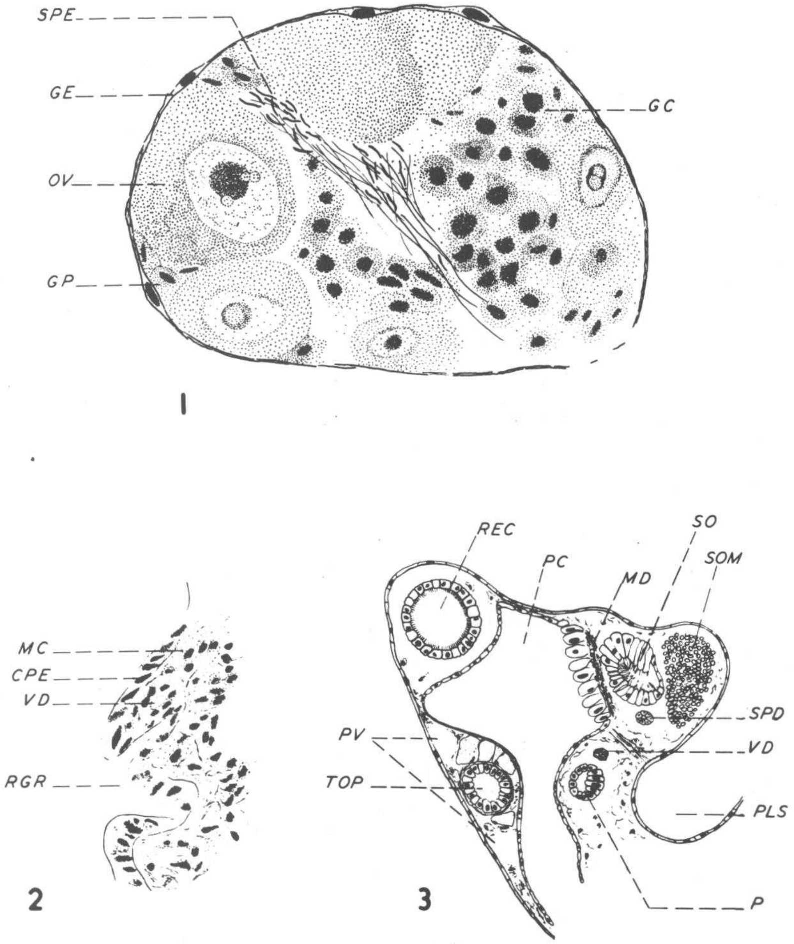
Abbreviations. AG - albumen gland; G - gonad; HD - hermaphroditic duct; P - penis; PNC - pneumostomal canal; RG - reproductive groove; SO - spermoviduct; SP - spermathecal sac; SV - seminal vesicle; VD - vas deferens.

pear-shaped cells, of glandular appearance. These cells project into the lumen of the pulmonary cavity (Plate XXV, Fig. 3), and their narrow end is attached along the diaphragm. Moreover, underlying this area is a prominent sheet of muscular tissue which is much thicker than anywhere else in the diaphragm. The muscular tissue of the aphallate specimens in this region again shows no special differentiation from the rest of the membrane.

In the aphallate specimens the ovotestis is situated in the sutural stricture immediately apical to the stomach but on the opposite side of the secondary cone. It is reniform in external outline; the thin wall of flattened epithelium is not constricted to form more than a single follicle (Plate XXIV, Fig. 1; Plate XXV, Fig. 1). Its greatest dimension is directed transversely in the secondary cone of which it occupies about half of the diameter. Most of the cavity of the ovotestis in the aphallate specimens is filled with ova, around the larger of which may usually be detected a thin, cellular follicle (not shown in Plate XXV, Fig. 1) which is much thinner than the wall of the gonad. Near the gonad wall, between the ova, are bundles of sperm, the long tails of which nearly extend across the organ. Toward the center of the ovotestis there occur numerous small, rounded cells having a granular cytoplasm and large spherical nuclei. These may be gametogenic cells but their exact nature was not determined. Intruded between the ova and near the gonad wall are smaller cells, more irregular in outline and with less granular cytoplasm, and oval nuclei. The exact nature of the peripheral granulocytes was not determined.

At its columellar end the ventral aspect of the ovotestis extends basally as a funnel-shaped vestibule, shortly narrowing to become the hermaphroditic duct. The latter passes directly basally, following the columellar axis rather closely, and going between the esophagus and stomach at the flexure of their junction. The hermaphroditic duct (Plate XXIV, Fig. 1) is very slim and straight with no convolutions in any part of its length. Its wall is a single layer of cuboidal epithelium not glandular or ciliated. At the region of the transition of the duodenum into the lower loop of the sigmoid intestine, in the lower part of the upper visceral complex, the hermaphroditic duct makes a lateral entrance into the spermoviduct. The latter continues apically beyond this junction following the coil of the primary cone for about half a whorl. The portion of the spermovidical tube above the junction with the hermaphroditic duct is apparently the homologue of the albumen gland in other pulmonates. Below this junction the spermoviduct continues to follow the trend of the primary cone passing to the parietal isthmian hemocoel and through it to its apertural end where the duct opens to the exterior of the animal on the body stalk, high in the

PLATE XXV



Details of the reproductive system. FIG. 1. Histological detail of the gonad of an aphallate specimen. FIG. 2. Cross section through the reproductive groove of a phallate specimen. FIG. 3. Cross section through the pulmonary complex and isthmian hemocoels of a phallate specimen as seen in a contracted individual.

Abbreviations. CPE - epithelium of the lateral cephalopedal mass; GC - central granulocytes of ovary; GE - epithelium of gonad wall; GP - peripheral granulocytes of ovary; MC - musculo-connective tissue of tegument; MD - muscular diaphragm overlying spermoviduct; OV - ovum; P - penis; PC - pulmonary cavity; PLS - parietal lamella of shell; PV - pulmonary vein; REC - rectum; RGR - ridge in reproductive groove; SO - spermoviduct; SOM - suboviducal columellar retractor muscle; SPD - spermathecal duct; SPE - sperm; TOP - tube of the organ of Plate; VD - vas deferens.

pneumostomal canal.

The upper half of the spermoviduct shows a marked tendency to out-pocketing and folding presenting a slightly convoluted aspect. Its wall is of glandular, cuboidal epithelia which take an intense basic stain. The albumen gland consists of a tube which histologically resembles the spermoviduct though it shows less affinity for stain. It similarly shows a tendency to out-pocketing and folding. Except for its position the albumen gland is easily confused with the upper part of the spermoviduct in sections. In the lumen of both are vague, fibrous extensions from the inner surface of the epithelia which may represent aspects of glandular secretion. It was not possible to determine with certainty the presence of cilia in the upper spermoviduct and albumen gland.

In the middle of the parietal isthmian hemocoel the upper oviduct gradually narrows, losing its convoluted appearance and strong affinity for stain. The lumen in this lower portion is definitely ciliated and uniformly so over the inner surface except for a narrow band on the wall which fronts on the suboviducal columellar retractor muscle. Here the epithelium is flattened and overhung by the neighboring strip of columnar cells so that a non-ciliated groove is produced. This may correspond to a similar longitudinal differentiation in the uterine portion of the spermoviduct of Stylommatophora, which is termed the sperm groove, and receives the excretion of the follicular prostate cells along that tube. No comparable prostatic cells are present in *Carychium exiguum* nor in the material which I have examined of *C. minimum, C. tridentatum* and *C. stygium.* However, Moquin-Tandon (1855) figured an external longitudinal mass on the spermoviduct which he termed the prostate. The sperm groove is difficult to trace in the upper part of the spermoviduct although apparently present there; it was not detected in the albumen gland.

A short distance above the opening of the spermoviduct to the exterior of the body there arises a minute tube which passes apically through the parietal isthmian hemocoel, beside the spermoviduct, until it reaches the lower part of the upper visceral complex. Here it expands into a large spermathecal sac lying between the apical end of the pulmonary complex and the spermoviduct. These are the duct and sac of the spermatheca (Plate XXIV; Plate XII). The wall of the spermathecal duct is of squamous epithelia; neither seem ciliated internally. Occasionally in the interior of the sac could be detected a small agglutinated mass possibly of cellular nature. It was not possible to ascertain whether they might be ova and nothing resembling sperm was noted. The frequent assumption that the spermatheca of pulmonates constitutes a seminal receptacle has been shown by Larambergue (1939) to be open to doubt, at least in some species.

The position of the external reproductive groove has been described above (p. 52). In sections (Plate XXV, Fig. 2) this groove seems to be double having a narrow ridge dividing it into upper and lower troughs. No cilia could be detected in it.

The above description applies to the reproductive system of the aphallate individuals. The phallate condition seems to be merely a super-position of additional structures with slight modification of one or two already existing in that basic pattern. In the phallate specimen the ovotestis is much larger, its transverse section occupying about three-fourths of the secondary cone at that level. Through the space of the spire not occluded by the gonad passes the upper liver tube which reaches to the extreme apical end of the visceral mass. The shape of the ovotestis in phallate specimens may be compared to a hand with the fingers slightly flexed and the palm cupped. Thus the upper part of this gonad shows a tendency to several large rounded lobes; though the transverse constrictions do not cut deeply, it has some resemblance to the plurifolliculate gonads of other snails.

The interior of the gonad in phallate individuals has the same cellular elements found in the aphallate specimens, but sperm here constitute the greatest bulk of the cells; the spherical granulocytes are also present in abundance; ova are usually of smaller size than maximum examples noted in the aphallate specimens, though occasionally one is found which approaches such proportions,

After the hermaphroditic duct passes the gastro-esophageal flexure a short lateral tube from it expands into a small spherical sac. This tube and sac have an epithelium similar to the hermaphroditic duct; the interior of the sac is filled with masses of sperm. Therefore, it seems to constitute the seminal vesicle, a structure characteristic of lymnic Basommatophora but absent in the Stylommatophora. This vesicle was found in none of the aphallate specimens.

At the opening of the spermoviduct, and below the origin of the spermathecal duct, the vas deferens arises. This passes in the musculoconnective tissue of the tegument closely paralleling the upper margin of the external reproductive groove (Plate XXV, Fig. 2) until it reaches the lower end of the latter where it passes medially into the hemocoel. It extends across the hemocoel above the buccal mass and its associated structures to the left side of the cephalopedal mass. Here it enters the penis, apparently in a terminal or subterminal position. The penis is a continuous tube the upper half of which is about twice the diameter of the lower half. The wall of the penis and vas deferens are simple cuboidal epithelia and not ciliated or glandular. Running the length of the expanded part of the penis is a strip of columnar epithelium projecting into the lumen to form a pilaster. Little, if any, intrinsic musculature is present in the penis wall. Extrinsic muscles were observed in one specimen near the apex of the penis, but their similarity and approximation to compacted tegumentary muscles in the contracted specimen did not permit exact determination of their origin and insertion.

Sectioned specimens of *Carychium minimum* and *C. tridentatum* received from Hugh Watson likewise show both aphallate and phallate types of sexuality (Table 11). As the individuals were all contracted and few were examined it is not possible to report the anatomy in detail. However, the phallate type is again recognizable by the tube of the organ of Plate, the muscular and glandular diaphragm over the parietal isthmian hemocoel, the presence of vas deferens, penis and seminal vesicle, and the large ovotestis with a preponderance of sperm. All four of the specimens of *C. stygium* sectioned were typically aphallate.

The small number of ova (three or four) in the ovotestis of aphallate specimens of *Carychium exiguum,* when the ova are of maximum size, indicates there are about three or four eggs deposited at the phenological period. That ova of moderate size were found in all seasons of the year, even late summer, suggests that this species might live longer than a single year or that the snails become sexually mature by the time the shell is mature in late summer.

SUMMARY

1. The study is based on series of *Carychium exiguum* (Say) from 60 localities in the Lower Peninsula of Michigan.
2. Methods of collecting, culturing and techniques of study are discussed.
3. The problem of classification of pulmonates is presented by showing the ecological distribution of the major groups.
4. In Michigan, *Carychium* occurred in isolated colonies within microhabitats of a few feet major dimension. The essential ecological factors in these habitats are: high and constant moisture content throughout the year, decaying plant material, and darkness. Living *Carychium* colonies are exceptional in places where the moisture content varies, such as on flood plains of major streams.
5. *Carychium stygium* of Mammoth Cave, Kentucky, was found in a relatively simple environment presenting these essential ecological factors.
6. Locating microhabitats containing *Carychium* was most readily accomplished by seeking macrohabitats which might contain them. Such

macrohabitats are of three general types: *Thuja* forests, grasslands and hardwood forests of certain types.

7. Typical assemblages of mollusks associated with *Carychium* are listed.

8. Distribution records were obtained for most of the counties of the Lower Peninsula of Michigan north of the Saginaw and Grand River valleys, but for only three counties south of that major drainage divide.

9. Life history data were obtained mainly from field sampling. During most of the year *Carychium* populations contained 90% or more adults. In July, the sudden appearance of juveniles, mostly of minimal size, reduced the adult population to one-third of the total number of living snails. These small juveniles were present for about a month, during the latter half of which some of these young had already reached the adult size range of 3 1/2 - 4 1/2 suture whorls. In November the juvenile population dwindled to less than 10%. Eggs were not observed but the anatomical data indicated that this snail was oviparous rather than ovoviviparous.

10. Concepts of the snail's shell fitting a morphological pattern of a (primary) cone, which has coiled to form a secondary cone, are discussed. Heterostrophy, internal shell resorption, terms of dimension relationship, and determinate growth of the shell are all defined with respect to the two cones.

11. Observations on growth changes in the shell showed a lack of heterostrophy at all stages. Resorption of the shell partitions as well as growth of the shell's lamellae began with post-embryonic growth. Determinate growth was shown by the reflected, thickened lip of the ephebic shell; there was no gerontic growth.

12. From the variation of the form, size, sculpture, internal lamellae, number of whorls and extent of resorption of the internal lamellae, it was concluded that only one natural species is worthy of recognition in the material used for this study.

13. Significant characters in the external morphology were as follows: smooth integument, absence of a pedal groove, presence of a reproductive groove, a single pair of tentacles with eyes in their bases, no vestige of the anterior tentacles, the anus opening into the pneumostomal canal, and the occlusion of the hypopeplar chamber.

14. The resorption of the shell's partition was accompanied by a corresponding amount of fusion in the whorls of the visceral mass. Some organs of this mass are modified to fit the pattern of the secondary cone while other structures continue to follow the coiling of the primary cone. A simplification of structure was in evidence in several organ systems.

15. The mutually imbedded organs of the upper part of the visceral mass, a distinctive type of connective tissue forming a matrix for them,

the apertural extent of fusion of the whorls, the apical extent of the pulmonary cavity and the columellar muscle – all provide internal morphological criteria used to distinguish and limit the region referred to as the upper visceral complex. The rest of the snail's body, exclusive of the pulmonary cavity and the organs associated with its wall, forming the pulmonary complex, was termed the lower visceral complex.

16. The hemocoel situated between the upper visceral complex and cephalopedal mass and paralleling the pulmonary complex throughout the latter's extent was termed the isthmian hemocoel. It was found to be distinctive in *Carychium* in the way it was divided longitudinally by the approach of the shell's lamellae to the columellar side of the diaphragm, thus dividing it into parietal and columellar moieties.

17. The cephalopedal mass was bounded by cuboidal or columnar epithelium (rarely squamous) of which only that of the sole and area of the pneumostomal canal is ciliated. Spongy musculoconnective tissue subtending the epithelium was of several cell types but the eosinophilic granulocytes of the upper visceral complex were absent.

18. Connective tissue of the lower visceral complex formed definite membranes only in the base of the tentacles where a transverse sheet supported the eye capsule.

19. The digestive system was characterized by its simplicity. Neither the salivary glands nor the liver were branched, although the liver tubes showed shallow outpocketings which simulated vestigial branching. The musculature of the buccal mass showed the general pattern of the musculature of other pulmonates. A single sphincter-like muscle obliquely encircled the spherical stomach dividing it into three parts in a simplified fashion. There was no prominent musculature in other portions of the digestive tract. The duodenum contained a typhlosole with columnar epithelium.

20. The lower loop of the sigmoid intestine did not abut the upper margin of the pulmonary complex in the manner found in other snails but was situated a little above it. Between these two structures a part of the reproductive system was intruded.

21. The heart and pericardium showed little difference from the general pattern of that structure among other pulmonates. The arterial system was traced only as far as the branching of the anterior and posterior arteries. It is probable that the arterial system is no more extensive than observed.

22. The venous system is remarkable in the absence of vascularization of the peripheral portion of the pulmonary chamber and the uniform small size of the pulmonary vein throughout its length. The left pallial vein

entered the pulmonary vein just before the latter entered the auricle. The left pallial vein was much larger than the pulmonary vein and therefore seemed to be the chief course for the return of blood from the spacious marginal mantle sinus, which might be the primary site of external respiration.

23. The kidney was a simple sac without lamellae. A prominent renopericardial passage was present but cilia could not be detected. A large renal pore opened into the pulmonary cavity near the rectum. Some of the cells typical of the kidney sac lined the free surface of the rectal wedge, but no ureteral groove or tube was present.

24. The nervous system was diffuse as compared to the condition usually found in other pulmonates. Each cerebral ganglion has two accessory ganglia which were apparently not homologous with those of *Helix* or *Lymnaea.* Pleural ganglia could be recognized. Only two ganglia were present on the visceral nerve ring behind the pleurals. The distribution of nerves arising from them could not be determined and to avoid confusion they were termed innominate visceral ganglia. Chiastoneury was prominent in the pleuro-innominate connectives.

25. The eye was a relatively simple vesicle in which corneal and retinal portions could be recognized, surrounding a cavity containing a prominent lens. No special nervous elements could be recognized in the eye capsule. The epithelium of the tentacular tip and anterior margin of the labial palps was modified to form sensory tissue. It contained peripheral nuclei and basal sensory organelles, and each area is covered externally by a prominent cuticle. The possibility that the sensory area of the labial palps is homologous with the anterior tentacular pads of other Ellobiacea is considered. A large otocyst is attached to the dorsal aspect of each pedal ganglion but no special innervation for it could be detected.

26. Two distinct sexual types are defined by modifications of the reproductive system. The gonads of both contain sperm and ova. In the aphallate type the hermaphroditic gland was a single reniform vesicle containing about three ova when the latter were of maximum size. The hermaphroditic duct was straight, not convoluted, and lacked a seminal vesicle. The albumen gland was a continuation of the spermoviduct above the entrance of the hermaphroditic duct into the latter. The spermoviduct contained internally a groove, characteristic of the Stylommatophora, though no vas deferens or penis was present in aphallate specimens. A spermathecal duct had its origin from the spermoviduct near the opening of the latter and expanded at its upper end into a spherical spermathecal sac.

27. The reproductive system of phallate specimens showed a modifica-

tion of existing structures and superposition of new ones on the fundamental pattern presented by aphallate specimens. The ovotestis showed a tendency to be plurifolliculate and contained a preponderance of sperm. Ova of the maximum size observed in aphallate specimens were rarely found. A seminal vesicle was present on the hermaphroditic duct. The vas deferens arose from the lower part of the spermoviduct below the origin of the spermathecal duct. The vas deferens was situated inside the body wall parallel to the reproductive groove. At the lower end of the latter, it crossed the cephalopedal hemocoel to enter the penis. The penis opened at the lower end of the reproductive groove.

28. Besides differences in the reproductive system proper, the two sexual types were set apart by the tube contained in the organ of Plate in the phallate specimens, and by the muscular and glandular character of the diaphragm overlying the parietal isthmian hemocoel of the same sexual type. The organ of Plate was a glandular structure in the peripheral pulmonary wall, presumably homologous to a structure described by Plate in *Pythia.*

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