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LAND MOLLUSCA OF THE TIKAL NATIONAL PARK, GUATEMALA

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THE field collections upon which this report is based were made during the period from early February to the middle of May, 1956, and centered in the area adjacent to the ruins of the ancient Maya city of Tikal, Department of Petén, Guatemala. One purpose of the trip was to study the transition from "dry" to "rainy" seasons, and the effect of this change upon the land snails. However, as the season progressed, the expected rains failed to materalize, and the absence of water finally forced abandonment of our field camp. Nevertheless, living snails of several species, more or less active within limited habitats throughout the year, were collected wherever they were found. Of approximately 15,000 specimens brought back to Ann Arbor, most consist of shells only, fewer than ten per cent represented entire preserved animals.

This study would have been impossible without the aid and support of many persons, to all of whom I am deeply indebted. Through Dean Ralph A. Sawyer, the Horace H. Rackham School of Graduate Studies, University of Michigan, generously provided the funds for transportation and maintenance in the field. Henry van der Schalie supplied collecting equipment and the free use of the specimens and facilities at his disposal. The excellent cooperation of the government of the Republic of Guatemala in supplying air transportation, and its constant interest in Tikal, is gratefully acknowledged. Edwin M. Shook, Director of the University of Pennsylvania field camp at Tikal, was at all times extremely hospitable and took an active and personal interest in the success of our efforts.

To Irving J. Cantrall, Laurence C. Stuart, and Theodore H. Hubbell, my mentors in the field, I am particularly grateful for their continued encouragement and friendly advice. The bulk of the diffi-

cult task of identification of specimens was done by Fred G. Thompson; Alan Solem aided with the identification of a number of troublesome shells.

Knowledge of the molluscan fauna of the Petén region has increased slowly but steadily since the pioneering expeditions of Arthur Morelet in 1847. The region around Lake Petén was visited by Osbert Salvin in 1861, and the report of his collections appeared two years later (Tristam, 1863). The work of these and other early collectors was summarized by von Martens (1890–1901) in the invaluable volumes which form a portion of the Biologia Centrali-Americana series.

More recently, the extended collecting expedition carried out by Henry van der Schalie in 1935 added greatly to our information on the mollusks of this area, and the report of his work (Goodrich and van der Schalie, 1937) forms an important nucleus for further studies in the region.

Our field camp was located approximately one kilometer from the center of the ruins of Tikal, 17° 10′ N, 89° 25′ W. The ruins lie within a rather uniform forest termed a "quasi-rain forest" by Lundell (1937), and typical of the Northern Petén region which he delimited. A relatively thin layer of immature, calcareous soil covers the ground, except for some hills and slopes on which the underlying limestone is exposed in outcrops. In samples of soil taken from well-drained areas, soft white crumbs of limestone form a conspicuous component. The limestone substrate, probably of Oligocene age, represents a southward extension of the Karst-like topography characteristic of much of the Yucatán Peninsula.

The temperature in this part of Petén varies from about 20°C in February to about 30°C in May and June, and the scanty data available regarding rainfall indicate that there is an annual precipitation of about 1750 mm., almost all falling from May to October.

The presence of the once great metropolitan center of Tikal indicates that the forests were at one time extensively cleared, but in the millenium since the abondonment of the city by the Maya, the vegetation of the climax forest has become reestablished. Nevertheless, the present distribution of tree types may reflect a lingering influence of selective cultivation on the part of the orginal natives, for there is little doubt that such useful trees as the ramon (*Brosimum alicastrum*), zapote (*Achras zapota*), and others were grown, or at least preserved, by the ancients.

The high forest itself is composed of many dozens of types of trees. The most common large tree in many areas is the zapote, exploited

commercially in recent years for its latex, which is used in the manufacture of chewing gum. A local association within the forest in which this tree is dominant is termed a "zapotal," and similarly one may find himself in a "caobal," in which there is a concentration of caoba or mahogany trees (*Swietenia macrophyllum*), a "ramonal," etc. The canopy of the high forest may be 50 meters from the ground, and its density sufficient to exclude most of the sunlight from the forest floor. As a consequence, the absense of small shrubs and herbaceous vegetation gives an almost park-like appearance to many places deep within the forest. A profusion of vines and lianas may be found draped around most of the larger trees. On hillsides which receive more light smaller shrubs often grow, and a luxuriant, though temporary, growth of herbaceous vegetation appears in sunlit openings left by the downfall of the forest giants. Excellent descriptions of the area have been provided by Bartlett (1935), Lundell (1937), and Stuart (1958).

Within the high forest, several microhabitats of special importance for land snails are distinguishable. These are not peculiar to the Petén, for their counterparts may be found in most tropical and temperate deciduous forests. They include the following:

(1) Microhabitats closely associated with the soil,
   (a) Under stones: *Bulimulus, Neocyclotus, Lamellaxis.*
   (b) On the surface of the soil at the bases of limestone outcrops: *Licina, Neocyclotus.*
(2) Within the leaf litter and mulch layer: smaller Oleacinids and Zonitids?
(3) Within decaying logs and bark: *Neocyclotus, Lucidella, Spiraxis, Caecilioides, Synopeas, Thysanophora, Microconus, Xenodiscula, Averellia, Guppya, Habroconus,* and other tiny snails.
(4) On the trunks and leaves of trees and larger shrubs: *Oligyra, Helicina, Euglandina, Drymaeus, Oxystyla, Averellia.*
(5) In higher foliage, particularly bromeliads: *Oxystyla, Euglandina?* Helicinids? (bromeliads are rare in the Tikal area).

In collecting, an effort was made to find association between species of snails and particular types of vegetation. No constant relationship was found, although it should be pointed out that live individuals of many species of mollusks were not collected. Since it is practically impossible to guess the habitat of snails whose shells are found on the forest floor, it is evident that ecological work on the land mollusks of this area can be carried out only during the rainy season when living animals should be more abundant.

An opportunity was presented at Tikal to observe a young secondary growth area which was developing between the field camp and the airstrip, a few hundred yards distant. This patch had been completely cleared and burned over a few years previously. With the return of vegetation, many low shrubs and bushes, as well as grasses and other herbaceous plants began to grow in the area. The most outstanding feature of this secondary growth was the presence of a number of guarumo trees (*Cecropia* sp.), from which the association takes the name of "guarumal." These are extremely fast-growing trees belonging to the family Moraceae; their wood is so soft and watery that one stroke with a machete is often sufficient to fell a tree ten or twelve feet tall. On these trees aestivating specimens of *Oxystyla princeps* were often found.

Another major type of forest in the Tikal area is found in the "bajos." These are patches of low ground, often quite extensive, and easily identified from the air because of their lower canopy and distinctive coloration. In a typical bajo, the soil is of a heavy, clayey texture, very dark in color, and cleft by deep fissures in the dry season. A network of rootlets and rhizomes covers the soil, over which a scant half inch of leaf litter may accumulate. The surface of the ground is not flat, but rather irregularly rolling, with many depressions and channels which apparently are the pools and arroyos of the rainy season. Small mounds of hard, almost brick-like soil are formed at the bases of fallen trees which have pulled up masses of earth packed among their roots.

Scattered sedges, grasses, and low shrubby plants grow in these areas, but never so thickly as to obscure the ground beneath. Larger shrubs and bushes are not usually found in the bajos, since perennial xerophytic plants would be killed by the standing water which collects during the rainy season. The trees are for the most part small and spindly, with occasional resistant larger trees, such as zapote, cedro (*Cedrela*), and caoba, particularly around the periphery of the bajos. Palms are abundant, with the spiny escoba (*Crysophila*) and the botan (*Sabal*) perhaps the most common. Many fallen logs lie scattered on the ground in various stages of decay, and many types of vines and lianas, often armed with needle-like thorns, trail from the trees and along the ground. These thorny vines often occur in thick, tangled masses, and make passage through the bajo painfully difficult.

The canopy of the forest in the bajos is from 10 to 25 meters in height, relatively open, with a large proportion of open sky visible from almost any spot on the ground. In general, the bajos support

only a poor and spotty molluscan fauna which appears to have no species of land snails not found in the surrounding high forest. The large shells of *Pomacea flagellata* are found scattered on the ground in bajo areas, but I was unable to find any live specimens.

Somewhat similar to the bajos are a number of deeper depressions of much smaller extent which retain water throughout most or all of the year. These watering places or "aguadas," which resemble ponds, serve as the major source of drinking water for many of the larger animals of the region. Temporary camps of the "chicleros," men who collect the chicle from the zapote tree, are invariably located adjacent to such aguadas. The aguada near our camp supported a heavy growth of emergent and floating hydrophytes and harbored several species of turtles and frogs, as well as one crocodile. Most of the aquatic mollusks found within this aguada have not yet been identified with certainty, but they include a large *Physa* (or *Aplexa*), several species of Sphaeriidae, an ancylid (*Ferrissia aguadae?*), and several small planorbids, among which *Drepanotrema lucidum* (Pfeiffer) and *Tropicorbis albicans* (Pfeiffer) have been identified by Harold W. Harry.

Several techniques were employed in collecting. The arboreal snails, when found alive, were picked off the trunks and leaves of trees, *Bulimulus* and a few other forms were found beneath stones. Many of the minute species were found within decaying logs or in the rich, fine mixture of windblown soil and humus which collects in open depressions in logs and stumps. The dead shells, which form by far the bulk of the collection, were secured in large numbers from soil samples collected at stations in the forest floor and brought to the camp "laboratory" in cloth bags. Samples were first sifted through wire mesh to remove pebbles, larger shells, and other objects. The sifted soil was then spread, a tablespoonful at a time, on a white enameled plate where tiny shells could be removed with the aid of a camel's hair brush. Often several hundred tiny shells could be recovered from two or three pounds of soil.

The annotated list which follows includes all of the recognizable species of terrestrial mollusks collected at Tikal. Even though several months were spent in intensive collecting in a fairly small area, it is possible that additional species will be added to this list, particularly if roads and trails are cut connecting Tikal with other areas, and if ecological conditions are altered by development of the site as a park.

The Tikal area, lying between the more arid forests of Yucatán and the wetter forests of southern Petén, is not demarcated by any

particularly distinctive natural boundaries. Thus, the land mollusks would not be expected to show any high degree of endemism. Many of the species found here may be placed in the faunal assemblage which Bequaert (1957) has described within the Chiapas-Guatemalan subregion. About 30 per cent of the species listed by him as occurring in the Selva Lacandona, Chiapas, México, are found at Tikal. Roughly 25 per cent of the species listed by Bequaert and Clench (1933, 1936, 1938) for Yucatán, and 40 per cent of those discussed by Harry (1950) for the same general area are found at Tikal. However, only about 17 per cent of the species of land snails from the department of Alta Vera Paz, Guatemala, which are mentioned by van der Schalie (1940) also occur at Tikal. The difficulty of making accurate identifications of many obscure species without having a large and properly determined reference collection, and the variety of names which appear in the literature make faunal comparisons with other regions complicated and hazardous. Most of the forms represented are members of biological complexes whose ranges extend from the region of Veracruz to Panamá, and eastward to the islands of the Caribbean. The area included is a vast one, and workers in the field have been few. It is quite likely that additional collecting in all parts of Central America will demonstrate that many of the named "species," originally believed to be distinct, will fall into place as clinal variants of wide-ranging and plastic species.

SYSTEMATIC LIST OF SPECIES[1]

SUBCLASS PROSOBRANCHIA

Family Cyclophoridae

Neocyclotus dysoni cookei (Bartsch and Morrison).—With the exception of one active specimen collected near the edge of the camp aguada and two from the base of a limestone outcrop, all live animals of this species were found aestivating within rotting logs. Twenty-two live animals and 428 shells of this subspecies, the only representative of its family at Tikal, were taken. The type locality of *N. d. cookei* is Uaxactún, Department of Petén, about 16 kilometers northeast of Tikal, and the form has been collected at several other localities in the Petén, and in British Honduras to the east. Solem (1956) has con-

[1]The references which follow the discussion of each species present information about the distribution and biology of that form in Central America. The works of von Martens (1890–1901) and Goodrich and van der Schalie (1937) discuss so many of these species that I have felt it unnecessary to repeat references to them each time. No attempt has been made to give an exhaustive coverage of the literature.

sidered *cookei* to be closely related to the larger *Neocyclotus dysoni ambiguum* of southern México. The genus *Neocyclotus* is found from Veracruz southward to Venezuela, Ecuador, and Colombia, and also on the islands of the West Indies. (Bartsch and Morrison, 1942; Morrison, 1955; Pilsbry, 1891, 1920.)

Family Pomatiasidae

Licina radiosa (Morelet).—This species seems always to be associated with exposures of limestone. Some of the best collections of *L. radiosa* were made on and within the buildings of the Tikal ruins. Many dead shells and occasional live specimens were taken from the cracks and fissures between the building stones. Outside of the ruins area, this species was encountered only at the bases of limestone outcrops. Sixty-six live animals and about 250 shells were collected. *L. radiosa* ranges from the Petén region to the Department of Alta Vera Paz, Guatemala. Closely related forms are known from southern México and several islands of the Caribbean. (Baker, 1928; van der Schalie, 1948, related species.)

Family Helicinidae

Oligyra oweniana oweniana (Pfeiffer).—One of the most common snails of the Tikal area. The shells vary in color from white to yellow, pink, and light brown. Many show banding in various patterns. After a rain, *O. o. oweniana* may be found crawling actively on tree trunks and leaves. The species has been recorded from Tabasco and Chiapas, México, and Alta Vera Paz, Guatemala. More than 800 animals and several thousand shells were collected. (Baker, 1922*a*; Bequaert, 1957; Pilsbry, 1892; van der Schalie, 1940.)

Helicina amoena (Pfeiffer).—The rarest helicinid snail found at Tikal. Only two lots totalling eight specimens were collected. This arboreal species is found in most of Central America, from the southern states of México southward to Panamá. (Bequaert, 1957; Pilsbry, 1926; van der Schalie, 1940.)

Helicina rostrata Morelet.—Fifteen live animals were collected, all from the trunks of trees or the undersurfaces of large leaves, particularly those of young palms. About 200 shells were found on the forest floor. Most of the shells are banded, with olive, yellow, pink, and tan stripes over a white base. They may be found on the vegetation which covers the pyramids within the ruins area. This species has also been collected from several localities in the Department of Alta Vera Paz, and ranges southward to Honduras and Nicaragua. (Baker, 1922.)

Lucidella lirata (Pfeiffer).—Only five living animals of this wide-ranging species were collected, all from beneath the bark of the same log. Shells of *L. lirata* are common in the soil, and more than 800 were secured from soil samples. Baker (1922) believed that this species is "almost semiaquatic." Known from Veracruz and Yucatán to Venezuela, and a number of related forms occur on many of the Carribean islands. (Baker, 1922, 1928; Bequaert, 1957; Bequaert and Clench, 1933; Pilsbry, 1891, 1903, 1926, 1926*a*, 1930.)

Family Pilidae (Ampulariidae)

Pomacea flagellata, subsp.—By far the largest gastropod at Tikal, this aquatic species is included here because shells are often found on dry land after the aguadas and bajos have dried up. Many forms of this exceedingly complicated species are known from México to northern Colombia. (Baker, 1922; Bequaert, 1957.)

SUBCLASS PULMONATA

Family Oleacinidae

Euglandina cumingi (Beck).—Twenty-one animals were collected from a number of habitats, including tree trunks, damp straw on the ground, and upon stones. When confined with snails of another species, the *Euglandina* are extremely voracious and quickly devour their companions. One large specimen ate 14 *Bulimulus unicolor* in about 45 minutes, after which the *Euglandina* retired into its shell and hung from the roof of a glass jar for several days. Besides the live animals, 64 shells were collected.

E. cumingi is widespread in Central America, and ranges southward into Colombia and Venezuela. (Baker, 1925, 1943; Pilsbry, 1926, 1930; van der Schalie, 1940.)

Salasiella guatemalensis Pilsbry.—No live animals were found, but 179 shells referable to this species were collected at Tikal. This is one of a series of closely related forms which extends from the region of San Luis Potosí in México south into Panamá. (Baker, 1923; Pilsbry, 1919.)

Salasiella modesta (Pfeiffer).—Thirty-nine dead shells from Tikal. Most of the records of *S. modesta* are from Veracruz and eastern México. (Baker, 1940.)

Streptostyla meridana (Morelet).—Soil samples yielded 116 speci-

mens of this species, previously reported from several localities in Yucatán. (Bequaert and Clench, 1933, 1936; Harry, 1950.)

Spiraxis alvaradoi Goodrich and van der Schalie.—Seventy-four shells collected, all from soil. This tiny snail is probably a resident of decaying logs and stumps. *S. alvaradoi* is known only from the Petén. The difficult genus *Spiraxis* contains a great many essentially similar forms, found over a large part of México and Central America. It is possible that our collections from Tikal contain other species of *Spiraxis* than the two listed here.

Spiraxis funibus Goodrich and van der Schalie.—No live animals of this species were found. One hundred fifty-eight shells were obtained by examining soil samples.

Family Achatinidae

Caecilioides consobrina veracruzensis Crosse and Fischer.—This minute mollusk is common at Tikal, and hundreds of shells were recovered from soil samples. The distinction between this subspecies and *C. c. prima* is not entirely clear, the main difference between the two being in the fine spiral striations on the shell surface. These forms are known from tropical México and Central America. (Baker, 1930; Harry, 1950; Pilsbry, 1930; van der Schalie, 1948.)

Lamellaxis martensi (Pfeiffer).—This species seems to be a ground inhabitant of lowland jungles; 66 specimens were collected at Tikal. It is known from Veracruz, Yucatán, the island of Cozumel near Yucatán, and a number of localities in the Petén. (Baker, 1923; Bequaert and Clench, 1933, 1936; Harry, 1950; Richards, 1937.)

Lamellaxis gracilis (Hutton).—According to Pilsbry (1946) this is perhaps the most widespread of all land snails, and is found in the tropics of both hemispheres. I collected 106 shells, mostly in soil samples. (Baker, 1927; Bequaert and Clench, 1933; Pilsbry, 1926, 1930, 1946.)

Lamellaxis micra (d'Orbigny).—Like the last species, this small snail is common in many tropical areas, perhaps spread by the activities of man. (Bequaert and Clench, 1933; Harry, 1950; Pilsbry, 1903, 1926, 1930; Richards, 1937.)

Synopeas beckianum (Pfeiffer).—Only four dead shells of this species were collected, two from a decaying log and the others from the surface of the ground in the forest. While not abundant at Tikal, the species ranges very widely, extending from Veracruz to Brazil and

Peru. (Baker, 1923, 1927; Bequaert, 1957; Pilsbry, 1920, 1926*a*, 1930; van der Schalie, 1940.)

Leptinaria elisae (Tristam).—A few of the 30 specimens found did not have the parietal tooth and thus might be considered as referable to *L. stolli* or *L. livingstonensis*. The population appears to be uniform in other respects, however, and probably represents a single species.

Family Bulimulidae

Bulimulus unicolor (Sowerby).—About 150 animals of this species were collected, most of them living beneath stones in the area of the camp clearing. In contrast with the three other species of the family which are found at Tikal, *B. unicolor* is not a tree snail. Several hundred dead shells were taken from the forest litter, usually in close association with stone outcrops. This is a common shell of Yucatán and most of Central America. (Bequaert, 1957; Bequaert and Clench, 1933, 1936; Harry, 1950; Pilsbry, 1926.)

Drymaeus shattucki Bequaert and Clench.—Rare at Tikal. Only twelve shells and one animal were found; the live snail was suspended from the underside of a botan palm frond cut for thatching. Aside from the direction of coiling, the shell of this species is almost identical with that of *D. tropicalis*. Known from Yucatán and several localities in the Petén forest. (Bequaert and Clench, 1933, 1936; Pilsbry, 1946; Richards, 1937.)

Drymaeus tropicalis (Morelet).—Only one shell of this sinistral species was found at Tikal. (Bequaert and Clench, 1933.)

Oxystyla princeps (Broderip).—Common at Tikal. Many specimens were collected in the small patch of second-growth bush between the camp and the airstrip. Weathered shells of *O. princeps* are a common element of the leaf litter layer of the forest floor. This large tree snail is found from tropical México to Panamá, and the many names which have been applied to separate populations show it to be quite variable over its range. (Baker, 1923; Bequaert and Clench, 1933, 1936; Harry, 1950; Pilsbry, 1891; 1920, 1926, 1930; van der Schalie, 1940.)

Family Sagdidae

Thysanophora caecoides (Tate).—No live animals of this tiny species were found, although 156 shells were recovered from soil samples. Probably this snail is an inhabitant of decaying logs and leaf litter. It is known from Yucatán to Panamá. The various species of *Thysano-*

phora, such as *T. plagioptycha, T. conspurcatella,* and *T. caecoides* are difficult to distinguish, and it is possible that more than one is represented in this collection. (Bequaert and Clench, 1933; Harry, 1950; Pilsbry, 1926, 1930; Richards, 1937.)

Microconus rufus Thompson.—At present known only from localities in the Petén forest. Several hundred specimens of this small reddish shell were collected from logs and soil samples, of which 124 were selected by Thompson (1958) as paratypes.

Hyalosagda turbinella (Morelet).—A single lot containing five shells was collected at the top of Temple IV, within the Tikal ruins. This very rare shell, originally described from the Petén forest, has near relatives on the island of Jamacia. (von Martens 1890–1901.)

Xenodiscula taintori Goodrich and van der Schalie.—Besides the Petén and one locality in Alta Vera Paz, the only known locality for this genus is in Venezuela. The systematic position of *Xenodiscula* is unclear and it has been assigned only provisionally to the family Sagdidae. Several hundred specimens of this minute shell were removed from sifted soil samples. (Pilsbry, 1919.)

Lacteoluna selenina (Gould) .—Only present in one lot from Tikal, this species apparently has not previously been reported from the mainland of Central America. It is known from Florida, several of the islands of the Caribbean, and Bermuda. (Pilsbry, 1940*a*; van der Schalie, 1948.)

Family Fruticicolidae

Averellia coactiliata (Deshayes); *Averellia suturalis* (Pfeiffer).—I have not been able to assign the 65 specimens of *Averellia* to either of the above species with certainty. About seven live snails were collected from the soft wood within a decomposing log, and one was taken by Irving J. Cantrall from the bark of a tree. (Baker, 1922.)

Family Zonitidae

Hawaiia minuscula (Binney).—Common in the Tikal area. Several hundred shells were taken from soil samples. This small snail has been introduced into many areas throughout the world, and is found commonly in North America, Central America, the West Indies, and some Pacific islands. (Baker, 1930; Bequaert, 1957; Bequaert and Clench, 1938; Pilsbry, 1946; van der Schalie, 1948.)

Guppya gundlachi (Pfeiffer).—This species is found fairly abundantly at Tikal. It is known from Florida and Texas to Venezuela, and in

the West Indies. (Baker, 1922, 1925; Pilsbry, 1903, 1926, 1930, 1946; Richards, 1937; van der Schalie, 1948.)

Guppya gundlachi orosciana (von Martens).—Sometimes considered to be a separate species, this form is characterized by a greater tendency towards carination of the whorls. Known from México to Venezuela, usually occurring together with typical *G. gundlachi.* (Baker, 1922, 1925, 1930.)

Habroconus elegantula (Pilsbry).—Most of the 179 shells collected were in soil samples, but several were found beneath the bark of rotting logs, a favorite habitat of many zonitid snails. *H. elegantula* has also been taken from low vegetation in the state of San Luis Potosí, México, by H. B. Baker (1930). Specimens in the University of Michigan Museum of Zoology are from several states in southern México and from the Petén. (Baker, 1922, 1930.)

Habroconus trochulina (Morelet).—One shell, taken from a log of the ramon tree, is the only representative of this species found at Tikal. *H. trochulina* was collected commonly in Petén by van der Schalie in 1935. According to Bequaert (1957), it is known only from Veracruz, Chiapas, and Petén. (Baker, 1925, 1930; Bequaert, 1957.)

Family Pupillidae

Gastrocopta pellucida hordeacella Pilsbry.—One of the rarer of the tiny species, this form is represented by about two dozen specimens recovered from soil samples. Known from New Jersey to Tampico, México. (Pilsby, 1903, 1948.)

Pupisoma dioscoricola insigne Pilsbry.—This small pupillid is found commonly in the soil, from which several dozen dead shells were taken. The species is found in Florida, Texas, and Central and South America; subspecies *insigne,* distinguished by its coarser sculpture, is known from Texas, México, Yucatán, and Jamaica. (Baker, 1923, 1925, 1928; Pilsbry 1926, 1948.)

Family Ellobiidae

Carychium exiguum mexicanum Pilsbry.—A very common species at Tikal. Many hundreds of specimens of this minute shell were brushed from soil samples, but no living animals were found. This form represents the tropical stock of *C. exile* and seems to intergrade with the typical form in Texas. The genus *Carychium* is widespread in Europe, Asia, and North America. (Baker, 1930; Pilsbry, 1891, 1903, 1948.)

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