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INTRODUCED GULF COAST MOLLUSCS

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Abstract

Of the ten species of molluscs which are known to have been introduced into the Gulf Coast area of the United States, four have been studied over a five year period; two of these, *Bradybaena similaris* (Ferussac) and *Lamellaxis gracilis* (Hutton), were given concentrated attention; the other two, *Rumina decollata* (Linnaeus) and *Gulella bicolor* (Gould), while not studied as intensively, were used for comparative purposes. Study of dispersal since introduction showed that these animals are still spreading. The means of dispersal appears to be through man's activities relating to the transport of plants. Studies of biological requirements and tolerances by the snails indicate that they are well adapted to the types of habitats found in this area. Life history and ecological data reveal that further spread is likely.

Introduction

Some members of the gastropod fauna of the United States are not native. They have been introduced in various ways to our shores from other land masses. Such biological introductions often pose problems in the control of the immigrant species, largely because we have no knowledge of rates, and in many cases the means, of the distribution or changes of ecological tolerances on the part of the introduced organisms.

The goal of this study was to take a segment of an introduced fauna and try to determine from whence it came, when and how it was introduced, and the rate and means of dispersal since being introduced. It was proposed also to study some of the ecological factors influencing the distribution of these introduced species, including a morphological study. Data gathered in this latter study will be published separately.

The reported introduced fauna of the Gulf Coast study area (Houston, Texas to Mobile, Alabama: Figure 1), at the inception of this study numbered ten species. From these, four were selected for the purpose of study. They were chosen on the bases of availability and ease of raising in the laboratory. Two of them, *Lamellaxis gracilis* (Hutton) and *Bradybaena similaris* (Ferussac), were selected for intensive study while the others, *Gulella bicolor* (Gould) and *Rumina decollata* (Linnaeus), were examined more casually. The reason for limiting the study to these four was simply a matter of keeping the work involved within reasonable limits.

Procedural Methods

Effecting the proposed study resulted in dividing it into several phases:

1. Points of Origin; When and How Introduced

   This phase of the project dealt largely with the correlation of past and present molluscan distributions with ship routes, cargoes, and currents. It involved literature searches and discussions with port authorities and shipping companies. It was necessary here to become acquainted and maintain contact with the members of the United States Department of Agriculture Quarantine Division.

2. Rate and Means of Dispersal

   This phase of the study consisted of making collections of these animals throughout the Gulf Coastal study area

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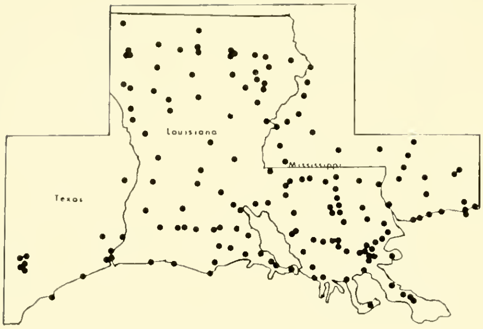

Figure 1. The study area. From Houston, Texas to Mobile, Alabama and northward to the level of the northern border of Louisiana. Dots indicate collection sites.

to determine present distributions (Figure 1) and the making of several follow-up collections to determine if further dispersal is occurring at present. Correlated with this phase of the study were visits to major United States collections to check further on distributions. Determining *means* of dispersal proved to be a difficult task. Involved in this was the questioning of individuals such as nurserymen, gardeners, and so forth and it was not always easy to obtain accurate answers. Sometimes these individuals became suspicious that we might somehow be accusing them of wrong-doing in having these animals and they would then become defensive and not give complete answers. Most, however, were very helpful. Careful surveys of all nurseries and greenhouses in New Orleans and Baton Rouge were made to determine what introduced species were there (Dundee and Watt, 1962; Hermann, Strickland and Dundee, 1965). Time limitations made it necessary to concentrate detailed studies of this phase at the Port of New Orleans.

3. Habits of Introduced Molluscs

It was also necessary to study in detail the habits of the molluscs both in field and laboratory. Laboratory colonies were begun in 1959 and from then through 1967, there were only brief periods when we were without colonies of these animals. Data on food habits, reproductive habits, longevity, variability, ecological tolerances, and life histories, were gathered from these laboratory colonies.

Colonies were easily maintained in the laboratory. Clear plastic containers of various sizes were used. Into each was put a layer of sand with a piece of paper toweling over part of it. The containers were kept damp with tap water in an air-conditioned room where the temperature ranged between 22–25°C and the relative humidity near 40 percent. The significant humidities in the containers were much higher but no special check of them was made in routine daily care. One side of the room, which had an eastern exposure, contained large glass windows, hence the animals were regularly exposed to daylight. Food consisted of head lettuce leaves. The containers were cleaned and the toweling replaced at least every other day.

Simultaneously, similar data were gathered from field stations for each of these species. In addition, marking of field individuals with nail polish gave some information on rates of movement.

Acknowledgments

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My husband, Dr. Harold A. Dundee, has accompanied me on many of the field trips and has helped make many of the collections. To him I owe sincere thanks.

Findings

1. *Points of Origin; When and How Introduced*

This discussion will be based entirely upon the Port of New Orleans. Of necessity, the discussion of introductions must be speculative since there is no record of the actual moment and method of introduction.

The first recorded use of the port was in 1699 with the first settlements in the area of present-day New Orleans (Sinclair, 1942).

Table 1. Point of origin of each species of mollusc and its distribution in the period 1699–1905.

SPECIES	ENDEMIC TO:	DISTRIBUTION DURING PERIOD
Bradybaena similaris (Ferrusac)	Southeast Asia	Brazil, W. Indies, Hawaii, Mauritius
Lamellaxis gracilis (Hutton)	Tropical Americas	Tropics of world; Mobile, 1885 (Binney)
Gulella bicolor (Gould)	India, southeast Asia	Tropics of world; W. Indies, Cuba, S. America
Rumina decollata (Linnaeus)	Mediterranean area: S. France, Italy, Sicily, Canary Islands	In Bermuda and Havana (Smith, 1912); in Philadelphia 1897 (Johnson, 1900)

Thus we know that these species must have been introduced after that time. The first record of each of them in the New Orleans area is as follows:

Bradybaena similaris (Ferussac) (Harry, 1948) 1939
Lamellaxis gracilis (Hutton) (Pilsbry, 1946) 1905
Gulella bicolor (Gould) (Dundee, 1961) 1958
Rumina decollata (Linnaeus) (Pilsbry, 1946) 1906

Gulella bicolor (Gould) was observed about 1940 by Dr. H. Harry (personal communication) but was not reported. Knowing when the port was first used and the first recorded date of the animals in the city sets the time of introduction of these species. If one now determines the point of origin of each of the species and the distribution at the turn of the 18th century as shown in Table 1, one then can compare those geographical positions with points of origins of cargoes inbound to New Orleans (Table 2)

Table 2. Brief history of the Port of New Orleans.

DATE	IMPORTS	ORIGIN OF IMPORTS
1699	Provisions	France
1710	Provisions, brandy, tobacco	Cuba, Santa Domingo, Martinique, W. Florida
1710	Furs	Ohio Valley
1718	FOUNDING OF NEW ORLEANS	
1720	Slaves	West Africa
1763–1776	Powder, lead, clothing	Great Britain
1803	Provisions, first coffee	France, Spain, Brazil
	LOUISIANA PURCHASE—MANY PEOPLE MOVING IN	
1806–1813	Various items pirated from Spanish ships and smuggled into the port	Spain
1812	FIRST REGULAR STEAMBOAT FROM NATCHEZ, MISSISSIPPI	
1812–1862	Wines, brandies, cutlery, tools, China, cotton goods, sugar, rum, coffee, fruits, mahogany, rosewood, silver, cochineal, pimento	France; Great Britain, Cuba and the islands
1862	BLOCKADE OF THE PORT. No imports except cotton, sugar, and rice.	
1862	QUARANTINE OF PORT AGAINST YELLOW FEVER	
1865	ALL CIVIL WAR RESTRICTIONS REMOVED. MANY NEW SHIPPING LINES ESTABLISHED	
1871	FIRST RAILROAD	
1874	Bananas	Colon, Ecuador, Honduras, Guatemala, Costa Rica
1899	Tropical fruits	United Fruit Company established
Late 1800's	Rubber, palm kernels, sisal, hardwoods	W. Coast Africa, Belgian Congo

TABLE 3. United States Department of Agriculture interceptions of molluscs during 1959 and 1960 in New Orleans (Morris, 1959, 1960).

GENUS	CARGO	POINT OF ORIGIN
Bulimulus corneus (Sowerby)	Bananas	Ecuador
Chilina cf. *fluminea* (Maton)	Plant	Brazil
Cochlicella barbara (Linnaeus)	General cargo	France, N. Africa
Helicella (4 spp.)	General cargo	France, Greece, N. Africa
Limax marginatus Müller	Cut flowers	Guatemala
Solaropsis monile (Broderip)	Bananas	Ecuador
Succinea sp.	General cargo	N. Africa
Theba pisana (Müller)	General cargo	N. Africa, Italy, France
Zonitoides arboreus (Say)	Orchid	Philippines

and arrive at a logical conclusion as to approximate time and means of introduction. These animals are assumed to have arrived by ship, since New Orleans was surrounded by a swampy wilderness divided by a network of waterways. Road and railroad travel were limited until much later (Civil War period). The first railroad travel was available in the 1870s. Even as late as the early 1800s overland travel by means other than railroad was practically non-existent thus negating the likelihood that snails were brought in from Mexico and/or Central America overland.

Table 2 summarizes the history of the Port of New Orleans in relation to this discussion.

Since 1865 many ships have included New Orleans on their regular itineraries. Some of those arriving from endemic areas for these snails carry cargoes which are likely ones for harboring such animals.

Actual interceptions of molluscs by the Quarantine Division, United States Department of Agriculture in New Orleans in several recent years point out the potential for molluscan introductions. For example, in relation to this present problem, in 1960 one of the interceptions at the Port of New Orleans was *Lamellaxis mauritianus* (Pfeiffer) on an orchid from Venezuela (Morris, 1960). Table 3 summarizes several such interceptions during the years 1959, 1960. Studies on other molluscs have also revealed that they too are arriving in this country on imported materials and it would seem that nursery stocks provide an ideal method of entry. Inspections will not reveal each single individual which might be hidden on the plant parts or the ova which might be in the soil around the roots of the plants.

It rapidly became obvious that these animals are arriving through man's activities rather than being passively carried on floating vegetation or the like. Also, it is obvious that most of the introductions are accidental even though there have been cases where individuals have brought snails from another country to use as food items here. Many of these "foreign" snails can be bought alive in the markets of our country as food items (Figure 2). The question then becomes: what is to prevent them from crawling out of the container and establishing a colony? It is my belief that that is exactly how species such as *Helix aspersa* Müller and others originally were established in the port area of New Orleans.

2. *Rate of Dispersal*

All four of the migrants with which this paper is concerned are widely distributed in the warm areas of the world at the present time. Within the United States both *Bradybaena similaris* and *Rumina decollata* seem to be pushing northward as evidenced by our collections. Figure 3 shows the present known distribution of *B. similaris* while

Figure 2. Snails for sale. *Helix aspersa* at 35¢, and *Otala lactea* at 75¢.

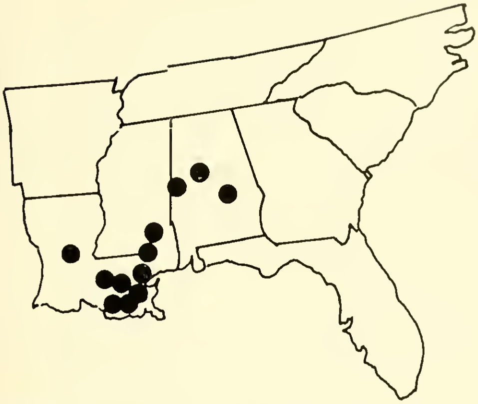


Figure 3. Present distribution of *Bradybaena similaris* in the United States.

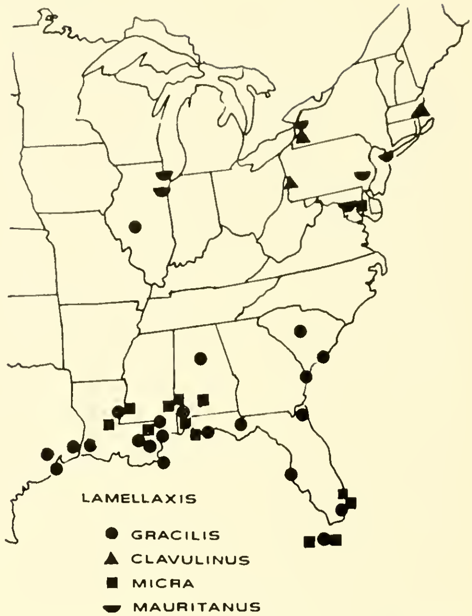


Figure 5. Present distribution of *Lamellaxis* in the United States.

Figure 6 gives that of *R. decollata*. *Gulella bicolor* (Figure 4) by contrast, still seems to be confined to the area where it was introduced—at least here in the Gulf Coast area. *Lamellaxis* (Figure 5), at first glance, would seem to be widely distributed in the eastern half of the United States; however, most of the northern records are greenhouse localities.

Within the designated study area *Bradybaena* and *Lamellaxis* are both slowly widening their distribution as shown by our repeated collections of the area (Figures 7 and 8). When this study began in 1959, *B. similaris* seemed to be limited to the New Orleans-to-Baton Rouge and Mobile areas. By 1961 we found it on the Mississippi Gulf Coast, spreading northeastward into southwestern Mississippi and northward to Alexandria, Louisiana. By 1962 it had been introduced to Hammond, Louisiana on the north and to Houma and Jeanerette on the south, and towards the mouth of the Mississippi River on the southeast. In 1964 it had moved into Thibodaux, Louisiana on the southeast. Complete further checks have not

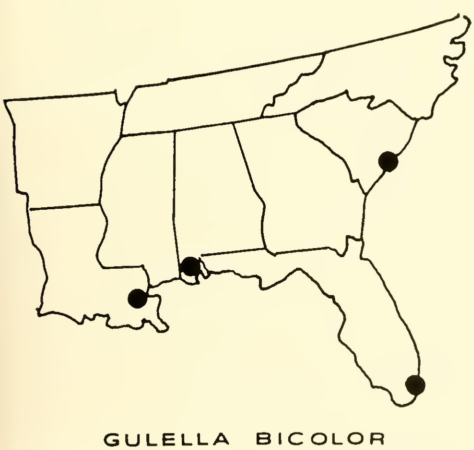


Figure 4. Present distribution of *Gulella bicolor* in the United States.

Figure 6. Present distribution of *Rumina decollata* in the United States.

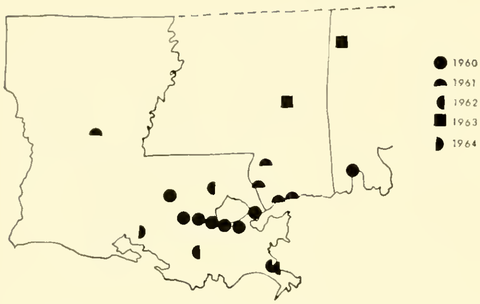


Figure 7. Study area distribution of *Bradybaena similaris* showing dispersal over a 5-year period.

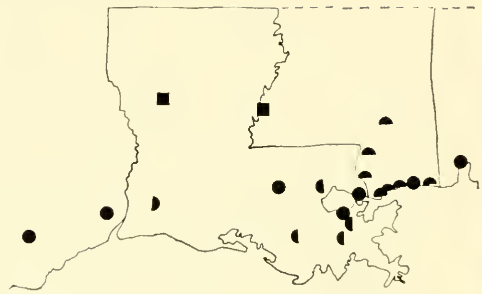


Figure 8. Study area distribution of *Lamellaxis gracilis* showing dispersal over a 5-year period. Explanation as for Figure 7.

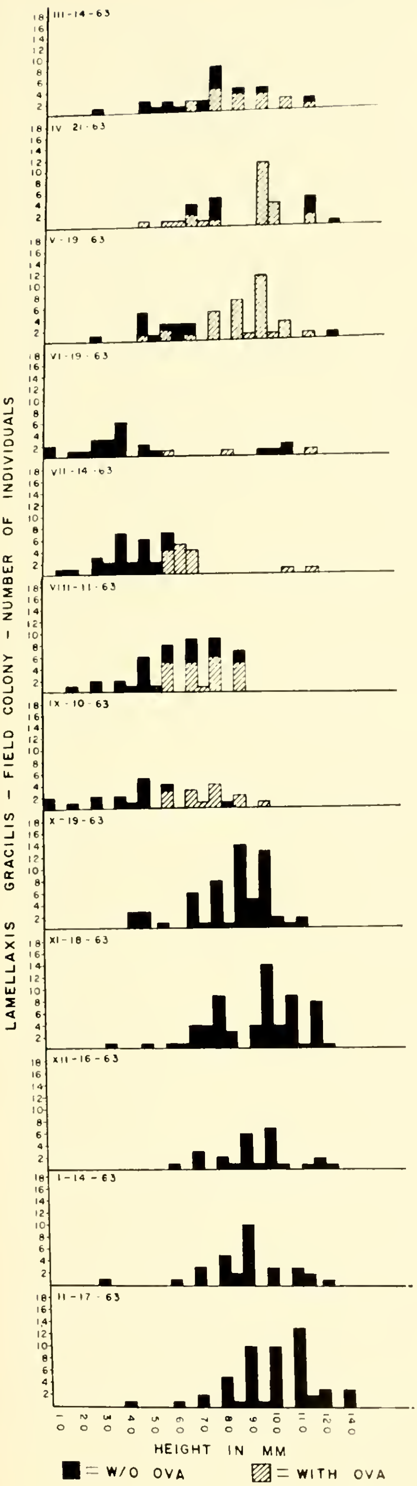
been made since; however, plans are to survey again soon.

Lamellaxis gracilis distribution has also been carefully observed over a five year period (Figure 8). By 1959 and 1960, *L. gracilis* seemed to be limited to New Orleans, Baton Rouge, Biloxi, Houston, and Beaumont. In 1961 we found it spreading from the Biloxi locality into neighboring Gulfport, Moss Point, and Pass Christian in Mississippi. At the same time it was found in Picayune and Hattiesburg, Mississippi, probably originating from New Orleans. The year 1962 found it established to the south of New Orleans in four localities and in one more to the north. By 1963 it had managed to extend about 200 miles further north into Natchez, Mississippi and Natchitoches, Louisiana. In 1964 it was still pushing westward from New Orleans along the lower half of the state. More recent findings show it in Pensacola, Florida on the east and Lake Charles, Louisiana and Galveston, Texas on the west.

3. *Means of Dispersal*

There are two ways in which land molluscs are distributed: actively by their own movement, and passively by being transported by other organisms or the environment. Doubtlessly most of the distribution of molluscs which we see today can be accounted for by the activity of the molluscs themselves over millions of years. However, with the numerous forms of transportation of modern man, many molluscs such as those involved in this work find themselves in areas far from their native habitats. Such introductions often pose severe problems in the control of introduced species. With the absence of natural population checks (predators, diseases, and the like), the immigrant is free to "run wild" biologically until a balance is again established in the ecosystem.

The questions often asked are these. How are these organisms being transported? Why are we unable to stop introductions? Answers, of course, vary with the organisms in question. It has become increasingly obvious during this study that the four mollusc species herein considered are being transported through the movements of plant materials. This is being further borne out by another study on introduced slugs now in progress. It was also found to be true in New York state (Karlin and Naegele, 1960). We first suspected this in noticing that these molluscs were always found in association with man's activities—in cultivated areas, near import centers, and so forth. Never have we found them away from man's activity areas even though habitats elsewhere appear to be satisfactory. If then we were correct that these snails were moving about as passengers on vegetation, where would be the most likely spots to find them? In gardens, public and private. In cemeteries. In nurseries and greenhouses. Private gardens were ruled out immediately as a study source because of the problems associated with entering such property. Checking public gardens and cemeteries resulted in finding many new localities for the snails. If we could find the same snails in greenhouses, we could reasonably assume that they got there with the plants (as opposed to riding on bird feet, drifting on floating materials and so on). Such examinations did reveal the snails in many cases.



It also revealed other molluscs not previously reported from the area.

Our next question was that of why it is that these snails are not discovered and killed. Many discussions with owners and operators of nurseries and greenhouses made us aware that there is a constant battle between man and snail. All owners and operators use some type of molluscacide and are constantly trying to prevent plant damage from these animals. It also became obvious that, despite the fact that they wish to rid themselves of such pests, they are not thorough enough. We were able to find many molluscs under the tables where nothing economically important was being grown and where they are not using the chemicals. It was difficult to find snails on the about-to-be-sold plants, however. How then, were these snails being distributed? Our studies have revealed that they spread largely through transport of snail ova which have been deposited in the soil around the plants.

4. *Future Dispersal*

If, in the five years of studies, these snails have spread considerably through much of the study area, what then of the future? How far can they go? Baker (1958: 143) summarizes it well: "In time, dispersal means that each species would occur everywhere unless it be stopped by barriers . . ." Basically there are two types of barriers which prevent an organism from spreading everywhere: physical (geographical) and ecological. Since we have already established in this particular case that physical barriers are easily spanned with the aid of man, the immediate question becomes: Are there any ecological barriers which will stop the spread of these animals? Can they exist wherever man takes them? To answer these questions it was first necessary to determine something of the biology of the animals.

A. Life History: *Lamellaxis gracilis.*

In Figure 9 one can see that, in the New Orleans area, the reproductive season is initiated in mid-March at which time ova may be seen through the shell. This situation prevails to late May at which time the ova are deposited. Young of various ages are present

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Figure 9. Field colony, *Lamellaxis gracilis.*

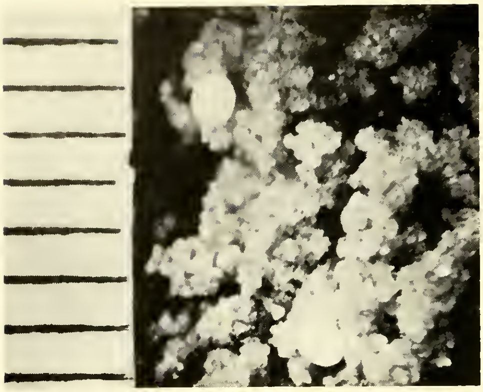

Figure 10. Ova in soil, *Lamellaxis gracilis.*

from early June through the summer (Figure 9). By about October they have grown to approximately 4–5 mm in height. Early October is another period of ova deposition followed by some young overwintering in the 3 mm stage.

Laboratory colonies maintained for over a year tend to behave in a somewhat different manner in that March to June is a period of ova production and is followed by an interval of no ova nor young and then by another peak of production of ova in late summer followed by constant low ova production for the rest of the year. This is most likely the result of the colony being in a more or less constant temperature-humidity atmosphere (temperatures from 22–25°C and relative humidities constantly in the 40 percent range).

The maximum number of ova ever seen in one snail was 10; the average number per gravid snail was 5 seen at one time. However, based on laboratory experiments, the average number of ova deposited per snail per breeding season is 79. In lab colonies 55 percent of the ova hatched. These ova (Figure 10) of *Lamellaxis gracilis* are almost spherical, white, have "hard shells," and are deposited singly in the surface of the soil, but not covered by soil. There appears to be no effort at "nest building"; the ova are simply placed individually in the soil; usually several ova will be found together as a clutch.

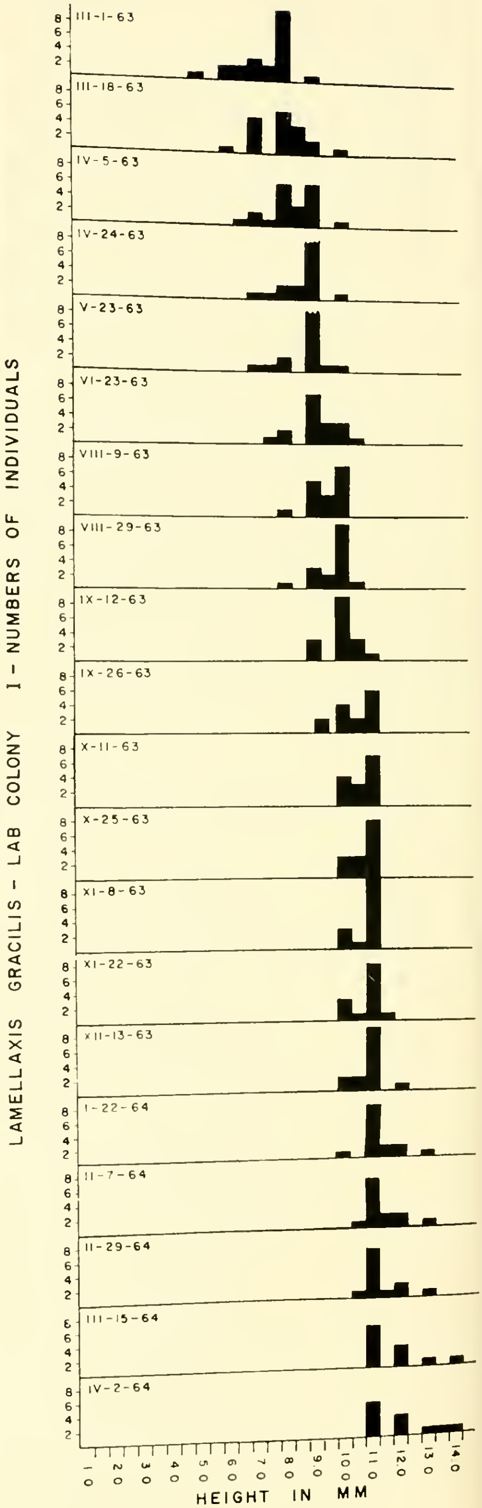

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Figure 11. Laboratory, *Lamellaxis gracilis.* Colony begun with 21 individuals and all ova and/or young removed from it regularly.

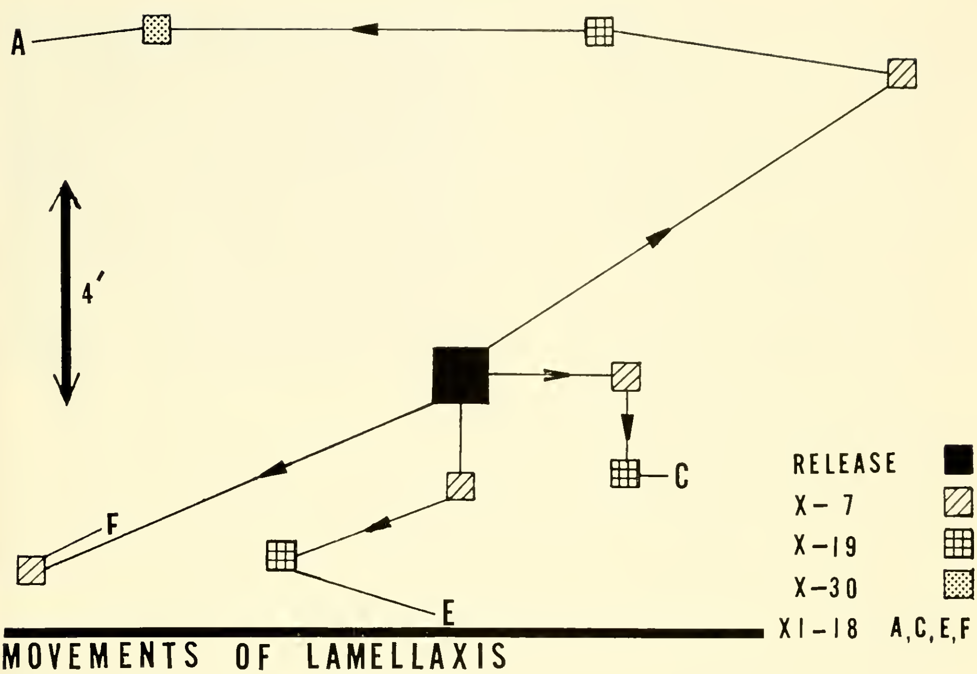

Figure 12. Movements of marked individuals, *Lamellaxis gracilis*.

These ova are small enough (0.5–0.9 mm in diameter) to be easily overlooked by individuals transporting plant materials.

Incubation time in nature is approximately 10 days. However, on 2 occasions in the laboratory incubation was completed in 7 days. *Lamellaxis micra*, by contrast, had an incubation time of 15 days in the laboratory. Its ova are similar but smaller.

Lamellaxis gracilis growth rate is approximately 1 mm/month. Those young which hatch in mid-June are in the 5 mm class by late October to early November. This rapid growth rate then seems to slow with a continued constant, gradual growth until death. Figure 11 shows a laboratory colony which was begun with 21 adults of various sizes. Constant removal of all ova and/or young immediately upon discovery kept this colony intact for over a year. During that time 10 individuals died and the remaining 11 continued growth as shown on the histogram.

Adult *Lamellaxis gracilis* (as evidenced by the initiation of reproductive cycles) range in size from 4–14 mm in height and have whorl numbers between 5.5–10. Individuals exceeding 12 mm in height are rare. *Lamellaxis micra* adults range in size between 4.5 and 7.2 mm in height.

The life span of an individual *L. gracilis* appears to be approximately one year with some apparently surviving through most of the second year. These observations need substantiation since it was impossible to obtain recapture of marked individuals after a lengthy period.

B. Habitat and Habits: *Lamellaxis gracilis*.

These snails are found in areas of man's activities—in particular, in areas where man has been active and then has allowed the area to stand idle for a period. A prerequisite is cover of some sort—boards, bricks, leaves, or other objects which can provide shelter. The snails are always under these objects during periods of dryness. After rains they are easily available crawling about on the surface. At no time are they more than 1.3 cm or so above ground. As cooler weather arrives, *Lamellaxis gracilis* descends into the soil. During one period of −5° C, the animals were found 7.6 cm down in the soil. During a January period when the soil temperature stayed close to 8° C, the snails, despite heavy

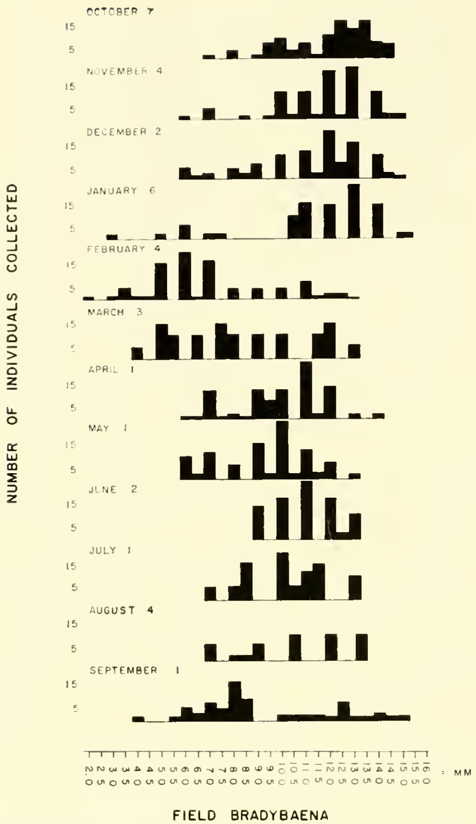

Figure 13. Field colony, *Bradybaena similaris.*

rains, remained from 2.5–7.6 cm below the surface. Even at these depths individuals are grouped together; for example, in a 4.5 × 10 cm area 27 individuals were found 1.3 cm down in the soil. Under the circumstances described in this paragraph the individuals are lying dormant (hibernation?).

Feeding experiments were run in the laboratory. Individuals were offered plant parts of each of the species of plants found in the habitat. Results indicated that they will feed readily on leaves of *Laportea canadense*, *Panicum* sp., and *Crepis* sp. Other plants from the habitat were not acceptable. Karlin's (1956) assumption was that since *Lamellaxis* and two other species were never found more than an inch above soil surface, they were feeding "only on plant matter in the mulch. . ." The observation of the closeness to the soil is in accordance with our findings; however, it seems likely that these snails do use the leaf matter described above in their normal living but probably rely on those leaves which drop off or are low down. In the laboratory any of the species of *Lamellaxis* seem to survive for long periods on nothing more than lettuce leaves.

Repeated marking experiments all met with failure. One is shown in Figure 12. Here 6 snails were marked differentially with nail polish and released as indicated on October 1. One week later we were unable to find 2 of them (B, D). By a month and a half later (November 18) the other 4 were in the positions shown. With the advent of colder weather shortly thereafter, we were unable to get further recaptures of these. It is believed, however, that enough other recaptures were made—albeit not after lengthy periods—to state tentatively that *L. gracilis* seems to remain within 10 ft or less of its point of release; whether this is true during the entire life is unknown.

C. Life History: *Bradybaena similaris.*

In the New Orleans area *B. similaris* deposits its ova in January and by early February many young snails are present (Figure 13). The older members of the colony appear to die off soon after the winter season as shown in Figure 13. Through spring and summer the young are growing and a middle-aged group is present. Again in late July there is a brief period of egg deposition so that by mid-August to early September there are again a few young present in the population. In this area these young reach a subadult stage before cooler weather occurs. Just as with *Lamellaxis* the laboratory colonies continue producing ova and young throughout the year in small numbers.

Bradybaena ova (Figure 14) by contrast with those of *Lamellaxis*, are clear and gelatinous when first deposited. They are frequently stuck together (probably accidentally) and always laid as a cluster. The adult usually makes a concavity in which the ova are placed; they are not covered with soil. Each ovum is spherical and measures approximately 2 mm in diameter. In laboratory colonies the average number of ova per snail per breeding season was 38.

Incubation time in the lab was 11 days and in the field it ranged from 10–15 days.

The smallest *Bradybaena similaris* at hatching measure 1 mm in height, 1.75 mm in

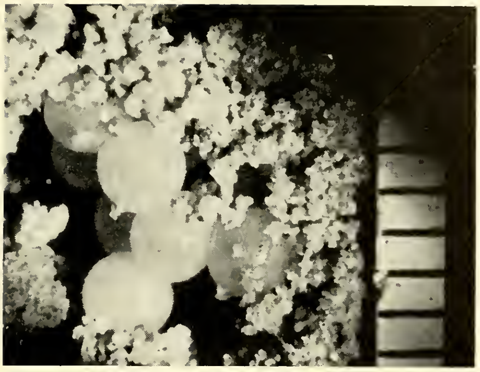

Figure 14. Ova in soil, *Bradybaena similaris.*

diameter, and have 1.75 whorls. Six months later most of these had reached 3.25 mm in height, 5.25 mm in diameter, had 3.5 whorls, were sexually mature and reproducing. All newly hatched young were without color bands which are characteristic of 91.1% of the population here. The bands began to show by the time the snail had reached 2 mm diameter and 1.5 mm in height. Of the 1566 *Bradybaena similaris* checked, 3.9% had no bands at all in the adult and 6% showed only very faint banding. The remainder have a characteristic light yellowish shell with a brown band. This stands in contrast to the same species in Japan (Komai and Emura, 1955) where there are 4 distinct genetic types: the 2 mentioned above plus brown forms with and without bands. Why these introduced forms lack the brown phases is not known at this time.

Adult *Bradybaena similaris* in this area also differ much in size from those reported by Komai and Emura (1955). They report them to be "18 mm in diameter and 12 mm in height at most of its size." The tallest *Bradybaena* we have recorded in many measurements is 11 mm and the one of greatest diameter was 15.5 mm. These are rare. This smaller size, plus the absence of the two color phases, suggests that some factor in the habitat, present in Japan but missing here, is exerting a considerable influence on these snails. We plan to do some follow-up work on this phase.

D. Habitat and Habits: *Bradybaena similaris.*

It has been suggested that this species is closely associated with sugar cane (Pilsbry, Hyatt and Cook, 1912). While we have found it in close proximity to sugar cane fields here, it is not necessarily associated with them. Many of the colonies are found living in various types of tall grasses in vacant lots, along railroad tracks, and so forth. Others, however, have become established in gardens. Sugar cane was introduced from Santo Domingo to this area between 1771 and 1775 in Jesuit Bend, a community 15 miles south of New Orleans. Since *B. similaris* was known from the West Indies at that time (Table 1), it is quite probable that it was introduced here with the sugar cane.

In feeding experiments we were unable to get *B. similaris* to eat anything but monocots and, in particular, the grass, *Panicum brachyanthus* and a lily, *Lilium canadense.* All of the plants from their normal habitats were offered.

These snails are much less secretive than *Lamellaxis.* They are just as likely to be found out in the open (either active or dormant) as under objects. Occasionally they are seen a few feet high on vegetation or on the sides of vertical objects. Usually they are not found over 15 cm above the ground on the plants. Most often they are seen at night crawling about on grass which previously has fallen down and dried. Often hundreds of them can be seen in this type of situation.

Marking experiments in 3 different localities revealed that individuals move little at any time. The maximum distance traveled away from one point of release by any one individual was just under 3 m in a 2 month period. This, of course, is not taking into consideration how much movement occurred within the 3 m radius during that period by this individual. Marking was done with nail polish; this seems to lead to an early death in the snails.

E. Ecological Tolerances.

(1) Temperature: An experimental device similar to, and patterned after, that used by Dainton (1954) was used to determine temperature tolerances of these snails. This device consists of a trough in which a temperature gradient can be maintained. Different ranges can be had by using different water temperatures at the inputs. Snails are introduced throughout the length of the

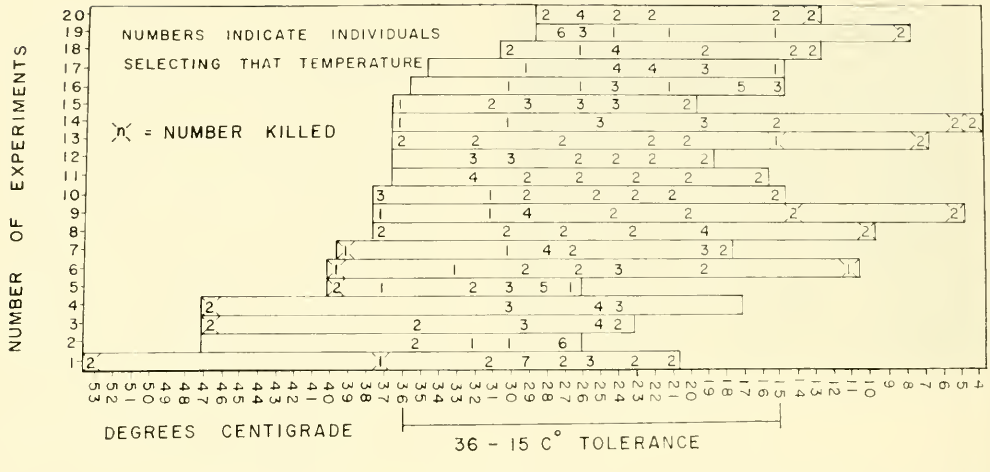

Figure 15. Temperature selections, *Lamellaxis gracilis.*

trough and allowed a period in which to select the temperature most suitable for them. The results are recorded after 30 minutes. After repeated trials for each species, during which the temperature ranges were varied (Figure 15) so as to include all reasonably possible temperatures, it was found that the range of tolerance for *Lamellaxis gracilis* is 15–37°C while that for *Bradybaena similaris* is slightly greater: 12–38°C. Interpretations of these data must be made in conjunction with other factors. If one were to use only these temperature data, one would be forced to conclude that these snails can live nowhere in the United States except Florida; as has already been shown (Figures 3 and 5) the snails *do* live elsewhere. If one plots upon the present distribution picture the average minimum temperature for January, one finds that these snails, which, according to our experimental data can tolerate no less than 12°C, are living in areas where the average January minimum is 6°C. Here again, it is of interest to note that Komai and Emura (1955) found that –7°C for an hour or 2 killed nearly all adults; perhaps these snails are able to tolerate much lower temperatures in their native homeland. When one considers that these snails protect themselves from the cold as described above, then it is not too surprising to find them living in colder areas than the laboratory experiments indicate are possible. During the period in which we were recording soil temperatures, the lowest reading was a December one of –2°C at a 3 inch soil depth. The snails at this level were aggregated and they had their epiphragms in position, but many of them were dead. This was true for both *Lamellaxis* and *Bradybaena.*

The upper limits of tolerance of these snails are such that they should be able to tolerate temperatures anywhere in the United States since the highest average July temperature falls easily within their range of tolerance. The maximum could be withstood through the use of shelter.

(2) Desiccation: Experiments consisted of merely placing the snails in dry bowls (one per bowl) at room temperature (23–29°C) and humidity (40%) and examining them at intervals to see if they were still alive. It was found that dead ones could be easily identified by shining a narrow beam from a spot lamp through the shell and looking to see if the animal was intact. Surprising differences in tolerances to desiccation were revealed in our experiments. In several hundred trials, the time which *Bradybaena* was able to remain alive ranged from 30–217 days with an average time of death being 122 days, or approximately 4 months. In contrast, the maximum time which *Lamellaxis* was able to remain alive was 121 hours, or approximately 5 days. To evaluate these data one must keep in mind that the 40% relative

TABLE 4. Molluscan associates of the introduced species.

SPECIES	STATION 1	STATION 2	STATION 3	STATION 4
Bradybaena similaris		x	x	x
Guella bicolor		x	x	x
Rumina decollata		x		
Lamellaxis gracilis	x	x	x	x
Helicina orbiculata	x	x		x
Polygyra texasiana		x	x	x
Retinella indentata	x	x		
Hawaiia miniscula		x	x	x
Pupoides marginatus			x	x
Polygyra septemvolva		x		x
Praticolella griseola		x		x
Mesodon perigraptus		x		
Strobilops texasiana		x		
Deroceras laeve		x		

humidity found in the lab during these experiments is low in contrast to that in the environment in this Gulf Coast area and the microenvironment of these snails. Thus, the animals should be able to withstand periods of drought longer in nature than they can in the laboratory. The fact that 3 of the 4 species treated here can survive adverse conditions for long periods of time through estivation is doubtlessly of high survival value. It is of interest that *Lamellaxis gracilis*, despite the fact that it is widely distributed over the world now, does not have this ability. Obviously, a combination of other factors has overcome this one factor which would appear to be a distinct handicap to an introduced species.

Similar experiments with *Rumina decollata* and *Gulella bicolor* revealed that under the circumstances described some individuals of both species are able to survive at least 7 months. One *Gulella* was still alive at the end of 214 days. Rascop (1960) found that relative humidity below 15% and a temperature above 85°F (29°C) caused *Rumina* to estivate. Further, Rascop found that snails estivating at room temperature for 8 months lost an average of 55.56% of their body weight.

(3) Soil pH: Throughout our studies we found pH ranges at the various study stations of 6.4–7.1 for both *Lamellaxis gracilis* and *Bradybaena similaris*. Karlin (1956) concluded that pH could not be considered a critical factor in greenhouses since the mean pH where *L. gracilis* and others lived was 5.9. He pointed out that while it is well-known that snails are scarce on acid soils, other factors such as the addition of gypsum and the presence of other minerals compensated for the low pH.

(4) Moisture: None of these 4 snails is associated with visible moisture in the form of swampy or marshy conditions. All live in well-drained areas. Among the 4, they could be ranked on the basis of 5 years of observation both in the field and in the lab, according to their moisture tolerances (from wettest to driest): *Lamellaxis, Bradybaena, Gulella, Rumina*. Observations lead us to believe that moisture, in the form of relative humidity, is of far more direct importance to the land mollusc than standing or falling water. Relative humidities of 85% and up are not uncommon in this area even in the day. A dry day would have a humidity in the 40% range. From this standpoint, then, conditions in this Gulf Coast area seem to be ideal for these snails.

(5) Relative Population Densities: *L. gracilis* and *B. similaris* are, in the habitats described, extremely abundant. One can easily collect hundreds of specimens within half an hour. The habitats, however, are frequently widely separated so that this heavy abundance actually forms a spotty type of distribution. Some populations were large enough that we were able to remove 50 or more individuals every two weeks without any noticeable change in the numbers present. In contrast, *Gulella bicolor* and *Rumina decollata* are abundant nowhere in this area. The distribution is not only spotty but within a given habitat one would be likely to find no more than 10 individuals in the half-hour period.

(6) Associates: Table 4 reveals that there are no associates which are always found with a given introduced species. The most common joint occurrence is that of the two introduced species, *B. similaris* and *L. gracilis*. Apparently no significance may be attached to the presence of any of the molluscan associates of these introduced snails.

Other associates such as ants (Formicidae) do seem to be extremely significant to the well-being of these snails, however. Ants are very common in this entire study area. We observed repeatedly that whenever ants invaded a habitat such as the area beneath a large boulder it would not be long before the snails would all be dead. We do not know the reason. We did run several simple experiments of enclosing the snails and the ants in gallon jars together and again the results were the same—the snails soon died (controls did not). This, perhaps, might be investigated further with a view towards biological control if such is ever needed.

5. *Economic Considerations*

Fortunately, at the present time, none of the introduced molluscs in the Gulf Coast area have become severe pests under natural conditions. Even though they are a problem in greenhouses and nurseries, this is a different matter. *B. similaris* is an annoyance in a few flower gardens, but no more so than endemic species such as *Mesodon thyroidus*. In any event, no serious damages to crops nor any nuisance from numbers of snails such as was the case with *Achatina fulica* (Mead, 1961) has occurred in this area.

Discussion

We can, after examining the foregoing data, return to the question posed in the beginning of section 4 of this paper: Can these snails (in particular, *B. similaris* and *L. gracilis*) exist wherever man takes them? The general answer, of course, is no. There are many areas, however, where they do not now exist but where they could easily survive. There is no cause to think that they will not spread further northward, eastward, and westward. They should be able to live throughout the lower half of the United States from southern Pennsylvania, the lower half of Ohio, Indiana, and Illinois, southern Missouri and Kansas, southeastern Colorado and along the entire west coast. The average winter minimum temperatures of this area are no less than −2°C (28.4°F). Since we are considering only average temperatures the snails in the northernmost part of this area would have to remain confined to sheltered type habitats and, therefore, should be much more spotty in distribution than elsewhere.

Drier parts of this range, namely in west Texas, New Mexico, Arizona, and southern California should act as barriers to the general spread in that direction. However, again, cultivated areas should provide habitats which have adequate moisture to maintain high enough relative humidites in the microhabitats, especially for small snails such as *Lamellaxis*.

Through follow-ups on this study we will know definitely whether, by a brief survey of such factors as have been dealt with in this paper, one would be able to predict the future dispersal of an introduced land mollusc. It seems now that such will be the case.

It appears that most of the introduced snails which do become established do not become agricultural pests. Of the 10 species which are known to have been introduced in the New Orleans area at the inception of this study, 4 have failed to become established, 4, as shown in this paper, are still spreading, and 2 other species are also established and spreading. None of these has yet become a real pest to agriculture or horticulture.

It appears also that preventing the entrance of these foreign invaders into this country is impossible. The United States Department of Agriculture is doing an admirable job of keeping down the numbers entering but even they are not preventing the entrance of many. As long as we import materials we will accidentally import snails. One of the best sources of foreign land molluscs in this country is the nursery. It is ideal for their reception, maintenance, and distribution.

The key to whether or not one of these immigrants will become a severe pest seems to lie in its food habits and its reproductive potential, assuming of course that it is able to find a suitable habitat. It appears that if an investigation of a species' reproductive and food habits were undertaken as soon as an introduced land mollusc is discovered, it should be easily possible to predict whether the immigrant would become a severe agricultural pest; if so, immediate control measures could be instituted.

Perhaps such a program could be undertaken by the United States Department of Agriculture through a program which would encourage malacologists and other interested biologists to be on the alert for new introductions in their areas. If and when such is found the ideal situation would be for the United States Department of Agriculture to request that a study be made by a malacologist, supported by U.S.D.A., to determine if the immigrant is likely to become a pest. If chances are good, then control action could be initiated promptly; if not, there would no longer be a need for constant vigil at our ports for that species.

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