Some Insects of the Between Tides Zone.

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All insects, except a few species which live entirely in the water and have functional gills, are air breathing animals, breathing by means of tracheæ. Thus we may desire to know how air breathing insects living in a zone which is submerged twice a day, prevent themselves from being drowned; or, if breathing by means of gills, they protect themselves from superoxygenation during the low tide. We may further be interested in any adaptations, or unique instincts, which make the inhabitants of such a locality especially adapted to their environment.

The following observations on the habits of the insects of the between tides zone, were made in the region directly north of Jones' bath house at the head of Cold Spring Harbor Bay; which is included in the lines drawn from 600 E., 200 S., to 200 N., 400 E; and 200 N., 800 E., on map of Inner Harbor made by Johnson and York. Many observations were made on the extreme outer limit of the *Spartina cynosuroides* 275 N., 400 E. The slope of the shore to the west of the boat landing from the outer limit of the Spartina to within two feet of the inner limits of the Spartina is about 6%. From the latter point to the inner limit of the Spartina the slope is more abrupt. The Spartina is here replaced by a short (about six inches high), densely matted grass, *Juncus Geravdi*. This covers the entire region around the bath house with the exception of a few pebble-covered areas on which there is a sparse growth of *Spergularia Marina*. (Map 2.)

The highest tides of the summer, July 8, 9.2 feet; August 3, 8.8 feet; submerged the region as far as the bath house. From July 11 to July 29 the Spartina area was never entirely submerged, due to the low tides and the absence of any strong easterly winds. The observations extended from July 1, to August 5, 1913.

Megamelus Marginatus.

This yellowish brown, 2.5 cm. long, leaf-hopper is a common inhabitant of the salt marshes from Connecticut to Florida (Van Duzee). This insect I found only in the Spartina area, never more than a few feet from the inner limit. Due to the alertness of this leaf-hopper on sunny days and its inconspicuousness, many hours of observation failed to reveal its whereabouts during high tide, until one rainy morning, while watching their actions from a boat, I found them resting head downwards on the inner part of the shallow "U's" formed by the grass blades. They remained in this position as they were slowly covered by the incoming tide. Their position on the blade is especially advantageous as it encloses large bubbles of air under their wings which serve the double purpose of supplying them with air and of making them inconspicuous by giving them a silvery appearance which makes them resemble closely the stem of the Spartina on which they rest, which also has a silvery appearance due to bubbles of air on its surface. On a cloudy day they cling so tenaciously to the blades of the Spartina that the blades may be cut off and placed in a jar of water. On July 18, 9 a. m., I put eight of them under sea water by this method. I kept them submerged for twenty-seven hours. On lowering the water in the jar they were still able to fly. I kept them submerged for two days on several occasions, with apparently no ill effect.

Besides this reaction to the tides, which prevents them from being washed away, and their inconspicuousness, which makes them invisible to their natural enemies, the inhabitants of the sea, they have a spur on the third pair of legs which is peculiarly modified to secure their survival in a region at times covered with water. To secure a larger contact area with water to allow them to remain at rest on its surface as well as to hop upon it, this spur has been developed until it is as long as the proximal tarsal segment. The prominent hoods at the distal end of the tibia and also on each tarsal segment, are other modifications for the same purpose. They never walk on the surface of the water, but can hop on it with great ease. The two hooks on the terminal segment of the leg enable it to secure a firm hold on the Spartina blade at the time of submergence.

This leaf-hopper was never found further inward than the inner limit of the Spartina area. It can be readily distinguished from the leaf-hoppers inhabiting the higher regions of the salt marsh by the prominent

hoods on its legs, by the greatly developed spur, and by the great length of the proximal tarsal segment in comparison to the tibia. In the other species the tibia is at least four times the length of the proximal tarsal segment, while in this species it is only twice as long.

See Plate 1, figures 1, 2, and 3. 1, Megamelus; 2, Leaf-hopper from the Juncus area; 3, Leaf-hopper from the area never covered by ordinary tides. The species whose hind leg is figured in 2 retreated before the tide, but on no occasion during the summer was the region it inhabited completely submerged. These figures show a peculiar development of structures of advantage in each particular environment. No. 3 has no hoods, No. 2 has them somewhat developed, in No. 1 we find the greatest development. If, as I have suggested, these hoods have been developed to aid in hopping on the surface of water, No. 3 would have no use for them and they would necessarily be useless structures.

The chief enemy of the Megamelus marginatus, is the only other permanent resident of the Spartina area, a small spider, Grammonata trivittata. Its principal source of food is this leaf-hopper.

The hoods on its feet, the greatly developed proximal tarsal segment, and the spur, are the peculiar modifications which determined that this leaf-hopper should inhabit this particular region. But why it is only found in the Spartina region, is not as easily answered. It may have been the severer competition in the other regions of the marsh, or perhaps the Spartina grass is its favorite food, the one on which it is especially adapted to live; or, again, the habits necessary for its continued existence in the tidal zone may make it the easy prey of its natural enemies living in the other areas.

I could not compare the resistivity of this leaf-hopper to drowning with that of those farther back on the marsh, because I could not get any of them to remain under water without placing them in vials covered with cheesecloth. Two to four hours submergence usually killed them. Even the leaf-hopper of the Spartina could only survive for several hours when submerged in this manner. This may suggest that the leaf-hopper may secure its air supply from the Spartina by piercing the blade to the air channels. I have no experimental evidence to prove this.

Grammonata Trivittata.

This spider inhabits the salt marshes from Long Island to Maine (Emerton). The females are about 3.5 mm. long. Their color is a dark

reddish brown. These spiders are very abundant in the Spartina region. A short search will reveal a number of them running up and down the Spartina blades or resting head downward on them.

As the tide comes in, they retreat up the Spartina grass. When the tide has once chased them out on the isolated blades of Spartnia (6 to 8 inches from the tip), they retreat to within about two inches of the tip where they remain head downward until the water almost touches them. Then they begin to run wildly up and down the blade, from tip to water, from water to tip, as if they were very much afraid of the water. After doing this a number of times they will calmly walk down the blade under the surface of the water until they come to the pit formed by the union of the stem and the blade. Here they remain until the tide retreats. The pit furnishes them protection from aquatic enemies and supplies them with air, for there is always a considerable amount of air left in the pit. That this reaction is due to an effort to secure protection and air, was shown in several experiments. When they were placed on blades of grass weighted to the bottom of the jar which was slowly filled with water, they went down the blades and attempted to crawl under objects at the bottom of the jar. However, to get under some object did not satisfy them, they kept on moving until they came to a bubble of air. Their actions were especially interesting when safety pins were used to weight down the blades. They would walk entirely around the wire part of the pin until they came to the sheath where there was a quantity of air. Into this they crawled. They always cling tightly to the wire, never attempting to leave it. It is however not essential for them to find a bubble of air. I kept a number of them submerged for three days without any noticeable bubbles being present. When they go below the surface, they always entangle numerous small air bubbles in their short, dense hairs, which are curved backward seemingly for this special purpose. I performed many experiments to compare the resistance of this spider to drowning with that of other species by submerging them in water. In my experiments I used practically all species found farther back on the marsh; Tetragnatha, Lycosa, Epeira, Attidæ, Themsidæ. This was the only species, with the exception of the young Clubonia, which could be submerged in water when resting on a grass blade; i. e., the other species did not hold fast, but tried to escape on the surface of the water. The most striking difference between these spiders when they were placed in small vials whose mouths were covered with cheesecloth and then submerged in a large glass jar of sea

water, was the difference in the size of the air bubbles clinging to the different species. No prominent bubbles were noticed on the Grammonata, while the other species entangled large bubbles in their comparatively long hair which made them almost entirely helpless. Regardless of the disparity in the size of the air bubbles, the Grammonata could withstand a much longer submergence without causing death. The limit for the hardiest of the other species was twelve hours. When placed in vials in a similar manner and the air bubbles withdrawn by means of a pipette, the Lycosa communis, the hardiest of all other species, did not survive more than three hours submergence, while the Grammonata could remain for twenty-four hours in the same jar with no ill effect. This would seem to indicate that this species must have some special modification, as perhaps greatly developed air sacs, "lungs", to enable them to resist drowning so successfully. None of the other marsh spiders, with the exception of the crab spiders, are as free from long flimsy hair, which greatly impedes an animal's movements in water, as the Grammonata. Even the Lycosa Communis, whose habitat borders on the between tides zone, has comparatively few long hairs, and these are comparatively stiff.

The food of this spider, Grammonata, consists chiefly of leaf-hoppers, but it also captures the small flies which frequent its habitat during the low tide. It is always attached to the tip of the grass blade by a thread which enables it to run on the surface of the water after food without being washed away.

This spider, as the leaf-hopper, Megamelus marginatus, is found only in the Spartina area. Its great resistance to drowning, its unique covering of hair, and the instinct which causes it to seek safety by clinging to the object on which it rests, instead of seeking safety in flight as other species, all have determined that it could survive in the Spartina area; but as to the reason it is only found there, I cannot explain.

Clubonia Sp.

This was an immature spider, light tan in color, largest specimen 7 mm. The first specimen was found August 1 after a period of very low tides, at which time I found them in practically the entire Spartina area (rare in other areas). The frequent use of a sweep net as well as searching on the ground, failed to reveal an adult spider of this species. The probable solution is that they had hatched, during the low tide period, from eggs laid the previous year. I was very unfortunate in that they

first appeared during my last week at the laboratory, so that my observations did not extend over a period long enough to determine if they were permanent inhabitants of the area, or whether they had just migrated there as several species of Tetragnatha had. This last supposition I consider very improbable, as I found no Clubonias in any other part of the marsh.

Their reactions to the tides were such as would prevent them from drowning or being washed away, but they afforded little protection from their aquatic enemies save that secured from their inconspicuousness. When the tide came in, they crawled to the under side of the Spartina blades. When resting in this position with their long legs stretched out along the edges of the blade, they are difficult to see. That they are not destroyed by the tide was shown by the fact that on August 5, after the Spartina area had been submerged by the tides of three successive days, I still found them in abundance. I placed several of them, in the position I found them on the grass when covered by the tide, in a jar of sea water and kept them submerged for thirty hours. They were apparently unaffected, showing that this spider, as well as the Grammonata trivittata, must have some unique modification to prevent drowning. This spider, however, entangled more air bubbles in its longer, flimsier hair. Its feet are provided with toothed claws, perhaps developed to secure a firm hold on the grass blade.

I am anxious to secure more data concerning this spider. Is it a permanent resident of the Spartina area? What accounts for its sudden appearance? Where were the adults, or when? Its resistance to drowning is great enough to allow it to be a permanent inhabitant, but I doubt if it is sufficiently well protected from the inhabitants of the sea. However, the pads on its feet, which resemble those of a water strider and the one large toothed claw as well as several smaller ones on each foot may be structures of particular value to a resident of a between tides zone. The pads would enable it to move on the surface of the water, while the claws would enable it to secure such a firm hold on the grass blade that it could not be washed away.

INSECTS OF THE OUTER JUNCUS AREA.

Bembidium Constructum.

Of all the insects whose habits I observed, this brownish-black, 5 mm. long, beetle had the widest range. It was the only one to live in both

places that are daily covered by the tides and in places that are not. Its outer limit is 14 N., 4 E. (map 2). They are very abundant in the gravel which covers the wooden platform and also in the region of the tidal drift, especially under the newly washed up sea-lettuce (Ulva). In regions daily covered by the tide it is rarely found except in gravel covered areas. By crawling under the gravel it prevents itself from being washed away and protects itself from aquatic enemies. Its actions may be readily observed by hunting for them as the tide rises and the digging a channel around the place where they are found. As the water rises, they will run from place to place, darting under one stone only to leave it for another. They may approach the channel, but will rarely attempt to cross it. Before the tide has completely submerged the place, the bembida will crawl under the gravel to remain there until the tide retreats. When the place is covered by the tide, they may be found at a depth of from three or four inches. The water, when it covers them, encloses a large bubble of air under their wings.

Their action may be easily determined under artificial conditions by placing them in jars containing moist sand and gravel and slowly filling them with water. Several times, when filling the jars, I poured the water in so rapidly that some were swept to the surface. They would then swim wildly on the surface; but when a grass stem was thrust into the sand so as to extend above the surface of the water, they would swim to it and crawl down into the sand. The bubble of air under their wings is so large that should they lose their footing, they will immediately rise to the surface. Their ability to withstand submergence is wonderful. At the end of one day the bubble of air will have almost disappeared and they will have become stupid. By the above gravel jar I kept eight out of ten specimens alive for three days in sea water. Several recovered after five days' submergence, showing a great resistivity to drowning.

This beetle, as well as the Heterocerous undatus and Salda sp(?) lives on the carrion of the small animals so abundant in the between tides zone.

Heterocerus Undatus.

This beetle is very rare in this area. Several were found between 4 and 6 N., to 12 and 16 E. (Map 2.) They live in burrows in the ground, only venturing out for food at low tide. Their resistance to drowning is equal to that of the Bembidium.

SALDA Sp(?).

This shore bug is very active and very difficult to catch and hard to find except on sunny days, when their shiny black wings make them rather conspicuous. They are found chiefly in the area covered by the Spergularia Marina. They live in burrows in the ground, and only venture forth in search of food on sunny days at low tide.

Their resistance to drowning is not nearly as great as that of the beetles; twenty-four hours submergence usually being sufficient to kill them. Twelve hours had very little effect. Like the beetles, they enclose large bubbles of air under their wings. On several occasions I placed several of them on the surface of the water when the area was covered by the tide. They swam on the surface until they came to floating fucus thallus (other floating materials being rejected). They would then crawl to one of the deepest submerged branches, where they would remain. They were almost invisible on the thallus, due to the resemblance of the fucus to their wings with the enclosed air bubble. This, undoubtedly, is a protective instinct.

BDELIDÆ Sp(?).

This reddish-brown plant louse (2 to 3 mm. long) is widely distributed throughout the salt marsh. Their outer limit borders on the inner limit of the prevailing tides. They are never found beyond the inner Spartina limit, 6½-foot level. Their mouth parts are especially adapted to sucking plant juices and they live on decaying plants. They are especially abundant on fresh drift weed.

As stated, they are seldom found in the areas covered by the prevailing tides, yet on occasions of a sudden rise in tide levels, they may be found walking on the ground when it is covered by the tide. They do not seem to have any objections to such unusual conditions as they apparently make no effort to escape. They are easily washed away by the tide when once lifted from their feet, as their long slender legs are to their disadvantage. After the retreat of such an unusually high tide, they are not as numerous as they were previous to it, due perhaps to the fact that they have no protection from aquatic enemies, and also because many of them are washed away. There is little danger of drowning. One morning, at 6:45, I placed six of them in vials and submerged them in sea water. At 5 p. m. they were all lying on their backs, apparently dead, but on exposure to the air they all revived. I also placed several in an un-

covered glass cylinder and placed it where it would be covered by the tide. As the tide filled the jar they made no effort to change their positions. Those on the grass blades remained in the same position, as did also those on the ground. The Bdellidæ were still alive in the cylinder after it had been submerged by two tides; i. e., two periods of submergence of five hours each, one period of terrestrial conditions of four hours.

Lycosa Communis.

Although the inner limit of the tidal drift, with its myriads of flies should furnish abundant food for spiders, this is the only species prevalent in the drift covered areas. This is a greyish spider from 4 mm. to 5 mm. in length. They venture out beyond the high tide limit, but will always retreat before the incoming tide. Their long, strong legs, which enable them to run rapidly, make them especially adapted to a region where safety lies in retreat. I often found them running inward on the Juncus when the ground was already covered by the tide. On several I found them isolated on the blades of Spartina grass. When this position was no longer conducive to dryness, they would run rapidly inward over the surface of the water. This is the only insect without wings, frequenting the between tides zone, which retreats before the tide. The Lycosæ, are not only the most rapid runners among the spiders, but can also withstand several hours more submergence than the other spiders of the salt marsh, Grammonata and Clubonia, of course, excepted.

Many winged insects, beetles, flies, etc., are found on the Spartina during the low tide; but, although I made no especial study of them, they seem to be only temporary residents. They are never abundant, or even present, immediately upon the retreat of the tide. I never found any submerged on the grass when covered by the tide. They are all good fliers and most undoubtedly retreat before the tide.

On the morning of August 5, when we had the first high tide which covered the outer Spartina area entirely for several weeks, I noticed many Tetragnatha spiders retreating up the Spartina blades because of the rising tide. As the water chased them to the tip of the blade they spun out a long thread which the north wind carried to the higher areas. They ran inward on the thread. When they accidentally became wetted by the water they became helpless. Should the wind have come from the south, they would have been destroyed. No Tetragnatha were found in areas that had once

been submerged by the tide. They had migrated to the outer Spartina areas during the low tide period. They are very abundant in the higher marsh areas.

It would be extremely interesting to know something of the life histories of the insects of the between tides zone, especially as to where they spend the winter, as to the methods of egg laying, and as to the types of larvæ.

Conclusion.

In almost every insect of the between tides zone there appears to be some peculiar protective feature; as, unique instincts, especially adapted external parts, or a greater resistivity to drowning.

Unique instincts, to prevent themselves from being washed away by the tides, are well shown in the tenacious clinging to the blades of Spartina by the Grammonata trivittata, Megamelus marginatus, and Clubonia sp (?). Another feature of the same type is the crawling of the Bembidium constructum under the gravel. That the environment has undoubtedly led to the formation of these instincts is illustrated by the comparison of the habits, when submerged, of the spiders of the Spartina area with those found higher on the marsh. Another instinct which serves the same purpose is the venturing forth for food by the Salda only on sunny days at low tide. The Grammonata trivittata and Megamelus marginatus undoubtedly rest head downward on the Spartina grass to prevent themselves from being caught unawares by the rising tide.

Inconspicuousness as a means of protection from aquatic enemies is shown by the swimming of the Salda to the Fucus thallus when disturbed during high tide. Other reactions serving the same purpose, are illustrated by the resemblance of Megamelus to the Spartina blade, the crawling the Grammonata into the pits at the junction of blade and stem, and the living of the beetles in burrows.

That one of the factors which determines the surviving species in a between tides zone is an ability to resist drowning, is shown by a comparison of the resistivity of Grammonata and Clubonia with that of other spiders.

A modification of the external features as an adaptation, is shown in the greatly modified legs of the Megamelus marginatus and in the short, stiff hair of the Grammonata trivittata. The legs of Lycosa communis are not essentially different from those of other Lycosæ; yet their long,

strong legs, which are conducive to swift movements and which give them the designation of running spiders, make them especially fitted to inhabit a zone in which safety may lie in retreat.

The terrestrial conditions which prevail for one-half of the time in the between the tides zone, make it necessary that the permanent inhabitants of such a zone be insects which breathe not by means of gills, but that they be air breathing insects. Terrestrial conditions are the normal ones for their activities. They are inactive during the high tide, or the period of submergence. The most striking phenomena is the strictly zonal distribution of the insects of the between the tides zone. Each species is undoubtedly specialized in some way to fit it to inhabit this area, and this specialization has rendered it incapable of surviving in other zones. Even the Megamelus marginatus, which travels with comparative rapidity, never migrates to the Juncus areas. To determine the exact reasons why the insects of this zone cannot survive in the higher areas of the salt marsh, more extensive studies of their life histories and habits must be made. Further observations concerning these features, I believe, will add much to the already extensive and fascinating data relating to adaptation among insects.

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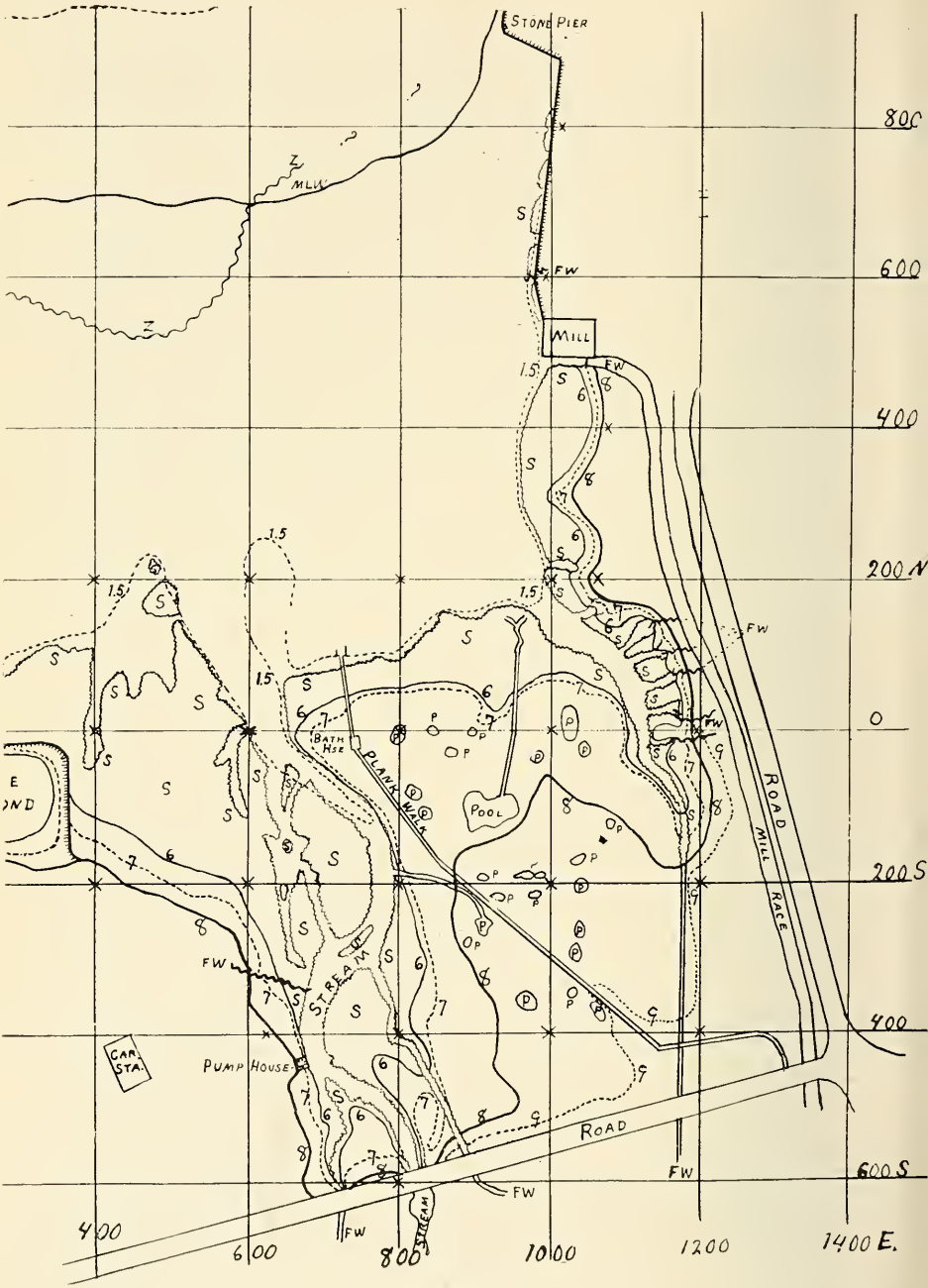
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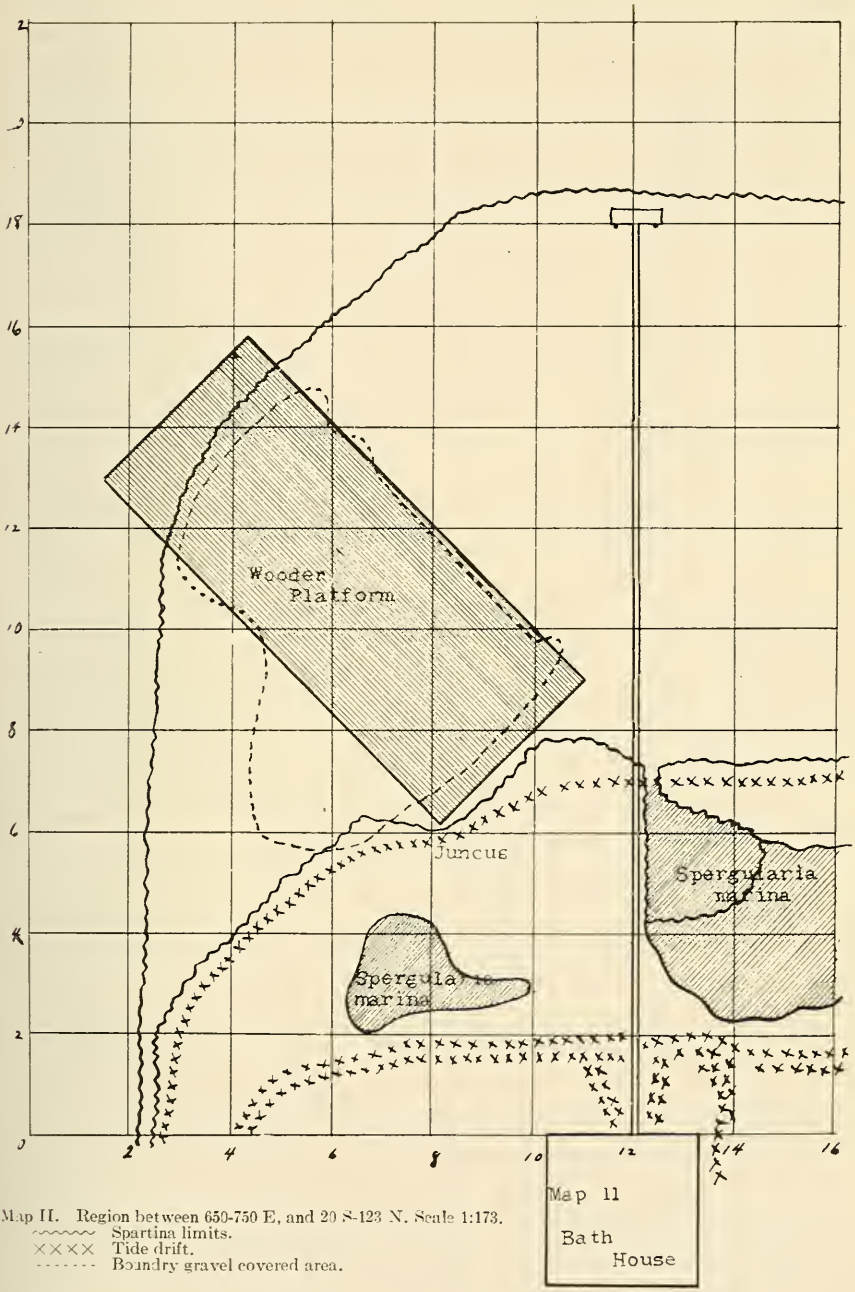
Map I.



Map II. Region between 650-750 E, and 20 S-123 N. Scale 1:173.
~~~~ Spartina limits.
×××× Tide drift.
------ Boundry gravel covered area.
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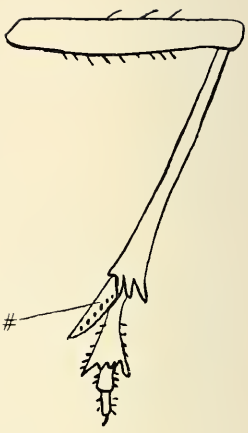

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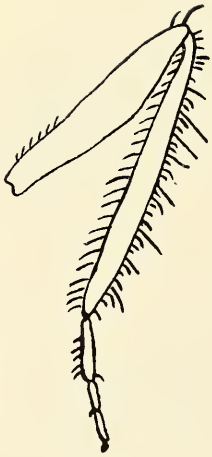

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PLATE I