
OBSERVATIONS ON THE SWIMMING, RIGHTING, AND
BURROWING MOVEMENTS OF YOUNG HORSE-
SHOE CRABS, *LIMULUS POLYPHEMUS*¹

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ABSTRACT

This paper presents a record of observations made on the swimming, righting, and burrowing movements of twelve young horseshoe crabs, *Limulus polyphemus* (L.), kept in a salt-water aquarium in New London, Ohio, during 1965 and 1966.

Activity occurred primarily at night. *Limulus* swam inverted, using its legs and gills for propulsion and its tail for steering, while the sloping front of the cephalothorax acted as a hydroplane to lift the body as it moved forward through the water. Arching its body and using its tail as a lever, *Limulus* could right itself when turned over on its back. Burrowing involved both leg motion and body flexing.

INTRODUCTION

Limulus polyphemus (Arthropoda: Merostomata: Xiphosura), commonly known as the horseshoe crab, is truly a living fossil. According to Shrock and Twenhofel (1953), the first merostomate forms appeared in the Cambrian, flourished during the mid-Paleozoic, and then declined through the Mesozoic to its present state of a single surviving genus, *Limulus*, which dates from the Triassic and is represented today by five species. Barnes (1963), however, assigns these five species to three different genera: *Tachypleus gigas*, *T. tridentatus*, *T. hoeveni*, and *Carcinoscorpius rotundicauda* from the Pacific coast of Asia, and *Xiphosura* (*Limulus*) *polyphemus* from the Atlantic coast of North America. This Atlantic species ranges from Maine to Yucatan from the shoreline out to depths of 30 or 40 feet (Stephens, 1964). It is this Atlantic species with which this paper deals.

Structurally, *Limulus* can be divided into three parts: a cephalothorax, an abdomen, and a tail spike. The cephalothorax, or carapace, resembles an upside-

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down pan; in some areas *Limulus* is known as a "pan crab," presumably because early settlers used the carapaces as pans (Stephens, 1964). The concave ventral side of the cephalothorax contains seven pairs of appendages: one pair of chelicerae, five pairs of walking legs, and one pair of chilaria. The first four pairs of walking legs are chelate and aid in passing food to the mouth. The fifth pair of walking legs bear four leaf-like processes which spread out when the appendage is thrust against the substrate, so that either some sand and mud is pushed back or the animal is pushed forward (Lochhead, 1950).

A triangular abdomen is attached to the cephalothorax by powerful muscles, so that the body can be flexed or extended at this joint. The ventral side of the abdomen contains six pairs of flap-like, membranous appendages, each pair of which is fused along the midline. The first pair form the genital operculum, in which the genital openings are located. The last five pairs contain the book gills, which provide the actual surface for gas exchange (Barnes, 1963). Figure 2A shows the locations of the walking legs and abdominal appendages.

The tail spike, which articulates with the posterior of the abdomen, is not used as a weapon, but as an aid in swimming, righting, and burrowing.

METHODS

Twelve young specimens of *Limulus* (ranging from two to four inches in total length), collected near Sarasota, Florida, for the biology laboratory at New London (Ohio) High School, were transferred to me in June, 1965. Unfortunately, the collector did not record the water pH, temperature, or salinity of the collecting site. Therefore, the aquarium in which the specimens were kept was maintained at approximately the yearly normals for the collecting area (pH 7.8, temperature 75°F., and 12 ‰ salinity). The aquarium was equipped with an undergravel filter operating through a coarse sand substrate. The salt-water solution used was a mixture of synthetic sea salts (sold as "Rila Mix" by Ward's Natural Science Establishment, Rochester, New York) and actual sea water.

The horseshoe crabs were fed standard dry "fish food", living and dead guppies, and raw hamburger. Three of the original twelve crabs survived over a year in captivity.

The behavioral descriptions discussed in this report, as well as the illustrations, are based primarily on visual observations, although some of the activity was filmed for a more detailed study at a later date. Lochhead's (1950) report that *Limulus* is most active during the night was confirmed during the course of this study.

OBSERVATIONS

Swimming

The young *Limulus* generally stayed close to, or burrowed through the substrate. Occasionally they swam (Lochhead (1950) states that swimming is quite common in young horseshoe crabs). When swimming, the animal was usually positioned upside down, with its back oriented downward. Adults are also reported to swim when coming inshore to breed. Stephens (1964) notes that occasionally a horseshoe crab comes off the bottom in a half-loop and swims on its back. However, during this investigation, no horseshoe crabs were observed to come off the open bottom in this manner. Rather, they only left the bottom when they ran into an obstacle and started to climb up and over it. When their body was nearly vertical, balanced on the tip of its tail against the obstacle, the animal pushed off with its legs and then swam upward and over in a half-loop, propelled by the powerful rhythmic beating motions of its walking legs, operculum, and gills (fig. 1).

Limulus apparently swam in an inverted position because of its body design,

the sloping front of the cephalothorax acting as a hydroplane as the animal moved through the water. If *Limulus* were right-side-up, this hydroplane effect would force the body down against the bottom. However, with the animal inverted, this same effect would cause the body to lift as it moved ahead through the water.

The tail aided in steering. When it was in line with the body, the animal swam straight forward. When it was swung to the side, the body tilted and the animal swam along an arc in the direction toward which the tail had been moved.

During swimming, all five pairs of legs moved forward slowly, while retracted within the concave ventral side of the cephalothorax, then extended and moved rapidly to the rear in a powerful stroke (fig. 2B). The legs then retracted and moved forward again in preparation for the next power stroke. Approximately twelve power strokes occurred during every five seconds.

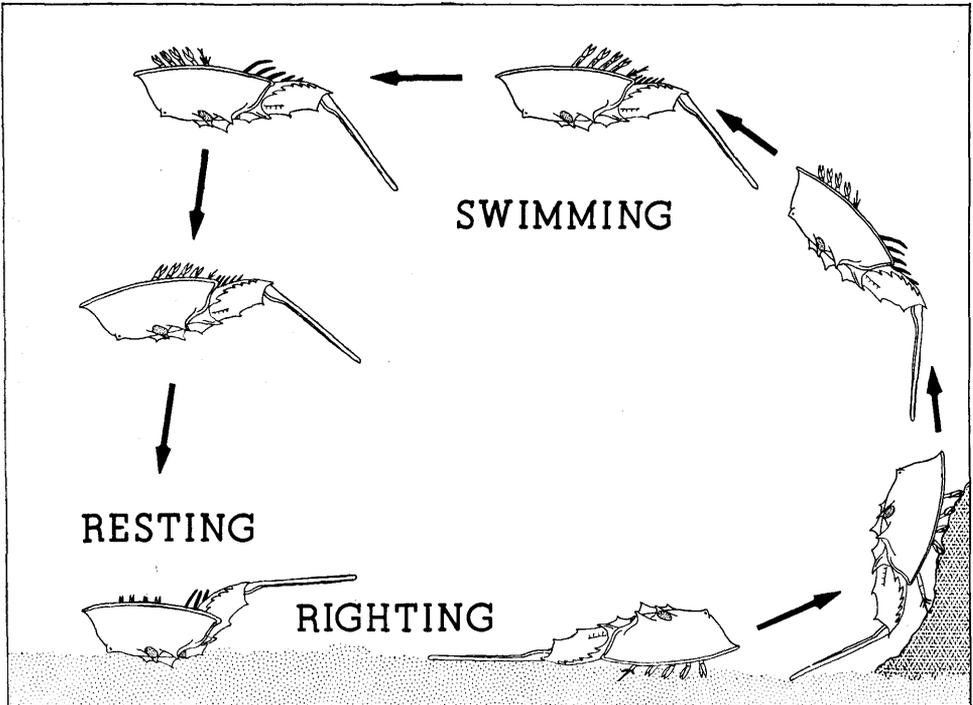


FIGURE 1. Swimming cycle of *Limulus* in an aquarium.

The operculum and the first three gills moved in unison with the legs, whereas the last two gills moved together almost 180 degrees out of phase with the anterior appendages. As shown in Figure 2C, the operculum and gills beat in a four-step cycle. At the beginning of the cycle, gills 4 and 5 moved forward while the operculum and gills 1, 2, and 3 were moving backward in a power stroke (fig. 2C-1). At the end of their power stroke, the operculum and gills 1, 2, and 3 reversed direction and moved forward with gills 4 and 5 (fig. 2C-2). Gills 4 and 5 then reversed and moved backward in a power stroke, while the operculum and gills 1, 2, and 3 continued their forward movement (fig. 2C-3). The operculum and gills 1, 2, and 3 then reversed direction again and moved back in a power stroke, accompanied by a power stroke of the legs (fig. 2C-4). At the same time, gills 4 and 5 reversed and began to move forward again, and the cycle repeated.

After some 80 to 90 power strokes (about 40 seconds of swimming), the beat of the legs and gills weakened and *Limulus* sank slowly to the bottom, still upside-down, and rested (fig. 1). When resting, the body was doubled up at the cephalothorax-abdominal joint to about one half its maximum extent, and the tail was horizontal (figures 3B and 4A). The legs were retracted, and the gills moved slowly through one-fourth to one-third of their full range of movement.

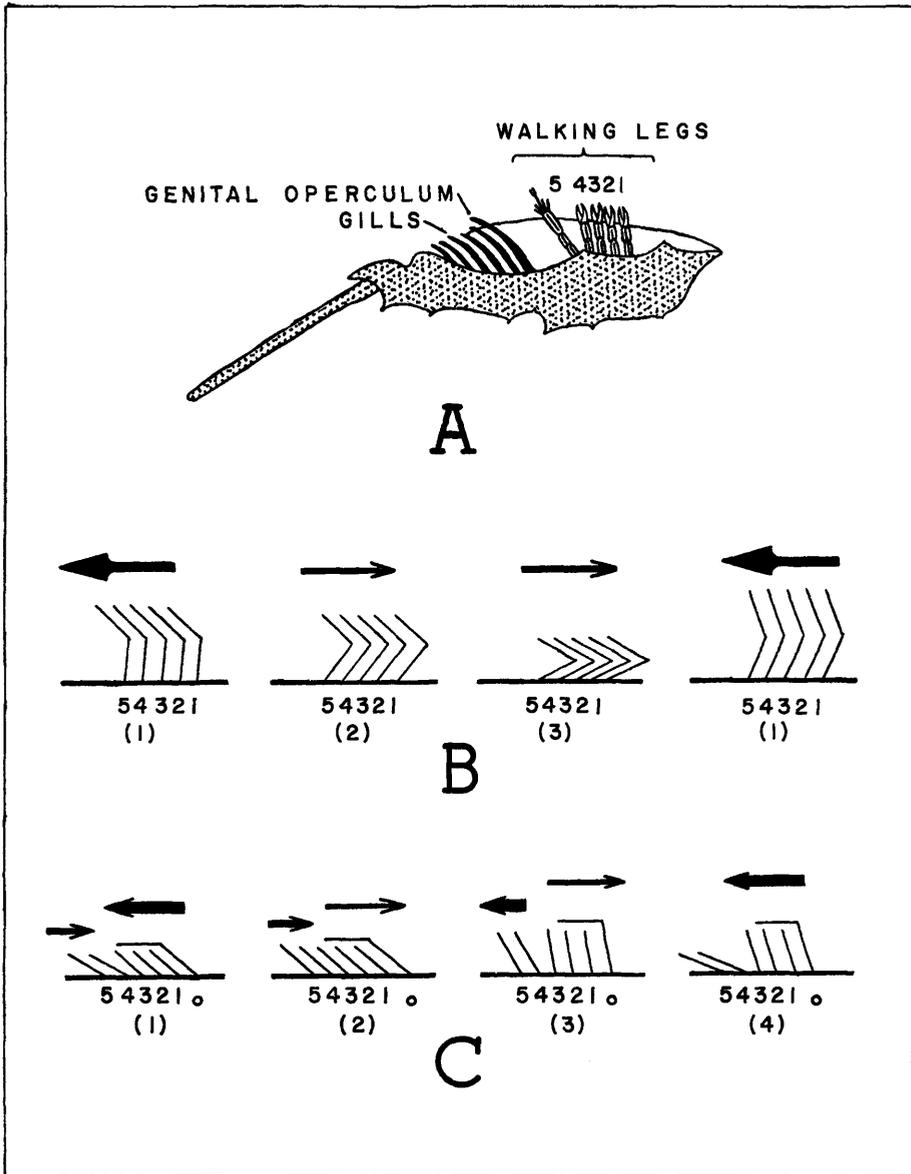


FIGURE 2. Cross-section of *Limulus* in swimming position, showing location of appendages (A), and schematic movements of legs (B) and operculum and gills (C) during swimming. Heavy arrows indicate power strokes; light arrows indicate return strokes.

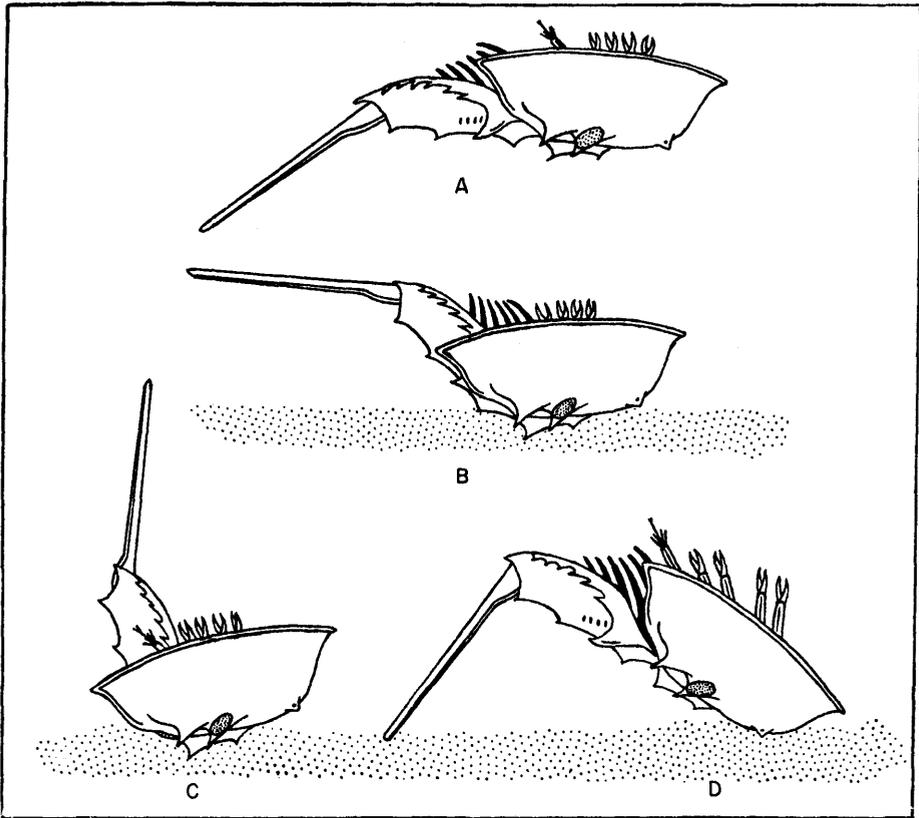


FIGURE 3. Characteristic body positions during (A) swimming, (B) resting, (C) maximum doubling-up, and (D) maximum arching.

According to Lochhead (1950), the beat of the gills is usually rather leisurely and serves only to aerate them.

After swimming, *Limulus* came to rest upside-down. This position was also reached by simply falling over backwards after climbing up on an obstacle, or by being turned over by sudden currents or by other animals, including larger members of its own species. *Limulus* appeared to become exhausted much more quickly when on its back. The animal would attempt to right itself for 30 seconds or so, and would then rest for over a minute before attempting to right itself again. However, if it was righted by some external force, it suddenly became as active as it was before being turned upside-down.

Righting

In the aquarium the horseshoe crabs righted themselves in three ways, although one method definitely dominated over the other two. The righting process was a complex combination of body arching and leg, gill, and tail movements which, in effect, caused the inverted body to rock sideways until the legs could gain a foothold on the substrate (fig. 4).

In the most common method, *Limulus*, starting from the resting position (figures 3B and 4A), first doubled up as far as possible (figures 3C and 4B). The legs and gills were almost inactive at this stage. *Limulus* then quickly arched its back coming to rest on the tip of its tail and the front of the cephalothorax while the legs and gills beat rapidly (figures 3D and 4C). After these initial moves,

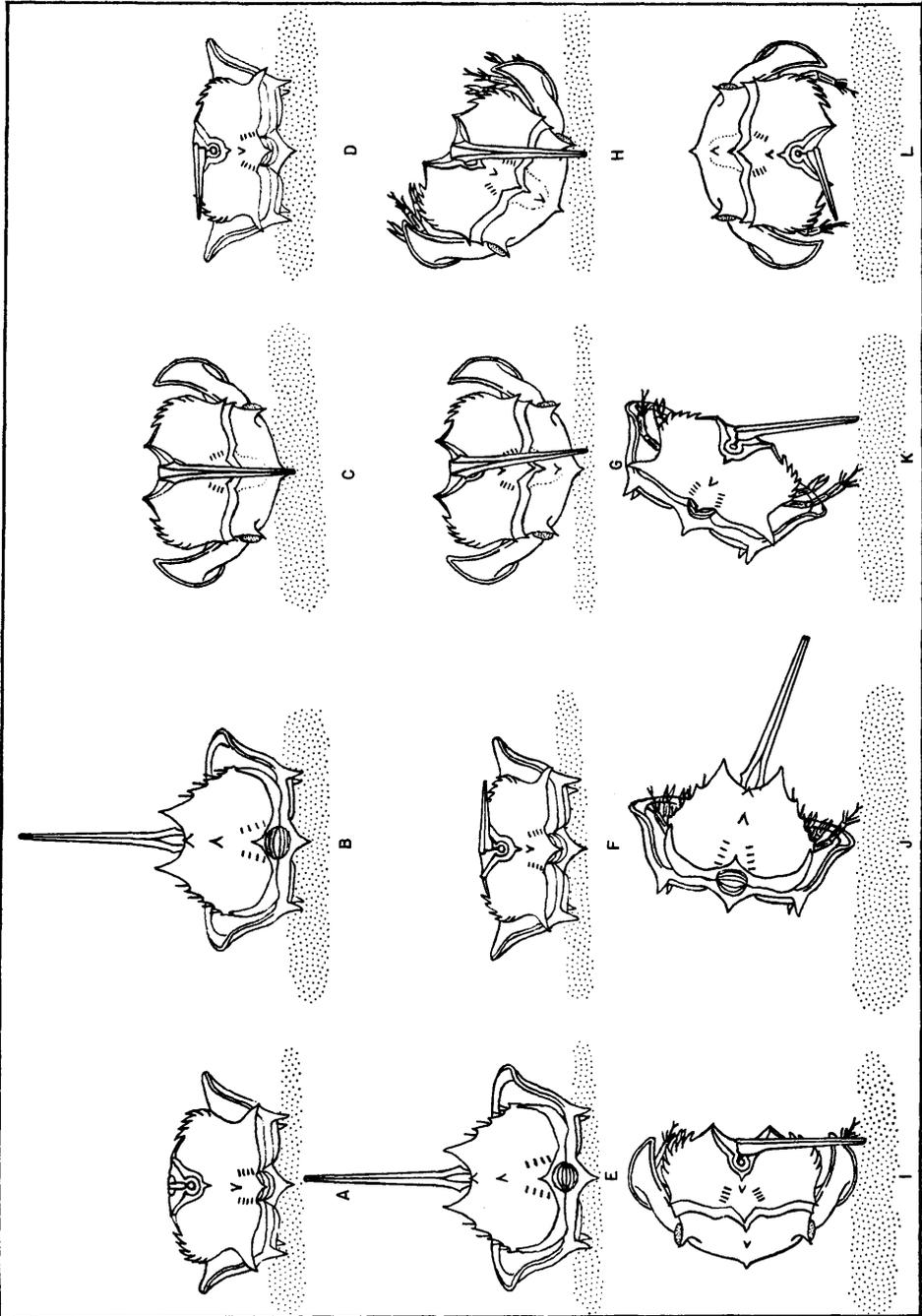


FIGURE 4. Body and tail movements during righting of *Limulus*, starting with inverted resting position (A) and ending with righted body settling to the bottom (L).

Limulus alternately doubled up and then arched its body in the same manner as before, while the tail was swung in either a clockwise or counterclockwise circle (fig. 4, D through G). Every time the tip of the tail engaged the bottom (fig. 4G), the body was given an added thrust to the side. This lateral push, combined with the instability of the body in the arched position and the beating of the legs and gills, eventually caused the body to roll over on its side (fig. 4, H and I). (The importance of the tail in righting was demonstrated by one *Limulus* with a deformed tail which could not right itself because it lacked the leverage normally provided by the tail.) The legs then began moving independently, at random, until those on the lower side engaged the substratum and were quickly extended, pushing the body up off the bottom in a quarter-roll toward the upright position. At the same time, *Limulus* doubled up, shifting its center of gravity so that its body continued on over and settled onto the bottom, right-side-up (fig. 4, J, K, and L).

Limulus usually did not succeed in righting itself on the first try. It usually doubled up and arched its body many times before succeeding in rolling far enough to the side for the legs to engage the substrate.

Another method of righting was occasionally observed. An increased beating of legs and gills while the body was in the arched position caused the body to pivot tail over head in a vertical half-circle and to come thus to rest right-side-up.

A third and seldom-observed method of righting occurred when the horseshoe crab swam to the bottom, rolled on its side, and engaged the substrate with its lowermost legs while still swimming. Thus, *Limulus* had made possible the righting of itself before it had settled to the bottom.

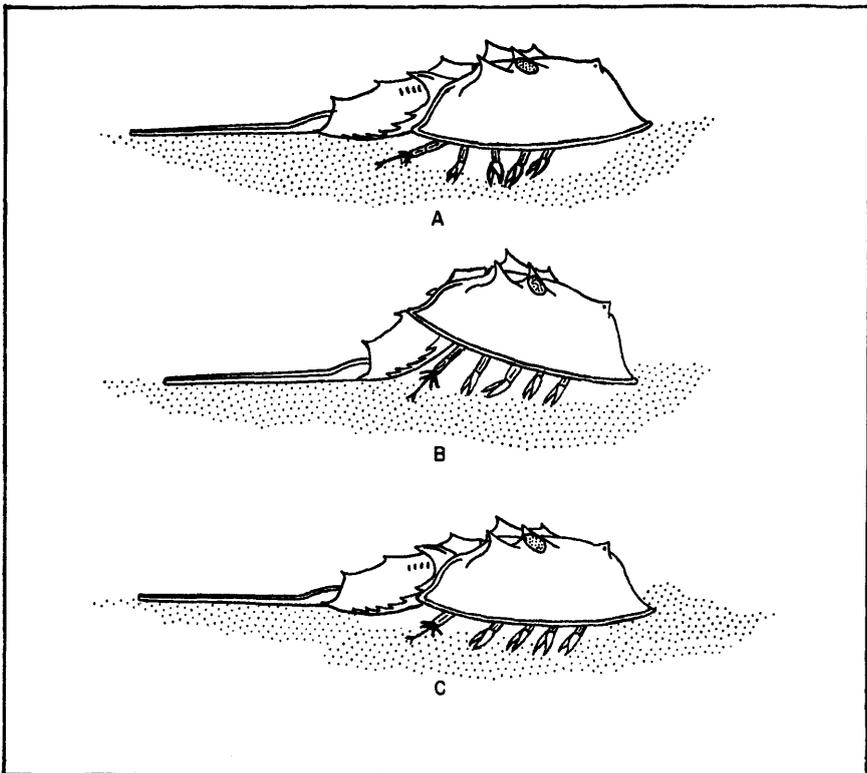


FIGURE 5. Burrowing movements of *Limulus* showing scooping of material from under body (A), arching of body (B), and thrusting of body under substrate (C).

Burrowing

Stephens (1964) states that *Limulus* burrows when the water temperature drops and when predators (namely sharks and some of the larger rays) are present. Burrowing may also serve to keep the shell free of fouling organisms. The young specimens of *Limulus* in the aquarium were observed to burrow partially or wholly during periods of general inactivity in the aquarium.

Observations of these specimens indicated that burrowing involved three steps repeated over and over until burrowing was completed. During the first step (fig. 5A), a depression was scooped out from under the body by the walking legs. The first four pairs of legs moved material from the margin of the cephalothorax toward the center of the body and then toward the rear where the fifth pair pushed it out from under the body through the gaps between the cephalothorax and abdomen. The legs of each of the first four pairs moved either together or moved separately, whereas the legs of the fifth pair usually moved together.

In the second step (fig. 5B), the animal pushed down against the substrate with its fifth pair of legs, causing the body to arch and the anterior margin of the cephalothorax to slide back and down into the depression. The tail remained in place on the substrate during this step, rather than being thrust into it as Lochhead (1950) suggests. In the third step (fig. 5C), *Limulus* pushed back against the substrate with all of its legs and straightened its body causing the anterior margin of the cephalothorax to be thrust somewhat under the substrate.

Limulus repeated these three steps several times until it was completely buried, or, in the case of the specimens observed, until the median eyes (located on each side of the central anterior carapace spine) were covered. In this latter position, *Limulus* was about one-half buried, with only the carapace around the lateral eyes, the abdomen, and the tail exposed. On several occasions, however, the horseshoe crabs burrowed completely under the substratum.

SUMMARY

The observations made on the activities of young horseshoe crabs kept in a salt-water aquarium lead to the following conclusions.

- 1) *Limulus* is most active at night.
- 2) The body design of *Limulus* prevents it from swimming right-side-up. When the animal swims which here occurred only after it had climbed up on an obstacle, it assumes an inverted position, in which the sloping front of the cephalothorax acts as a hydroplane to lift the body as it moves forward.
- 3) *Limulus* swims by powerful rhythmic beating motions of its legs, operculum, and gills. The posterior two gills beat almost 180 degrees out-of-phase with the rest of the appendages.
- 4) The tail aids in steering during swimming and provides important leverage during righting.
- 5) The righting process is a complex combination of body arching and leg, gill, and tail movements, which cause the inverted body to rock sideways until the legs can gain a foothold on the substrate and push the animal on over to an upright position.
- 6) *Limulus* appears to tire quickly when on its back.
- 7) *Limulus* tends to stop burrowing, in the aquarium at least, when its median eyes are covered.

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