119322

THE BORING HABITS OF THE SHIPWORM

By Dr. ROBERT CUNNINGHAM MILLER

UNIVERSITY OF CALIFORNIA

THE method by which the smooth-walled, perfectly rounded burrows of the shipworm are excavated in wood has excited the curiosity of man since an early time. In the first century A. D. the Roman naturalist Pliny the Elder remarked upon it. "What teeth (Nature) has given the teredo," he exclaimed, "even for perforating oak! . . . And also she has made from wood its principal nourishment."[1]

This conjecture as to the purpose of the denticles on the shell appears to have gone unchallenged until 1733, when the Dutch investigator Sellius[2] objected that the shell of *Teredo* does not appear adequate to the task of boring, especially in the harder woods. He believed the boring to be accomplished by a kind of suction with the foot, aided by the action of the water which is being continually taken into and forced out of the burrow.

The opinion of Sellius precipitated a discussion which has been carried on intermittently for nearly two hundred years. Certain experimental difficulties having interfered with direct observations of the shipworm in action, the debate has been more or less academic, the nature of the premises and the vigor of the discussion suggesting analogies with a well-known medieval controversy regarding the number of teeth of the horse.

While a majority of writers have favored the view that boring is carried on by movements of the shell, not a few have insisted that the burrows are excavated by a slow but continuous wearing away of the wood by friction and suction with the foot. Still a third group has maintained that a chemical action of some sort is involved in the boring process.

The theory of boring by means of the shell rests largely on morphological grounds. The shell of *Teredo* has been reduced, relative to the size of the animal, until it covers only a small portion of the anterior part of the body. It is a subglobular structure, gaping in front for the protrusion of the foot, and behind for the protrusion of the long, slender body. It consists of two valves, which are capable of rocking back and forth on specialized dorsal and ventral knobs, so that the anterior and posterior adductor muscles oppose

[1] Caii Plinii Secundi Historia Naturalis, Book XI, Chap. 1.

[2] Godofredi Sellii Historia Naturalis Teredinis seu Xylophagi Marini, pp. 78 ff. Trajecti ad Rhenum, 1733.

each other in action. The anterior portions of the valves are equipped with sharply denticulated ridges, the projections of which are directed outward and backward. The structure of the shell, coupled with the fact that the posterior adductor muscle is somewhat more than thirty times as large by volume as the anterior adductor, strongly suggests that boring is accomplished by movements of the valves, repeated contractions of the large posterior muscle causing their forward edges to spread apart and rasp the wood.

To this it has been objected by advocates of the theory of boring by means of the foot that the shell is inadequate to the task of boring, that it does not show signs of wear as would be expected if its function were that of rasping wood, and that the walls of the burrow of *Teredo* are too smoothly polished to have been rasped mechanically. It has been further pointed out that certain forms, such as *Patella,* are able to make depressions in rocks by means of the foot.

Proponents of the theory of boring by chemical means have little to offer in support of their views except a presumed inadequacy of both shell and foot to accomplish the observed result. Nevertheless, this theory had the backing of such authorities as Gray, Deshayes and De Quatrefages, all of whom during the nineteenth century made noteworthy contributions to the knowledge of marine borers.[3]

In order to determine if possible by direct observation which of the foregoing suppositions is correct, the writer recently tried the experiment of carefully opening the burrow of a teredo near the anterior end and sealing over the opening with a glass cover-slip, thus making a small window in the burrow, through which the movements of the occupant could be observed with the aid of a binocular microscope and a narrow shaft of light. Most of the animals disturbed in this fashion would retract about a third of the length of the burrow, so that they were entirely out of sight from the window, and after a few days' quiescence they would bore off in another direction. But after a number of repetitions the experiment finally proved successful. One specimen was found which carried on boring operations directly in view of the small glass window, and the process was observed in considerable detail.

The boring is accomplished by rasping with the valves, which are held in position by the combined action of the foot, attached to one wall of the burrow, and the dorsal fold of the mantle, distended by turgor, pushing against the opposite wall. The typical boring position is seen in Fig. 1a.

[3] Readers who desire a fuller account of the various theories of boring are referred to Miller: "The boring mechanism of *Teredo,*" Univ. Calif. Publ. Zool., vol. 26, pp. 41–80. 1924.

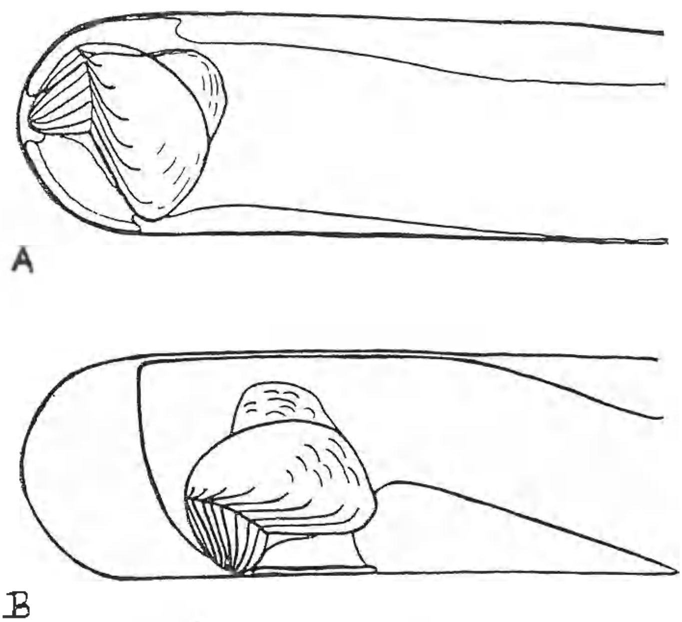

FIG. 1. *Teredo*. a. Typical boring position. b. Boring position when beginning a side passage at a right angle to the former course of the burrow.

The effective stroke of the valves is the outward and backward one, as had already been assumed from the direction of the points of the denticles on the shell, and from the extraordinary development of the posterior adductor muscle. At each stroke of the valves the foot takes a new hold. As the backward stroke of the valves is completed, the foot is relaxed and its margins spread out so far that they overlap the edges of the shell. Then, by a sudden contraction, the margins of this structure are drawn in and the valves brought forward into position for a new stroke. Then follows the slow, labored contraction of the large posterior adductor, causing the forward edges of the valves to spread apart and rasp the wood on their outward thrust. That the valves do actively scrape the wood on this stroke is indicated by the fact they were observed frequently to slip, the backward margins being drawn together with a jerk instead of the usual slow, steady pull. The boring movements occurred rhythmically, from 8 to 12 times a minute.

The anterior tip of the burrow is mined out by the anterior lobe of the shell; the movement of the shell is necessarily in a direction longitudinal to the ridges of this area, so that their serrate edges act upon the wood as so many small saws. The serrations on the ridges of the anterior area are extremely fine, as compared with the

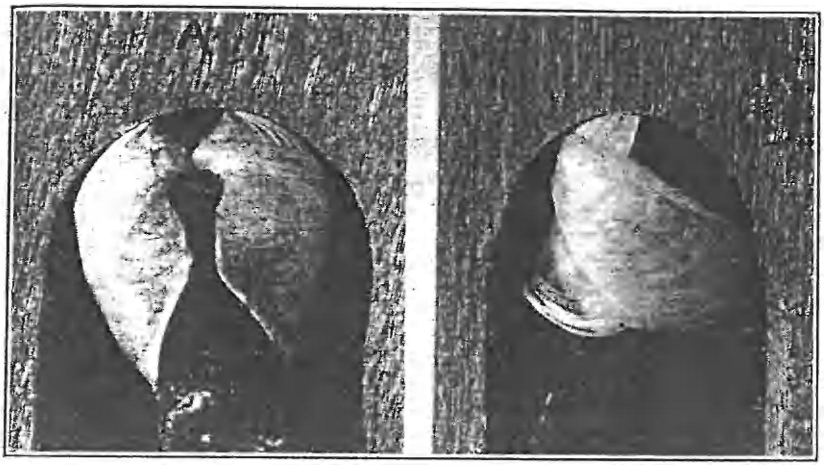

FIG. 2. Shell of *Teredo navalis* mounted in position at end of burrow, x 10. a. Dorsal view, b. Lateral view.

denticulations of the anterior portion of the median lobe of the shell, and hence better fitted to act as the advance boring edges. Also the shape and position of the anterior lobe especially adapt it to working in the extreme tip of the burrow (see Fig. 2). The marks of the work of the anterior lobe of the shell are often plainly evident on the wood (Fig. 3).

While the ridges of the anterior lobe are working saw-fashion in the tip of the burrow, the coarser, wedge-shaped teeth of the anterior portion of the median lobe of the shell are at the same time working rasp-like, enlarging the diameter of the burrow and advancing the peripheral portion of its cupped extremity. Thus, while the tools might be compared to saw and rasp, their work is in effect that of drill and reamer.

The disposal of the rasped-off particles of wood it was not possible to observe, because of their minute size. There is, however, every reason to believe that they are swept by the cilia of the periphery of the foot into the range of the cilia of the esophagus. Apparently all the rasped-off wood passes through the digestive tract, where a considerable portion of it is utilized as food by the animal,[4] as Pliny had further surmised.

The position assumed by *Teredo* in boring off at a right angle to its former direction of progress is seen in Fig. 1b. One would hardly have supposed that such an awkward position is assumed by the animal in changing the course of its burrow, were this not

[4] *Cf.* Dore and Miller: "The digestion of wood by *Teredo navalis*," Univ. Calif. Publ. Zool., vol. 22, pp. 383–400, 1923.

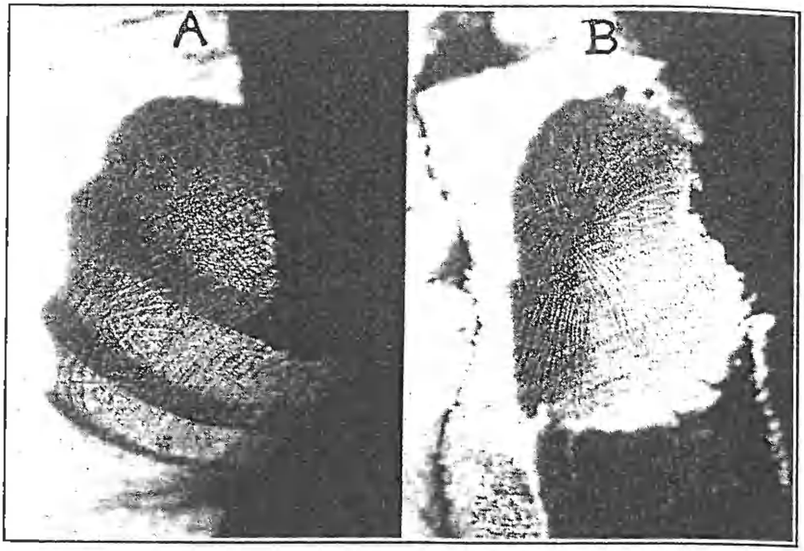

FIG. 3. Cupped extremity of a burrow showing marks of the work of the shell, x 10. a. *Teredo navalis*. b. *Teredo diegensis*.

actually a matter of observation. Apparently the valves function without difficulty under such circumstances. This explains how *Teredo* is able to make the abrupt changes in the course of its burrow which are so often found, especially in heavily riddled piling, where such changes of direction are necessary in order to avoid breaking through into neighboring burrows.

The commonly made statement that one *Teredo* will never bore into or cross the burrow of another is not, strictly speaking, true. Occasional instances have been found in which one burrow passed directly through another. Such cases are rare, however, and it is probable that the first animal was dead before the second entered its burrow, as otherwise it would doubtless have been able to protect itself by a thickened wall of nacre. In heavily riddled timbers the teredos will sometimes adopt unusual expedients, such as to cross a crack of considerable magnitude in order to find new wood to attack. One instance was observed in an aquarium where a teredo had bored completely through a piece of wood, so that its shell and the anterior part of the body protruded into the water. This animal was doubtless abnormal.

The foot appeared, from observation, to be an organ of sense and a means of limited locomotion about the narrow confines of the burrow. The animal under observation through the window made in the burrow was seen to turn from left to right and back again a number of times, as though exploring the wall of the burrow with the foot, before it made any boring movements. Probably thus in some way *Teredo* becomes aware of neighboring burrows, so as to turn aside and avoid them. In executing these turning movements, the foot several times passed directly across the glass, so that the manner in which it functioned could be well studied. The organ was first flattened against the surface of the glass, and its margins spread out so that they extended beyond the edges of the shell. Then, apparently by contraction of the retractor muscles of the foot, the margins were rather suddenly drawn in and the central disc of the foot slightly cupped, obviously constituting a sucker. After each contraction the foot sought a new attachment, moving laterally about 0.5 mm and hitching the shell along to a new position.

During the course of this exploration of the walls of the burrow, the animal was observed to turn about its long axis 260 degrees in one direction and 220 degrees in the other, or a total of 480 degrees. The body was obviously twisted, owing to the animal's being attached to the burrow at the posterior end, but this twisting appeared to occasion it no inconvenience. Thus is solved the problem of how the shell can be brought into the various positions necessary for excavating the regularly cupped, perfectly rounded burrow. It was obvious from the markings shown in Fig. 3 that the shell must have been rotated by slow stages through at least 180 degrees in each direction in order to produce the striations radiating in all directions.

The further possibility that *Teredo* might facilitate its boring by the use of some secretion which has a solvent action on certain constituents of the wood was also investigated. It would seem that the action of such a substance, if it occurs, should spread at least for a limited distance through the cells of the wood at the extremity of the burrow. The tracheids of Douglas fir are from 1 to 3 mm in length, and it is hardly conceivable that a secretion applied to one end of a tracheid should not spread through its entire length. Probing in the extremity of the burrow with a needle, however, did not reveal any area of softened wood, as would be expected on this hypothesis. Micro-staining with hematoxylin, which is a selective stain for cellulose, did not reveal any diminution in the cellulose content of the wood at the end of the burrow. It was further attempted to compare quantitatively the composition of shavings of wood immediately adjacent to the burrows of *Teredo* with that of shavings from sound portions of the same timber. An analysis of these samples did not indicate that any substances had been removed by the enzymes of the borer from the wood forming the wall of the burrow.

While the writer does not consider that the possibility of the use of a glandular secretion to facilitate boring is definitely disproved by these experiments, the evidence strongly indicates that boring is performed entirely by mechanical rasping of the valves on wood that has been to some extent softened and macerated by the presence of water in the burrow.

The experiment was tried of rasping the surface of a piece of Douglas fir wood under water with a medium-sized teredo shell held between the thumb and forefinger. By this method a depression 6 mm in diameter and 1.2 mm deep was made in 30 minutes, at the end of which time the denticles of the shell, examined under the microscope, showed not the least trace of wear. A similar attempt to rasp dry wood, however, resulted in the speedy destruction of the shell. Thus it appears that the action of water alone is sufficient to greatly soften the wood and accordingly facilitate boring. The assumption of a chemical action on the wood by some unknown secretion produced by the borers is quite unnecessary.

It is not the intention of the writer to defend the somewhat moth-eaten scientific reputation of the blandly uncritical Pliny, but in this instance at least he appears to have hit upon the right conjecture, both as regards the mechanism of boring and the utilization of the wood as food. It was perhaps the very simplicity of the actual method of boring of the shipworm which led so many later investigators to overlook it in a search for some more obscure explanation.