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Snapping Behavior of the Shrimp Alpheus californiensis

Abstract. *A pair of very smooth disks, located on the claw of the snapping shrimp* Alpheus californiensis, *are temporarily held together by cohesive forces of water. This allows the closer muscle of the claw to generate a large amount of tension before these cohesive forces are overcome, and results in a rapid closing movement.*

Snapping shrimps (family Crangonidae) have one greatly enlarged claw. Rapid closure of this claw, resulting in the expulsion of a jet of water and an audible snap, is a principal component of the defensive and aggressive behavior in these animals. While this behavior has been well known for several years (*1*, *2*), its mechanism has not been adequately described. The work reported here shows that for at least one species, *Alpheus californiensis*, the snapping behavior is made possible by the cohesive forces of water and a modification of the animal's exoskeleton.

Electrophysiological recordings, made with copper wires inserted through the exoskeleton and into the closer muscle of the propus, indicate that the dactyl is temporarily held in the open position even while the closer is being excited (Fig. 1). After the dactyl has been opened, large muscle potentials are observed in the closer muscle, but the dactyl does not move for 0.2 to 0.4 second after these muscle potentials are initiated. By the time the dactyl does move, the closer muscle has developed a large amount of force and snaps the dactyl closed.

The dactyl of an intact animal or an isolated claw can be set manually in the open (cocked) position. Once the dactyl of an amputated claw has been cocked, it will stay open until forcibly closed. By using a calibrated force transducer to close the dactyl, the force that the closer muscle must overcome to move the dactyl from the cocked position has been found to be 2.0×10^5 dynes, with a standard deviation of 0.36×10^5 dynes.

Since a claw that has been isolated from an animal for several hours can still be cocked, the mechanism for holding the dactyl open cannot be muscular action. This is further demonstrated by severing the opener muscle tendon of an isolated claw. Such an operation has no effect on the ability of the dactyl to remain in the cocked position.

Both the propus and the dactyl of the claw possess a hardened exoskeletal disk (Fig. 2a). When the dactyl is open these disks abut each other perfectly. A small, thin scratch on the surface of either of the disks completely disrupts an animal's ability to keep the dactyl open. The disks thus appear to be the structures responsible for holding the dactyl in the cocked position (*3*).

Scanning electron micrographs of the disks show some interesting features. The two disks are almost perfectly matched in size and shape (Fig. 2, b and c). The propus disk appears to have a layer of a soft substance spread over its surface; the substance cracks during preparation for the scanning electron microscope and looks much like dried clay (Fig. 2d). This layer is probably the epicuticle. If so, it is much thicker here than in any other part of the exoskeleton, including the dactyl disk. High-power micrographs of the troughlike rim surrounding the propus disk reveal many pores (Fig. 2d, inset). These pores are seen only in the rim area, not on the main surface of the disk. They may be from tegumental glands, which are thought to function in either the secretion or the maintenance of the epicuticle (*4*). The surfaces of the disks are remarkably flat and smooth (Fig. 2e). Micrographs at a magnification of 2000 reveal nothing to detract from the smoothness of these surfaces, aside from the cracks in the propus disk epicuticle. There are no structures that could be interpreted as minute latching or suction devices.

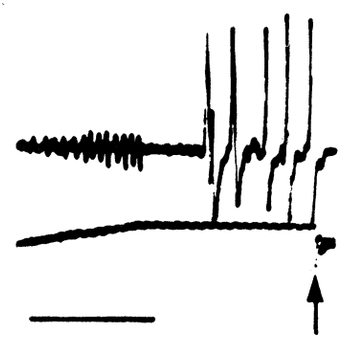

Fig. 1. Extracellular recording of muscle electrical potentials during a snap. The top trace is from the muscles of the propus. The bottom trace is from a movement transducer attached to the dactyl. In the transducer record, up is opening of the dactyl and down is closing. The snap occurs at the sharp downward movement of the transducer record (arrow). The large potentials are from the closer muscle. Note that there is no closing movement until after the last large potential. The small potentials that occur during opening are from the opener muscle, which is approximately 1 cm from the electrodes. Calibration, 200 msec.

There are several ways of explaining how the disks are held together. The soft substance on the propus disk may act as an adhesive. While this possibility cannot be completely eliminated, it is difficult to imagine an adhesive that would become completely ineffective when a small scratch is made on its surface or on the surface it would adhere to. Also, the alignment of the disks seems to be critical. If the articulation between the dactyl and the propus is damaged so that the disks no longer match precisely, the cocking mechanism is completely disrupted. This would not be expected if an adhesive were responsible for this mechanism.

Another possibility is that a vacuum is formed between the two disks, and the soft epicuticle on the propus disk acts as a seal. If this were true the force needed to separate the disks under standard conditions of temperature and pressure should be just enough to overcome a pressure of 1 atm. On the claws used to determine the force required to uncock the dactyl, the area of the disks was 0.7 mm^2. One atmosphere of pressure on an area of 0.7 mm^2 is equal to 0.7×10^4 dynes. Since the force needed to uncock the dactyl has been measured to be 2.0×10^5 dynes, a vacuum mechanism appears to be insufficient to account for the force holding the dactyl open (*5*).

The most reasonable hypothesis seems to be that forces of cohesion of the water between the disks are responsible for keeping the disks together. The amount of force that could theoretically be developed in this manner can be calculated by using the heat of vaporization of water, which is a measure of the amount of energy needed to separate water molecules from one another. Multiplying this figure by the

density of water gives a value in terms of energy per cubic centimeter. This is equal to (force × centimeters)/cubic centimeter, or force per square centimeter. For an area of 0.7 mm², this value would represent a force of 1.5×10^8 dynes. This is only an ideal figure, but it indicates that a cohesion mechanism could withstand a force of 2.0×10^5 dynes and therefore would be adequate to account for the adhesion of the two disks.

The ideal figure of 1.5×10^8 dynes could be attained only if extreme precautions had been taken to remove all impurities from the water. No such precautions were taken, nor would this be possible in nature. Any impurities in the water would provide cavitation nuclei. Cavitation due to vaporization of the liquid phase would greatly decrease the tensile strength of the water (*6*). Thus, the measured force of 2.0×10^5 dynes is not an unreasonable value. Furthermore, cavitation nuclei can also take the form of irregularities on the surfaces surrounding the water. Even the slightest crevices on the surfaces would provide a place for gases to be trapped. These gases would in turn provide sites for cavitation. This would explain why the surfaces must be remarkably smooth, and why a very small scratch on either surface completely disrupts the cocking mechanism (*7*).

The thick, soft epicuticle on the propus disk may play an important role in ensuring that the two surfaces of the disks match perfectly. This soft layer would mold itself to the surface of the dactyl disk, and in this way correct for any small nonconformities between the two hardened surfaces.

It seems, therefore, that the snapping behavior of *A. californiensis* is made possible by a modification of the chitinous exoskeleton. The behavior is started by a contraction of the opener muscle, which raises the dactyl into a fully open or cocked position. At this point the disks on the dactyl and propus meet and are held together, probably by the cohesive forces of the water between the two surfaces. When the closer muscle is excited and begins to contract, the disks prevent the dactyl from moving until the closer muscle develops enough tension to overcome the cohesive forces that hold the disks together. When the dactyl finally does move, the closer muscle acts like a stretched spring and causes the dactyl to close rapidly and with great force, producing an audible snap.

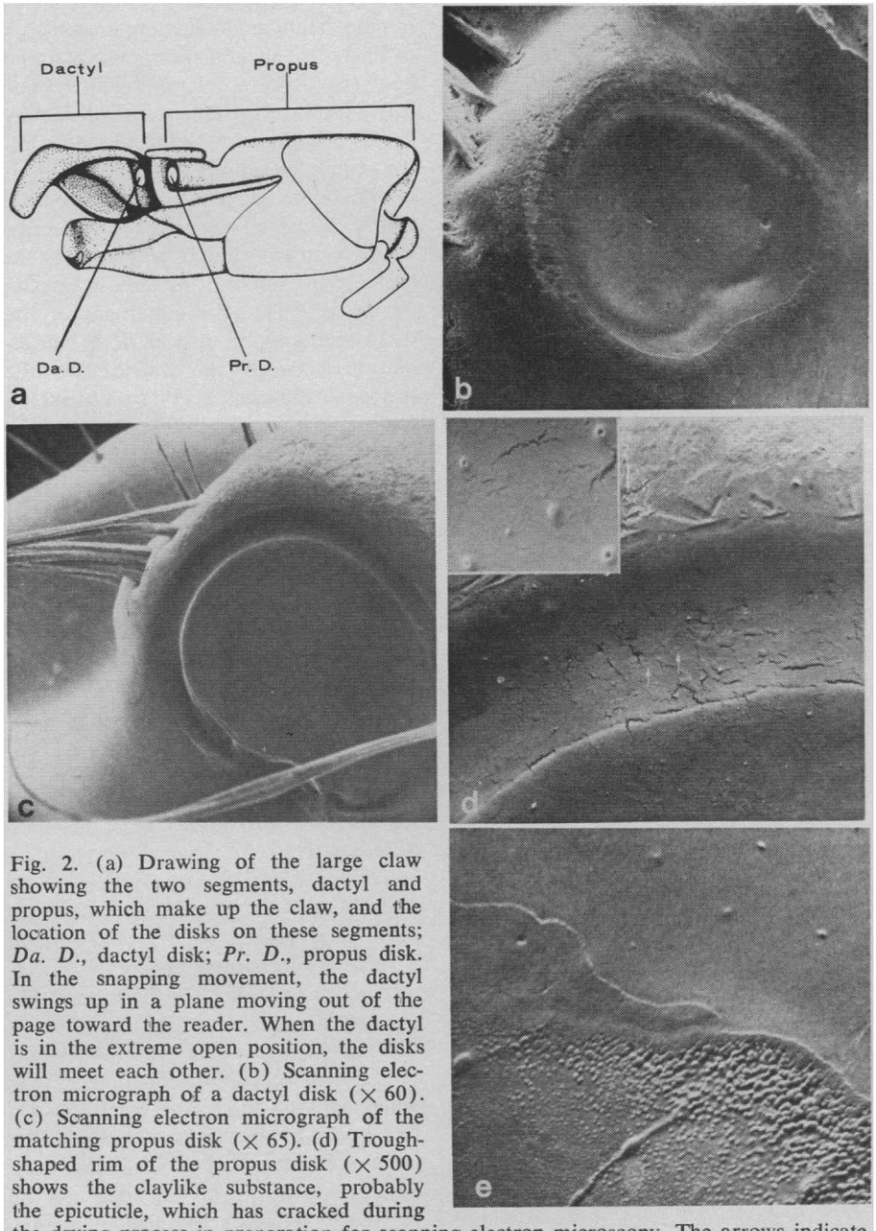

Fig. 2. (a) Drawing of the large claw showing the two segments, dactyl and propus, which make up the claw, and the location of the disks on these segments; *Da. D.*, dactyl disk; *Pr. D.*, propus disk. In the snapping movement, the dactyl swings up in a plane moving out of the page toward the reader. When the dactyl is in the extreme open position, the disks will meet each other. (b) Scanning electron micrograph of a dactyl disk (× 60). (c) Scanning electron micrograph of the matching propus disk (× 65). (d) Trough-shaped rim of the propus disk (× 500) shows the claylike substance, probably the epicuticle, which has cracked during the drying process in preparation for scanning electron microscopy. The arrows indicate the positions of two pores through which this substance may be secreted. The inset shows the pores (× 1500). (e) Edge of a dactyl disk (× 1000). The upper right half is the surface of the disk, the lower left half is the surrounding chitin. Note the extreme smoothness of the disk surface compared to the surrounding chitin.

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References and Notes

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2. R. E. Knowlton and J. M. Moulton, *ibid.* **125**, 311 (1963).
3. Johnson *et al.* (*1*) also felt that the disks were used in this way. However, they based their claim solely on the observation that the dactyl of a dead animal could be held open. Knowlton and Moulton (*2*) later disputed this observation and claimed that the disks could not be used in this way.
4. R. Dennell, in *The Physiology of Crustacea*, T. H. Waterman, Ed. (Academic Press, New York, 1960), p. 499.
5. Johnson *et al.* (*1*) referred to the disks as suction disks. Since the mechanism is not one of suction, this is an improper name for the structures.
6. For a review of cavitation and the tensile strength of water see R. F. Apfel, *Sci. Amer.* **227**, 58 (December 1972).
7. Knowlton and Moulton (*2*) may have failed to repeat the observation of Johnson *et al.* (*1*) that the disks held the dactyl in the open position because they somehow damaged the surface of one of the disks or loosened the articulation between the dactyl and the propus so that the two disks did not meet perfectly.
8. I thank Dr. Glenn Stoner for help with the scanning electron microscope, Susan Sparrow for the drawing in Fig. 2a, Dr. Rimmon C. Fay for supplying animals and identifying their species, and Drs. DeForest Mellon, Jr., Carl P. Spirito, David J. Prior, Charles Kaars, and Paul Fishbain for critically evaluating the manuscript. Supported by PHS grant NS 04989 to DeForest Mellon, Jr.

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