

THE MECHANISM OF PIPPING IN BIRDS¹

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THE pip, or first break in the eggshell by the hatching bird, is the initial phase of hatching. It furnishes the bird with a weakened point at which to begin cutting the shell and complete the hatching process. The typical pip on a chicken egg is a flatly conical area about one-third of the distance from the large end, near the widest portion of the egg. Approximately 0.2 cm in height and 1 cm in diameter, it is proscribed by cracks in the shell, and has four or five additional cracks radiating from the center. The cracks are parted to varying degrees, depending upon the force from inside the shell that caused the pip. Sometime after pipping the chick begins to rotate within the egg and, starting at the pip, to jab with the egg tooth and beak tip and cut away the shell and shell membrane almost completely around the egg. It then pushes off the loosened cap thus formed at the large end of the egg and tumbles out of the shell, terminating hatching.

The *Musculus complexus* or "hatching muscle" is a paired structure located on the anterodorsal portion of the neck in birds, originating on several anterior cervical vertebrae and inserting on the occipital crest at the rear of the skull (Fisher, 1958; Bock and Hikida, 1968). In chickens this muscle, as well as the subcutaneous area around it, starts to swell with lymph a few days prior to hatching until it reaches its peak size at the time of pipping. It then loses the fluid in a few days and assumes the appearance of normal muscle rather than being clear or yellowish and bulbous. In the adult bird it functions to raise or elevate the head. The *M. complexus* is probably present in enlarged form at hatching in most birds, having been described in grebes (Fisher, 1961), ducks (Keibel, 1912; Fisher, 1966), the coot, *Fulica americana* (J. Fisher, 1962), Franklin's Gull, *Larus pipixcan* (H. Fisher, 1962), the Bobwhite, *Colinus virginianus* (Johnson, 1969), chicken (Fisher, 1958, and many others), and possibly in the House Sparrow, *Passer domesticus*, and Red-winged Blackbird, *Agelaius phoeniceus* (Fisher, 1958).

As the peak in fluid content of the *M. complexus* is concurrent with pipping, it is difficult to discount the idea that it must have some role here. Keibel (1912) was apparently the first to attribute the function of breaking the eggshell to the *M. complexus*, and he felt that the pip was due to a contraction of the muscle, lifting and extending the beak to force the egg tooth through the shell. Pohlman (1919: 103) believed that the muscle could not contract because of its turgid condition and that

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pipping came about by "pressure rather than a sudden muscular effort." Fisher (1958: 399) felt that the "M. complexus provides the power" for the initial break in the shell.

Smail (1964: 499) believed the pip was the result of steady pressure rather than a sudden jab. He placed the M. complexus in a direct role by proposing that it pressed against one side of the shell and, as it swelled with fluid, forced the beak tip, by "hydraulic pressure," to push against the opposite side until it broke through. He alternatively speculated that if this were not the action of the muscle, then it probably functioned as a "turgid cushion against which contractions of the other muscles . . . [underlying the M. complexus] . . . or even of its own muscle fibers would effect the same result." Bock and Hikida (1969: 105) conclude that the muscle serves as a "cushion to brace the head when the egg tooth is forced against the shell," an indirect role, but they do not entirely discount the possibility that its contraction aids in pipping. Hamburger and Oppenheim (1967) also agree that the M. complexus acts as a turgid cushion but, in addition, imply that it is active in the pipping process by stating (p. 184) that "there is no doubt that the cracking of the shell is accomplished by backward thrusts of the beak." This puts the muscle in a direct rather than the passive role proposed by Smail.

Studies involving injection of steroids into 19-day chick embryos (Brooks, MS) cast doubt on a direct role of the muscle in pipping. Although certain steroids brought about increased fluid uptake by the muscle, making it relatively larger, pipping in treated chicks occurred later, or at least no earlier, than in control chicks, but the percentage that pipped was higher than that of the controls. These results were interpreted to mean that the M. complexus has no hydraulic action but, when more turgid, has greater ability to function as a cushion or brace.

METHODS AND MATERIALS

White leghorn chicken eggs were incubated in a cabinet-type incubator with close temperature and humidity control. To watch pipping directly it was necessary to cut an opening in each egg and place a sealed window over it. Windowing eggs is a standard procedure in embryological studies, but the windows are generally quite small so that gaseous (oxygen and carbon dioxide) exchange through the porous shell is only slightly hampered, allowing the embryo to respire and live. Our study required a large oval opening, at least 3×2.5 cm, to show as great a portion as possible of the chick within. Cutting through the calcified portion of the shell on the side of the egg near the large end with a small electric rotary saw, we left the shell membrane intact, and then sealed to the shell the lower edge of a strip of pliable styrofoam (0.5 cm wide) that had been previously formed into a ring or collar and coated with paraffin. Then cutting the shell membrane, we removed the flap of shell from the opening and sealed a slightly warmed glass plate (4×4 cm) to the top edge of the collar, leaving the underside of the glass plate 0-1 cm above the embryo.

Hamburger and Oppenheim (1967), whose work was unknown to us at the time of the experiments, did not cover their windows with glass plates. We found through experimentation that it was advisable to have a solid substitute for the shell at the proper level, so that the chick's normal pipping position was not altered by part of its body protruding from the opening. Consequently we placed all our later windows 0 cm above the chick.

The sealed window and collar covered approximately 20 to 25 per cent of the egg, greatly reducing the area for gaseous exchange. Because gravity pulls the blastodisc or developing embryo to the upper side of the egg, therefore to the relatively airless side beneath the window, in eggs incubated less than 14 days the lack of oxygen killed the embryos a day or two after windowing. Considerable experimentation shows it necessary to incubate the eggs for at least 15 days until the highly vascularized embryonic membranes, where gaseous exchange occurs, have enlarged and extended completely around the egg. Mortality was approximately 50 per cent, even in eggs windowed on day 17 of incubation, so that finally we did not window the eggs until the scheduled day of pipping (day 19 in these experiments). Windowing on this day afforded the additional advantage of allowing the chick no time to move into an unfavorable position relative to the window, e.g. beak protruding into the window space or wedged under the waxed area, and if the chick initially was in an undesirable position it could be gently rotated and usually did not return to that position before pipping. Also sterile conditions were unnecessary because the chicks would pip before any introduced disease became sufficiently advanced to cause sickness or death.

Nearly constant observation of the windowed eggs in the incubator commenced on day 19 of incubation and continued until they pipped, usually by day 20. Generally a dozen eggs was the maximum number windowed on any one day, as there was neither space nor enough eyes to watch a greater number at one time. Mirrors placed beneath and beside the eggs made it possible to see almost the entire shell. Watching for the pip was facilitated by marking the shell at the approximate position that it would appear. This was determined by viewing the portion of the chick visible through the window and comparing it with the normal embryo position. The estimated position of the pip was not always easily determined and many pips were missed because they were "off-target."

RESULTS

Of about 70 eggs windowed, approximately 30 pipped. Of these we actually witnessed only four in the act of pipping. Several others we missed by a few minutes and in these we noted only the behavior and position of the chick up to and after, but not during, pipping. The others were missed completely because they pipped either "off-target" or during intermissions in the observation period.

Three aspects of pipping are in question here: (1) whether the pip is caused by a muscular contraction, and if so, which muscles are involved, (2) whether the M. complexus contracts or can contract, and (3) the exact position of the chick at the time of pipping. Observations concerning these aspects are taken up in order following the descriptions below. These descriptions are taken from notes recorded at the time of pipping in each of the four eggs in which this was seen. The observations were

quite consistent with each other and with observations of the pre- and postpipping behavior of the majority of chicks that pipped but were not actually witnessed doing so. Therefore they are believed to be representative.

Chick 1.—For a few minutes immediately preceding the pip there was increased activity in the egg in the form of sudden strong overall body convulsions (rapid, extensive muscular contraction), each causing the body to expand once and then immediately relax. Concurrent with one of these convulsions the pip appeared. Subsequent activity was similar to that prior to the pip, overall body convulsions occurring at regular intervals.

Chick 2.—Single strong whole-body convulsions interspersed with short bouts of body quivering were seen for some time prior to the pip. There was no movement immediately before the pip, but at the time the shell was broken there was a strong whole-body convulsion, apparently including contraction of the M. complexus, which was pressed against the glass window (the muscle widened, and although we could not see it shorten because it was partially obscured by the shell, we have interpreted the movement as a contraction. We saw the muscle shorten in other chicks, see below). The chick was quiet for about 30 seconds, then movements continued similar to those seen before the pip.

Chick 3.—Little activity was seen during the 2 hours preceding the pip. At the time of the pip the chick made one strong whole-body convulsion; it then remained quiet except for normal breathing movements.

Chick 4.—Intermittent strong overall body convulsions and short bouts of quivering preceded pipping. The pip was accompanied by a single, sudden, and strong movement of the entire chick. After pipping the amount of activity within the egg increased.

It is noteworthy that in all these cases the pip was accompanied by a violent convulsion apparently caused by contraction of the muscles of the *entire* body. Although the pipping convulsion may have been more powerful, it was not noticeably different from similar ones seen before and after the pip. Such convulsions were witnessed, not only in these four eggs but in the majority of eggs windowed. These convulsions seem to correspond to the Hamburger and Oppenheim (1967) type III motility pattern, although we considered them quite rapid.

It will also be noted that in two cases intermittent short bouts of quivering (one of the type II motility pattern "startles" of Hamburger and Oppenheim) were manifested for a variable period before and after the pip. Although not present in all cases, this seems to be fairly characteristic behavior, as it was noticed in most other eggs near the time of pipping. In several cases where the pip appeared unseen on a nonvisible

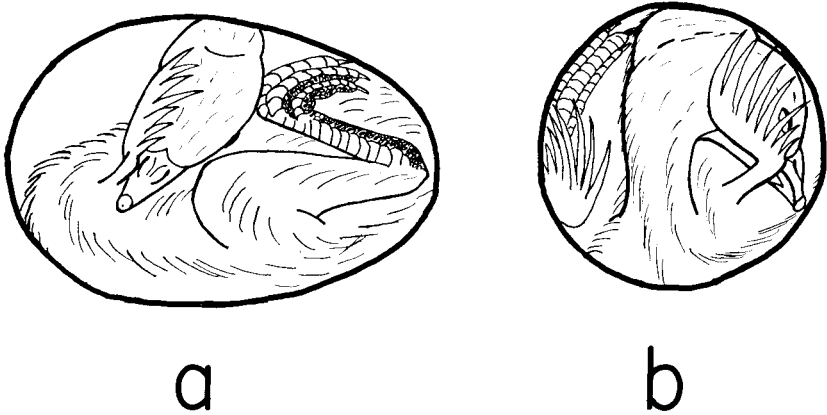


Figure 1. The normal pipping position of the 19-day chicken embryo in the egg. The *Musculus complexus* is apparent as a sizable bulge on the back of the neck at the top of the shell. a, Side view showing chick laying on back, with right wing covering right side of head. Bill tip is wedged between shell and side of body near base of wing. b, End view from the large end of the egg showing the bill tip with egg tooth approximately at the 4 o'clock position on the side of the egg.

portion of the shell or "off-target," the fact that a pip was about to occur or had occurred was surmised because of this behavior.

We noted in one case that the *M. complexus* contracted appreciably during the pipping convulsion. It was also seen to contract (shorten and bulge) with concomitant slight lifting of the head in several other chicks during body convulsions that did not produce pips, particularly in chicks whose entire muscle protruded into the window space. We were able to make the muscle contract simply by jabbing it with a needle shortly after pipping, and contraction has also been caused by electrical stimulation (Bock and Hikida, 1968). Thus the muscle can and apparently does contract at pipping, contrary to what Pohlman (1919) and others have contended.

The position of the chick in the egg at the time of pipping was determined for most of the eggs by opening the shell after the pip and by observation through the window. The position (Figure 1) in all cases was nearly as described by Smail (1964: 502) with the important exception that the tip of the beak was *never* "directed at the shell at a point opposite the side contacted by the neck." If the egg is viewed from the large end and if the *M. complexus* is pressed against the exact top of the shell, we found that the egg tooth and beak tip are adjacent to the shell (and the pip occurs) at about the 4 o'clock position (Figure 1b) rather than the 6 o'clock position that Smail's description would require. In addition, the

distance from the back of the neck to the beak tip is not so great as that across the egg at the place in the egg where the head is located at the time of pipping.

In most of the eggs we observed, the pip did not occur as near the large end of the egg as various other workers have indicated. It was generally located as shown in Figure 1a, although in some cases it was nearer the large end. As the chick moves around within the egg, this position no doubt varies prior to pipping, but it appeared to be the usual position attained at the time of pipping in our experiments. A slight movement of the head to the left is all that is necessary.

DISCUSSION AND CONCLUSIONS

Our data support the contention of Bock and Hikida (1969) that the hypotheses of Keibel (1912), Pohlman (1919), and Fisher (1958), as well as Smail's (1964) hydraulic pressure hypothesis, are no longer tenable. The probable contraction of the *M. complexus* (also implied by Hamburger and Oppenheim, 1967), along with a whole-body convulsion simultaneous with the appearance of the pip, provide this support.

Smail's hypothesis is also weakened by clarification of the position of the chick in the egg at pipping and by the fact that in some cases we have seen a chick pip twice—shortly after the first pip it produced a second typical pip mark overlapping or near the first. In these cases the initial break in the shell is generally incomplete; little bulging occurs and the cracks are not parted. Bock and Hikida (1969) also mention a somewhat similar situation with other birds. Too little time elapses between pips for the *M. complexus* to build up pressure and, in addition, the muscle is probably at peak turgidity at the time of the first pip.

We found that at time of pipping the tip of the beak and the egg tooth were always in contact with the inside of the shell, rather than a few mm away as Hamburger and Oppenheim (1967: 174, 184) suggest. This was seen clearly in cases where the beak tip was lodged under the shell only a short distance from the edge of the window. Smail's (1964) work also indicates that the beak tip is wedged against the shell. (See also the discussion of the egg tooth, below.)

Our hypothesis on the mechanism of pipping is as follows: The beak tip is wedged between the shell and the chick's dorsolateral thoracic area (ventral to the scapula) at this time, with the egg tooth directed toward and touching the shell (Figure 1). The strong whole-body convulsions occurring prior to and at the time of actual pipping produce two important actions here. Expansion of the thoracic area of the body underlying the entire beak forces the dorsum of the beak, and especially the beak tip, hard against the shell. This body expansion toward the beak may come

about as a result of inhalation (as in the Bobwhite: Johnson, 1969), or of arching the body and bracing or pushing with the tarsi so that the shoulder region is braced strongly against the shell (a very important part of the mechanism) as described by Hamburger and Oppenheim (1967), or likely a combination of both. At the same time contraction of the dorsal cervical musculature, at least of the *M. complexus*, elevates the beak and forces its tip in the same direction. The latter contraction would also tend to pull the head backward to some extent, but this is prevented by the turgidity of the *M. complexus* bracing itself against the shell. Successive convulsions prior to pipping probably weaken the shell at the beak tip, providing that the tip is kept at or very near the same point on the shell, until eventually a convulsion causes the shell to break. The pip thus is not the result of a jab, but rather of pressure, as Pohlman (1919) and Smail (1964) proposed. However the pressure is neither passive nor steady.

This mechanism differs from that proposed by Hamburger and Oppenheim (1967), and although it is very difficult to repudiate their excellent work, we feel that our inclusion of a glass plate as a shell substitute is an important difference—one that might well have brought about some of the discrepancies noted. The mechanism described herein is supported by our observations, and also by the fact that when body weight and size are less than normal at the scheduled time of hatching, pipping is delayed until they do become normal (Romanoff, 1960). The body in these cases may be too small to press the beak against the shell with sufficient force to break it.

A major problem of the chick at this time is holding the beak tip at the same location on the shell during successive body convulsions. The egg tooth and *M. complexus* probably function here. The small, sharp point of the tooth is directed forward, so that it catches on the shell membrane if the head moves forward but not if the head moves toward the rear or the side. If, as Hamburger and Oppenheim state, the beak tip is usually held a few mm away from the shell, this would naturally preclude the function of the egg tooth as we, Smail (1964), and others have advanced it. The tooth is small and light, and these characteristics coupled with the forward direction of its point indicate that it could not function satisfactorily as a pick or hammer. The point of the tooth would be unnecessary if the structure were present only to protect the beak from abrasion or other damage. It also appears remote to suggest that its major function is to penetrate and cut the various membranes, in particular the shell membrane. Although the latter membrane is resilient and does not break easily, the beak could probably break through without the tooth. In this connection, also, the point would not need to project forward rather

than vertically; indeed it might even be expected to project rearward, as the head motion described by Hamburger and Oppenheim is in that direction.

As the egg tooth normally must catch and hold at one place for successive convulsions to be effective, and because the head tends to be displaced backward by the body convulsions, the M. complexus pressing against the shell at the back of the neck and head functions to counteract this tendency and hold the beak tip at one place. Because it contracts simultaneously with the rest of the body musculature during a convulsion, it becomes thicker and more firm at the time displacement of the beak would occur and retards any substantial displacement that might be caused by its own contraction or by pressure from the body (this latter displacement of the conical beak would be similar to the action of squeezing a slippery bar of soap in the hand). In addition its turgidity may give it a shock-absorbing function that brings the egg tooth back to the original point from any short distance that it *may* be displaced. That the turgidity of the M. complexus is necessary for pipping is demonstrated by the fact that windowed eggs were not pipped when the collar held the window away from the chick, and when the M. complexus extended into the window space. In these cases the muscle was not braced against any solid support, and with each body convulsion the head and neck moved rapidly backward into the window space, then returned forward after relaxing. The beak was never held firmly in the same place during the repeated convulsions.

The egg tooth, found almost universally among birds, appears to be a structure functioning to catch and hold the beak tip at one point on the shell, as Smail (1964) suggested. That it is not absolutely necessary for pipping is shown by certain breeds of chickens that have genetically lost the egg tooth; in these pipping still occurs, although the percentage is greatly reduced (Landauer, 1948 *in* Smail, 1964). The M. complexus seems to function in part to keep backward displacement of the beak tip at a minimum, and to return it to its original position should it be displaced slightly by a body convulsion. The pip or opening itself is brought about by whole-body convulsions in which the M. complexus (and probably other dorsal cervical muscles) contracts, and the thoracic region expands toward the beak to press it strongly against the shell, repeatedly if necessary, until the weakened shell breaks at the point where the beak tip was held. Here the position of the chick in the egg is very important. The beak tip must be wedged between the shell and the thoracic region of the body for the convulsions to have their maximum effect.

Although this study has utilized the chicken as the experimental bird, the structures and the body position involved in pipping are found in

most, if not all, other birds, with only slight modification. Thus the mechanism described here probably applies to birds in general.

SUMMARY

The pipping process of the chick was investigated by direct observation through a window cut in the eggshell. We witnessed 4 of 30 chicks in the act of pipping. The pip is apparently produced by one of a series of strong whole-body convulsions that presses the beak tip through the shell. The beak at this time is wedged between the shell and the chick's lateral thoracic area. The beak tip is probably held at one point on the shell by combined action of the egg tooth and the *Musculus complexus*, ensuring that the pressure produced by the repeated convulsions is applied to one location on the shell, thereby successively weakening it.

LITERATURE CITED

- BOCK, W. J., AND R. S. HIKIDA. 1968. An analysis of twitch and tonus fibers in the hatching muscle. *Condor*, 70: 211-222.
- BOCK, W. J., AND R. S. HIKIDA. 1969. Turgidity and function of the hatching muscle. *Amer. Midl. Naturalist*, 81: 99-106.
- FISHER, H. I. 1958. The "hatching muscle" in the chick. *Auk*, 75: 391-399.
- FISHER, H. I. 1961. The hatching muscle in North American grebes. *Condor*, 63: 227-233.
- FISHER, H. I. 1962. The hatching muscle in Franklin's Gull. *Wilson Bull.*, 74: 166-172.
- FISHER, H. I. 1966. Hatching and the hatching muscle in some North American ducks. *Trans. Illinois State Acad. Sci.*, 59: 305-325.
- FISHER, J. R. 1962. The hatching muscle in the American Coot. *Trans. Illinois State Acad. Sci.*, 55: 71-77.
- HAMBURGER, V., AND R. OPPENHEIM. 1967. Prehatching motility and hatching behavior in the chick. *J. Exp. Zool.*, 166: 171-204.
- JOHNSON, R. A. 1969. Hatching behavior of the Bobwhite. *Wilson Bull.*, 81: 79-86.
- KEIBEL, F. 1912. Wie zerbricht der ausschlüpfende Vogel die Eischale? *Anat. Anz.*, 41: 381-382.
- POHLMAN, A. G. 1919. Concerning the causal factor in the hatching of the chick, with particular reference to the *Musculus complexus*. *Anat. Rec.*, 17: 89-104.
- ROMANOFF, A. L. 1960. *The avian embryo*. New York, Macmillan Co.
- SMALL, J. R. 1964. A possible role of the *Musculus complexus* in pipping the chicken egg. *Amer. Midl. Naturalist*, 72: 499-506.

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