

THE "HATCHING MUSCLE" IN THE CHICK

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THE mechanism of hatching is little understood, and few investigators have concerned themselves with it. It has generally been accepted that the egg-tooth on the dorsal tip of the bill is a part of the apparatus that ruptures the shell. About 130 years ago Yarell (Rosenstadt, 1912) described the tooth and suggested its function. The tooth is usually pressed against the inner surface of the first "pip" or opening in the shell, but what causes the strong thrust that breaks the shell?

Since the chick's head and neck are flexed inside the shell, it is logical to presume that extension of the head or any of the cervical vertebrae could force the tooth against the shell. Keibel (1912) believed that *M. complexus* (Fig. 1) extended the head and thus pro-

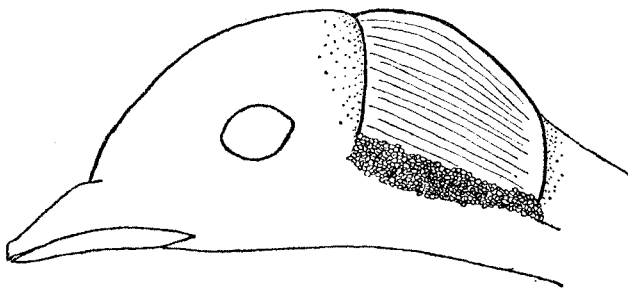


FIGURE 1. Diagrammatic lateral view of *M. complexus* of chick at hatching.

vided the force. The development of the egg-tooth and *M. complexus* seem to parallel each other. The tooth first appears at 7 or 8 days of incubation, is not outstanding at 10 days, but thereafter develops rapidly to reach its greatest size at 20 days. *M. complexus* is present and somewhat enlarged as early as 7 or 8 days, judging from the enlargement observable in chicks (Lillie, 1919: figs. on pp. 212 and 213) and in the House Sparrow (*Passer domesticus*) and Red-winged Blackbird (*Agelaius phoeniceus*) (Witschii, 1956: figs. on pp. 326 and 316-317, respectively). Neither of these authors mentioned the muscle; unless one takes particular note of it, the enlargement seems to be a part of the usual cervical flexure. Pohlman (1919:98) noted that *M. complexus* reached its maximum development at about the 20th day of incubation and rapidly became smaller after hatching.

Despite the manner in which these two develop together and the apparent function of the mechanism, doubt has been cast on the ability of this muscle to contract vigorously. At least part of the

increased size is accumulated lymph. Pohlman (1919:101), who studied this muscle in some detail, stated that the lymph hinders muscular action and that this muscle "... is relaxed at the time of picking through the shell."

This paired muscle overlying *M. spinalis* and *M. biventer cervicis* originates from the neural spines of cervical vertebrae 3, 4, 5 and from fascia overlying the deeper muscles. It inserts fleshily and widely on the posterior edge of the parietal bones (Figs. 1 and 2). The muscle is composed of three segments separated by tendinous intersections; the segments are not usually visible from the 19th day of incubation to the 2nd day of age. A large lymph gland lies along either lateral surface of the muscles.

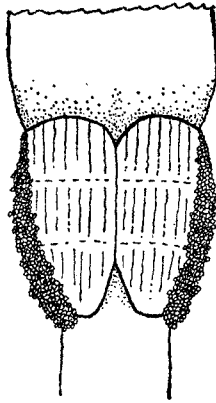


FIGURE 2. Diagrammatic dorsal view of *M. complexus* of chick at two days of age.

The homology of this transitory muscle is uncertain, but it is evident that the muscle is in an excellent structural position to provide a strong upward thrust of the egg-tooth.

Pohlman (1919:102) discounted the role of *M. complexus* in hatching. He believed that the extension was largely in the cervical region and that the force involved was touched off by a respiratory reflex—the drinking-choking reflex which is characterized by extension of the neck and head (Pohlman did not mention head-extension, although it is quite evident in this reflex in adults.) This reflex is reported to result from distention of the abdomen when the yolk sac is absorbed, or perhaps injected, into the digestive tract by *M. levator ani*, according to Pohlman.

In view of the conflicting opinions of Keibel and Pohlman, it was felt that further study of the development of this muscle and its function would be valuable.

MATERIALS AND METHODS

Eggs of Rhode Island Red chickens were incubated and samples taken daily, starting at 15 days of incubation; prior to this stage the muscle is so small that biometric study would involve large errors. Numbers of young so sacrificed are indicated in the tables. Forty-three pipped, but unhatched eggs were obtained on the 20th and 21st days of incubation; in most instances the embryos were already dead.

When the embryos were removed from the egg, the yolk sac was clipped off near the body. Surface moisture on the feathers was removed by gentle blotting, and the embryo was weighed to the nearest tenth of a gram. The muscle was dissected out, weighed in milligrams on a Roller-Smith torsion balance, and then immersed in Bouin's fixative.

Later, these muscles were sectioned (cross and longitudinal) and stained in haemotoxylin and eosin for histological study.

In the same recognizable part of each cross-section, counts were made of the numbers of contracted (densely stained) and of relaxed muscle fibers per unit of area. It was thought that these data might indicate stages of maturity and development and might also be an indirect measure of the infiltration of lymph, in that the fibers per unit of area should decrease as they are pushed apart by lymph. The same square-ruled ocular disk was used in all counts. It was difficult to make these counts with 100 per cent consistency from section to section of the same muscle, but variation was about 10 per cent.

Photographs were made of sections typical of the different age groups.

Later, two procedures were used to make it more difficult for chicks to pip the eggs and crack the shells to emerge. Two dozen eggs were hardboiled and the shells sawed transversely to form two cups, after removal of their contents including egg membranes. These paired cups of shells were placed over unhatched eggs at 15 days of incubation. A narrow band of cellophane tape held the cut edges together to form a second layer of shell over the unhatched chick. The second procedure was to wrap a three-fourths-inch wide strip of cellophane tape around the usual plane of pipping and cracking; this was also done at 15 days of incubation.

The reason for the use of these methods was that extra difficulty in hatching might cause excess strain and perhaps hemorrhage in the muscle, if the muscle functioned in hatching.

RESULTS

The segmented condition of the muscle is frequently obscured by the turgidity resulting from the infiltration of lymph. From the 19th day of incubation to the 2nd day of age, the segmentation can be observed only upon dissection. After the chick hatches, the muscle appears to widen anteriorly; the distance between the anterolateral corners of the two muscles increases. The insertion on the skull moves laterally on either side, and *M. biventer cervicis* and parts of the *splenius* complex become visible in dorsal view.

In Table 1 are data showing the gradual increase in weight of the muscle (in per cent of body weight) up to the 20th day of incubation.

TABLE 1

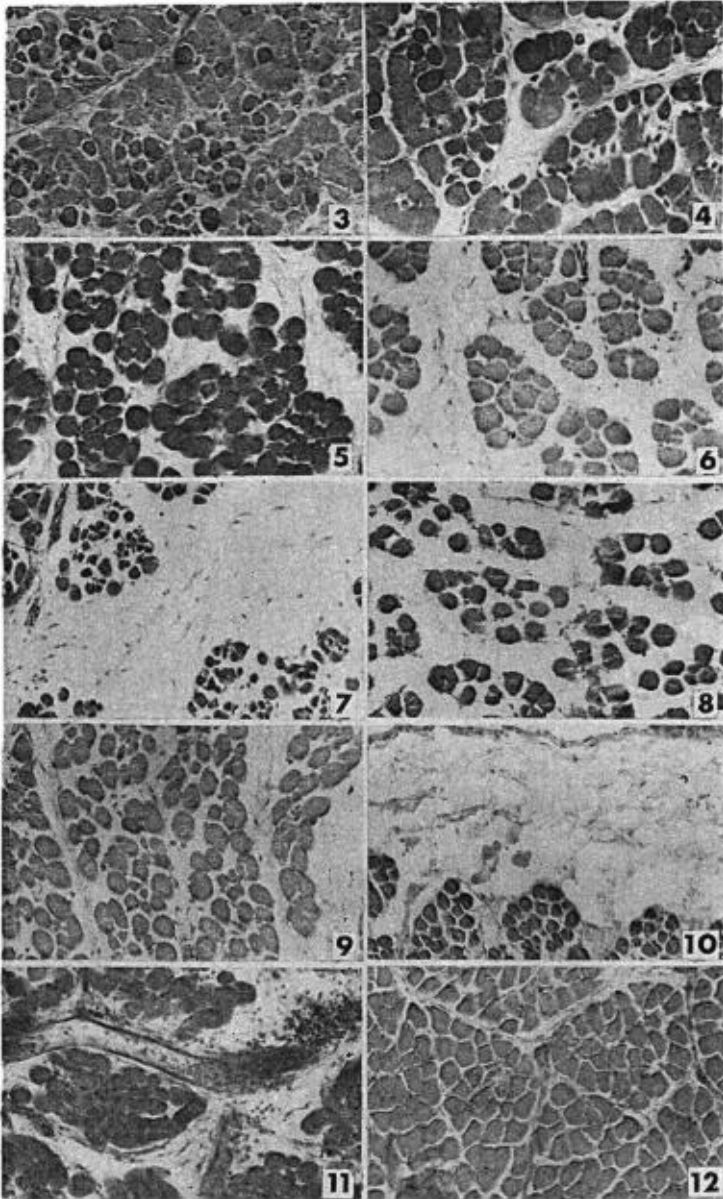
SIZE OF *M. COMPLEXUS* IN CHICKS OF DIFFERENT AGES, IN PER CENT BODY WEIGHT

Age	No. spec.	Mean	Range	St. dev.	Coeff. var.
15 days incubation	10	0.43±0.015	0.381-0.494	0.046	10.7
16 days incubation	10	0.56±0.038	0.376-0.742	0.113	20.2
17 days incubation	10	0.66±0.055	0.335-0.837	0.165	25.0
18 days incubation	10	0.95±0.074	0.627-1.379	0.221	23.3
19 days incubation	10	1.57±0.193	0.745-2.529	0.578	36.8
20 days incubation	10	1.93±0.280	0.689-3.406	0.841	43.6
At hatching	7	1.85±0.324	1.088-3.017	0.795	43.0
Pipped, but not hatched	43	1.34±0.065	0.68-2.41	0.423	31.6
1 day after hatching	10	1.16±0.098	0.60-1.63	0.295	25.4
2 days after hatching	10	1.04±0.084	0.69-1.53	0.252	24.2
3 days after hatching	10	0.63±0.172	0.37-1.93	0.516	81.9
4 days after hatching	10	0.50±0.069	0.31-0.98	0.208	41.6
5 days after hatching	5	0.28±0.022	0.22-0.33	0.044	15.7
6 days after hatching	5	0.49±0.053	0.35-0.63	0.105	21.4
8 days after hatching	5	0.27±0.015	0.23-0.30	0.029	10.7

Size on the 21st day is not significantly different. After hatching, there is a gradual decrease in weight, at least until the eighth day. Note that at 4 to 6 days of age the muscle has about the same gross size as at 15 days of incubation. Further, the maximum increase occurs between the 18th and 19th days of incubation, and the maximum decrease occurs within 24 hours after hatching.

In the 43 chicks which had pipped the egg but could not emerge, the muscle was only 1.34 per cent of body weight compared to 1.93 per cent in 10 embryos on the 20th day of incubation (Table 1). These values are significantly different at the 5 per cent level.

In Table 2 are representative counts of contracted and relaxed muscle fibers per unit of cross-sectional area. The number of contracted fibers decreases rapidly between the 15th and 19th days of



Cross-sections of *M. complexus* of the chick. 15 microns, haematoxylin and eosin. Figures: 3) at 16 days of incubation; 4) at 17 days; 5) at 18 days; 6) at 19 days; 7) at 20 days; 8) at 21 days, hatching; 9-11) pipped but not hatched; 12) chick 5 days of age.

TABLE 2
NUMBER OF MUSCLE FIBERS PER UNIT CROSS-SECTIONAL AREA

<i>Age</i>	<i>Number specimens</i>	<i>Contracted</i>	<i>Relaxed</i>
15 days incubation	8	18 (8-40)	67 (40-86)
16 days incubation	5	11 (1-30)	49 (39-64)
17 days incubation	2	4 (3-13)	38 (32-46)
18 days incubation	4	3 (1-5)	40 (26-52)
19 days incubation	4	2.5 (1-5)	28 (18-36)
20 days incubation	9	1.1 (0-3)	24 (14-28)
At hatching	10	1.4 (0-6)	44 (27-66)
Pipped only	12	1.6 (0-3)	55 (22-110)
1 day after hatching	5	2.8 (0-7)	42 (30-62)
3 days after hatching	3	0	64 (30-105)
5 days after hatching	2	2.0 (0-4)	70 (32-94)

incubation, reaching its lowest level just prior to and at the time of hatching; there is no significant change after hatching. Numbers of relaxed muscle fibers decline gradually from the 15th day (67) to the 19th and 20th days (28 and 24, respectively) and then gradually become more numerous (70) on the 5th day after hatching. There was no observable difference in numbers of contracted fibers between chicks which pipped the shell but did not emerge and the chicks that hatched; but there were 25 per cent more relaxed muscle fibers per unit area in the "pipped" than in the "hatched" group.

Photographs (Plate 21) show the changes. In Figure 3 observe the numerous contracted fibers and the closely approximated muscle fibers. Note that contracted fibers are few after 17 days of incubation, and that there is a progressive separation of the bundles of fibers (Figs. 5-7) by the infiltration of lymph. By the 20th day (Fig. 7) the fibers are separated within the bundles, and lymph fills the central part of the muscle. Figure 8 shows that great infiltration is still present between and within the bundles of fibers; however, the centrally-located mass of lymph is not as obvious. The accumulation of lymph in the thin layer of connective tissue surrounding the muscle (Fig. 10) follows the same pattern. After hatching, there is a gradual decrease in lymph content until at least the 8th day, but the muscle already shows a nearly normal condition when the chick is five days old (Fig. 12).

Histological examination of the sections revealed that the cross-sectional area of muscle fibers was apparently less at 20 days of incubation (Fig. 7) when the greatest amount of lymph was present. Six of the nine chicks examined at this age showed this lesser area, but no quantitative studies were made of it.

Gross examination of the M. complexus in chicks which pipped the egg but did not emerge revealed diffuse to massive hemorrhages. Such bleeding occurred in 39 of 43 of these chicks, but in only 3 of 67 control chicks examined before or at the time of hatching. Microscopic examination of these tissues showed typical hemorrhages (Fig. 11). It is also interesting to note that, in these embryos which failed to hatch, the muscle fibers appear larger and closer together (Fig. 9) than in chicks of the same age that have hatched (Fig. 8).

Only 11 chicks emerged from the 24 eggs which had the experimental double shell; only one of the six eggs with cellophane tape hatched. In both these experiments the unbroken eggs contained fully developed chicks which in most instances were still alive at 22 days of incubation.

Twenty-seven of these 30 chicks showed slight to heavy hemorrhages in M. complexus. Two of the three chicks without the hemorrhages were ones that managed to hatch. It is possible, but not probable, that diffusion of oxygen was hindered by these procedures. However, this uniform hindrance could not account for the differential results obtained.

Five chicks in these series produced from two to four separate pips in attempting to hatch; two pipped the inner shell but were unable to break through the outer, added shell; and one pipped the shell in four places beneath the tape before finally breaking off the small end of the egg and backing out of the shell. The four pips were in a 220-degree arc around the larger end of the egg.

DISCUSSION AND SUMMARY

Wet weight of the paired M. complexus increases rapidly, relative to body weight, at least from the 15th to the 20th day of hatching and with the major increase between the 18th and 20th days. Relative weight on the 21st day is approximately the same as on the 20th day, but there is a marked decrease in wet weight for three days after hatching, followed by a gradual decline at least until the 8th day of age.

In general these trends in size are similar to those reported by Pohlman (1919) for Rhode Island Red chickens. However, his graph (chart 1, p. 93) and Table 3 (p. 94) show the maximum weight on the 21st day. On page 98, he stated that "... the complexus muscle attains its maximum development at the twentieth day of incubation"; this is in agreement with the findings of the present study.

It is of at least momentary interest that the wet weights reported by Pohlman are less than those in this study, prior to hatching time, but agree well with the present ones for chicks one to eight days of

TABLE 3
WET WEIGHTS OF *M. complexus*

Age	Pohlman		Fisher	
	mgms.	% body wt.	mgms.	% body wt.
19 days incubation	234	0.46	428	1.57
20 days incubation	350	0.68	542	1.93
21 days incubation	656	1.44	456	1.85
1 day of age	416	1.09	473	1.16
2 days of age	325	0.87	376	1.04
3 days of age	262	0.76	247	0.63
5 days of age	150	0.39	135	0.28
8 days of age	95	0.27	135	0.27

age. I can see no significant explanation for the differences in weights during the incubation, since the post-incubation data agree. The most logical explanation is that Pohlman's 19-day chicks were really at 18 days of incubation (wts. for 18-day chicks in the present study averaged 234 mgms.). If this be the explanation, then the muscle reached its greatest size at 20 days in his chicks, not 21 days.

When the weight of the muscle is considered relative to body weight and the present data are compared to Pohlman's, there is close agreement after hatching, but inconsistencies prior to this time. Embryos in this study had muscles as large at 16 and 17 days as Pohlman's had at 20 days. Pohlman stated (p. 92) that his series represented "... roughly the 19th, 20th, and 21st day. . . ." Thus, I believe the present data, obtained from eggs laid within an eight-hour period, refrigerated overnight, and then incubated, provide a more accurate picture of development.

There can be little doubt as to the infiltration of lymph. Pohlman demonstrated this by comparing wet and dry weights of whole muscles, and weights of solids and of lymph. Counts of sections through muscle fibers show a decreasing number per unit area from the 15th through the 20th day of incubation, with a gradual increase thereafter until the 5th day of age when the fiber count is the same as on the 15th day of incubation. These changes are interpreted as results of lymph infiltration—first, between bundles of muscle fibers and, second, between fibers within a bundle—which forces the fibers apart.

Although the infiltration is evident in all muscles, it is most obvious in *M. complexus*. I have no explanation for this difference except to point out the presence of the pair of well-developed lymph glands which lie next to the lateral edge of each *M. complexus*. These glands follow a pattern of enlargement similar to that of the muscle, and I

cannot find any other lymph glands which even approximate the size of these.

Pohlman (1919:103) has postulated that the infiltration results from the absorption of the yolk sac, the resulting pressure, and perhaps an excretory malfunction. There seems to be little evidence for or against this theory.

The function of M. complexus, and even of the egg-tooth, has been questioned. Rosenstadt (1912) regarded the egg-tooth as a "phylogenetically old organ" which has "no particular physiological significance." Keibel (1912) thought M. complexus was the primary factor making the egg-tooth effective, but Pohlman (1919) believed that the infiltration of lymph was great enough to make the muscle ineffective. Although Daniel (1957:353) noted that the spinalis and biventer muscles were somewhat heavier in the Red-winged Blackbird than in the chick, he also observed that these muscles in the Red-wing are used in extending the head and neck when food is begged. If this be a primary function of these muscles, one would not expect their efficiency (measured by size) to decrease so soon after hatching. All evidence has been and is either speculative or circumstantial.

The coincidence of hatching and the best development of a transitory muscle may or may not be significant. The fact that the muscle in chicks which pipped the shell but did not emerge was significantly smaller than in just-hatched chicks seems to be important. It is a curious fact that there appears to be less infiltration of lymph in chicks which are fully developed and pip the egg, but do not hatch. If lymph does hinder the action of muscles, and if accumulated lymph is the factor hampering the activity of M. complexus, the muscle in these chicks should be better able to carry on its function; yet these chicks can not break out.

There are, of course, many other possible factors in failure to hatch. Further, hemorrhages in the M. complexus of these "picker" chicks and in the experimental series where additional shells or tape were added might indicate excessive strain when the muscle is being used to pip the egg. At the same time, it is possible that the increased pressure, postulated by Pohlman, ruptures the vascular capillaries. If so, why do these ruptures occur for the most part only in M. complexus?

Interpretation of the "contracted" muscle fibers is difficult. In Table 2 and in the photographs it is evident that their numbers decrease from the 15th to the 20th days of incubation, a period of time corresponding to the accumulation of lymph. This could be construed to mean that the lymph is "forcing" relaxation of the fibers,

which would support Pohlman's thesis of lymph hindrance. However, the number of these contracted fibers is apparently the same in the 21-day, just-hatched, and "picker" chicks, despite the lesser infiltration of lymph in the latter chicks. In addition, the "picker" chicks show a much greater proportion of their lymph in the connective tissue on the dorsal side of the muscle (Plate 21, fig. 10); here, it might be presumed, the pressure of the lymph and its effect on the fibers would be less than when the lymph is deeper and actually surrounding bundles and individual fibers.

Although the evidence is far from conclusive, my present belief is that the egg tooth ruptures the shell at hatching and that *M. complexus* provides the power.

SUMMARY

M. complexus is a muscle extending from the vertebral column to the dorsal surface of the head. Its action is to raise the head and bill. The muscle is apparent at 7 days of incubation, reaches its maximum size at 20 or 21 days of incubation, and then gradually disappears. This developmental history parallels that of the egg-tooth, which is thought to be effective in pipping the egg shell at the time of hatching. Histological study of the muscle and experimental procedures indicate that *M. complexus* is active at the time of hatching. It is believed that the muscle aids in forcing the egg-tooth against the shell.

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