TOOTH SUCCESSION IN THE SMOOTH DOGFISH, MUSTELUS CANIS

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The arrangement of the teeth of sharks in a series of rows is well known. In some species, such as tiger sharks and sand sharks, with large conical teeth, newly formed teeth appear to be formed in the back rows while older teeth are in front. This impression led Owen in 1866 to state, ". . . the whole phalanx of their numerous teeth is ever marching slowly forwards in rotary progress over the alveolar border of the jaw, the teeth being successively cast off as they reach the outer margin, and new teeth rising from the mucous membrane behind the rear rank of the phalanx." Owen's theory of tooth replacement in sharks is the commonly accepted one today and is found in most comparative anatomy texts. This theory apparently was based only on morphological evidence without experimental proof; a search of the literature has failed to reveal reports of any experiments testing the theory. However, the morphological evidence is quite convincing and accounts for the general acceptance of the theory.

Within recent years Owen's hypothesis has been challenged by Cawston in a series of papers (1939; 1940a, b, c; 1941a, b, c; 1944; 1945). He has doubted that sharks shed their teeth but if they do he denies the possibility of replacement occurring by the forward movement of teeth from the rear. That sharks shed their teeth is confirmed by Breder (1942) who noticed the sloughing of teeth by sand sharks (*Carcharias littoralis*) in the tanks at the New York Aquarium. Whether the lost teeth are replaced and the manner of this replacement if it occurs apparently has not been observed. It is the purpose of this investigation to inquire experimentally into the question of polyphyodonty in selachians.

Materials and Methods

It was thought at the beginning of this work at Woods Hole, Massachusetts, that both the spiny dogfish (*Squalus acanthias*), and the smooth dogfish (*Mustelus canis*) could be used. However, the spiny dogfish would not live in the aquaria. Perhaps this may be caused by normal summer salt water temperature in Woods Hole being lethal for the spiny dogfish but not for the smooth dogfish. This was suggested by William Schroeder, Jr., of the Woods Hole Oceanographic Institute who in conversation with the authors pointed out the coastwise migrations of the spiny dogfish paralleling temperature isotherms.

Since *Squalus* proved unsatisfactory, *Mustelus canis,* collected at Woods Hole, Massachusetts, were used in these experiments. A total of 23 adult animals were used, one group of 12 in the summer of 1946 and a second group of 11 in the summer of 1947. The animals ranged in size from 14½″ to 39″ with the majority being over 24″ in length; 11 were males, 12 females. They were kept in a large paraffin-lined cement tank supplied with running sea water and were fed every other day on chopped fish.

The dogfish were anesthetized by cooling in ice water according to the method of Parker (1937) and a varying number of teeth, as described below, were removed with forceps from the lower jaws. In order to follow the movements of the remaining teeth they were marked with silver nitrate solution precipitated with stannous chloride. While the stain subsequently was worn away from the surface of the teeth, sufficient amounts remained on the sides of the teeth to mark them adequately. This species has pavement teeth, somewhat diamond-shaped and arranged in compact rows (see Fig. 3). Sections were made of the jaws using both paraffin and celloidin technics following decalcification. Mallory's stain as well as haemotoxylin and borax-carmine was used.

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Experiments and Observations

The preliminary experiments were designed to determine if tooth replacement occurs in *Mustelus*. For this purpose 12 animals were divided into four groups. In the first group of three animals, six teeth of the first row in the mid-line of the lower jaw were removed. These animals died six, eight, and 11 days respectively after the operation. The cause of death was not ascertained although it probably was not the result of the operation since one of the unoperated controls died during the same period. The teeth were not replaced in this period. Serial sagittal sections at 10 μ revealed no change had taken place and the jaws presented the usual appearance with tooth buds in successive stages of development posterior to the area of the erupted teeth.

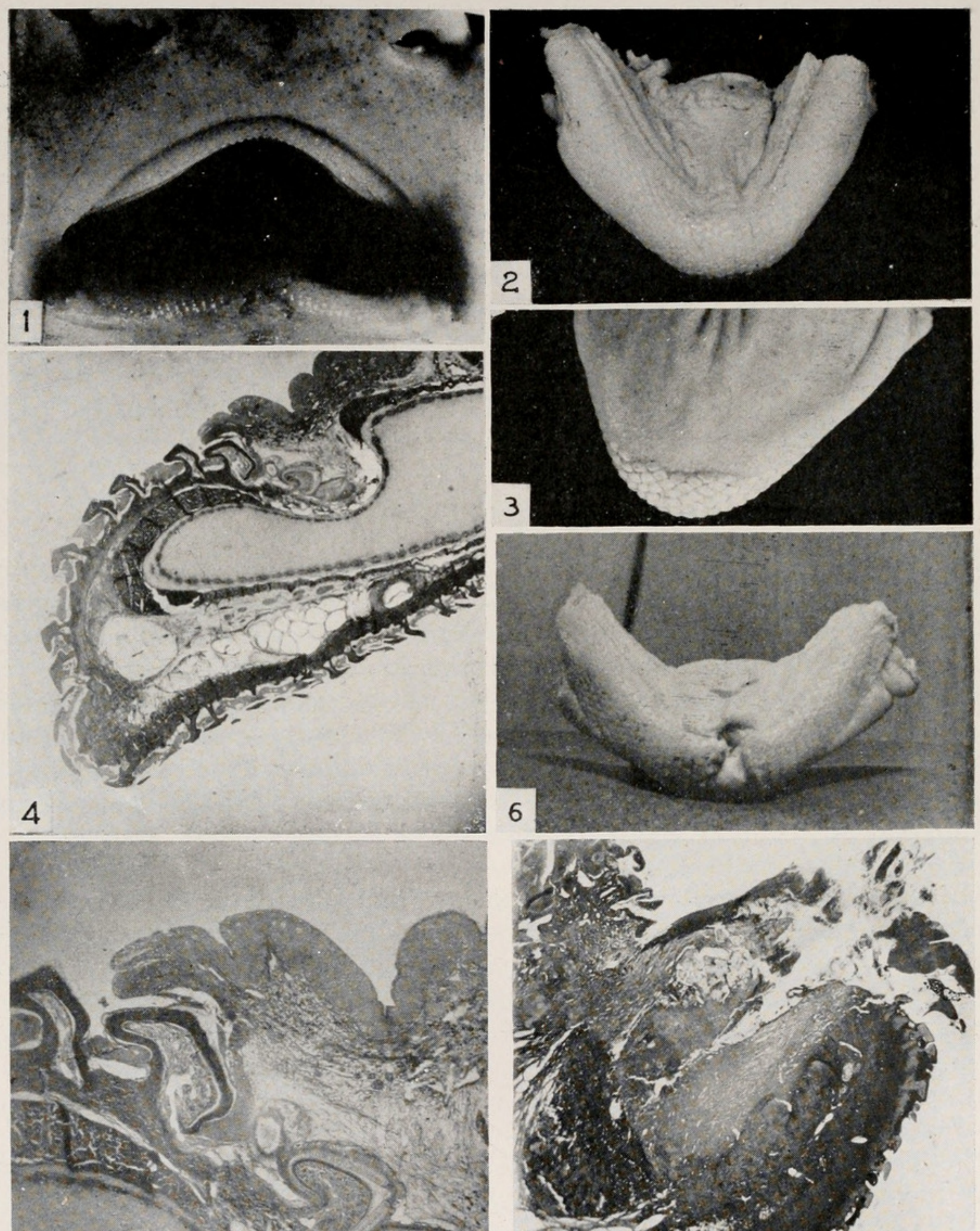
The second group contained four animals from each of which 22 teeth were extracted from a triangular area, five rows deep; the apex of the triangle pointed posteriorly. Figure 1 is a photograph of a jaw of this group. Two of the fish died before replacement occurred, after eight and 12 days respectively. The remaining two replaced the teeth within 50 days. Figures 2 and 3 are photographs of the jaw of one of these latter fish. It can be seen that the replaced teeth are arranged in the normal pattern. Sections of these jaws also were normal in appearance (Fig. 4).

The third group of three animals had the first row of teeth removed. Two died on the following day but the third had replaced the teeth when examined 93 days later. The rate of replacement was not obtained for this animal.

The fourth group consisted of the two control animals. Both were anesthetized by cooling but were not operated upon. One died the following day, the other in 18 days. The cause of death was not determined although the method of anesthetizing might have been a contributory cause.

The second series of experiments were designed to discover the manner in which the tooth replacement occurred. The 11 dogfish of this series were divided into three groups. In the first group of four, each of the fish had 12 teeth in all ex-

Plate I



tracted from the anterior first two rows in the center section of the lower jaw. The remainder of the teeth with the exception of the two first rows lateral to the extracted area were marked with silver nitrate. One animal died on the ninth day and no change in the teeth was found. The other three were examined 25 days later and all had replaced the extracted teeth with teeth bearing silver nitrate marks. In addition, the teeth lateral to the extracted area, previously unmarked, now were replaced by teeth bearing silver nitrate markings. This would seem to indicate, therefore, that within the 25-day period, two rows of teeth moved forward and replaced the former first two rows.

The second group of this series consisted of five animals in which either two, three, or four rows in the center section were removed, and the tooth-bud area back of the region from which the teeth had been extracted, was cauterized with an electric cautery. Four of these animals died in three, five, 12 and 13 days respectively. The remaining animal of the group lived and was killed 25 days later. In the three cauterized dogfish living 12, 13, and 25 days the tooth area in front of the region cauterized was disorganized: many teeth in addition to those extracted had fallen out and only a few scattered teeth remained in the center area. Figure 6 is a photograph of the jaw of one of these fish. No replacement of teeth had occurred in any of this group including the animal killed after 25 days. A section (Fig. 7) from this latter dogfish taken through the cauterized area and the region anterior to it shows the drastic disorganization resulting from the cauterization. The tooth buds were destroyed and parts of the jaw cartilage degenerated. The oral epithelium and underlying connective tissue appeared to be sloughing off.

The third group contained two animals in which all but the first two rows of teeth were marked with silver nitrate but no teeth were extracted. Both of these fish died six days later; there were no observable changes in the teeth.

Certain general observations of the teeth were made. It was found that the first or outermost row of teeth was irregular while the preceding rows are quite regular. This would seem to indicate that the teeth are normally lost singly from the first row as has been observed in other species. Great regularity was observed in the posterior rows and in the animals examined there were no indications of tooth-loss except in the first row. The number of exposed rows of teeth varied from eight to 11. No sexual differences in the teeth were seen. The arrangement of the teeth in the upper jaws appeared to be similar to that of the lower jaws.

PLATE I

FIGURE 1. View of jaws of dogfish showing triangular area in center of lower jaw from which teeth have been extracted. About one-third natural size.

FIGURE 2. Dorsal view of jaw of animal in Figure 1 fifty days after removal of teeth showing the complete replacement of the teeth. About one-third natural size.

FIGURE 3. Ventral view of jaw in Figure 2. About one-third natural size.

FIGURE 4. A sagittal section at 10 microns of the jaw seen in Figure 2. Tooth buds can be seen back of the erupted teeth. About $\times$ 10.

FIGURE 5. A view of the tooth bud area from Figure 4. About $\times$ 33.

FIGURE 6. A dorsal view of a jaw in which 4 rows of teeth were removed in the center section and the tooth buds back of this region were cauterized. No replacement had occurred after 25 days. About one-third natural size.

FIGURE 7. A sagittal section at 10 microns of the jaw seen in Figure 6, showing the disorganization resulting from the cauterization. About $\times$ 10.

Tooth-bud areas were never found except behind the tooth-bearing region. Figure 5 is a photograph of the tooth-bud area. The tooth buds can be seen to be progressively larger and more mature in a postero-anterior direction. Particular care was taken to search for buds underlying the outermost rows but none were found. It would appear, therefore, that the only source of new teeth are these buds back of the erupted tooth area.

Conclusions and Discussions

From the experiments described above it seems apparent that in *Mustelus canis* teeth can be replaced and that this replacement occurs in the manner hypothecated by Owen; that is, by the moving forward of the teeth from the rear. The fact that marked teeth from posterior areas were seen later to occupy areas where teeth had been removed seems conclusive evidence in favor of Owen's view. It is not certain from the experiments what the normal rate of replacement is since the animals which were to have been used to test this point died before such information could be obtained. However, the rate of replacement in the operated animals was quite rapid, being approximately of the order of one row replaced in ten to twelve days.

The experiment in which the tooth buds back of the center area of the jaw were removed by cautery was done to determine whether replacement occurred in the absence of the posterior tooth buds. In the one surviving animal replacement had not taken place although in the same length of time non-cauterized dogfish did replace teeth. While the experiment apparently bears out the role of the posterior tooth buds in replacement it may be criticized on the ground that the unexpected general disorganization and degeneration resulting from the cauterization would prevent replacement from any source. However, even if this experiment is omitted from consideration, there is sufficient evidence from the other experiments to support the contention that Owen's hypothesis is correct.

From a study of Cawston's papers it would appear that his views are based on gross examination only and without a study of histological sections. Otherwise it is difficult to account for his statement (1941a): "New tooth formation behind the normal number of rows of teeth in species of shark has never been observed, though dental germs should be present if the alleged replacement of teeth by revolving of the gum forwards ever occurred in adult specimens." In the same paper he also states: "At the anterior border of the teeth of *Mustelus canis* (Mitch.) one sees round or oval dental germs in process of development into the flattened closely set teeth of the adult, which reveal the characteristic wrinkled surface very early." As we have noted earlier, and as can be seen from the photographs of the sections (Figs. 4, 5), tooth buds are found back of the erupted teeth and are not found in the front region of the jaw. There is no evidence that new teeth are being formed in the front row of *Mustelus.*

In a later paper (1944), Cawston states that there is no provision for replacement of lost teeth in selachians and that growth may continue throughout life. In earlier papers (1939, 1941a) he considers that a tooth is renewed at the site where one is lost. He considers that this replacement obtains by vertical succession (1941b). Unless we are misinterpreting the statements it would appear that Cawston's viewpoint has changed from a possibility of vertical succession in tooth replacement to the hypothesis that no replacement of any type occurs.

Other observers besides Owen have concluded by studying the morphology of the jaw that replacement occurs by the forward movement of the back teeth. For example, Budker (1938) states: "Lorsque la dent est tombée, une autre, dite 'dent de remplacement' et provenant des rangées de remplacement disposées derriere les rangées fonctionelles, vient prendre sa place." This author also observed that tooth buds did not develop at the site of the lost tooth.

The cause of the falling-out of the teeth was also studied by Budker in various species such as *Scyliorhinus canicula*. He accounted for this loss by the destruction of the dentinal basal plates which anchor the tooth in the underlying connective tissue by specialized cells similar to osteoclasts which cells also reduce the dentine of the older tooth as a whole. Benzer (1944), on the other hand, reports that the dentine of *Mustelus* grows progressively thicker in older teeth. He did not note that the dentine was later destroyed.

The jaws of ten other species of sharks were examined by the authors through the courtesy of Mr. Schroeder at the Museum of Comparative Zoology at Harvard University. Included in the group were three species of the Port Jackson shark (*Cestracion* or *Heterodontus*) which have pointed biting teeth in front and flat crushing teeth in the remainder of the jaw. It was observed, however, that the teeth in any section of the jaw are the same in an antero-posterior direction and consequently could be replaced in the manner described for *Mustelus*. No morphological indications were found in any of the other species examined contradicting Owen's hypothesis.

Summary

1. Twenty-two teeth extracted in a triangular area five rows deep from the front of the tooth-bearing region of the lower jaw of *Mustelus canis* were replaced within 50 days.

2. Marking of the posterior teeth with silver nitrate indicated that extracted teeth were replaced from behind by these marked teeth. The replacement rate was approximately one row in 10 to 12 days.

3. Tooth buds were found only back of the erupted teeth and never elsewhere.

4. Destruction of the tooth buds by cautery prevented replacement.

5. It is concluded that Owen's hypothesis of the replacement of sharks' teeth by the forward movement of the posterior teeth is correct and that Cawston's objections to the theory are not tenable.

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