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A. GORDON EDMUND

Sequence and Rate of Tooth Replacement in the Crocodilia

OYAL ONTARIO MUSEUM — UNIVERSITY OF TORONTO

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INTRODUCTION

The orderly replacement of teeth in the lower vertebrates was discussed in detail by Edmund (1960). It was noted that crocodilians apparently are an exception, in that they frequently display a random distribution of teeth in all stages of replacement.

The present study, based on examination of crocodilians of all ages, explains this deviation from the common orderly sequence, and presents data on the time required to complete the replacement process.

HISTORY

Dentitions of crocodilians, especially embryonic crocodilians, have been intensively studied by numerous workers including Röse (1893), Bolk (1912), and Woerdeman (1919 and 1921). All agree that there is a continuous replacement of teeth intiated long before hatching. In the field, Adams (1867) found "quantities of deciduous teeth of various sizes strewn along the slimy sides of the pond" inhabited by crocodiles. Ditmars (1933) similarly noted that often a dozen cast-off teeth were found each week in a pool in the New York Zoological Park which contained five large alligators.

McIlhenny (1935) gave an interesting account of the life history of the American alligator. His description of the dentition contains the only verified statement known to the writer to show that tooth replacement in alligators ceases in old individuals. He states that the only way he could recognize a really mature animal is by an examination of the teeth, the walls of which have been greatly thickened by the deposition of dentine, at the expense of the pulp cavity. Smith (1958) briefly mentions crocodilians in connection with implantation and oligophyodonty. The most recent general view of the literature on crocodilian dentition is Wettstein (1937). Kvam (1958 *et seq.*) is currently active in the field of crocodilian tooth replacement.

It has long been known that the replacement of old teeth by new is a phenomenon common to most, if not all, vertebrate groups. Replacement is greatly restricted in the mammals, but occurs frequently in most lower vertebrates. Furthermore, it was realized that in most groups the teeth are replaced in a definite sequence, and not randomly as a result of wear, injury, etc. Parrington (1936), Romer and Price (1940) and Edmund (1960) showed that this replacement frequently occurs in regular waves passing along the jaw, usually from back to front, affecting alternately numbered teeth. Thus, in any particular area of the jaw, the odd-numbered teeth are replaced by one wave, followed by replacement of the even-numbered teeth by a succeeding wave.

Deeply entrenched in the literature of tooth replacement is the Distichy Theory of Bolk (1912 *et al.*). This states that there are separate loci for the development of odd- and even-numbered teeth. (1) All of the teeth produced at one set of loci comprise one odontostichos. (2) A complete dentition, according to Bolk, is made up of the alternating elements of two odontostichi. (3) This gives rise to simple alternate replacement, i.e., all of the teeth of one odontostichos are replaced at one time, followed by simultaneous replacement of all of the teeth of the other odontostichos.

Bolk described crocodilian embryos in which there appeared to be simple, alternate replacement. The same observation was noted earlier by Röse (1893) and by others. Woerdeman (1919 and 1921) studied crocodilian embryos by serial sectioning, and showed that Bolk's concept of two sites for the production of replacement teeth was in error.

Vorstman (1922) reviewed the work of Bolk and Woerdeman and, while not working specifically with crocodilians, derived some interesting generalities. Unfortunately, the terminology used by Bolk, Woerdeman and Vorstman is confusing and occasionally misleading. Edmund (1960) explained and redefined the essential terminology.

The dentitions of a number of post-embryonic crocodilians were analysed by Edmund (1960) who remarked that the regular pattern of replacement seen in other archosaurs was often lacking. Some specimens had replacement occurring in waves progressing from back to front. In others the reverse was noted. Some showed no recognizable pattern. Since this differed so markedly from the usual reptilian pattern, and from the simple pattern described by Bolk, the need for further study became obvious.

METHODS

Unfortunately, all of the previous tooth replacement studies have utilized only dead material. Usually these have been ample to demonstrate the existence of a replacement pattern (Edmund 1960). The dead animal, however, gives us only a still picture of the process, whereas a live animal can provide not only a dynamic moving picture of the process, but also supply a measurement of the time involved in the process. Crocodilians have the added inherent disadvantage of having their teeth set in thecae which prevent the direct observation of their bases and young replacements except by radiography or destructive preparation.

The use of live animals in tooth replacement studies presents several difficulties. It is usually expensive and inconvenient to keep living speciments of most of the lower vertebrates for prolonged periods. Secondly, their teeth are usually small, so that identification and examination are difficult. Furthermore, it is usually almost impossible to subdue a living animal for the length of time needed for a careful examination.

These objections were overcome by the use of young specimens of *Alligator mississippiensis*, since these crocodilians are hardy, inexpensive, and have relatively large teeth. To solve the examination problem, the animal was subdued with an intraperitoneal injection of the barbiturate "Nembutal". An hour after the injection the animal could be easily handled, yet a few hours later normal activity was resumed. Deep surgical anaesthesia is dangerous and unnecessary.

Since the marking of individual teeth by painting, notching, truncating, etc., is unsatisfactory for various reasons, radiography was selected as the method of observation. The mouth of the animal was propped open with a thin stick and near-lateral exposures were made, one for each jaw quadrant. X-ray protective gloves were used to hold the animal in position during the exposure. By means of lead shields, all four jaws were registered on one sheet of 5 in. × 7 in. film. A 65 K.V.P. dental X-ray unit and Kodak AA industrial film gave good pictures with excellent contrast and fine grain. The use of radiographs permits the observer to see replacement teeth hidden within pulp cavities, to measure the thickness of the tooth wall, and to see the undisturbed spatial relationships within the alveolus.

The radiographs were made at monthly intervals, and were read under a low-powered microscope using bright transmitted light. For record purposes the radiographs can be placed in a photographic enlarger and projected on to bromide paper with good results at up to thirty magnifications. In the present study the height of each tooth at each position was recorded in tenths of its definitive height, and the date of the loss of the remains of the old tooth noted.

DESCRIPTION OF CROCODILIAN DENTITION

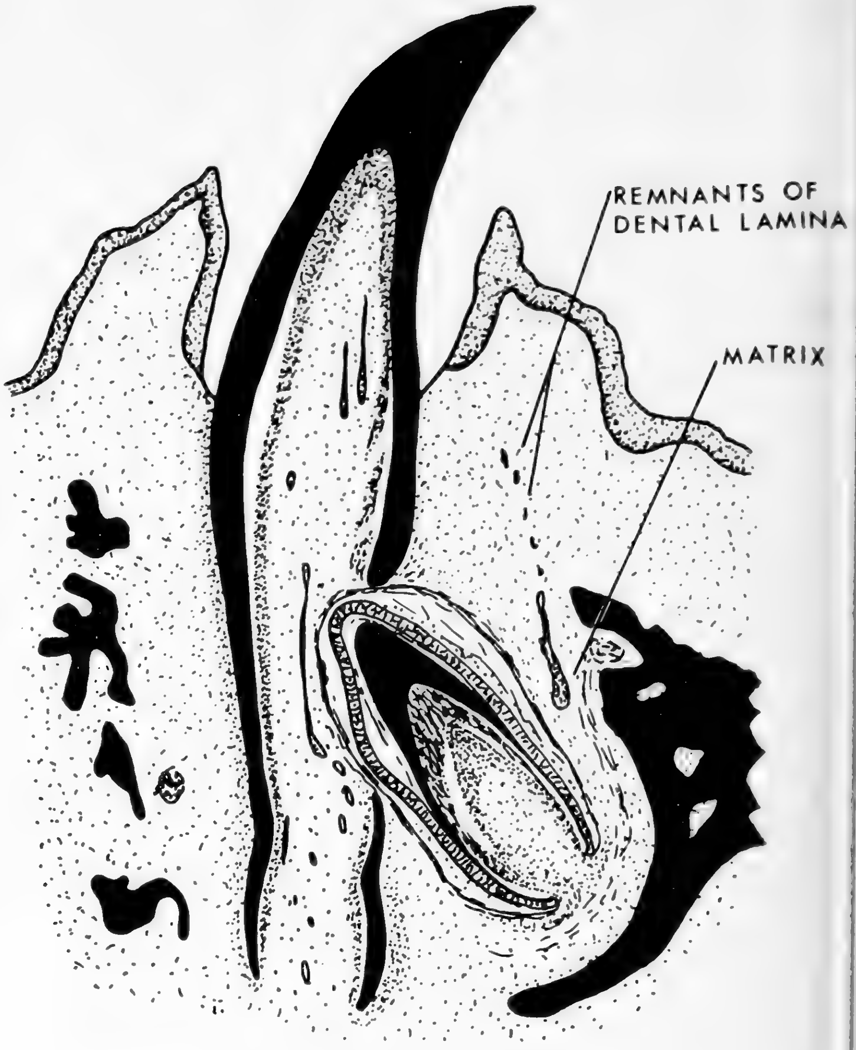
The purpose of this paper is not to describe the dentitions of the various taxa of crocodilians, but to discuss the method of replacement of individual teeth and the rate and sequence in which each tooth in the dentition is replaced.

A typical individual tooth of a crocodilian consists of a crown and a base separated by a more or less distinct neck or constriction. The base is usually relatively thin-walled and the pulp chamber is wide open. The crown has heavy walls, and may contain little or no pulp. The shape of the crown varies between species and between different regions in the same jaws. In most species the anterior teeth are elongate and pointed, while the more posterior teeth are shorter and with rounded crowns. There is usually a "canine" or two in each jaw, one of those in the lower jaw usually fitting into a notch or pit in the upper jaw.

Implantation in the crocodilia is thecodont. Older individuals have all of their teeth set in discrete sockets, while in very young specimens many of the teeth at the posterior end of the tooth rows are in deep, relatively unconstricted grooves, which in later life become divided by inter-dental septa. This process is progressive from front to back. There is no bony ankylosis in the crocodiles. Of all living lower vertebrates only the crocodilians possess a periodontal membrane. Indeed, Owen (1840) remarked that the relation of tooth to alveolus in the crocodile is more similar to that of mammals than that of any other living vertebrates. It is now known, of course, that this condition was probably held in common with all archosaurs.

Figure 1 illustrates the relationship of the replacement tooth to its predecessor. The replacement is always formed in soft tissue directly lingual to the base of its predecessor, close to the open root. There is a distinct crypt at the base of each tooth for the accommodation of the replacement and its attendant structures. Each is confluent with the canal running the length of the maxilla or dentary as the case may be. These canals carry the blood vessels and nerves which supply the teeth, and branches from these

Fig. 1. Frontal section of a lower jaw of an embryo of *Crocodylus porosus*. After Woerdeman.



can be seen forming a plexus in each alveolus around the replacement tooth and its predecessor. This is discussed briefly in Brown and Schlaikjer (1940) and Edmund (1957). A detailed account of the innervation is given by Fischer (1852). James and Wellings (1943, Fig. 10) give an excellent sectional view of a tooth position of a young *Caiman* showing an old tooth with large replacement beneath it, and a very young replacement on the lingual side, attached to a fragment of the dental lamina.

As with all vertebrates, the teeth of crocodilians are formed from germinal material on the free margin of the dental lamina, a plate of specialized, invaginated oral epithelium. The derivation of this is shown diagrammatically in Figure 14. According to Woerdeman (1919), as each alveolus is formed by the division of the dental groove, the dental lamina is divided into clumps of cells, one clump per alveolus. Each of these retains the ability to generate replacement teeth. From time to time, a new tooth is produced by this material (termed the tooth matrix by Bolk) and the new tooth undergoes much of its early development in the crypt.

The series of isolated teeth (Fig. 2) shows the stages in the degradation of the base of an old tooth. When the replacement, lying in its crypt lingual to the base of the old tooth, begins to enlarge, a shallow depression appears on the lingual wall of its predecessor. This depression deepens, and

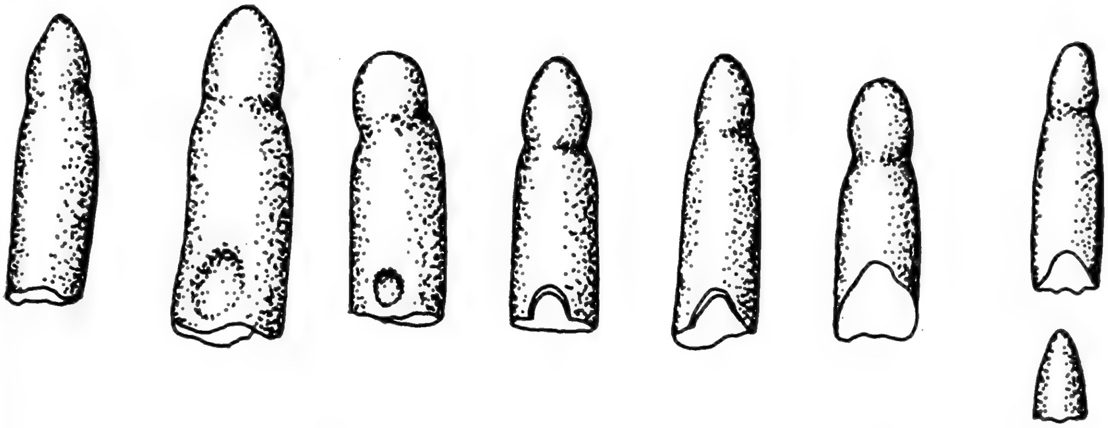


Fig. 2. Teeth from a Pleistocene specimen of *Alligator* mississippiensis, U.S.N.M. 5995, showing successive stages in the resorption of the base. Lingual view.

at the same time the area of the base adjacent to the depression becomes progressively thinner, so that there is produced an emargination or "bite" out of the wall. The replacement passes through this opening and into the pulp chamber. Since the definitive size of the new crown is not larger than that of the inside of the pulp chamber, the new crown, and often its neck as well, can grow to full size without seriously impairing the mechanical strength of the old tooth. As the new tooth approaches full stature, the remains of the old base are resorbed, and the crown, held only loosely by connective tissue, is eventually lost. The replacement tooth has thus grown to a considerable size protected by its predecessor, and is erect and requires only the rapid elaboration of its base in order to become a full-sized functional tooth.

Stages in this process can be seen in the radiographs of adult crocodilians (Fig. 3), many of which show the circular perforations in the lingual side of the tooth bases. This suggests that in many cases the replacement undergoes quite a lengthy period of growth inside its predecessor before the old base suffers much degradation.

SEQUENCE OF ERUPTION

Mention has been made of the regularity of the pattern in which replacement occurs in most lower vertebrates. Since the carnivorous dinosaurs are fairly close relatives of the crocodilians, an example from this group is given for comparison. The theropods were also thecodont, and the young teeth developed in crypts in the alveoli just as in the crocodilia. They differed in that the replacement tooth did not enter its predecessor's pulp cavity at an early stage, but seems to have been associated with a progressive lingual resorption, with the resulting appearance of having dissolved its way into the lingual wall. The new tooth does not become central in the alveolus until it is about half grown, and much of its predecessor has been resorbed. Frequently a replacement tooth can be seen in the alveolus lingual to its predecessor, the latter being still perfectly functional. Because the new tooth is visible during much of its early life, and because it undergoes considerable growth after the loss of its predecessor, the relative age of a tooth can be estimated by the degree of eruption. In the crocodilia this is

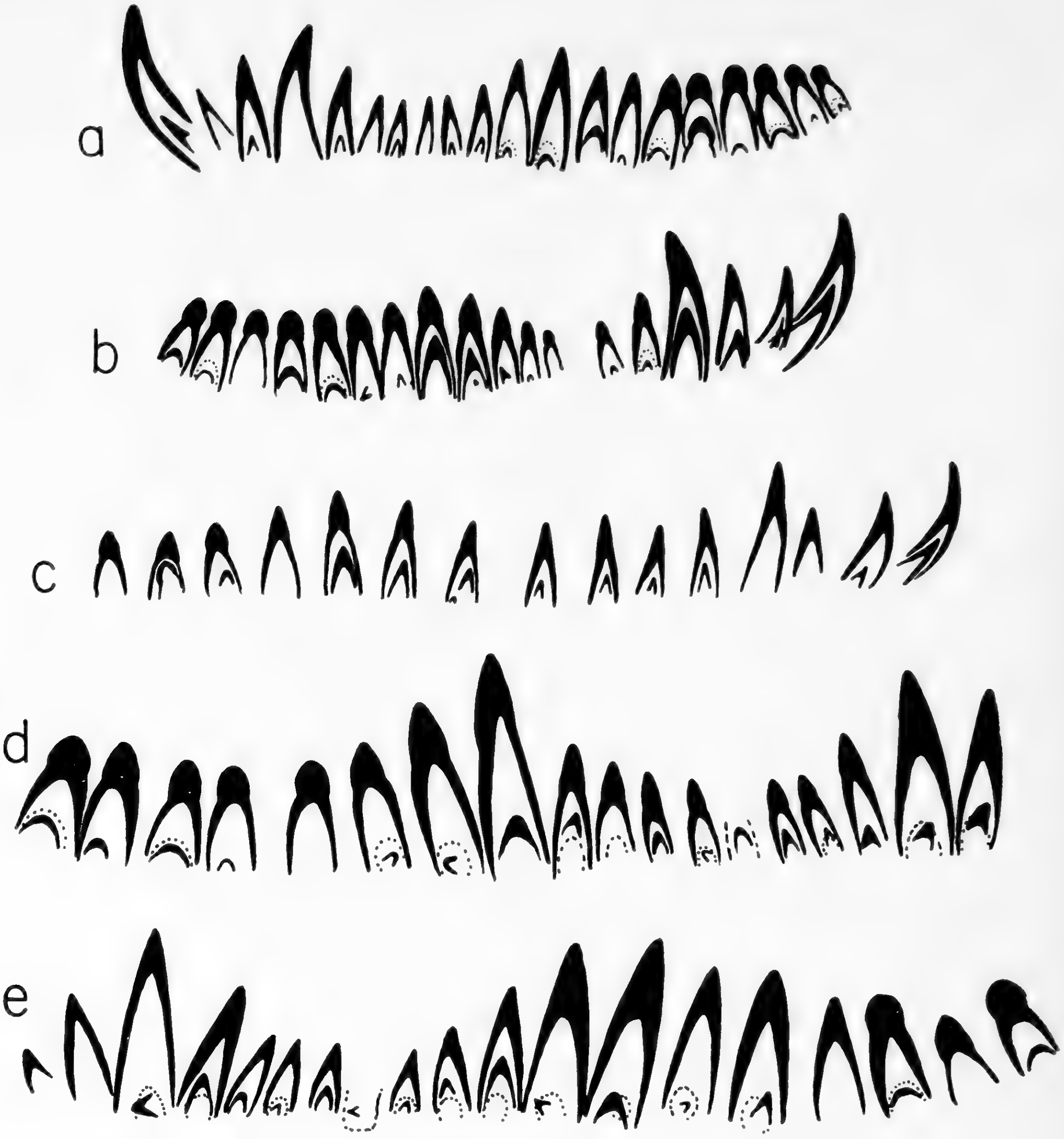


Fig. 3. Radiographs of adult crocodilian dentitions.
a. Caiman sclerops fuscus C.N.H.M. 69852.
b. Caiman sclerops fuscus C.N.H.M. 69852.
c. Crocodylus acutus, C.N.H.M. 5776.
d. Alligator mississippiensis C.N.H.M. 25946.
e. Alligator mississippiensis C.N.H.M. 25946.

impossible without radiographs, since the new tooth is hidden by the cap of its predecessor until a relatively late stage.

A stylized drawing of part of the dentition of *Gorgosaurus libratus* N.M.C. 2120 (Carnosauria, Therapoda) is shown in Figure 4. In the two dental series shown, several of the teeth have not reached their definitive heights. It is obvious that if we consider the odd-numbered and even-numbered teeth as separate series, there are definite sets of teeth grading downward in size from back to front. For example, in Figure 4b, teeth 12, 10, 8, 6 and 4 decline in size toward the front. This indicates that the teeth at the rear are older, since they have had time to develop further. Clearly, there is a wave of replacement passing along the even-numbered series, with the youngest visible tooth at position four, and the wave is progressing cephalad, i.e., mesial, or toward the anterior mid-line.

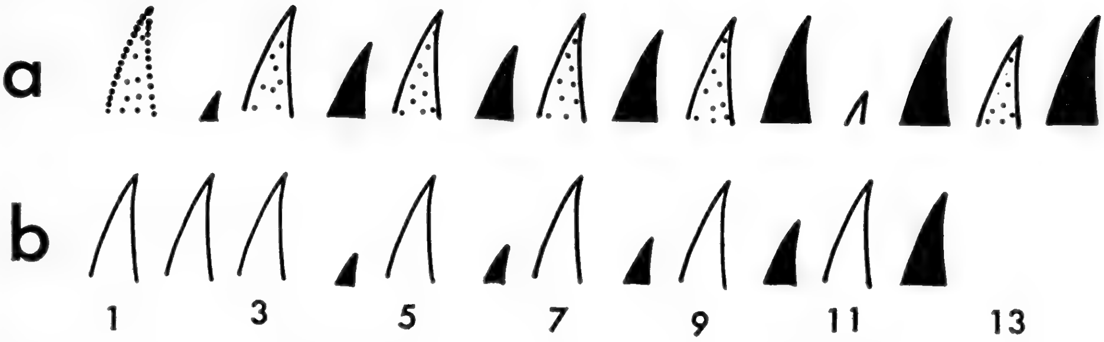


Fig. 4. Diagrams of the dentition of *Gorgosaurus libratus* Lambe. N.M.C. 2120.
a. Right dentary.
b. Right maxilla.

A further noteworthy phenomenon is seen in Figure 4a, where a wave in the even-numbered series has been established by position 10, only to be succeeded by a wave in the odd-numbered series beginning at positions 11 and 13. In every case, a wave in the even-numbered series is followed by one in the odd-numbered series, and vice versa. In jaws with numerous teeth, several such waves follow one another. The explanation for this lies in the synchrony in which the tooth buds are initiated on the dental lamina, and is graphically shown in Edmund (1960). Replacement by regular cephalad waves is the rule in the archosaurs. The writer was surprised to find that the crocodilians formed an exception to the rule, showing both cephalad and caudad waves, as well as instances with no apparent pattern whatsoever.

MATERIALS STUDIED

Both live and dead materials were used. The former, discussed in detail below, give by far the most satisfactory results. Unfortunately, most institutions are not equipped to handle a variety of live crocodilians of various species and sizes for a lengthy period of time.

Dead material consisted of skulls, dried heads with the flesh intact, and preserved specimens. Skulls frequently proved disappointing, since it appeared that during preparation many of the teeth, especially the posterior ones, were dislodged. Because of this, the replacement teeth were lost. Such tooth positions are obvious in the radiographs, the old tooth showing the opening which admitted the replacement but the pulp chamber empty. Often a shadow representing plaster or cement is seen. Consequently, a large proportion of completely cleaned skulls had to be rejected.

Skulls on which the flesh has dried are usually trustworthy for the present purpose, since their teeth have had no opportunity to drop out. Preserved specimens fall into the same category.

Many of the specimens studied were borrowed from the Department of Herpetology, Chicago Natural History Museum, and the writer wishes to acknowledge gratefully the cooperation of Dr. Robert F. Inger and Mr. Hymen Marx. Thanks are also due to Dr. Rainer Zangerl of the same institution, and to Dr. G. H. Poyton of the Faculty of Dentistry, University of Toronto, for assistance in making radiographs of some of the larger specimens.

Because of the obvious disadvantages of using dead material, two live alligators were observed monthly, one for nearly two years, the other for nearly three. Since the results of the two studies were similar, most of the analysis deals with the smaller specimen which was observed for the longer period. Where significant, reference is made to the second animal. The initial skull length of the smaller specimen was about 75 mm., age about one year. The larger specimen had a skull length of about 110 mm. at the start of the experiment and was two or three years old. Despite adequate care and abundant food, the alligators did not increase significantly in size throughout the experiment, yet remained in apparent good health.

OBSERVATIONS ON DEAD SPECIMENS

Because of the indecisive conclusions resulting from the examination of a small number of specimens (Edmund 1960), it was decided to study longer series of modern crocodilians of various ages and species. Consequently, thirty-eight specimens representing eight genera were examined, and graphs, such as those in Figure 5 were constructed from radiographs. These were analyzed to see if trends could be found in the replacement pattern. It was obvious in most cases that the basis of an alternating pattern was present, as in most other reptiles. In a few cases, such as Figure 5, c and d, there was a regular alternation of teeth, with each alternately numbered tooth in about the same stage of the replacement cycle. In other cases, each of the alternately numbered tooth series showed wave-like patterns, with the size of the replacement teeth grading downward either to the anterior (Fig. 5, a and b) or posterior (Fig. 5, e and f). This, of course, indicates that replacement had been occurring in waves passing either cephalad (i.e., mesially or toward the anterior mid-line) or caudad (i.e., distally or away from the anterior mid-line). In most cases there was no difficulty in tracing these waves. This agrees well with the observation in most other reptiles that the two alternately-numbered series in each jaw undergo replacement as more or less independent units, i.e., there is a unity within each alternately numbered series, although the replacement pattern in that series may be simple or complex. In only a few cases, notably in older individuals, (Fig. 5, g and h) was it impossible to detect a regular pattern.

The following data were obtained from the radiographs and from the charts derived from them:

1. Regularity or irregularity of the replacement pattern.
2. Direction of progression of the replacing wave, i.e., caudad or cephalad.
3. Number of teeth involved in each wave.
4. Skull length.

Since no difference between species could be detected for the variables listed, the data will be lumped together in the construction of the graphs (Figs. 6 and 7) and in the ensuing discussion. A list of the specimens used in this study is given in the appendix.

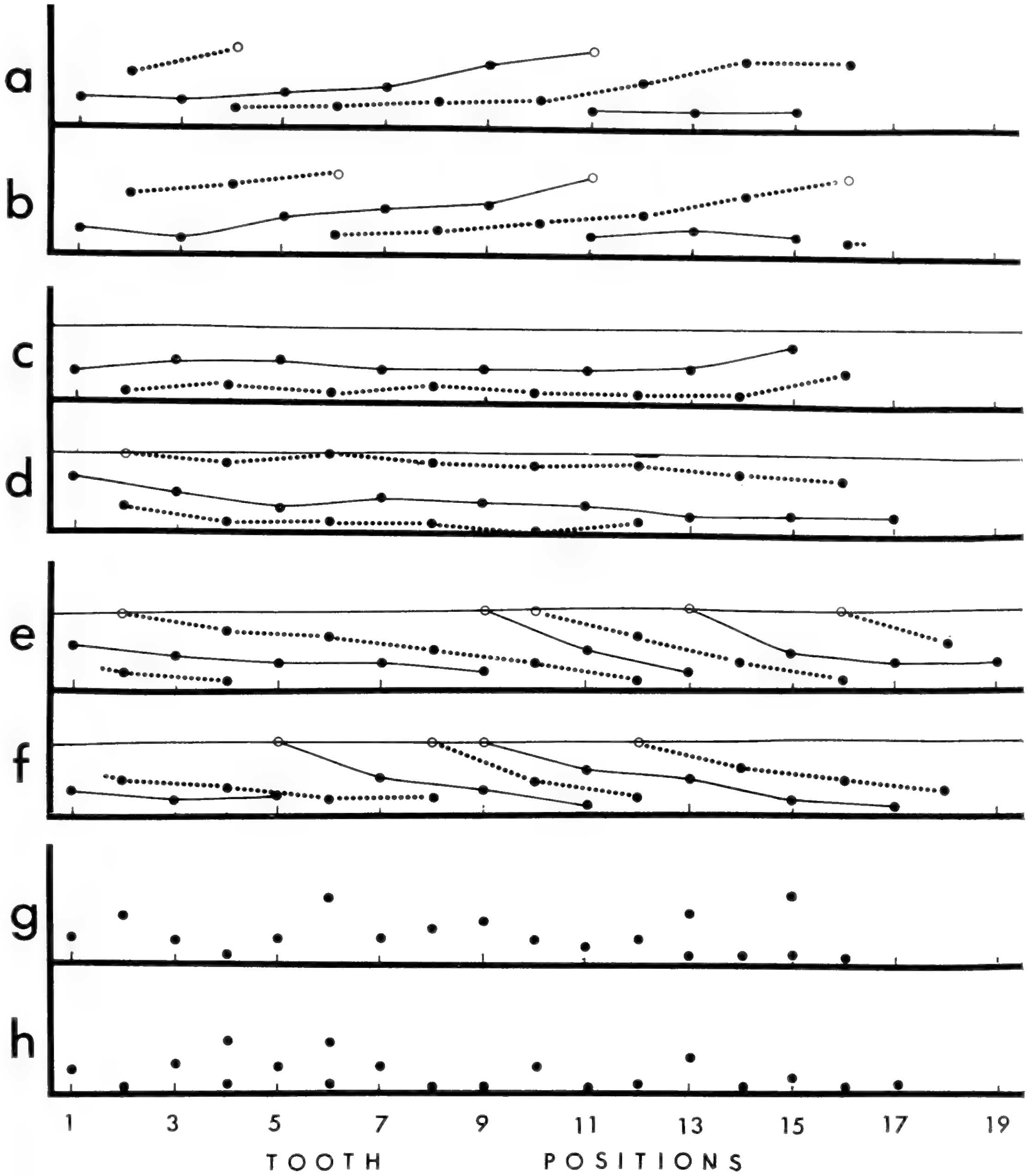


Fig. 5. Tooth replacement patterns in crocodilians.

a. Upper left.
b. Upper right, of *Crocodylus porosus*. R.O.M. R 149.
c. Lower right.
d. Upper right, of *Caiman sclerops*. R.O.M. R 144.
e. Lower right.
f. Lower left, of *Alligator mississippiensis*. C.N.H.M. 6576.
g. Lower left.
h. Upper left, of *Crocodylus sp*. R.O.M. R 264.

REGULARITY OF WAVES OF REPLACEMENT

As was mentioned above, when replacement tooth size is plotted against tooth position number (counting from anterior, midline) as in Figure 5, it is usually possible to detect more-or-less regular trends in the replacement sequence. In many cases the familiar imbricating pattern was noted (Fig. 5, a, b, e, and f) or less frequently, simple alteration (Fig. 5, c and d). In other cases, however, no pattern could be recognized, or else the pattern was so distorted that regular trends were absent, (Figs. 5 g and h). It was

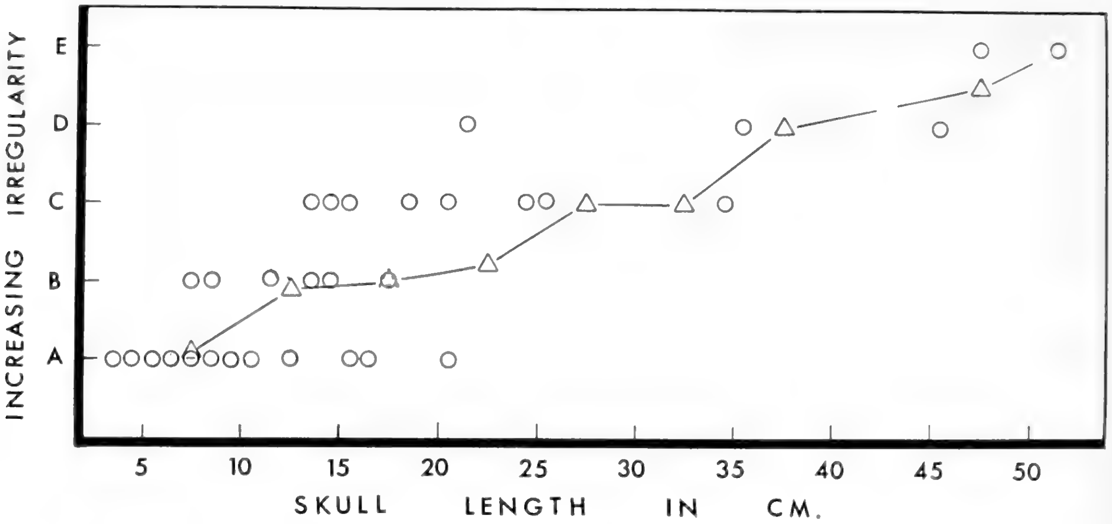


Fig. 6. Graph showing relationship between skull length and irregularity in the replacement pattern of several species of crocodilians. The triangular symbols are running averages; the circular symbols represent individual specimens.

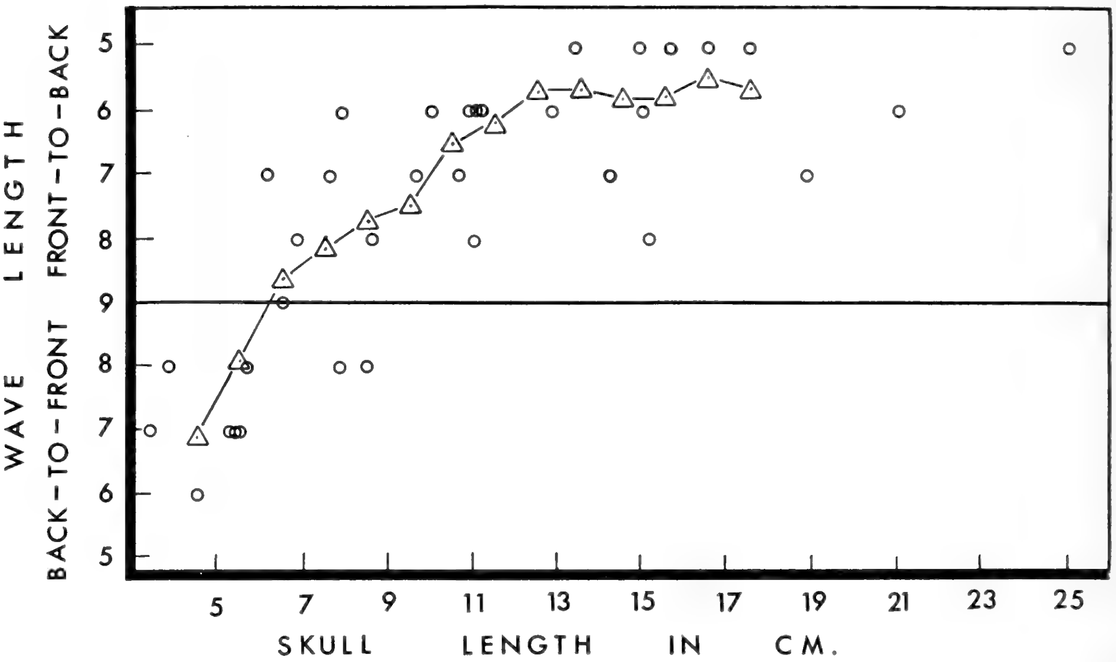


Fig. 7. Graph showing the relationship between skull length and wave length and direction. The triangular symbols represent running averages. The circles are observations of individual specimens.

noted (Edmund 1960) that crocodiles, especially older individuals, often appear to have no regular replacement pattern. To determine if age could be a factor in influencing the regularity of this pattern, regularity was plotted against skull length, which is the best available criterion of age. Degree of regularity was assessed in the following manner:

A. All four jaw quadrants of the specimen show a regular pattern.
B. Three of the jaw quadrants with regular pattern.
C. Two of the jaw quadrants with regular pattern.
D. One of the jaw quadrants with regular pattern.
E. None of the four jaw quadrants with a regular pattern.

When these five classes were plotted against skull length (Fig. 6) it was apparent that irregularity did indeed increase with age. All specimens with a skull length of 7 cm. or less were quite regular in all four jaw quadrants, whereas no specimens above 21 cm. had all four quadrants regular. A suggested reason for this decrease in regularity in replacement comes from the observation of Woerdeman (1919) that the dental lamina becomes discontinuous in older crocodiles. Presumably, when the individual thecae are formed by division of the earlier long groove, the clumps of germinal material lying on the free margin of the dental lamina become separated. Synchrony of replacement is probably dependent on the continuity of the free margin of the dental lamina. It may be that tooth buds are initiated by an impulse, possibly hormonal in nature, passing along the lamina. In the absence of a continuous lamina, the individual clumps of germinal material may begin to function independently, and thus lose synchrony.

DIRECTION OF WAVE PROGRESSION, AND NUMBER OF TEETH PER WAVE

These two factors were plotted against skull length in Figure 7. For each specimen, the wave lengths for all waves in all four jaw quadrants were averaged, so that for reasonably regular specimens, each symbol represents the measurement of at least four replacing waves. To simplify plotting, a wave length of nine or more teeth was considered to show simple alternation, and is plotted as nine on the vertical axis. To indicate the direction of wave progression, the figures in the upper part of the graph represent front-to-back waves, while the lower part shows back-to-front waves. The triangular symbols represent running averages which more clearly show the trend of the scattered points.

The distribution of points on the graph clearly shows that a change in the direction of the replacing wave occurs during life. Very young individuals (in their first year) with skull lengths up to about 6 cm. (as well as a few up to 8 cm.) all showed a wave progression from back to front. Between 6 and 11 cm., some specimens exhibited little or no gradient while many others showed distinct front-to-back waves. No specimen with a skull length of under 60 mm., had a front-to-back wave, and no specimen with a skull length over 90 mm., had a back-to-front wave. Since the 250-mm. specimen was the largest in which a regular wave pattern could be discerned, larger specimens were not included in Figure 7. The significance of this correlation between skull size and wave progression will be discussed below.

LIVE ALLIGATOR OBSERVATIONS

The results of monthly radiographic examination of the younger captive specimen are summarized in Figures 8 and 9. In lateral radiographs, teeth numbers one and two, and often twenty, are not always visible, and thus are omitted here. The bars on the graph indicate the length of time each tooth is exposed in the functional dentition—i.e., from its first appearance until the appearance of its successor. Thick and thin bars are used alternately to separate one generation from the next, and also to attempt to

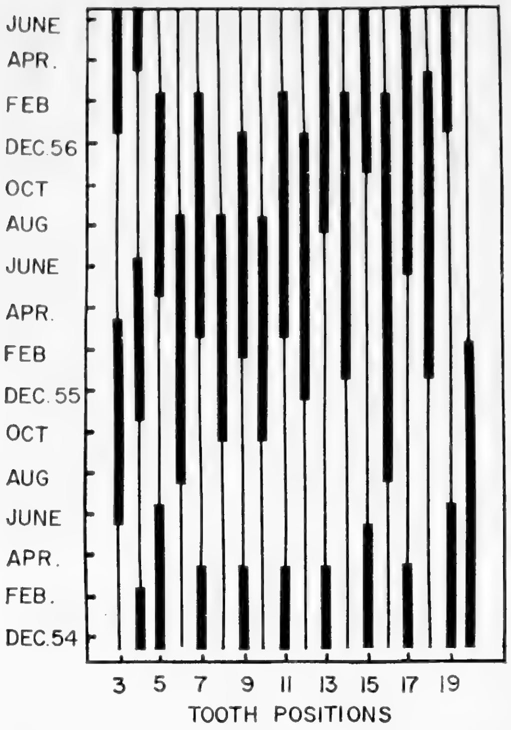


Fig. 8. a. Chart showing times of replacement of teeth in a young captive specimen of *Alligator mississippiensis.* Upper Right jaw.

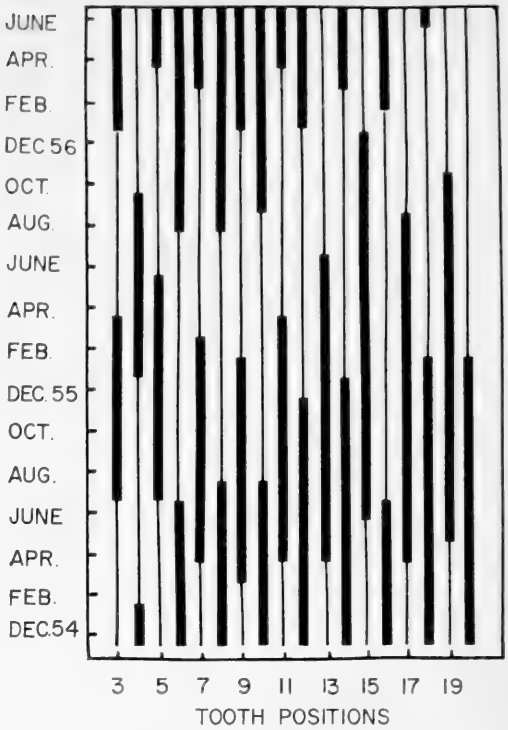


Fig. 8. b. Chart showing times of replacement of teeth in a young captive specimen of *Alligator mississippiensis.* Upper Left jaw.

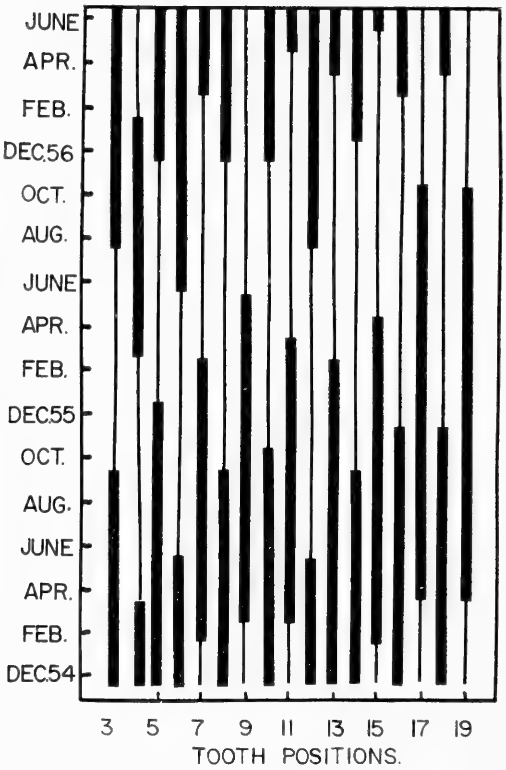


Fig. 9. a. Chart showing times of replacement of teeth in a young captive specimen of *Alligator mississippiensis.* Lower Right jaw.

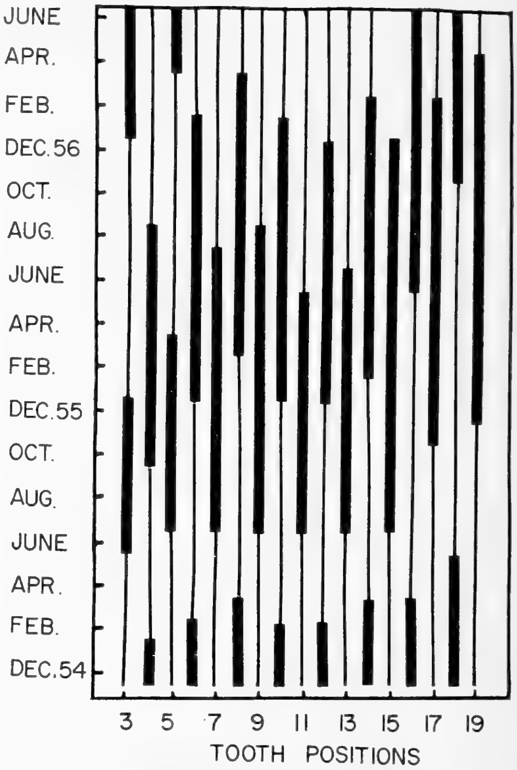


Fig. 9. b. Chart showing times of replacement of teeth in a young captive specimen of *Alligator mississippiensis.* Lower Left jaw.

indicate synchony, where present. The two types of lines are, of course, of equal value.

The graphs indicate that replacement did not take place in a regular pattern in every case. The upper right and lower left dentitions began fairly regularly, but soon showed as much variation as did the other two jaws. The lower left jaw (Fig. 9b) will be used as an example. In the even-numbered series most of the teeth were replaced in the relatively short period between January and March 1955. The odd-numbered teeth were replaced with remarkable uniformity, mostly in June, but the two most posterior teeth were greatly delayed. The next wave of replacement in the even-numbered teeth occurred about a year after the first, and the irregularity is more obvious, with an "S" shaped curve developing. The fourth replacement wave, this time in the odd-numbered set, is closely parallel to the third. The fifth wave, as far as can be determined, seems to follow the same pattern.

The other three jaws are similar. The upper right is not quite as regular to begin with as the lower left, but it rapidly loses most of its regularity. The upper left and lower right are moderately irregular from the outset, and become more irregular with time. An interesting feature, however, is that once the shape of the irregular wave is established, the succeeding waves adhere closely to it. This is obvious in all four graphs.

Another constant feature, and one characteristic of the dentitions of all lower vertebrates, is the essential cohesiveness of each alternately numbered tooth series. That is, although the shape of the replacing wave may be irregular, a wave in one series continues to act as a distinct entity, separate from its neighbouring waves in the other alternately numbered series. At any area of the jaw, the teeth in one series are replaced while the adjacent teeth in the other series are relatively intact. Usually the synchrony is such that a tooth in one set is replaced at about the mid-point of its neighbours' term in use. A wave in one alternately numbered series never overlaps one in another series, although in very rare instances, parts of two waves may almost coincide. The common arrangement is that seen in Figure 5, a or b, where a wave in the odd-numbered teeth remains clearly distinct from the succeeding one in the odd-numbered teeth. Even in those graphs where the regular wave-like pattern is lost, some mechanism continues to impose a sort of synchrony on the replacement sequence, so that adjacent teeth are rarely seen to be undergoing replacement concurrently.

A further trend is visible on all four of the graphs. The irregular waves all slope generally downward from the right to left. This is seen to a slight degree in the early observations, but becomes much more marked in later times. From this, one can deduce that the teeth toward the rear of the jaw remain in use a little longer than those at the front. The same observation was made on the periodic radiographs of the larger alligator.

The average times required for the replacement of the teeth at various tooth positions are plotted in Figure 10, a and b. These graphs, representing the two animals which were studied by radiographs, show that the average functional life for an anterior tooth is about nine months, and for a posterior tooth about sixteen. The average for all generations at all positions was 13.3 months for the young animal, 11.5 for the older one. It

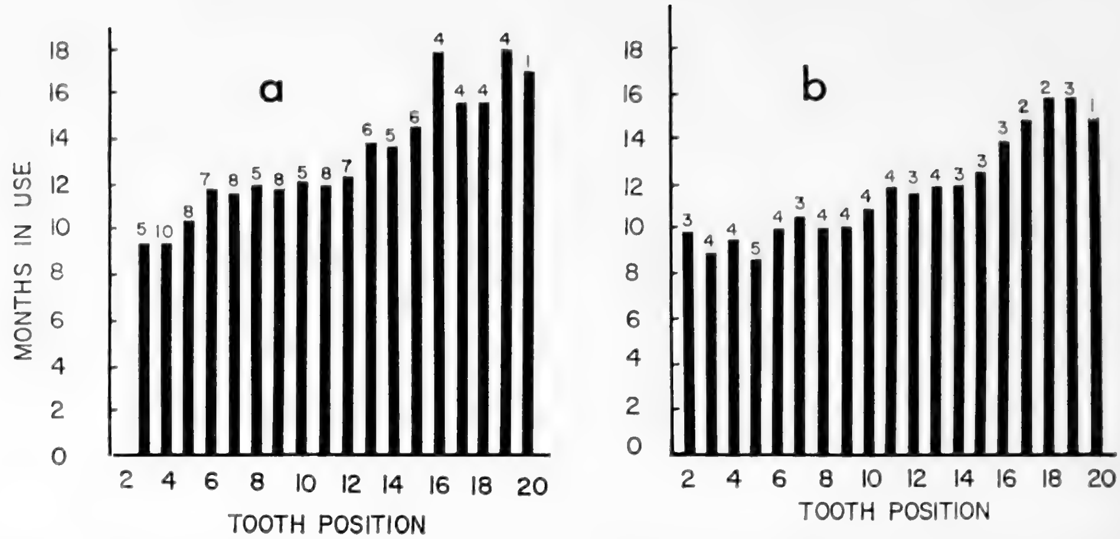


Fig. 10. Histograms showing the number of months required for tooth replacement at different tooth positions.
a. For the young captive specimen.
b. For the older captive specimen.
The small figures indicate numbers of observations.

would not be wise to assume from this single observation that the replacement process is faster in older animals. Indeed, it will be shown below that the opposite case is more likely to be correct.

The average life of a tooth in its definitive or functional position is thus approximately twelve months. This, however, is the time from the loss of the cap of its predecessor until its loss in turn. In actual fact the new tooth becomes visible on the radiograph at about the time of the loss of the cap of the old tooth. The life of the radio-visible tooth is therefore, about twice that indicated on the graph. The earliest stages of the development of the replacement tooth are not visible in radiographs, even with the refined techniques used in this study. Thus, it is safe to say that the average life of a tooth in a young alligator is in excess of two years.

The graphs showing times of tooth exchange (Fig. 10, a and b) suggested that the duration of a tooth in the functioning dentition might change as the animal got older. Figure 11 illustrates this feature. The curve with the triangular symbols represent the time required for the complete generations at each position during the early part of observation period. This probably took place largely during the animal's second year of life. The curve with the circular symbols is the same for the last complete observed generation, largely occurring in the late third and early fourth years of life.

The two curves are very close for the more posterior teeth. For the anterior teeth, however, the "early in life" curve shows that these teeth existed in the functional dentition about one month less than did the "later in life" teeth. That is, in the anterior part of the jaw, as the animal gets older, its teeth remain in use for a longer period. This is consistent with the observation that the growth rate of the animal's jaws decreases with age. (McIlhenny 1955) Continuous tooth replacement is not entirely a process for the provision of fresh, unworn teeth, but is necessary also to provide teeth of appropriate size for the rapidly growing jaws of the animal. Thus, one would expect the younger, more rapidly growing animals to have more rapid turnover of dental elements.

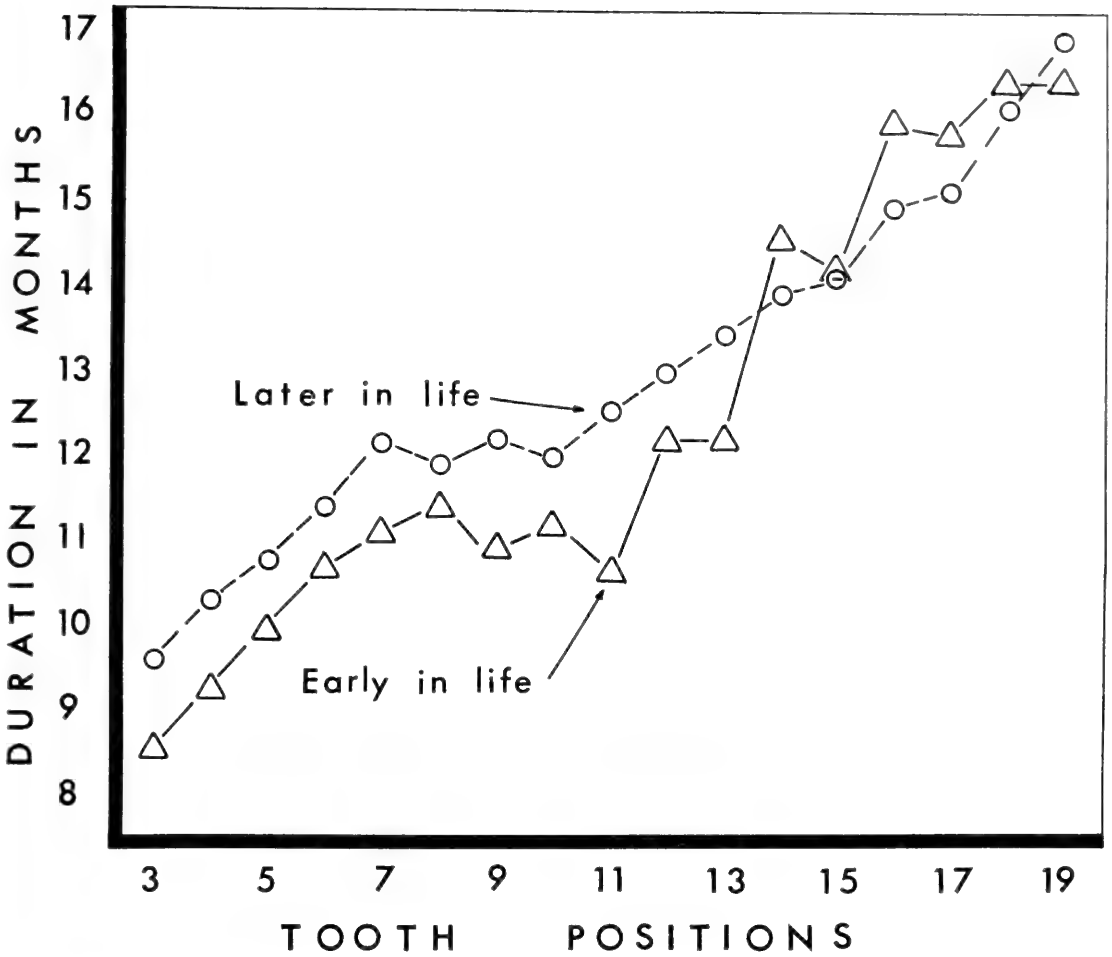


Fig. 11. Graph showing the length of time teeth existed in the functioning dention at different tooth positions. The triangular symbols represent the youngest available data, the circular symbols, the oldest. Information is derived from the younger of the two captive specimens of *Alligator mississippiensis.*

SUMMARY OF OBSERVATIONS

A. From dead material

1. Replacement of teeth occurs at least in most young individuals in a sequence of waves passing along alternately numbered tooth series.
2. In very young animals, the waves pass from back to front, while in older animals the sequence is reversed.
3. Replacement of teeth in one series is synchronized with that in the other series so that neighbouring teeth are almost always in opposite phases of the replacement cycle .
4. As age advances, the regularity of the replacement process deteriorates.

B. From live material

1. In the two young animals studied, tooth replacement was occurring essentially in waves from back to front, although in some cases it was rather irregular.
2. Teeth near the back of the jaw required longer to be replaced than teeth at the front of the jaw.
3. As was observed with dead material, as age advances, irregularity increases.

Probably the most puzzling aspect of this series of observations is the switch from a back-to-front wave progression in the young animals to a front-to-back progression in older animals. The two live alligators studied had distinct front-to-back progressing waves even from the beginning of the observation period (Figs. 8 and 9). As time went on, these waves increased in slope—i.e., the teeth in the rear of the jaw persisted in the functional dentition longer than did the anterior teeth.

From an examination of the graph (Fig. 7), it would be expected that the 75 and 110 mm., live specimens would have front-to-back wave progression, and this is the case. How can this be reconciled with the back-to-front progression seen in those specimens under 60 mm. skull length?

To investigate this, a graphic reconstruction of a crocodilian dental history was made (Fig. 12). This was based on the following observations:

1. Anterior teeth are replaced at ten-month intervals, while posterior teeth are replaced at twenty-month intervals. These agree with the data from Figure 7. It was postulated that these replacement times remain constant during the period covered.
2. When the skull length is about 65 mm., simple, alternate replacement is seen. This is based on Figure 7. This stage was called $t = 0$.

Generations of teeth were then constructed for a period covering t minus 36 months to t plus 60 months, and lines were drawn across the graph at 12-month intervals. At each of these intervals the heights of the replacement teeth were estimated and plotted in Figure 13. The result is that all graphs made earlier than $t = 0$ show back-to-front waves, while all graphs made later than $t = 0$ show front-to-back waves. This is exactly what was actually observed in the survey of dead material plotted in Figure 7. Unfortunately, we have one graph plotted in skull lengths, the other in months, and no conversion is available. The form of the two graphs is, however, identical. There is a switch-over in direction of wave progression, and the number of teeth per wave decreases on either side of the switch-over point. A graph similar to Figure 7 could be derived from Figure 13, but would only be redundant.

At this point, we must consider a different time scale for Figures 12 and 13. If we take t minus 36 as representative of a time when tooth replacement has been established in the embryo, we can see that about three and a half tooth generations occur at position one before the switch-over in wave direction occurs. The early microscopists (Woerdeman 1919, etc.), demonstrated that several generations were generated and resorbed prior to hatching. Quite probably a few more occur before the skull length of about 65 mm. is reached. These generations are also probably accomplished much more rapidly than the 10- to 20-month periods allotted in the graph. Unfortunately, we do not have observations of the time involved in these early replacement waves, other than the observation that several generations are replaced before hatching. This embryonic period is only a matter of months, and therefore each generation requires only weeks. It seems probable then, that as age increases, each generation of tooth replacement requires a longer time. This was shown to a limited extent in Figure 11, especially at the front of the jaw.

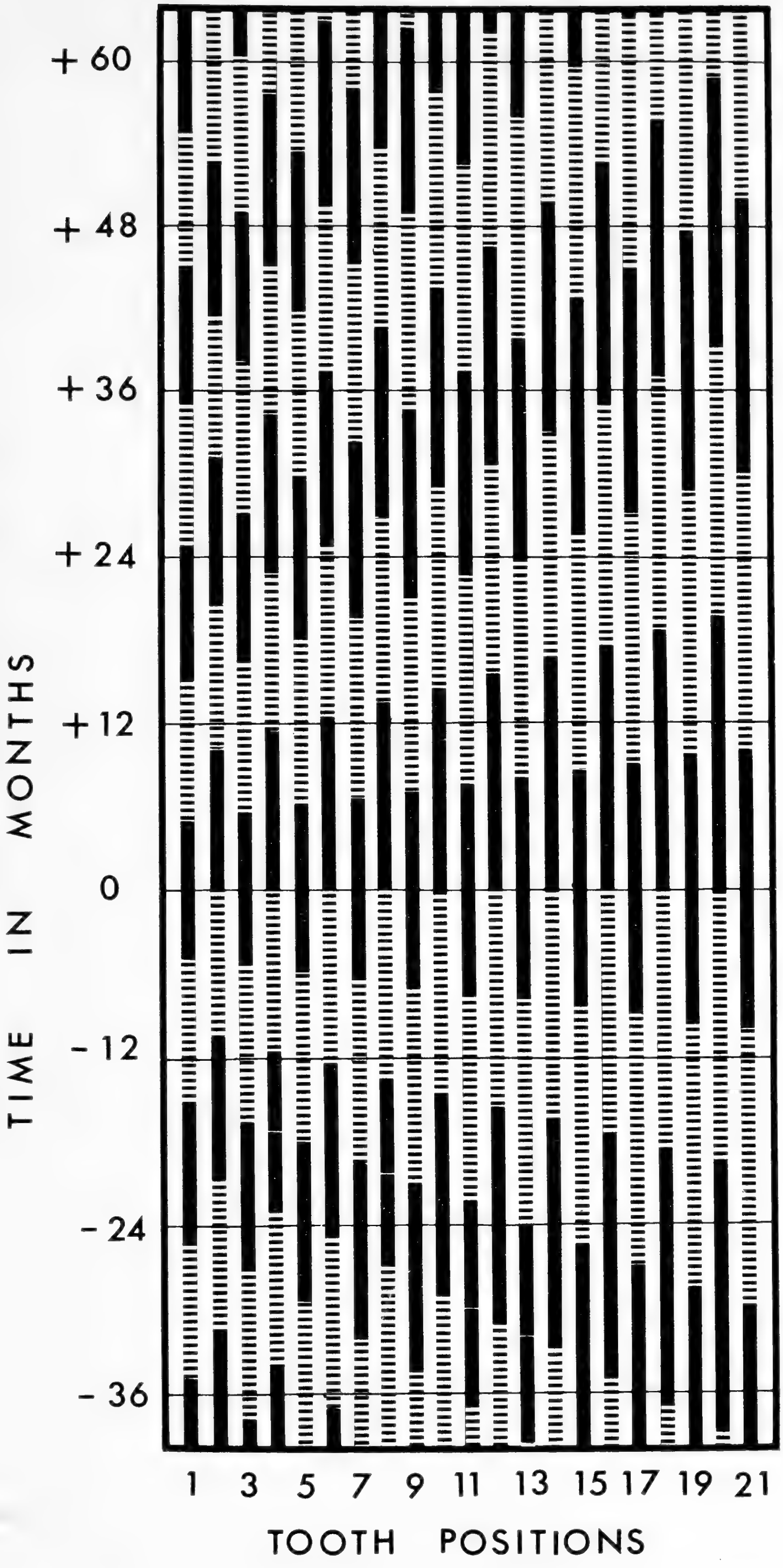


Fig. 12. Graphic model of the dental history of a young crocodilian. The divisions between solid and broken bars are the points where tooth replacement occurred. For an explanation of the graph, see the text.

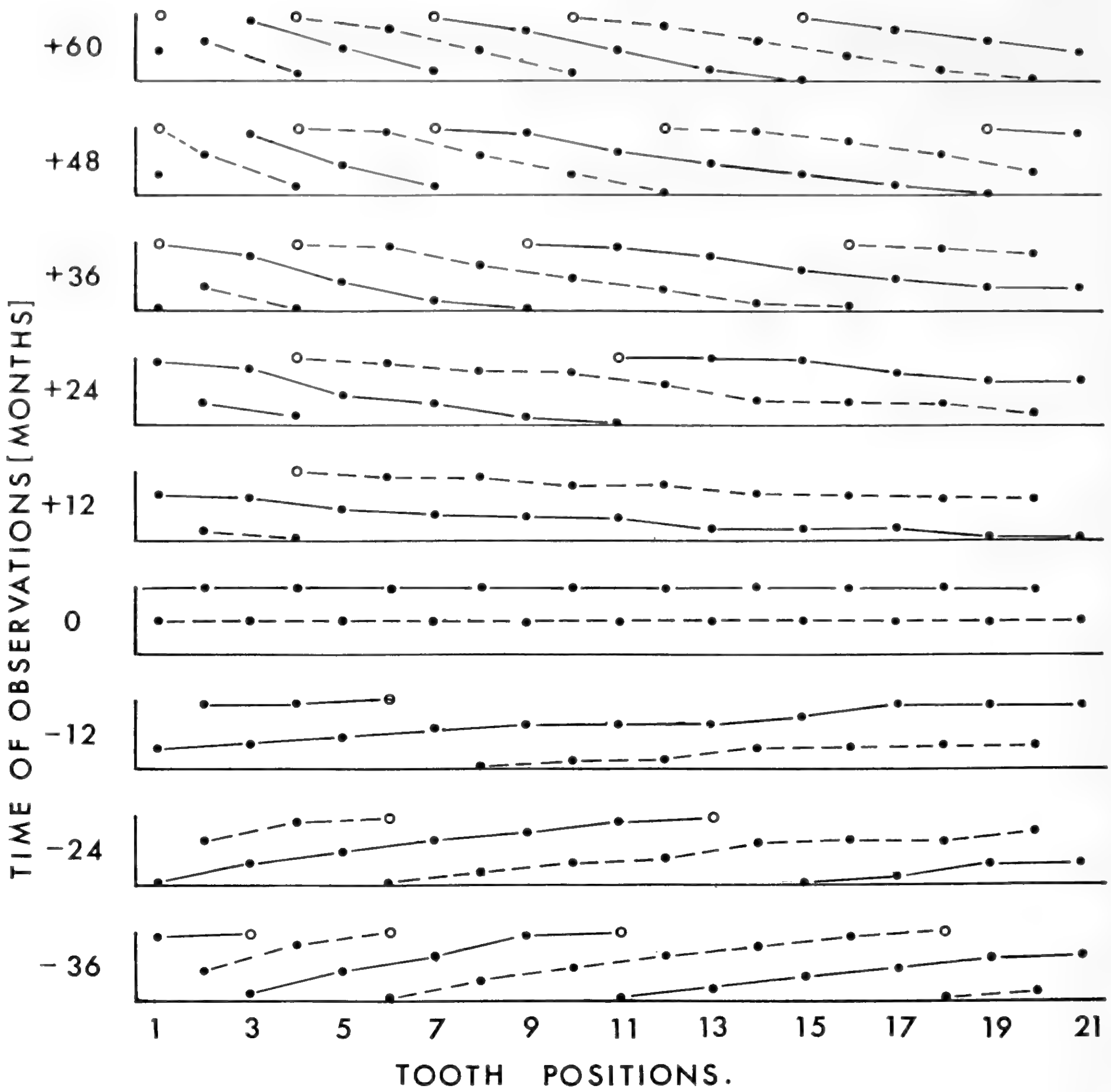


Fig. 13. Graphic presentation of the dentition of a young crocodilian derived from the graphic model, Fig. 12. The individual graphs represent the condition at 12 month intervals. Compare with the same type of graphs from actual specimens, Fig. 5.

Thus, it seems obvious that very young crocodilians have tooth replacement occurring in waves passing from back-to-front along alternately numbered tooth series. The more posterior teeth, however, remain in the functional dentition longer than do the anterior teeth. After a few generations of teeth have been replaced in this manner, a time is reached when all of the teeth in one of the alternately numbered series are replaced at the same time. This is simple alternate replacement. If the difference in replacement time between front and back teeth continues, the waves of replacement re-appear, this time progressing from front to back. We will return to a consideration of this phenomenon later.

HISTORY OF EMBRYOLOGICAL WORK ON CROCODILIANS

Most of our knowledge of the dental embryology of crocodilians stems from European microscopists who worked mainly between 1890 and 1923. Their observations and conclusions have been quoted and used with little question for decades. The most significant observations have come from four workers, Röse, Bolk, Woerdeman, and Vorstman. On the basis of the study of modern and fossil dentitions as well as the embryological evidence, Edmund (1960) demonstrated the essential similarity in the origin and arrangement of dentitions in all vertebrates. Crocodilians are no exception to this pattern.

FORMATION OF THE DENTAL LAMINA

The first teeth in the crocodilian embryo are formed on the surface of the oral epithelium. Röse (1894) showed the appearance of the earliest anlage in an embryo of 5¾ mm. skull length. The first dental elements are papillae which form rudimentary teeth. These never become functional but disintegrate into clumps of dentine which sink into the mesenchyme and are resorbed. The band of dentigerous epithelium continues to produce teeth for the life of the individual, but undergoes profound changes. By a process of opercularization and invagination, the tooth field (*Zahnfeld* of German literature) is overgrown and pushed under the surface of the oral epithelium, so that it forms a double-walled fold, the dental lamina (*Zahnleiste*). This lies on the lingual side of the tooth bearing bones (dentary, premaxilla and maxilla); only the labial wall produces teeth, since it represents the original tooth field. The lingual wall is derived from the opercular fold. The process is illustrated in Figure 14. Apparently the relative amounts of opercularizing and invagination vary from one group of animals to the next, but the end result is a plate of specialized oral epithelium with one

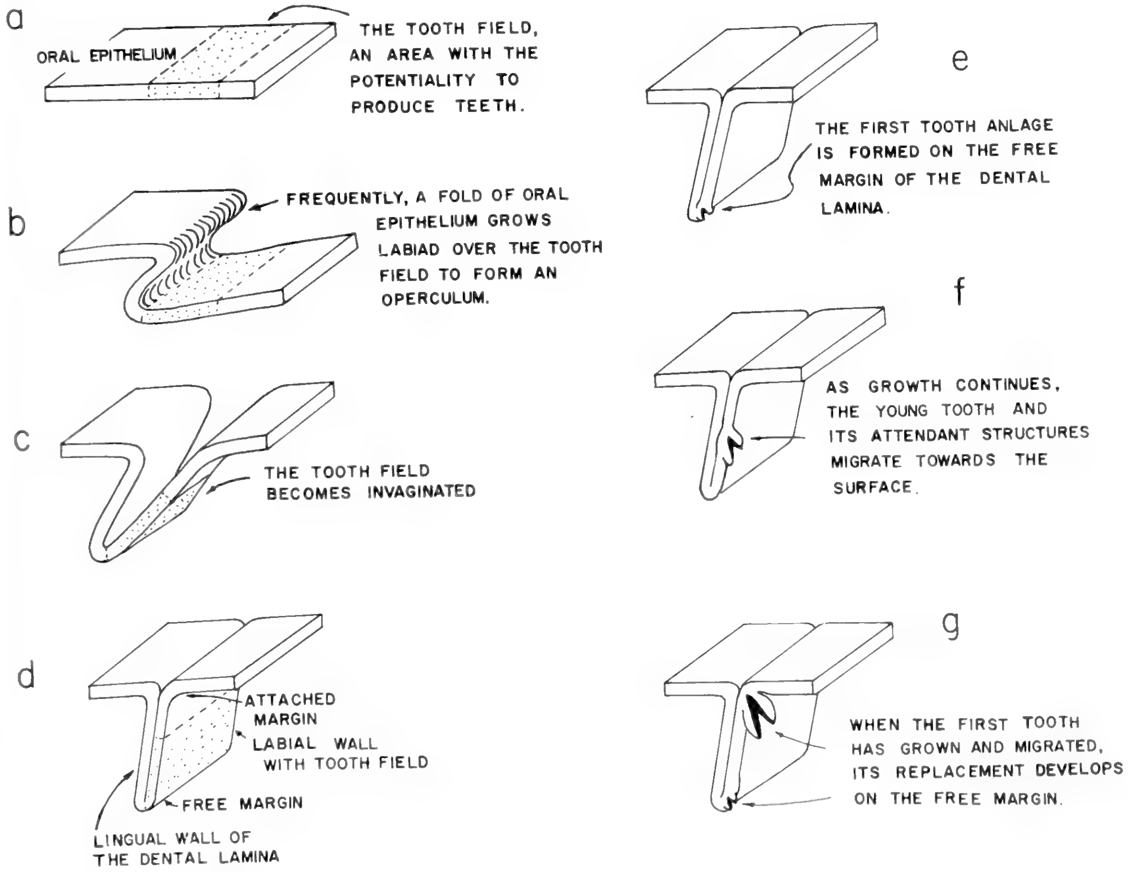


Fig. 14. Stages in the production of the dental lamina and its products. Derived from Bolk, Röse and Woerdeman.

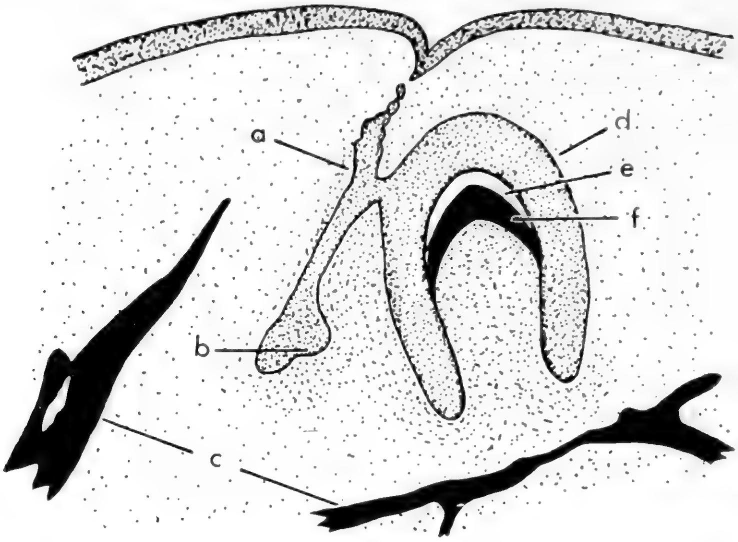


Fig. 15. Frontal section through the lower jaw of an embryo of *Crocodylus porosus*, 27 mm. skull length.
a. Dental lamina.
b. Tooth bud on the free margin of the lamina.
c. Parts of the embryonic dentary bones.
d. An older tooth bud.
e. Enamel.
f. Dentine.

end attached to the oral surface, the other end deeper in the soft tissue of the jaw. Figure 15 shows a dental lamina of a crocodile with one advanced tooth bud and one very early anlage. Since the dentigerous epithelium is restricted to the free margin of the lamina, all tooth buds begin their growth there and migrate towards the attached margin.

THE MATRIX THEORY

Friedmann (1897) pointed out that in many fishes, when the first tooth anlagen are formed, strands of dentigerous epithelium sink below the surface of the oral epithelium, one strand at each definitive tooth position. This is apparently the equivalent of the invagination process described above for the production of the dental lamina. All subsequent teeth are formed by the clumps of cells which were invaginated. The same situation prevails in cases where a definite lamina is present. The groups of specialized dentigerous epithelial cells were called matrices by Bolk. Each matrix produces all of the teeth at each tooth position throughout the life of the individual, and the products of each matrix are called a tooth family. James and Welling (1943) and James (1953) propose the term "dental unit" to replace Bolk's term "tooth family". I can see no advantage to this, since "dental unit" is even more ambiguous than "tooth family", whereas "tooth family" serves to emphasize the genetic relationship of the various elements at each position.

The genetic connection between members of a tooth family is shown in Figure 16, a section of a jaw of an embryo of *Esox lucius*. Of special note is the obvious cellular connection between individual members of each family, and the increasing size and degree of development as the tooth buds migrate away from the free margin of the dental lamina.

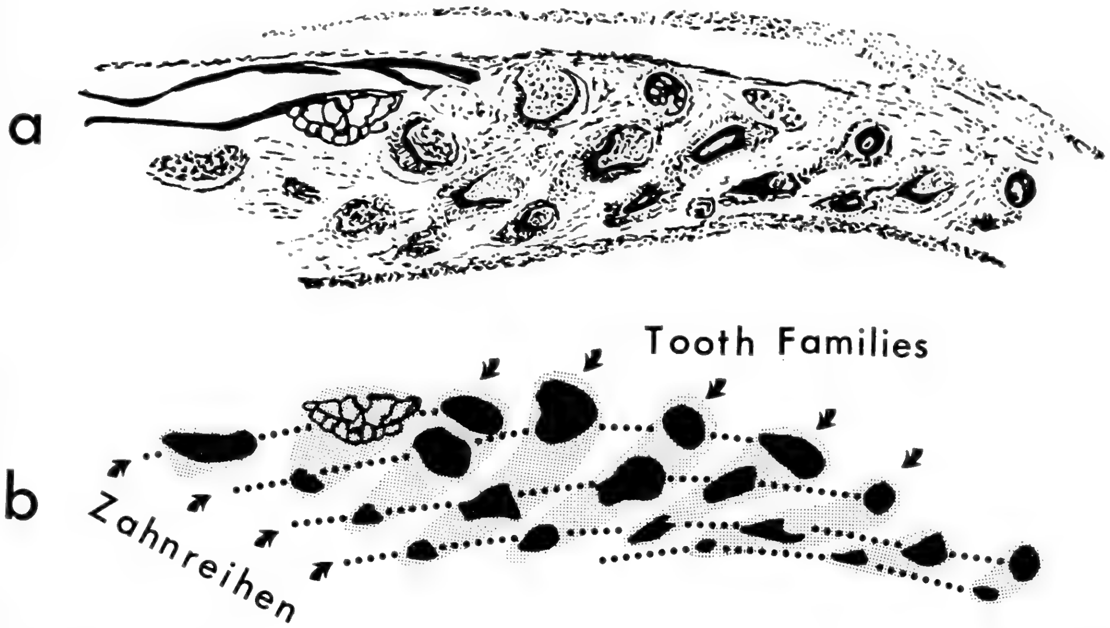


Fig. 16. a. A section of the lower jaw of a 7 cm. specimen of *Esox lucius,* showing the relationships of dental elements. After Vorstman.
b. Vorstman's interpretation of the section. The shaded areas indicate tooth families, the dotted lines Zahnreihen.

BOLK'S DISTICHY THEORY

L. Bolk wrote numerous papers on various aspects of dental embryology. Of particular interest here is his theory of Distichy, or two-rowedness. This theory has been shown to be false by several authors, but because of its firm entrenchment in the early literature, it still frequently appears.

In embryos of *Crocodylus porosus* Bolk saw anlagen, some on the labial wall of the dental lamina, some on the free margin. He called the first kind parietal, the second terminal. In the specimens studied by Bolk the terminal and parietal anlagen alternated with one another in a very regular fashion. Since the parietal anlagen were always further developed than the terminal anlagen, it was suggested that the terminal anlagen might be destined to replace the parietals. Bolk proved this to be incorrect, however, since the terminal anlagen are later pushed between the parietals, to form with them the series of functional teeth. Besides this, Bolk was able to show that both the parietal and terminal anlagen later are provided each with their own replacements.

Thus, according to Bolk, in the embryo there are two rows of tooth anlagen running along the dental lamina, one row on the free margin, one part way up the labial wall. (Each was called an Odontostichos.) The row on the free margin, or terminal position, he termed the endostichos and the row part way up the wall (parietal position) he named the exostichos. The functional dentition, which appears to be a single row of teeth of common origin, is, according to Bolk, formed by the combination of alternating members of one endostichos and one exostichos. This condition was termed a "Scheinmonostichismus", although Bolk considered it to be truly distichic. Edmund (1960) assembled convincing evidence to show the fallacy of the distichy concept.

EMBRYONIC HISTORY OF CROCODILIAN DENTITION

Observations on the order of appearance of tooth anlagen were made by Röse (1893 and others) and Woerdeman (1919). Both workers employed serial sections of jaws of embryos of various ages. Woerdeman analyzed his findings and those of Röse in his Beitrag I, although his work was strongly influenced by that of Bolk. These observations are very significant, however, and require only a certain amount of re-interpretation and clarification of terminology to become consistent with the results from other related studies.

Both Röse and Woerdeman described the formation of dental papillae on the open surface of the oral epithelium, before the formation of the dental lamina. The earliest embryo described had a skull length of 5¾ mm. and had only one anlage per lower jaw, with no trace of the production of dentine. In a 7-mm. skull length embryo there was a second small anlage A 7¾-mm. skull length embryo showed three anlagen, with the anterior one showing the deposition of dentine. A suggestion of the initial stages of a fourth anlage was also noted. In an 8-mm. skull there were four anlagen per lower jaw. These are arranged in a very significant order, however. The three teeth, corresponding to those of the 7¾-mm. specimen, grade downward in size and degree of development toward the rear. That is, the most anterior tooth of the three is more fully grown than is the second, and the second more than the posterior. The fourth tooth which has appeared, however, is lingual and somewhat anterior to the first, and is very young. Woerdeman considered it homologous with the first-developed tooth, but in degree of development, it more closely resembled the third. It thus seemed obvious that it was a member of the first (anterior) tooth family, being the second anlage produced by that matrix. Woerdeman termed the row of three teeth in the 7¾-mm. embryo the first "odontostichos", and labelled the anlagen O I^1, O I^2, and O I^3, always numbering from the anterior end of the jaw. As each tooth of the first "odontostichos" was laid down, it began to migrate labiad from its site of origin. In the 7¾-mm. embryo, the three teeth thus were increasingly younger towards the rear, and further from their site of origin at the front of the row. Woerdeman considered the fourth tooth, which appeared first in the 8-mm. embryo, to be the first member of a new "odontostichos", O II^1. The next stage was described by Röse, who had a 9½-mm. skull-length embryo with four teeth in the first "odontostichos" and three in the second. "In the lower jaw three new tooth anlagen have appeared; the first new anlage lies anterior, near the tip of the jaw. The other two are between the second and third, and the third and fourth." This is illustrated in Figure 18a iii copied from Woerdeman.

Woerdeman summarized the steps up to this stage, numbering the position of the elements according to their anterior-posterior sequence in

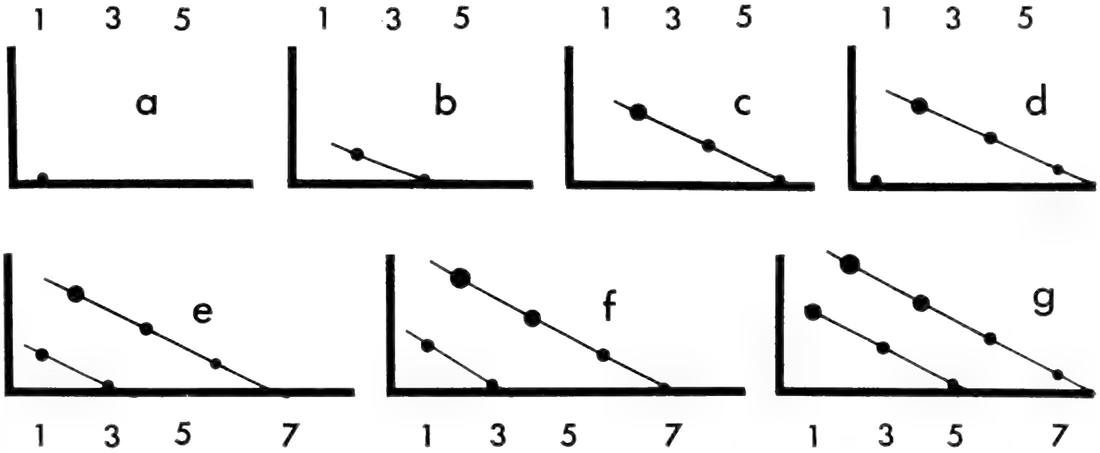


Fig. 17. Early stages in the development of the dentition of *Crocodylus* embryos. The sketches are by the author, based on a written description by Woerdeman (1919). For explanation, see text.

the jaw (Fig. 17). The first anlage to appear is in the second position, followed by those in the fourth and sixth positions. Then comes the first, third, seventh, and finally the fifth. It is obvious that two "odontostichi" are involved, consisting of the products of four matrices or tooth positions. In order of appearance, teeth two, four and six represent the first products of matrices one, two and three. The most anterior bud (number 1) is actually the second generation of the first matrix; number three is the second generation of the second matrix, and number five is the second

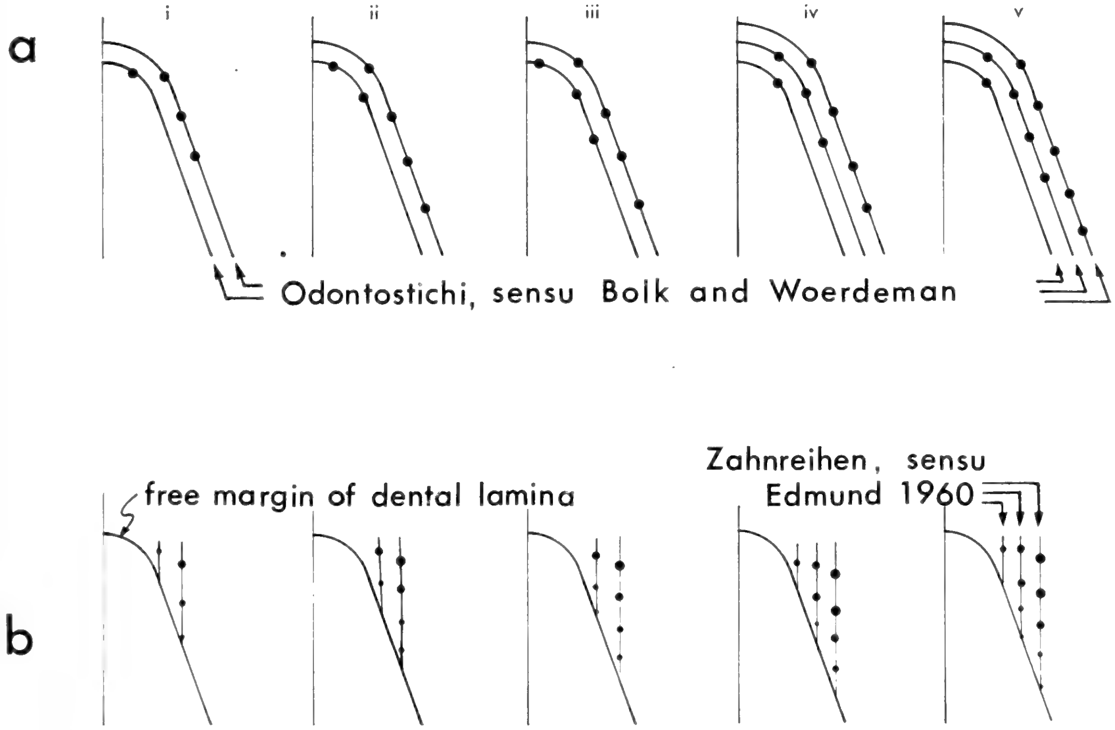


Fig. 18. a. Sequence of appearance and arrangement of embryonic dental elements in *Crocodylus*. After Woerdeman.

b. The same information arranged according to the concept of Zahnreihen. The curved line in these diagrams represents the free margin of the dental lamina.

generation of the third matrix. Tooth seven is, of course, the first generation of the fourth matrix. This arrangement is similar to that seen in Figure 18b iii.

It is important to note the relative degrees of development of the various tooth anlagen. Woerdeman gave a brief account of this for his "Stadium N" specimen (skull length 9.5 mm.) which is summarized in the following table. The arrangement of elements is shown in Figure 18b, iv.

Tooth No.	Odontostichos I	Odontostichos II	Odontostichos III
1	Well developed. A considerable amount of dentine has been laid down	Young anlage, very little dentine	Very young anlage —youngest of all
2	Few odontoblasts and only a little dentine laid down, but more than OII 2	Younger than OII 1, less dentine	
3	Young anlage, very little dentine	Very young anlage	
4	Very young anlage		

From this table it is evident that the more anterior teeth of each "odontostichos" is the oldest. Several older embryos were described by Woerdeman. In these, the older members of the "odontostichi" begin to show resorption, so that while more "odontostichi" are generated, there is a continual loss of older elements. In his stage E (no skull length given), "odontostichos" OI consists of seven elements, of which the first (anterior) five are undergoing resorption, and 6 and 7 are small enamel organs. OII also has seven elements, the anterior six possessing dentine. OIII has six elements, the anterior 5 with dentine formation. There are 5 anlagen in OIV, but all are very young. Woerdeman's crocodile embryo "0" is more fully described, with twenty-seven teeth arranged in six "odontostichi".

Odontostichos I:	1 to 3 are resorbed completely, 4, 5 and 6 are of a rudimentary type and are being resorbed. 7 is a rudimentary enamel organ.
Odontostichos II:	1 to 3 are resorbed, 4 to 6 are small, and rudimentary, but not as resorbed as 4 to 6 of O I.
Odontostichos III:	1 is strongly resorbed, 2 and 3 are rudimentary enamel organs undergoing resorption; 4 is a well-developed enamel organ undergoing resorption. 5 and 6 are younger teeth, not undergoing resorption.

Odontostichos IV:	Anlage 1 is well developed, but beginning to be resorbed. 2 and 3 have abundant dentine, and are not being resorbed. 4 and 6 are large enamel organs without dentine.
Odontostichos V:	has 3 anlagen with little dentine.
Odontostichos VI:	has 3 smaller anlagen with no dentine.

Stage F is an even older individual described by Woerdeman, although no skull length is given. In it, "odontostichi" I and II have completely disappeared. "Odontostichi" III and IV, with 8 and 7 anlage respectively, are represented by rudimentary elements, most of which are undergoing resorption. "Odonstotichi" V and VI each have 7 better-developed anlagen, and show no reduction. At the anterior end of the dentition, "odontostichi" VII and VIII have been laid down, each with two buds. The arrangement of these teeth is sketched in Figure 19. It is significant to note that the early tooth buds are described as being of a rudimentary type, while the older ones are more fully formed. Since the early teeth are destined for reduction, it might be expected that they would not be as well developed as the later ones.

TERMINOLOGY

The term "odontostichos" has purposely been used in quotation marks in the previous section, because it was used in a special sense. In an earlier section, the work of Bolk was discussed, and his odontostichi described. It is obvious that the odontostichi of Bolk's terminology are not the same tooth series as those described by Woerdeman. Bolk's odontostichi were defined as a series of teeth of equal age, whereas the series of Woerdeman consists of a number of teeth which by their times of origin are of different ages. Since it was shown that Bolk's odontostichi are merely artefacts caused by a fortunate arrangement of Woerdeman's "odontostichi", Edmund (1960) proposed the abandonment of the term in order to avoid confusion. He suggested the adoption of the German term *Zahnreihe*, which merely means tooth row or series. It was used several times by Woerdeman when he was discussing "odontostichi", and was frequently used by Vorstman to indicate the same concept. More recently the term has been accepted by Goin (1961) and Crompton (1962) although the former seems to have misinterpreted the concept.

It is unfortunate that Woerdeman attempted to force his Zahnreihen into the system of Bolk's odontostichi. This is seen in Figures 17a and 19a in which the graphs have been drawn so as to align the elements into an alternating pattern on the labial side, i.e., toward the attached margin of the dental lamina. Since the reference point should obviously be the free margin of the dental lamina, the Zahnreihen are not in their natural relationships. This is especially evident in Figure 19, a and b, where the odontostichi are of the type described by Bolk, and not the same series as the true Zahnreihen shown in Figure 17. In Figure 17b, the "odontostichi" of Figure 17a are drawn in a more natural arrangement, and their true

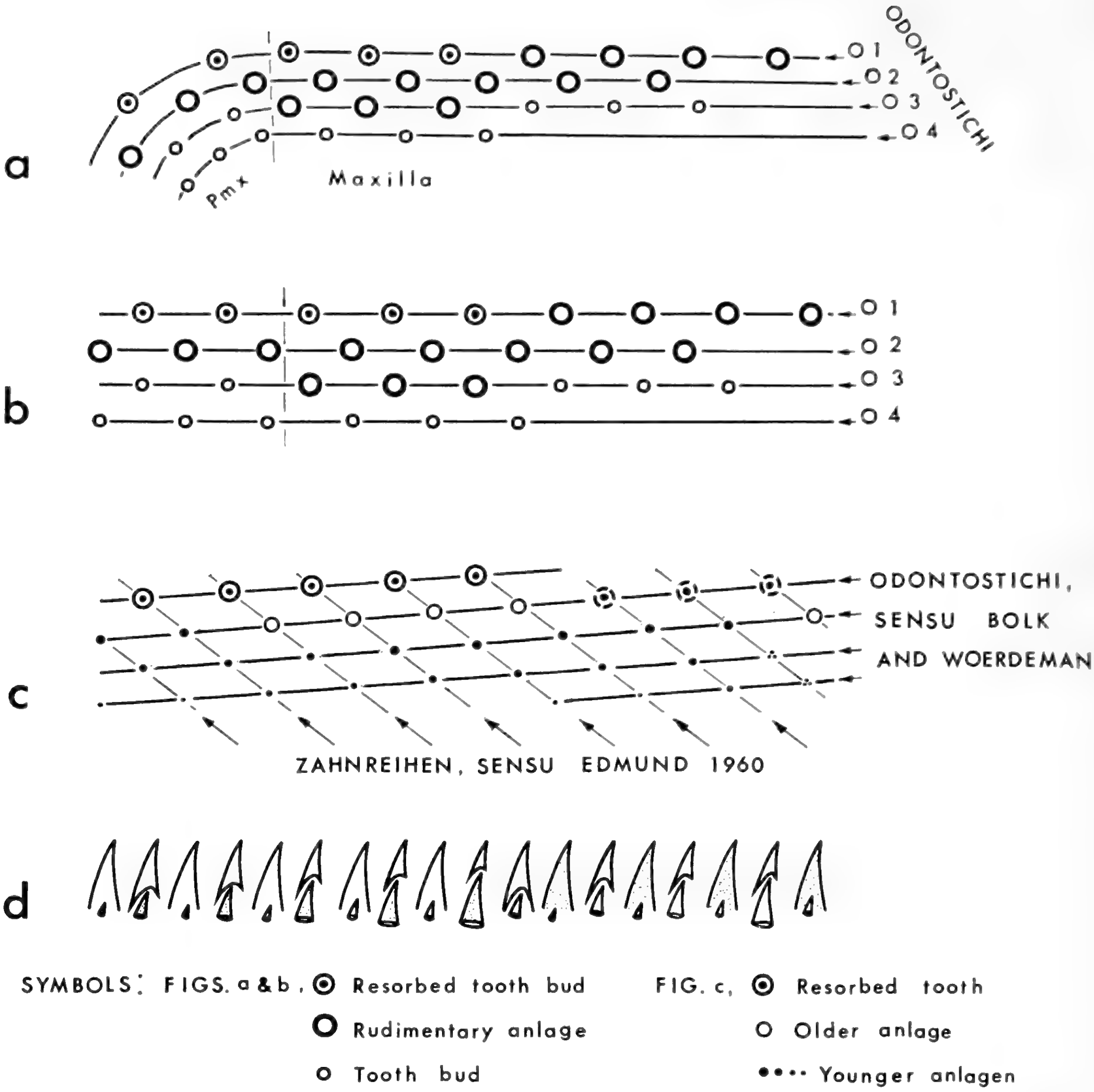


Fig. 19. Charts to show the difference in arrangement of dental elements as conceived by early authors and by the present writer.

a. A copy of Woerdeman's figure of the right upper jaw dentition of an embryo of *Crocodylus porosus.*
b. The same arrangement with the curve omitted.
c. The same elements arranged in a more natural order, so as to show their relative ages, and their organization into Zahnreihen.
d. A diagrammatic presentation of the same jaw. One alternately numbered series has been stippled to show a cephalad wave of replacement.

relationships become obvious. Similarly, in Figure 19c, the very artificial arrangement of Figure 19, a and b is corrected, so as to show what is probably the natural arrangement, demonstrating that a second type of Bolk-odontostichi could be selected. However, the true Zahnreihen are obvious, and they agree in orientation, spacing and in numbers of elements with the Zahnreihen seen in the earlier embryos in Figures 17 and 18. The symbolic representation of the actual dentition (Figure 19d) is derived from 19c, and indicates, as would be expected, that the teeth are being replaced in a wave-like pattern, the replacement progressing from back to front. In order to produce Figure 19c from Figure 19b, it was necessary to add three resorbed teeth and two young anlagen at the posterior end. Since these would probably have been fairly difficult to detect in his serial sections, it is not unlikely that they were overlooked by Woerdeman. They are shown in the figure by broken or stippled symbols.

Figure 17 is derived from written descriptions and therefore has not had to be re-interpreted. The relative size of the elements of each Zahnreihe is known, or can be inferred, and the elements fall naturally into the arrangements shown.

From this re-appraisal of the literature, it is clear that the terminology arising from Bolk's distichy theory should be abandoned. Since his concept of tooth matrix and tooth family seem valid, it is proposed that they be retained.

GRAPHIC MODEL OF THE SEQUENCE OF TOOTH DEVELOPMENT

The work of Röse and Woerdeman, especially the latter, demonstrated conclusively the pattern in which the anlagen of the teeth are laid down. Figures 17, 18 and 19 adequately show the sequence of origin, spatial and genetic relationships and movements of the dental elements. In order to summarize this process, and to investigate its consequences, Figure 20 was constructed. In this series of sketches it is assumed for simplicity that the dental lamina has been invaginated before the formation of the first anlage. Thus, there is a definite base line for the charts. Actually in the crocodilia the first anlagen are laid down as free papillae on the surface of the oral epithelium. Opercularization of the tooth field occurs, according to Woerdeman (1919) at about the time of the origin of the second Zahnreihe, i.e., at about an 8-mm. skull length. He states that a 9½-mm. embryo was partly opercularized.

For convenience, one may think of an impulse of some sort, possibly chemical, which passes along the free margin of the dental lamina (or its equivalent) from front to back. At regular intervals (corresponding to Bolk's tooth matrices) it causes the initiation of a tooth germ, as at Figure 20a. Once the first tooth bud has formed, it begins to grow and moves away from the free margin of the lamina. At the same time, however, the "impulse" progresses caudad, causing the formation of other tooth buds at successive matrices. With the passage of one "impulse" one series of teeth is produced. The teeth are youngest and closest to the free margin of the dental lamina at the posterior end, and older and nearer the attached margin at the anterior end. Because the dental lamina is often at a considerable angle to the vertical plane, movement away from the free margin is thus often also in the labial direction, so that Vorstman describes the arrangement as a "labio-lingual, mesio-distal orientation", and Woerdeman, despite his somewhat distorted figures, also describes "Reihentwicklung in mesiodistale und labiolinguale Richtung". This series of teeth is, of course, the Zahnreihe, and a Zahnreihe can be considered to be the series of teeth produced by a single passage of a hypothetical triggering impulse proceeding caudad along the free margin of the dental lamina.

After the first hypothetical impulse has begun its passage along the lamina, and a few tooth buds have been produced by it, a second impulse follows, as in Figure 20d. This produces the second tooth bud at position 1,

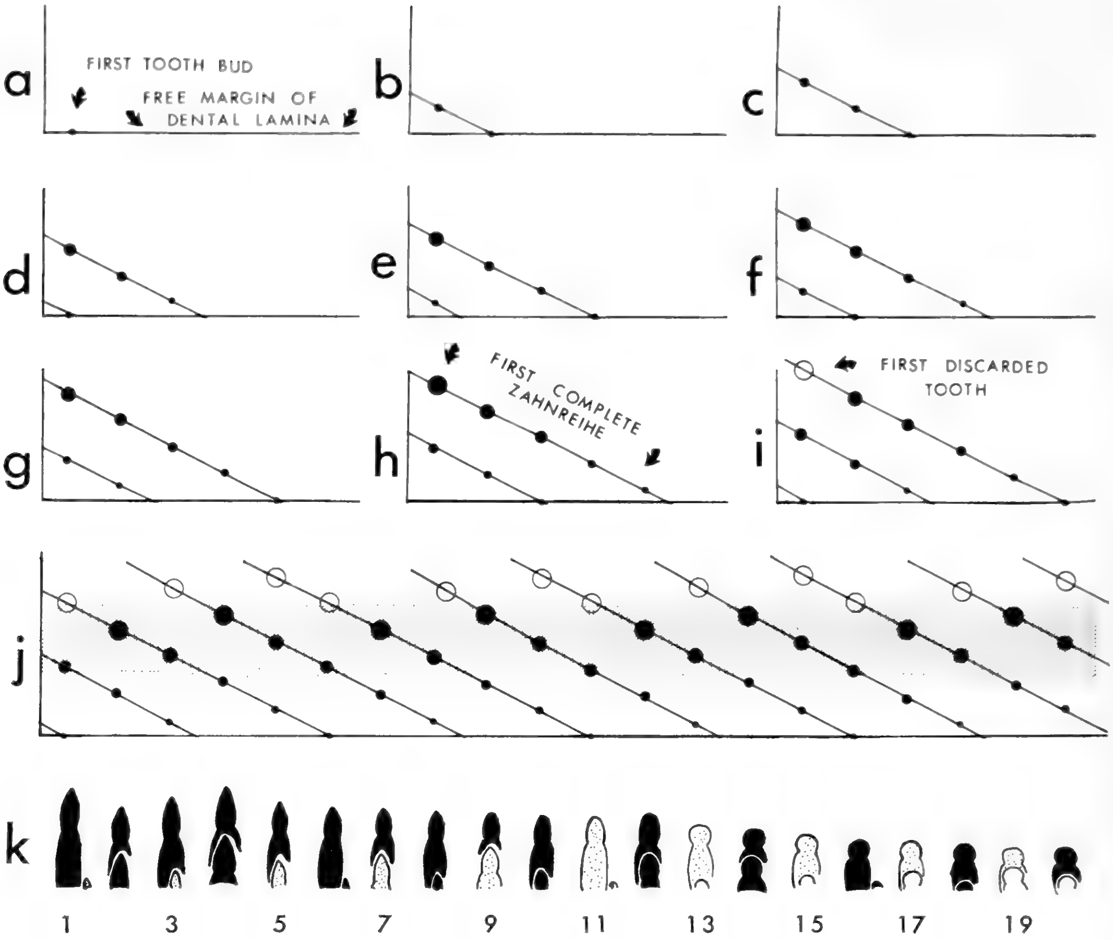


Fig. 20. Stages in the formation of the functional dentition.

a. to i. the sequence in which the tooth buds and Zahnreihen appear.

j. The arrangement of dental elements of all ages in a complete dentition. Elements in the grey shaded area are those in the functional stage. Those below are the developing replacements. The open circles are teeth which have been recently resorbed or cast off.

k. The actual appearance of the dentition in the above chart.

which, in turn, begins its migration toward the free margin. The spacing between the passage of the successive tooth-generating impulses is very important. Woerdeman (1919, p. 157) showed it to be about two and a half tooth spaces, and this is the figure used to construct the graphs in Figure 20. Graphic analysis of the effects of varying this spacing were considered in Edmund (1960, p. 164).

The complete dentition is built up of the products of a large number of Zahnreihen, as in Figure 20j. Dissection and radiography demonstrated that, in the Crocodilia, each tooth position usually has one functional tooth, and one, or occasionally two replacements. To produce this situation graphically, it is necessary to assume a Zahnreihe of six teeth. However, each jaw on hatching contains about twenty tooth positions. This means that as the impulse moves along, the teeth produced by it will reach their definitive size and must eventually make way for new teeth produced by subsequent Zahnreihen. This is shown in Figure 21, where the discarded teeth are indicated by open circle symbols. Since each Zahnreihe has six teeth, and the jaw has, say twenty-one positions, then 15 members of the first

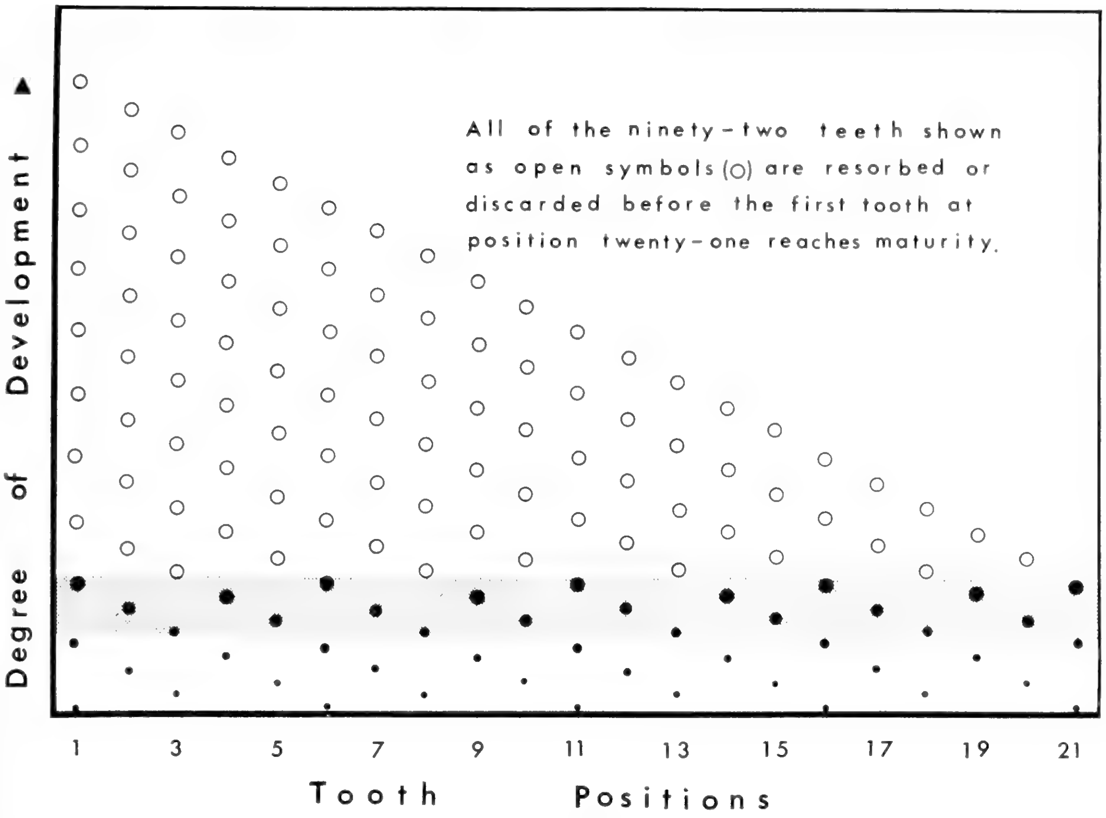


Fig. 21. Diagram to show the number of teeth which must be discarded before a complete functional tooth row can be laid down. The shaded area contains all of the mature teeth in use.

Zahnreihe are discarded before the first anlage of position twenty-one is laid down, and many members of the first seven Zahnreihen must be discarded before the first mature tooth is produced at position twenty. In the present example approximately ninety-two teeth are discarded before all of the twenty-one positions receive mature teeth. Woerdeman (1919, Beitrag I, p. 166) sums up this process, "Während der ganzen embryonalen Periode der Krokodile (bis zu Geburt) werden Zähnchen der Unterkeifergebisses resorbiert . . . Die genaue Zahl der rüdimentären Zahnreihen ist noch nicht bekannt (mindestens vier)". From the model constructed here, it is obvious that more than four tooth rows were resorbed. It is unfortunate that Woerdeman did not exploit the consequences of his discovery of Zahnreihen, since it explains the basis of so many dental phenomena.

What is the connection between Zahnreihen and the pattern of replacement seen in adult vertebrates? In most vertebrates (see review in Edmund 1960) tooth replacement occurs in a pattern of waves passing along *alternately numbered* tooth series. On a few occasions, all of the teeth in an alternately numbered series might be in the same stages of the replacement process, with the teeth of the other series in an opposite phase of the process. Vorstman (1923) was the first to point out that the tooth families and the Zahnreihen are at opposing angles to the free margin of the dental lamina, and to the jaw itself (Fig. 16). Thus, lines drawn through the two series intersect. The same effect is seen in Figure 20. Here, the tooth families are drawn perpendicular to the free margin of the lamina, but the effect is the same. At each position, the mature tooth is the oldest, second oldest, or occasionally the third oldest member of a Zahnreihe. The functional dention thus consists of the older members of a number of successive Zahnreihen. In Figure 21, for instance, the twenty-one positions are represented by members of nine Zahnreihen. The more mature members of these are shown in the shaded area, indicating teeth in the functional position. Some of these are old teeth, about to be replaced, while others are young, having only recently come into their definitive positions. The drawing, (Fig. 20) indicates the actual appearance of such a jaw, which agrees very well with that seen in young living crocodilians.

What of Bolk's odontostichi? The functional dention of most vertebrates does not show the regular alternation required for this sort of arrangement. However, over limited areas, it is possible to demonstrate simple alternation in some specimens. Woerdeman chose to illustrate the older embryo, Figure 19a here, and arranged the observed dental elements into four odontostichi. These showed perfect alternation in his figure. However, on the basis of the written descriptions, it is possible to re-arrange the elements as in Figure 19c. In this case, the longitudinal tooth series are much closer to Bolk's original description of odontostichi. In the first eleven positions, for instance, there is a fairly regular alternation of old teeth with younger teeth. Indeed, if Woerdeman's symbols are used the alternation is perfect. However, it is obvious that the various teeth in each odontostichos (*sensu* Bolk) are not of the same age, but are younger in the front, older in the rear. The "odontostichi", used in this sense, are the real waves of replacement.

The length of the waves of replacement depends on the spacing between Zahnreihen. As was explained above, after the hypothetical impulse has caused the initiation of a tooth at one position, it moves along causing the production of teeth at sucessive positions. After a certain interval has elapsed, a second tooth is generated at the same position, and is thus the first tooth of a second Zahnreihe. By this time, of course, the first impulse may have moved caudad several tooth spaces. The distance between the two Zahnreihen is very important. If this spacing is exactly 2.0 tooth positions, simple alternate replacement will occur. If the spacing is greater than 2.0, waves of replacement appear in the functional dentition, progressing from back to front. If the spacing is less than 2.0, the waves are in the reverse order. As the spacing between Zahnreihen approaches 2.0, from either direction, the wave length increases, so that at 2.0 it is theoretically infinite, thus giving simple alternate replacement. Thus, animals with short length waves have a Zahnreihe spacing considerably less or greater than 2.0. The spacing between Zahnreihen used in the construction of Figure 20j is 2.5 tooth positions. This is close to the spacing which Woerdeman found in his embryos, and, as would be expected, the resulting replacement pattern is similar to that seen in young live crocodilians. Most of Woerdeman's illustrations and descriptions indicate a spacing of greater than two and less than three positions.

EXPLANATION OF THE CHANGE IN WAVE DIRECTION IN CROCODILIANS

As was mentioned above, the spacing between Zahnreihen is the key to the direction of progression of the replacing wave. Almost all reptiles have tooth replacement occurring in cephalad waves. The ichthyosaurs and elapid snakes, however, are exceptions, both having replacement proceeding caudad. There is no need to postulate any unusual pattern of dental elements to explain this, since we need only assume that they have a spacing between Zahnreihen of less than 2.0 spaces. How does this explain the peculiar change in wave direction seen in young crocodilians?

The embryology of crocodilian dentition is very well known, and the arrangement of dental elements is as in Figure 20j. These young crocodilians, with a spacing between Zahnreihen of more than 2.0 have, as would be expected, replacement occurring in cephalad waves. If all of the teeth in the jaw were replaced at the same rate throughout life, the same replacement pattern would prevail. However, Figure 10 shows us that this is not the case. The anterior teeth are replaced much more rapidly than the posterior ones. The only way that this can occur is if extra Zahnreihen are added to the tooth row. In order to keep the number of functional teeth constant, the anterior teeth must mature more rapidly than the posterior and are thus replaced faster. Thus, the number of Zahnreihen per jaw increases, and in consequence the wave pattern changes, as in Figure 7. As would be expected, the wave length increases as the Zahnreihe spacing approaches 2.0, which apparently occurs with a skull length of about 6.5 cm. As more Zahnreihen are added to the jaw, the waves re-appear, but this time proceeding caudad. It should be noted that the change in Zahnreihe spacing is not drastic. If only a few Zahnreihen were added to the twenty position jaw shown in Figure 20, the change would be complete.

Probably after a certain period, the rate of Zahnreihe production slowly ceases to accelerate, with the result that the front-to-back pattern is retained, but the wave length remains about the same. This is shown in Figure 7, which shows little change in the wave length after a skull length of 13cm is attained. Thus, one can summarize the history of the replacement pattern in the crocodilians, by saying that they share with other reptiles a functional dentition consisting of the more mature members of a number of successive Zahnreihen. During early life there is an increase in the number of Zahnreihen in each tooth row, causing a switch in the wave-like replacement pattern from cephalad to caudad progression.

SUMMARY

The teeth of crocodilians are set in discrete sockets, held in by non-calcified connective tissue. Tooth replacement occurs through life in a definite sequence. Replacement teeth are formed from germinal material in pockets lingual to the base of the old tooth, and soon come to lie within the pulp cavity of their predecessors where they complete most of their growth. Early in life tooth replacement occurs in a pattern of waves passing along alternately numbered tooth series from back to front. Later in life the direction is reversed. The regularity of the replacement pattern decreases

with advancing age. No difference in replacement pattern or history could be detected between various genera. Live alligators examined periodically required between eight and sixteen months to replace any particular tooth. The anterior teeth were replaced more rapidly than the posterior teeth.

A review of the embryological literature showed that the teeth first appear in the embryo when the skull length is about 5¾ mm. Teeth are laid down in successive series termed *Zahnreihen*, which are the basic units of the dentition of all reptiles. Woerdeman's illustrations show a spacing between Zahnreihen of greater than 2.0 tooth spaces, which causes the functional dentition to have replacement waves running from back to front. A graphic analysis indicates that if the Zahnreihen are crowded more closely together, the replacement pattern will swing over to one of caudad waves, as was observed in an analysis of numerous modern crocodilians of all ages. This was correlated with the rapid replacement of the more anterior teeth in captive specimens, a phenomenon caused by the addition of extra Zahnreihen to a tooth row of limited length. As more Zahnreihen are added, the spacing becomes less than 2.0 positions, thus producing caudad waves.

APPENDIX

The following is a list of modern crocodilians used in this study. Under each species the figures refer to catalogue number and greatest skull length in centimetres.

Alligator mississippiensis

R.O.M. R 148	11.0 cm.
C.N.H.M. 35540	12.8 cm.
C.N.H.M. 6576	21.0 cm.
C.N.H.M. 25946	43 cm.
R.O.M. R 266	46 cm.
R.O.M. R 267	48 cm.

Caiman sclerops

R.O.M. R. 263	3.4 cm.
R.O.M. R. 261	6.5 cm.
C.N.H.M. 73449	6.8 cm.
R.O.M. R. 144	7.0 cm.

Caiman sclerops fuscus

C.N.H.M. 69839	6.08 cm.
C.N.H.M. 73751	7.64 cm.
C.N.H.M. 73750	11.2 cm.
C.N.H.M. 74903	14.2 cm.
C.N.H.M. 73753	17.5 cm.
C.N.H.M. 69852	20.6 cm.

Crocodylus sp.

R.O.M. R. 264	35.5 cm.

Crocodylus acutus

C.N.H.M. 5776	25.3 cm.
C.N.H.M. 69886	51.1 cm.

Crocodylus porosus

R.O.M. R. 262	4.5 cm.
R.O.M. R. 143	5.3 cm.
R.O.M. R. 149	5.5 cm.
R.O.M. R. 10	7.8 cm.
C.N.H.M. 15223	10.9 cm.
C.N.H.M. 15224	13.4 cm.
C.N.H.M. 15226	15.7 cm.
C.N.H.M. 14035	18.3 cm.

Osteolaemus tetraspis

C.N.H.M. 44442	7.93 cm.

Paleosuchus palpebrosus

C.N.H.M. 71835	3.8 cm.
C.N.H.M. 73450	8.6 cm.
C.N.H.M. 69872	15.1 cm.
C.N.H.M. 69867	18.8 cm.

Tomistoma schlegelii

C.N.H.M. 11084	13.6 cm.

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