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A. GORDON EDMUND

*Tooth Replacement Phenomena
in the Lower Vertebrates*

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TORONTO

A. GORDON EDMUND *Tooth Replacement
Phenomena in the
Lower Vertebrates*

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Preface

Scientists are motivated by one basic aim—to find general rules or laws which help explain observed phenomena, and which can be applied as widely as possible. When I began this study seven years ago, I realized that there might be some regular pattern common to certain reptilian groups, and thus I undertook to analyse systematically the information available from all reptilian groups. It soon became obvious that there were many superficially different replacement patterns, as well as different ways of implanting and replacing individual teeth. What did not appear obvious at the time, and only came out after much work, was the fact that there was a basic plan behind the dentitions of all vertebrates, and that that plan could be traced back in time, through the well-preserved fossil record, to the stem of the tetrapod line, in the Devonian crossopterygian fishes.

The problem was so immense, and so many interesting lines of research presented themselves, that it became absolutely necessary to limit the scope of the problem within practical bounds. The history of the development of the diphyodont condition of the mammals from the polyphyodont condition of the reptiles is a large study in itself and is properly the work of therapsid specialists. In many tetrapod lines there are rows of teeth in various positions, such as the palate, pharyngeal arches, and so on. In this work only those tooth rows on the premaxilla, maxilla, and dentary are considered, although brief references in appropriate sections indicate that the basic pattern of development and replacement applies regardless of the location of the tooth row.

To trace the evolution of various reptilian dental characteristics it was necessary to study both modern and fossil forms in the Reptilia and in their amphibian and piscine ancestors. When available, embryological evidence was also used. Thus, the investigation of the problem follows both phylogenetic and ontogenetic lines.

I wish to express my sincere thanks to Dr. A. S. Romer of Harvard University for suggesting that I undertake this study. I am deeply grateful

for his encouragement and constructive criticism. Dr. Tilly Edinger's wealth of experience and familiarity with both the literature and the fossil material have been freely given and gratefully received. Several other members of the staff of the Museum of Comparative Zoology at Harvard, especially Dr. E. E. Williams and Mr. Arthur Loveridge, have been of great assistance to the writer.

Thanks are due to many biologists and palaeontologists for permission to examine or borrow specimens in their care. The following have provided both specimens and encouraging advice: Dr. C. M. Bogert, Dr. E. H. Colbert, and Dr. Bobb Schaeffer, all of the American Museum of Natural History; Dr. D. Dwight Davis, Dr. Robert Denison, and Dr. Rainer Zangerl, of the Chicago Natural History Museum; Dr. Doris M. Cochran, Dr. David Dunkle, and Dr. Charles L. Gazin, of the United States National Museum; Dr. Joseph T. Gregory, of Yale Peabody Museum; Dr. Claude W. Hibbard, of the University of Michigan; Dr. E. C. Olson, of the University of Chicago; Dr. A. S. Romer and Mr. Arthur Loveridge of the Museum of Comparative Zoology, Harvard University; Dr. L. S. Russell and Dr. Wann Langston, of the National Museum of Canada; and Dr. S. P. Welles, of the University of California.

Dr. R. L. Peterson, Dr. W. B. Scott, Mr. E. B. S. Logier, and Miss E. McCormick of the staff of the Life Sciences Division, Royal Ontario Museum have given generously of their time in reading the manuscript. Their criticisms and suggestions have been most helpful. Finally, I must express my deepest thanks to Dr. F. A. Urquhart, Head of the Life Sciences Division, Royal Ontario Museum. Without his help and encouragement this work would not have been possible.

A.G.E.

Royal Ontario Museum

*Tooth Replacement Phenomena
in the Lower Vertebrates*

Introduction

The phenomenon of polyphyodonty in reptiles is generally recognized by all biologists and palaeontologists. It is a process of continuous dental replacement occurring throughout the life of the individual, not merely a process of replacement in response to wear or injury. An examination of a typical reptilian skull usually reveals teeth in every stage of growth and degradation, showing that replacement of the dentition as a unit is not a periodic process. This investigation was undertaken to determine the sequence in which tooth replacement occurs in reptiles, both fossil and recent, and to study the phylogenetic and ontogenetic implications of the process.

Owen, in his two-volume *Odontography*, summarized the knowledge of comparative dental anatomy up to 1845. He showed that replacement of teeth occurs in almost all fish, amphibians, and reptiles, and contributed many detailed descriptions of the replacement process in various genera. Although Owen apparently did not recognize that reptilian teeth are replaced according to a definite pattern, he noted a similarity between the arrangements of replacement teeth in certain reptiles and functional teeth in certain sharks. Owen's *Odontography* is, to this day, the only comprehensive work describing the dentitions of representatives of most vertebrate families. In his numerous descriptive works Owen was always careful to describe and illustrate the dentition of his specimens fully, a task unfortunately neglected by many modern palaeontologists.

The latter half of the nineteenth century and the early part of the twentieth saw great activity among microscopists, especially in England, Germany, and Holland. Much work was done in dental embryology and, although there was a certain amount of disagreement or even conflict, the foundations upon which future work on reptilian dentition could be based were laid.

The most significant observation reported by microscopists, such as Röse (1893 *et seq.*), Harrison (1901), Friedman (1897), and others, and by palaeontologists, such as Loomis (1900), was that the teeth in alternate

positions along the tooth row are often in approximately the same stage of development. That is, the odd-numbered teeth are replaced as a series, more or less independent of the even-numbered teeth, and vice versa. This phenomenon was observed in both adults and embryos of many fish, amphibians, and reptiles, and in fossil as well as modern specimens.

The first important paper on the regularity of tooth replacement in fossil specimens was by Loomis (1900). He was impressed by the regular alternation of functional teeth with those being replaced in the great carnivorous fish from the Cretaceous of Kansas. He found this condition in many species of fish, and remarked on the similarity between the replacement pattern in fish and that in amphibians and reptiles. Indeed, he became so fascinated with the study of tooth replacement that he devoted several pages of his essentially taxonomic paper to a discussion of it. Loomis' diagram of a generalized tooth replacement pattern (Fig. 1) is identical with that proposed by many later writers and is essentially confirmed by this study. It is interesting to note that Loomis made use of studies of comparative anatomy, quoting Friedman (1897) who showed the presence of the same replacement pattern in living teleosts, and also Röse, whose opinions (in correspondence) he used to explain various incidental phenomena.

Fig. 1. Diagram of generalized reptilian dentition as proposed by Loomis, 1900.

In many fossil amphibian and reptilian jaws it is common to find, over short sequences, that every alternate tooth position is empty, indicating post-mortem loss of unfused teeth. This condition is especially common in the labyrinthodont amphibians, where the phenomenon has frequently been described. In many groups, fossil as well as modern, either the replacement teeth or the visible effects of their presence on the structure of their predecessors remains. In these cases, there is no doubt that there is a regular alternation of functional teeth with those undergoing replacement. If, in a particular area of the jaw, the even-numbered teeth are in process of replacement, the odd-numbered teeth will be intact.

By the time L. Bolk began writing, it was generally accepted that replacement occurred, not in a haphazard pattern, but in the definite order described above. From 1912 to 1922 Bolk published numerous papers describing the embryological background for various tooth replacement phenomena seen in reptiles, and also attempted to explain the evolution of mammalian teeth. Much of Bolk's fame was gained through his suggestion that the phenomenon of alternation indicated the presence of two discrete dental series, the elements of which alternate along the tooth row. This was not an original observation, since Harrison (1901), studying the dentition of *Sphenodon*, said "It is difficult to avoid coming to the conclusion that we are here dealing with two dentitions." Röse, in several papers from 1892 to 1894, had made similar observations on *Crocodylus* sp. Bolk's early studies were essentially repetitions of Röse's work, demonstrating the formation of tooth buds on the dental laminae of various animals.

It will be necessary to digress momentarily to describe, in simplified form, the formation and topography of the dental lamina. The areas of oral epithelium with the potentiality to form teeth are differentiated in the very early embryo and lie lingual and subparallel to the future jaw margins (Fig. 2a). This area in each jaw ramus becomes involved in a longitudinal folding of the oral epithelium (Fig. 2b and 2c) so that the potentially dentigerous area of epithelium lies along the labial limb of the fold (Fig. 2d). The entire infolded structure is called the dental lamina.

Bolk's study of the arrangement of the buds on the dental lamina suggested the presence of two sites of formation: one on the "free" margin of the lamina (i.e., the bottom of the fold), the other on its labial (buccal) wall. These sites alternate, every odd-numbered one being in one row, every even-numbered one in the other. Bolk realized that this alternation of tooth buds, with two sites of formation, was correlated with the order in which the teeth were replaced in the adult. The tooth row which developed on the free margin and that which developed on the labial wall of the dental lamina Bolk termed *endostichos* and *exostichos* respectively, and he considered the dentition of the adult to be the combination of these two dentitions, whose members alternate with regard to both time of eruption and site of development. This concept was the basis of Bolk's distichy theory. Many critics attacked Bolk's work, especially the part dealing with the evolution of mammalian teeth, but his distichy theory was widely accepted and influenced students until quite recently. Bolk's concept of a typical reptilian dental lamina is shown in Figure 3.

Martin Woerdeman, a student of Bolk, took up Bolk's work, studying the development of the dental lamina and its products. At first (1919) he seems to have accepted Bolk's distichy theory in its entirety, but later (1921) he apparently came to realize that Bolk's interpretations were not consistent with all the facts. Bolk had studied the dental laminae mainly of older embryos in which several tooth positions had become established. Woerdeman, on the other hand, described the process of dental development beginning with the earliest stages and described the order and position in which the individual anlagen are laid down. He proved conclusively that

Fig. 2. Diagrams illustrating the development of the dental lamina in a typical reptile.

all teeth begin their development on the free margin of the dental lamina. Because of the sequence in which the anlagen are laid down and migrate towards the attached margin, the pattern in a more fully developed lamina at certain stages has the appearance of having two sites of development (Fig. 3).

This, no doubt, is what led Bolk to propose his distichy theory. Woerdeman, on the other hand proved conclusively that there is only one dentition and one site of development. The alternating appearance is attributable to the synchrony with which the teeth are laid down, as will be discussed in the embryological section of this paper. Many authors, despite doubts regarding the idea of two separate dentitions, still use the term distichy when they mean merely alternation. The term distichy was based on a misinterpretation of the evidence and should be abandoned.

The type of material used by Woerdeman has not been restudied, but more recent studies on teleostean fish (Vorstman 1922, Schnakenbeck 1936) have resulted in conclusions identical with Woerdeman's. Woerde-

Fig. 3. Bolk's concept of a typical reptilian dental lamina. The stereogram (above) was constructed from serial sections such as those shown a to g.

man attempted (1921) to use fossil evidence to illustrate alternating tooth replacement, but he used only a few inadequate specimens. He did not use the skulls of adult modern reptiles, although these afford abundant and convincing corroboration of many of his contentions, perhaps because most adult reptiles have a replacement pattern superficially different from that of the early embryos and Woerdeman may have purposely ignored them.

It is not uncommon to find skeletal or fossil reptile specimens in which, over a short sequence, every alternately numbered tooth is in about the same stage of the replacement cycle. This is what would be expected if Bolk's distichy theory were correct. However, if all of the teeth of one alternately numbered series are examined closely, each tooth will usually be seen to be more advanced in the replacement process than the tooth anterior to it. There appears to be a wave of replacement passing along each alternately numbered tooth series. Since the youngest teeth in each wave lie at the anterior end, it is apparent that the waves are passing from back to front.

At the anterior end of a typical replacement wave are small replacement teeth lying in soft tissue. These are followed by teeth of increasing size and degree of development. Near the posterior end are the mature teeth, intact and firmly attached to the jaw. The most posterior teeth are usually being prepared for shedding by some sort of resorptive process. Ideally, each replacement wave demonstrates all the stages in the replacement cycle, from the first appearance of the young tooth through growth, maturity, and

Fig. 4. Analysis of the dentition of a typical reptile, *Iguana iguana*, U.S.N.M. 65840 (upper left jaw).

- a. Drawing of the jaw
- b. Diagrammatic representations of the jaw.
- c. Graphic analysis of the jaw.

attachment, and finally to degradation and loss. The length of time required at each stage in the replacement cycle varies a good deal. A mature tooth may remain in the functional dentition for a considerable period with no obvious changes, or may be replaced quickly almost as soon as it has been established. The number of teeth in each replacement wave also varies greatly.

Since one replacement wave replaces the teeth laid down by the wave immediately ahead of it, the resulting pattern in any alternately numbered series is one of overlapping waves. Thus, a graphic presentation of the wave pattern, such as in Figure 4, shows the waves succeeding each other like shingles on a roof.

It is not surprising that the presence of an orderly sequence of tooth replacement has generally been overlooked. Where there are several overlapping waves in both of the alternately numbered series the basic pattern is not obvious. In most reptiles the jaw bears teeth in all stages of replacement, apparently randomly distributed. Only when the teeth in such jaws are analysed with alternation in mind can the presence of clear-cut waves be recognized.

Parrington (1936, a and b) was the first author to mention that tooth replacement in a reptile occurred in a wave-like pattern. His description of the sequence of replacement in a mosasaur showed waves in both the marginal and the palatine series and many of his conclusions were arrived at independently twenty years later by the present writer. Parrington's more

recent work has been on the therapsid reptiles; in this field a good understanding of tooth replacement is essential. Romer and Price (1940) and Romer (1949), describing pelycosaur jaws, reported the phenomenon of replacement by waves and gave an account of their significance to the animal. Largely because of Romer's work, other modern palaeontologists have become aware of the wave pattern of replacement, and more attention will undoubtedly be paid to it in the future. The possibility of waves of tooth replacement in various specimens has been considered in recent paleontological papers by Colbert (1952), Peabody (1952), Watson (1954), Vaughn (1955), and Romer (1956).

Another feature of reptilian tooth replacement mentioned originally by Romer and Price (1940) is that the areas of active tooth replacement in the two alternately numbered series are not coincident. "It will be noted that the waves of replacement are synchronized in the two series, so that when replacement is occurring at one locality in one series, the other is always functioning." This phenomenon was seen in hundreds of specimens in the present study, yet has had little mention in the literature.

The most extensive survey of tooth replacement phenomena to date is that of Edinger (1944). While a fellow of the Guggenheim Foundation in 1943-4 she studied both specimens and literature, but unfortunately her results were not published. Dr. Edinger's notes, containing many useful references and profound observations were generously turned over to the writer, who has found them both fascinating and stimulating.

Gillette (1955) carefully described the replacement mechanism in a frog, an unfortunate subject to choose since the perfect alternation seen in most reptiles is somewhat obscured in that amphibian. However, Gillette recognized the presence of a wave pattern similar to that of the reptiles. Bogert and Martin del Campo (1956) described the dentition of *Heloderma* and compared it to that of other lizards, and although they did not arrive at the general picture of tooth replacement as seen in practically all reptiles, they did recognize the presence of a wave-like form of replacement. Similarly Gans (1957), studying *Amphisbaena* recognized the presence of both an alternation and a wave pattern in many of his specimens.

Materials and Methods

The central purpose of this paper is to determine the sequence in which reptilian teeth are replaced. The ideal method would be to use live animals which have had each tooth marked or numbered. From periodic examinations it would be an easy matter to determine when various teeth dropped out and were replaced. This is obviously impossible in most cases. First of all, a large number of reptilian groups are extinct, represented only by fossils. Secondly, most of the living reptiles have small teeth which are difficult to mark, and it is also difficult to keep such animals alive in captivity and to temporarily subdue them for examination. For these and other technical reasons, it appears that no one up to the present has attempted to make periodic examinations of reptile jaws. In the present study, however, the writer has succeeded in using radiography to trace the course of replacement in alligators, with promising results, and the use of this technique on other reptiles is being investigated.

In the absence of the ideal information from living specimens, we must turn to dead material, and here the approach is necessarily less direct. The analogy between a moving picture and a "still" is apt. The periodic examination of a living reptile gives us all of the essential information concerning replacement including the time factor. But with dead material—museum skeletons of recent and fossil reptiles—we are forced to use a series of still pictures in which the action is "frozen" at the moment of the animal's death. From the evidence available we must reconstruct the action, and when the material is adequate we can, by arranging a series of "stills" in proper sequence, succeed in determining almost the entire replacement story, excepting, of course, those parts concerned with rates of growth and replacement.

To determine the sequence of tooth replacement from dead material, it is necessary to know the condition of a number of successive teeth in a jaw ramus. The word "condition" is used in this paper in a special sense. Essentially it is a description of the over-all dental picture at any one tooth

position, and includes the state of the old tooth, of the replacement tooth, of the socket when present, plus any other pertinent information. When the conditions of a number of alternately numbered teeth are assigned values and plotted on a graph, the replacement pattern becomes obvious.

Also important is a description of the mechanism effecting replacement. This requires knowledge of the site of formation of the replacement tooth, and the site of its later development, the changes in the old tooth as replacement progresses, as well as the method of disposal of the old tooth and the establishment of its successor. In many instances this information was available from the literature, but on the whole that source was not satisfactory. Most authors treating reptilian osteology or paleontology were either unaware of the significance of the tooth replacement pattern or were not interested in it. With the exception of a few works whose authors were either remarkably thorough or were particularly interested in dentition, most of the information from the literature had to be gleaned from the illustrations rather than from the text. Even these were not trustworthy in every case, since some artists reconstructed missing teeth without acknowledging that they had done so. As Edinger (1944) remarked, "it becomes obvious in such a study, that the best authority is the specimen itself."

This work is divided into three parts, introductory, descriptive, and discussion. Part II presents observations and graphic analyses of the dentitions of representatives of all available toothed reptilian groups. Part III includes discussion of tooth replacement in sub-reptilian groups (both modern and fossil), and a consideration of the dental embryology of fish, amphibians, and reptiles, with comparisons between ontogenetic and phylogenetic lines. Finally, all of the data from the three classes are analysed, a general case constructed, and conclusions presented.

The materials used in this study fall into three categories: (I) specimens "in the flesh"; (II) cleaned modern skulls; and (III) fossil skulls. The first group includes preserved whole specimens as well as living animals. Two methods of handling these were used by the author: clearing and radiographs. The clearing process for preserved material was a standard method of alkaline maceration, staining with Alizarin red S, and clearing with glycerin. This permitted the retention of the replacement teeth *in situ*. Several fish, lizards, and snakes were studied in this way, yielding information not otherwise available except by tedious serial sectioning.

Radiographs were used in many cases among the preserved specimens, especially with members of the Platynota, in which many of the teeth are not ankylosed. In the preparation of skeletal material, these loose teeth are frequently lost, but a radiograph taken before maceration reveals these *in situ*, thus insuring valuable data against loss in case of accidents during preparation, and in some cases obviating the need for maceration entirely. With modern fine-grain industrial films (Kodak type AA or M), a small focal spot, and a long tube-to-film distance, excellent detail can be obtained, permitting much enlargement, at least up to thirty diameters. Radiography was also used for periodic examination of live animals. Specimens of *Alligator mississippiensis* were kept alive and radiographed monthly. Some of

the results of the examinations of one alligator carried out over a period of nearly two years are presented in this paper.

The second group of specimens, skeletal preparations of modern reptiles, was usually the easiest to work with. Literally thousands of skulls were looked over, and hundreds of jaw quadrants selected for closer study. Unfortunately, over-zealous preparation resulted in the loss of the replacement teeth in many specimens, because in most cases the replacement teeth are retained only by soft tissues which are removed along with the other flesh. To gain the fullest information from some critical materials, the author carefully prepared several skulls by controlled maceration in sodium hypochlorite. The skull, after being skinned and roughed out, was immersed in fresh full strength laundry bleach for a short period, usually a minute or two, then removed and washed in a dish of water. The dentition was examined under the binocular microscope, and if it appeared that any unfused teeth were in danger of being lost, the specimen was allowed to dry. To protect the loose teeth, a "bridge" of connective tissue was preserved by being painted with a thin solution of Gelva, applied with a very fine camel hair brush. When dry, this treatment prevented the action of the bleach at that point for a considerable period, yet the amount of soft tissue retained was so slight as to be almost invisible. The process of macerating, washing, drying, and painting was repeated several times until the dentition was completely exposed, the use of this method permitting retention of practically all dental elements in almost every case. Some specimens which had been in alcohol for seventy-five years yielded excellent skulls. A competent operator can average about fifteen skulls per day. Care must be taken to use only fresh strong (10 per cent or more available chlorine) bleach, since long exposure to the high alkalinity of expended bleach attacks the bone rather than flesh, resulting in a flaking, chalky preparation. Fresh bleach works cleanly and quickly and is quite inexpensive. Since the process is an exothermic reaction, and the generation of much heat must be avoided, it is recommended that, where action is particularly vigorous, the specimen be immersed only for brief periods until the heat dissipates.

Fossils were the most difficult of the three types of material to study. For some forms, excellent specimens were available, but in other cases the material was meagre and poor in quality. On the whole, however, quite adequate information was obtained for members of most of the major fossil groups concerned. The main method of observation again was direct surface examination, as in modern skulls. X-rays and sections were occasionally used. Where sectioning was done, it was by serial, peel sections, as described by Darrah (1936). Radiographs frequently yielded good results with some fossil material, but often the presence of certain minerals in the bone or matrix caused too great a scattering of radiation or a lack of contrast.

Most of the data were obtained during visits to various museums. Because of the limited time available, records were made largely with the camera. This method enabled the author to examine a large amount of material while visiting museums, permitting close study and analysis to be postponed until later.

The information used in the embryological parts of this paper was obtained entirely from the literature. It was found that, although there were many disagreements on interpretation, the basic observations and descriptions presented independently by several authors generally agreed, and therefore these were taken as presumably reliable and were not checked by the present writer. As each reptilian group is considered, the method by which an individual tooth is replaced will be described and, where necessary, illustrations of significant specimens will be given. All of the drawings in this paper were produced by photographic processes. A photographic print was made, usually at least twice the size of the finished illustration, then a tracing on matte acetate was taken from it. This method ensures that the proportions are correct, the only artistic licence being the omission of extraneous details.

To determine the pattern of replacement in the dentition, the condition of all the teeth in the jaw will be described. This may be a verbal description in some cases, but usually, because of the large number of specimens under study, the information is in graphic form. In these latter cases the dentition is shown as a row of stylized symbols, each representing one tooth position. The essential information used in constructing these charts is the "condition" of each tooth position, that is, the over-all description of tooth replacement activity at any one location. Depending on the type of dentition, such criteria as degree of development of the replacement, degree of wear or degradation of the old tooth, or the general appearance of the alveolus, are used in assigning a condition value to any position. For convenience, five categories, termed A to E, were recognized, with A indicating the earliest stage in the replacement process. Assignment to categories of condition is necessarily somewhat arbitrary since the process is continuous, but the method is quite adequate for the purpose.

The symbols used are largely self-explanatory. The size of the tooth-like symbol is proportional to the actual tooth. A functional tooth is shown by an open-based symbol, a loose replacement tooth by a symbol with an elliptical base, and a tooth just becoming ankylosed by a symbol with a serrate base. Where basal resorption of the old tooth occurs, it is shown by a "bite" out of the symbol, the size of the bite being proportional to the size of the cavity. Odd-numbered symbols are shown stippled, even-numbered ones blank. Where there is reasonable indication of their condition, missing teeth have been restored as broken lines in the diagrams.

To introduce this method of presentation, and to illustrate a typical pattern of reptilian tooth replacement, a jaw of *Iguana iguana*, U.S.N.M. 65840 is completely analysed in Figure 4. In the Iguanidae the process of replacement of the pleurodont teeth is easily observed. A replacement tooth develops directly lingual to the base of the old tooth, and while it is still quite small an excavation appears in the base of the old tooth. At first this pit involves only the surface of the base of the tooth, but soon penetrates to the pulp cavity. The replacement tooth comes presently to lie within this pit, the tooth and pit increasing in size simultaneously. Eventually the tooth is completely undermined, with most of its lingual side resorbed. Following

this stage the crown of the old tooth is shed and the new tooth moves into its definitive position, where it completes its growth and becomes ankylosed to the bone.

Because of the constant relationship between the size of the pit and the size of the replacement tooth, the progress of tooth replacement can easily be followed, even when the loose replacement teeth have been lost during preservation or preparation.

In the iguanid lizards five conditions are recognized:

- A. Replacement tooth very small. Old tooth with a small pit in its base, but pulp cavity not invaded.
- B. Replacement tooth small to medium sized. Pit in old tooth has opened into the pulp cavity.
- C. Old tooth has been deeply excavated, and is often a mere shell. Replacement tooth is large.
- D. Old tooth has been lost. The new tooth has not yet become ankylosed, or shows definite evidence of being recently fused. The stage is often represented by an empty position in skeletons.
- E. Perfect tooth, well ankylosed. No resorption pit at its base.

In the right upper jaw of *Iguana iguana*, U.S.N.M. 65840 (Fig. 4a), teeth in all stages of replacement can be seen. Two positions, numbers 8 and 10, bear the basal remains of old teeth from which the crowns have been lost. Teeth 10, 16, 21, and 28 are shown with stippled bases, indicating the beginning of deposition of the ankylosing bone. These are obviously new teeth coming into use. Only three apparently sound teeth are present, numbers 1, 3, and 23. All of the remaining teeth bear resorption pits of various sizes at their bases. Only one unfused replacement tooth has been retained, number 26. The size of the lost replacements can be easily inferred, however, by reference to the size of the resorption pits in the bases of their predecessors.

A cursory inspection of the specimen seems to indicate that replacement is occurring in a random order. Teeth in various stages of replacement are found throughout the jaw. When assigned to their proper conditions and separated into two alternate series, however, the regularity becomes obvious. Figure 4, b and c reveals the presence of several discrete waves in both of the alternately numbered series. Each wave extends over about seven tooth positions, and the most fully developed and hence oldest tooth in each wave is at the rear. In life these waves obviously proceeded cephalad, with replacement beginning at the anterior end of each wave and becoming complete at its posterior end.

Frequently a tooth barely becomes full grown and ankylosed before it in turn is subjected to the degradation associated with replacement. This is seen here in the series 8, 10, 12, etc. There had been a large tooth lying within the shell of the base of its predecessor in position 8. Tooth 10 is one stage more advanced, having just become ankylosed, but it is not yet truly mature. Tooth 12 already bears a pit penetrating into its pulp cavity, indicating the presence of a small but fairly well-advanced replacement tooth. No doubt the duration of the resting phase, when no replacement activity is

occurring, is very short in this specimen. This, of course, varies with different reptilian groups.

This specimen also illustrates another constant feature of reptilian tooth replacement, namely, that in an area where the teeth of one series are being replaced, the teeth of the alternate series are intact. Thus, any tooth in the terminal stage of replacement, when it is functionally weakest, is flanked by relatively intact teeth. At no place in this specimen is there a gap of more than one tooth in the dental series, since intact teeth always alternate with teeth being replaced. This calls to mind the sine wave used in physics and mathematics, and we may consider neighbouring teeth in the two alternating series to represent opposite phases of the sine curve. For instance, a fully functional tooth at one point in one of the series could be compared with the 90° position on the sine curve. At the same point in the jaw, the neighbouring tooth would probably be far advanced toward replacement, and could be compared with the 270° position on the sine curve. In such a biological process, mathematical exactness is not to be expected, but the two waves are always close to being 180° out of phase, and the term "in opposite phases" will be used to describe this phenomenon.

No break occurs at the premaxilla-maxilla suture, which in this specimen is between teeth three and four. This continuity of replacement rhythm over the suture is general in reptiles.

In Part II each group of reptiles will be presented and analysed in the above manner. The order in which they are considered is usually that of Romer (1945). Because of their simple method of replacement and their early geological history, the synapsids are taken up immediately after the cotylosaurs. Since the therapsid-to-mammal line is not being followed, early consideration of the synapsids seemed advisable. The Squamata have been classified according to Romer (1956).

ABBREVIATIONS AND TERMINOLOGY

To conserve space, the following abbreviations are used.

(I) Designation of jaws: U.L. upper left; L.L. lower left; U.R. upper right; L.R. lower right

(II) Institutions possessing cited specimens:

A.M.N.H.	American Museum of Natural History
B.M.(N.H.)	British Museum (Natural History)
C.N.H.M.	Chicago Natural History Museum
K.U.M.N.H.	Kansas University, Museum of Natural History
M.C.Z.	Museum of Comparative Zoology, Harvard University
N.M.C.	National Museum of Canada (Natural History Branch)
R.O.M.Z.P.	Royal Ontario Museum, Division of Zoology and Palaeontology (now Division of Life Sciences)
U.C.M.P.	University of California, Museum of Paleontology
U.M.	University of Michigan
Y.P.M.	Peabody Museum, Yale University

(III) Special dental terms used:

Labial:	towards the lips, that is, the anterior surface of an anterior tooth, or the lateral surface of a cheek tooth.
Lingual:	towards the tongue, that is, the posterior surface of an anterior tooth, or the medial surface of a cheek tooth.
Mesial:	refers to that surface of a tooth facing along the tooth row towards the premaxillary or dentary symphysis.
Distal:	refers to that surface of a tooth facing along the tooth row away from the premaxillary or dentary symphysis.
Occlusal:	refers to the grinding or biting surface of the teeth.
Occlusal plane:	that imaginary plane joining the tips of all the fully erupted teeth in a jaw.

Class Reptilia

Subclass Anapsida

Order Cotylosauria

Because of their basic position in reptilian evolution, the cotylosaurs merit special consideration in a study of this sort. It is therefore especially regrettable that fossils representative of the group are rare and often poorly preserved, or preserved with the lower jaws firmly cemented to the uppers. Differences of opinion among several authorities on the general phylogenetic position of the few well-known cotylosaurs points to our meagre knowledge of the group, and an understanding of their dentitions would be helpful if it were obtainable.

Practically all modern palaeontologists recognize that the order Cotylosauria is a horizontal, rather than vertical assemblage. Within it are two fairly clearly defined phyletic lines, usually termed the Captorhinomorpha and Diadectomorpha. Most authorities agree on the assignment of most of the genera of cotylosaurs to one or other of the two groups. The main difficulty lies in tracing their origin and history.

The Diadectomorpha, as first defined by Watson (1917), consists of the diadectids, procolophonids, and pareiasaurs. Of the Captorhinomorpha, only a few genera are known in detail, and the only representatives with well preserved or prepared dentitions are those with extreme specializations. *Seymouria* and its relatives are forms close to the common ancestry of both the diadectomorphs and the captorhinomorphs, but whether they are extremely primitive reptiles or advanced labyrinthodonts is a matter of considerable uncertainty (see Watson 1917, 1951, 1954; Romer 1945, 1946; Olson 1947). *Seymouria* is here treated with the Amphibia in CHAPTER TWENTY.

SUBORDER CAPTORHINOMORPHA

Several genera belonging to this group have been described, but most are not represented by adequate dental material. *Captorhinus* is known from many skull and jaw fragments, as well as from almost complete skeletons.

Its dentition is well known, but because of its extreme specialization does not give us any indication of the dentition probably more typical of the group. Large numbers of jaws of *Captorhinus aguti* Cope from the Oklahoma fissure collections at C.N.H.M., A.M.N.H., Y.P.M., and M.C.Z. were studied, and all showed the same pattern, as illustrated in Figure 5, a and b.

The teeth are arranged not in a single row running parallel to the jaw margin, but in a band or field several teeth wide. In the specimens, all of the teeth are ankylosed, and none shows any evidences of the usual replacement processes such as basal cavities, gaps in the series, or obviously recently ankylosed teeth. The pattern in which the teeth are arranged (Fig. 5, a and b) is, however, quite significant. Rather than being distributed at random, the teeth are arranged in several rows, usually about five in larger individuals, oriented from mesio-labial to disto-lingual, one row overlapping the next like shingles on a roof.

This is exactly the pattern reported by Woerdeman (1921) as typical of the embryos of various reptiles (Figs. 54 and 55). Vorstman (1922) recognized the same pattern (Fig. 56) in both embryos and adults of many fish. In reptilian and piscine embryos, teeth are not produced at the same time by all of the definitive tooth positions. Rather, they are laid down in a regular succession consecutively, beginning at the anterior end of the lamina. Thus, the more anterior teeth will have become larger and have moved labiad and occlusad by the time the more posterior teeth begin their development. At any one time, the teeth in one of these series will be graded in size and in distance from the free margin of the dental lamina, with the more anterior teeth being older, larger, and nearer the labial margin of the jaw. (SEE CHAPTER NINETEEN of this paper for details). This is exactly the condition seen in *Captorhinus* (Fig. 5a and 5b). A second row is budded off the dental lamina and similarly moves labiad, with its anterior end again being more advanced than its posterior end. In most reptiles and in many fish and amphibians the earlier series of teeth are usually lost, to be replaced by subsequent series coming off the dental lamina. This is not the case in *Captorhinus*. Here, the first set became ankylosed and constituted the first functional dentition of the animal. Some very small *Captorhinus* jaws from the Fort Sill, Oklahoma, area show only one or two rows of small teeth arranged in the pattern described above. We must assume that the growth of these small teeth ceased once they became ankylosed and functional, since growth of a tooth is impossible unless it is free to grow by addition to its root. Therefore, the small teeth in the postero-labial series are not teeth which were still growing at the time of the animal's death, but represent a series laid down when the animal was small. These teeth are retained, and supplemented rather than replaced, by the larger, more antero-lingual series which are produced later.

The arrangement of teeth in diagonal tooth rows, called "Zahnreihen" by Woerdeman (SEE CHAPTER NINETEEN) imposes a limitation on the area of growth of the dentigerous bones. With growth of the animal as a whole there can be no caudad increase in the tooth row since this area is blocked by the first, diagonally oriented Zahnreihe, which obviously remains anky-

Fig. 5. Dentitions of Cotylosaurs.

- a. *Captorhinus aguti*, C.N.H.M. U.R. 338, occlusal view of a right lower jaw.
- b. *C. aguti*, C.N.H.M. U.R. 339, labial view of left lower jaw.
- c. *Labidosaurikos bakeri*, C.N.H.M. U.R. 113 occlusal view, right maxillary dentition.

losed for the life of the animal. Since new teeth must move labiad from the dental lamina, they cannot be added to the dentition posterior to the first-formed Zahnreihe. The growth of the dentigerous area could only occur anterior and lingual to the existing Zahnreihen, that is, towards the anterior midline. This type of growth is apparently confirmed by the finding of the largest teeth in the more lingual and anterior Zahnreihen. These larger teeth were, of course, produced when the over-all size of the animal was larger. Good series of growth stages of *Captorhinus* jaws are available at several museums, and in these specimens there is always an addition of Zahnreihen with larger teeth anterior and lingual to the existing Zahnreihen.

Resembling *Captorhinus* in its dentition is *Labidosaurikos* (Fig. 5c). The Zahnreihen are longer than in *Captorhinus* and lie subparallel to the jaw margin, but their general arrangement is that seen in *Captorhinus* and can be similarly explained. The specimen illustrated, *L. bakeri*, C.N.H.M. U.R. 113, is part of a right maxilla with five Zahnreihen. A smaller specimen of the same species C.N.H.M. U.R. 183 also has five Zahnreihen in the maxilla. In both, the multiple row arrangement is found only in the more posterior part of the jaw, the anterior part bearing a single marginal row.

The relation between this single row and the multiple Zahnreihen is not clear from the material available.

Two other genera represented by fairly good material have been described, but their dentitions are not adequately known. Romer (1946) re-described *Limnoscelis*, which is considered to be a more typical stem reptile than *Captorhinus*. He concluded (p. 163) that "There is little data on tooth replacement, but it may be assumed to have shown the waves of replacement of alternate series characteristic of primitive tetrapods in general." Unfortunately, the tooth rows of *Limnoscelis* have not been prepared lingually, and no useful information can be gleaned from either crown heights or general aspect of the labial sides. The illustrations of Williston (1912) and Romer (1946) show the teeth as regular featureless cones.

Two well-preserved and thoroughly-prepared lower jaws of *Labidosaurus hamatus*, C.N.H.M. U.C. 727 and U.C. 1198, were examined, but the writer found little evidence of replacement activity. In each jaw there was one tooth which had a cavity in the lingual side of its base, suggesting that resorption was taking place preparatory to the loss of the tooth. The alternate tooth following each of these excavated teeth did not appear to have been recently replaced, however; indeed all of the teeth appeared to be equally well ankylosed and evenly worn. Thus, *Labidosaurus* may have had tooth replacement of a type similar to that of *Iguana* described previously, but the process seems to have affected only one tooth at a time. A similar situation is seen in the pelycosaur *Edaphosaurus* which will be described later.

SUBORDER DIADECTOMORPHA

The type genus of the suborder, *Diadectes*, is represented by four species (Olson, 1947). The dentition of all species is similar, consisting of about four chisel-shaped incisors and a series of transversely widened cheek teeth in each jaw. The mode of replacement of individual teeth, as well as the sequence of replacement, can be easily determined from material on hand. Watson (1954) described the stages of replacement in detail, and the following account is based in part on his description and in part on the writer's observations.

The old, functional teeth have roots set in fairly deep sockets and are firmly ankylosed. The first sign of impending replacement is the appearance of a shallow pit on the lingual side of the neck of the old tooth near its attachment to the dentigerous bone. Presumably the germ of the replacing tooth develops in this pit. The size of the pit increases, resulting in a large excavation deep within the tooth, occupying the pulp cavity and involving the base of the tooth. The writer cut a section through a cheek tooth of *Diadectes* sp. (Fig. 6), which showed only a small pit in its neck and base, but proved to have a large crypt lying beneath the old crown, containing the wide but thin crown of a replacement tooth. Apparently the replacement tooth had entered the pulp cavity of its predecessor while it was only a few millimeters wide, since the diameter of the entrance was much smaller than the diameter of the replacement crown.

With the growth of the crypt keeping pace with the growth of the replacement tooth the base of the old tooth becomes so weakened that the crown and remaining base become lost. The root of the replacement is formed and at the same time the remnants of the old root are removed. This stage is represented in fossils by clean, smooth-walled alveoli; only rarely are loose, unankylosed teeth retained in any species during the processes leading to fossilization. The replacement tooth increases in vertical height (horizontal dimensions were attained while still in the crypt) until it reaches occlusal level, when the deposition of a bony substance begins at its base. Such a tooth, distinguished by its unworn crown and lack of basal pit, is then ready for use.

Fig. 6. Transverse section through a cheek tooth in the left dentary of *Diadectes* sp. 'a' is the pit in the lingual wall, 'b' is the developing replacement tooth.

A right dentary of *Diadectes* sp., No. R 500 in Watson's personal collection, is described in detail by Watson (1954). This specimen was collected in small fragments, permitting a study of internal conditions not obtainable in a whole specimen. Watson's descriptions will not be repeated here.

The following is a summary of the progress of tooth replacement seen in each of the alternately numbered series. Position 1 is either the first or second tooth on the dentary. Position 1 contains a young tooth just coming into function. The third tooth is well-fused and intact. Five is being attacked, and 7 has been lost. Positions 9 and 11 are also empty, but there are indications of deposition of a cement-like material. Tooth 13, the first tooth of a new generation, has been fused on, but already shows early signs of resorption. Thus, there is one complete cycle of replacement in the odd-numbered series.

In the even-numbered series, tooth 2 has been lost, but part of its base remains in the alveolus. A replacement was just beginning to become fused in position 4, but has been lost in the specimen. The replacement has become fused in position 6, and already bears a small resorption pit. A large cavity has formed in tooth 8, within which the crown of the replacement can be seen. Teeth 10 and 12 are similar to 8. In position 14 the old tooth has been lost and the new tooth not yet ankylosed.

Watson concludes that "The general pattern of tooth change is not evident, but it may be essentially an alternate replacement brought about by a wave of tooth shedding progressing along the jaw in some manner analogous to that found by Parrington in the mammal-like reptiles." This is obviously the case. Each of the alternately numbered series shows approximately one complete cycle of replacement, the pattern being one of waves passing from back to front along alternately numbered tooth series, as

shown in Figure 4. The waves in the odd-numbered series are clearly distinct from those in the even-numbered series, and are out of phase with one another, in the sense defined in the illustrative example.

An excellent right lower jaw of *D. lentus*, U.C.M.P. 33903, described by Welles (1941) was kindly loaned to the author for study. This well-preserved and well-prepared jaw shows all stages in the tooth replacement cycle. Tooth 1, at the symphysis, bears a deep pit containing the crown of a replacement. The third tooth is obviously new. Tooth 5 has a shallow pit not yet reaching the pulp cavity. The old tooth has been lost in alveolus 7 and the replacement not yet ankylosed. The ninth tooth is only slightly worn and is not completely buttressed by cementum, indicating that it came into use recently. Teeth 11 and 13 are intact. Fifteen and 17 are damaged, but appear to belong to the same generation as 11 and 13. Thus, there is a rapid replacement occurring through teeth 1, 3, 5, and 7, the remaining odd-numbered teeth apparently being in the resting state.

The even-numbered series is similar. Tooth 2 bears a shallow cavity not perforating the pulp cavity. Four is obviously a new tooth. Six is undergoing wear, but shows no basal pit. The eighth tooth is similar to number 2, showing a shallow pit. There is a large, deep pit beneath tooth 10, obviously the site of a large replacement tooth. Number 12 has only recently come into function. It is rotated slightly, as if it were not ankylosed *pre mortem*. Surprisingly, the next alveolus, 14, is empty except for a well-developed loose crown. This probably represents a replacement which was lying beneath a tooth lost just before, or possibly after, death. This area of the jaw is damaged so that we cannot be certain of the pre-mortem condition. It appears that in some areas of certain jaws the replacement waves run very close together, so that newly fused teeth undergo replacement almost as soon as they come into use. Also, the pit in a tooth may be deceptively small, not revealing the extent of resorption and development beneath the crown. In alveolus 16, the base of the old tooth has been resorbed and the unfused replacement lost. A fragment of tooth 18 indicates that it is the first member of the new generation to have become fused to the jaw. The replacement pattern of this jaw is graphically illustrated in Figure 7c. Several other specimens of *Diadectes* were examined, yielding patterns similar to those described above (Fig. 7, a and b). Among the better preserved jaws seen were those of Y.P.M. 805, C.N.H.M. U.C. 675, and A.M.N.H. 4839.

Stephanospondylus, originally described by Geinitz and Deichmuller

Fig. 7. Diagram of tooth replacement patterns in specimens of *Diadectes lentus*.

- a. Y.P.M. 805, upper right jaw.
- b. C.N.H.M. UC675, part of lower left jaw.
- c. U.C.M.P. 33903, lower right jaw.

(1882) as *Phanerosaurus*, has been placed in the Diadectidae by Romer (1925). No order of tooth replacement could be made out from the illustration of the fragmentary specimens, but the individual teeth are quite similar to those of *Diadectes*, and presumably it had a similar mode of replacement.

The other Diadectormorpha, the pareiasaurs and procolophonids are represented by many specimens, but little has been published which is useful in the interpretation of dental succession. Owen (1876) figured a section through the mandible of *Pareiasaurus*, showing that the replacement process is similar to that in *Diadectes*. The tooth is compressed rather than transversely widened, but there is the same type of large lingual resorption cavity containing a well-developed replacement tooth. About two-thirds of the lingual wall of the illustrated old tooth has been resorbed. The new tooth apparently had grown within the pulp cavity; however, it is not centrally placed beneath the old crown but somewhat lingual in position as in the pelycosaurs.

Owen's figure of *Pareiasaurus bombidens* (Owen 1876, Plate IX) shows most of a lower left jaw with all of the teeth in function. The third, fifth, and seventh teeth are somewhat less fully erupted than the second, fourth, and sixth, indicating an alternating pattern, although no waves could be determined. No doubt there is excellent pareiasaur dental material in the South African museums, but none useful in the present study was seen in the several United States museums visited. No specimens of procolophonids with adequately prepared or preserved dentitions were seen by the author, and the illustrations in the literature seem to indicate that others have not seen them either.

Bolosaurus striatus, the sole species of the family Bolosauridae, which appears to be a sterile offshoot of the cotylosaurs, has been studied by Watson (1954). On page 317, Watson states that "there is evidence that the teeth in the front of the mouth were worn out, shed, and replaced." His evidence seems to be the fact that all of the teeth do not show the same degree of wear. One specimen, M.C.Z. 4462, a left maxilla, bears a young crown lying in an otherwise empty alveolus. The process of individual tooth replacement is apparently similar to that described above for *Diadectes*, but no order of replacement could be made out.

Thus, a survey of the Cotylosauria shows that we know very little about the processes of tooth replacement in stem reptiles. *Diadectes* is represented by quite adequate material, and shows a method of replacement of individual teeth almost identical with that which will be seen below in several other reptilian groups. Its pattern or order of replacement is also typical of most other reptiles. Beyond *Diadectes* we have only the bizarre dentitions of *Labidosaurikos* and *Captorhinus* and the vaguely known pareiasaurs. The dentitions of *Captorhinus* and *Labidosaurikos* obviously represent a modification of an embryonic pattern which has become "frozen" and retained and added to in the adult. Such a specialization indicates clearly that these forms were not on the main line of evolution. Other captorhinomorphs, with typically reptilian dentitions, are yet to be studied from adequate material.

Class Reptilia

Subclass Synapsida

Order Pelycosauria

The structure of the teeth and their method of replacement are fairly well understood in the common pelycosaur genera, and have been described in some detail by Romer and Price (1940). The marginal teeth are simple, usually compressed cones set in a single row of sockets on the premaxilla, maxilla, and dentary. A more or less distinct groove lies alongside the bases of the teeth, probably bearing in life the dental lamina and its developing tooth buds. In fossil specimens the first evidence that tooth replacement is taking place is seen on the lingual side of the teeth and the adjacent bone. Romer and Price (1940, p. 91) continue

Here there is considerable resorption of adjacent skeletal materials to form the cavity in which the new tooth develops. The bone is resorbed beneath the site of this activity, the resorption in some cases even perforating the inner surface of the dentary or maxilla beneath the covering of the adjacent dermal bones. On the labial side of the groove the cavity expands into the area of the tooth to be replaced, with resorption of the basal portion of the tooth structure. As far as can be determined the forming tooth gradually moves laterally into its definite position as this resorption goes on, the enamelled tip of the replacing tooth being often found in a cavity beneath the crown of the old tooth while it still functioned. Frequently an empty socket is seen in the specimens without any trace of the replacing tooth; this, however, is surely due to the fact that the replacing tooth, not yet firmly attached to the socket, was lost post mortem.

The system permits the new tooth to develop to a fairly large size while enjoying the protection of its still functioning predecessor. The cavity in which the new tooth lies never progresses to the tip of the old tooth, the process of resorption causing loss of the old crown before the new tooth attains full stature.

Empty alveoli in pelycosaur jaws often bear parts of the bases of old teeth from which the crowns have been lost. From the evidence indicating the direction of progress of the replacing wave, it is apparent that these remnants of the old bases were later completely removed, resulting in clean smooth sockets before ankylosis of the new teeth took place. Because the new teeth grew within the old teeth, only the crowns could develop before the remains of the predecessors were shed, and more growth had to take place prior to establishment by ankylosis.

The pelycosaur group shows an interesting series of replacement patterns, as described by Romer and Price (1940), "In ophiacodonts tooth replacement is of such a nature that frequently little more than half the marginal teeth are functioning at a given time. In sphenacodonts a large majority of the teeth are usually functioning simultaneously, but there are usually gaps, and the formation of new teeth can generally be observed to be going on actively beneath many functioning teeth. In edaphosaurs there are relatively few signs of replacement, and seldom does a specimen show any gap in the tooth row."

The stages of replacement of individual teeth can usually be determined by surface examination of a well-prepared and well-preserved specimen. Although the early stages of replacement probably do not affect the old tooth, resorption at its base begins when the replacement is quite small, as shown by a few specimens in which the replacements have been preserved.

Fig. 8. Right lower jaw of *Ophiacodon retroversus*, M.C.Z. 1204.

SUBORDER OPHIACODONTIA

Specimens of two genera, *Ophiacodon* and *Varanosaurus*, were available to represent ophiacodont dentition. In *Ophiacodon* each lower jaw bears about forty tooth positions, but many of these are empty in the fossil specimens, indicating post-mortem loss of unfused teeth. The resorption pits in the fused teeth of all known specimens are also barren of contents, but from the size and distribution of the pits and gaps, graphs can be constructed giving a sufficiently accurate picture of the order of tooth replacement.

Ophiacodon retroversus Cope, M.C.Z. 1204, is a right lower jaw with thirty-eight tooth positions (Fig. 8). Alternation of elements of the odd- and even-numbered series is obvious from the figure. Old teeth are flanked by teeth being replaced, and vice versa.

One obvious series in M.C.Z. 1204 is that in the even numbers from two

to twenty. Teeth numbers 2, 4, 6, and 8 were younger members of the series, but being unfused they have been lost from the specimen. Numbers 10, 12, 14, 16, 18, and 20 are present, showing a gradation in the degree of fusion to the jaw, especially visible on the labial side. Tooth 10 seems to have been almost loose in its socket, while 20 is solidly fused. Numbers 20 and 22 are intact, being in the interval between fusion and degradation. Numbers 24 and 26 have resorption pits, and 28 and 30 have been lost except for traces of their bases. The first teeth of the new wave to become established were numbers 32 and 34 and these show increasing degrees of fusion. The final teeth in the even-numbered series, 36 and 38, are well fused. Thus, the even-numbered teeth show two waves, from empty alveoli through sound teeth, to resorption and empty alveoli, and back to sound teeth again.

In the odd-numbered series, teeth 1, 3, 5, 7, and 9 are in the resting condition, that is, well fused and not undergoing resorption. Numbers 11, 13, 15, and 17 present increasing stages of resorption. Alveoli 19, 21, and 23 are empty, the old teeth having been lost and the replacements not having been preserved. Progressive fusion is seen in 25 and 27, becoming complete in 29, 31, and 33. Number 33 is already under attack, while 35 and 37 are missing, although cracks in the specimen at these alveoli may have caused the loss of these teeth after preservation.

Of the thirty-eight tooth positions in the jaw, seventeen show evidence of tooth replacement. Where replacement is taking place, however, the unsound teeth are always flanked by functional teeth. In this jaw, we are fortunate in having information on the relative degrees of fusion of teeth to the jaw. Both this and the relative size of the pits indicate a definite back-to-front progression of waves of replacement, exactly as shown in the example of the iguana above.

A second dentary of *O. retroversus*, M.C.Z. 1203, has been cited by Romer and Price (1940) and Romer (1949) as an excellent example of back-to-front wave progression. The varying degrees of fusion are not as obvious as in M.C.Z. 1204, but both the fusion and the arrangement of resorption pits give the same picture as for M.C.Z. 1204. The wave length appears to be about nine teeth, somewhat shorter than that for M.C.Z. 1204, which has two waves of eleven and twelve teeth, respectively.

Specimen 4604 in the American Museum of Natural History is the type of Von Huene's *Therosaurus watsoni* (1925). This specimen, a partial left maxilla, is described by Romer and Price (1940, p. 243) as *Ophiacodon retroversus* (Cope), with the name *Therosaurus* placed in synonymy. The dentition of this specimen was described by Romer and Price as follows: "Number 1 is a very small tooth, 3 is small, 5, 7, 9, 11, and 13 are normal, 15 and 17 deeply excavated, 19 and 21 are out, while in the other series of the same bone, 2, 4, 6, 8, 10, and 12 are out, 16 is quite small, 18 fairly small, 20 and 22 are normal." Again, this pattern is similar to that described for M.C.Z. 1204. The replacement waves are not as markedly in opposite phases, but the general pattern of alternation and wave progression is identical.

Varanosaurus acutrostris Broili, is represented by a partial lower jaw, C.N.H.M. W.M. 34. Thirty-three tooth positions are preserved, all but three bearing teeth. The replacement pattern is similar to that of *Ophiacodon*, but with a higher proportion of teeth retained. In each wave only about two teeth are seen in the early stages. However, only the labial view of this specimen was available, and many early stages would undoubtedly be present on the lingual side of the jaw. As far as could be determined, the method of replacement of individual teeth was the same as in *Ophiacodon*.

Fig. 9. Dentitions of *Dimetrodon limbatus*.
 a. M.C.Z. 1113, lingual view, right maxilla.
 b. M.C.Z. 1908, lingual view, right dentary.

SUBORDER SPHENACODONTIA

The sphenacodonts display essentially the same replacement pattern as the ophiacodonts. Seven jaw fragments, all of the genus *Dimetrodon*, were used in this study. As shown in Figure 9, replacement occurs in waves proceeding from the back to the front of each jaw ramus. The waves are in opposite phases to each other, as in the ophiacodonts, but each wave involves fewer tooth positions. There are also fewer gaps in the dental series, showing that the number of teeth in their terminal, most vulnerable and least functional, stage is small. Since the number of teeth in any one stage of development in a jaw must be proportional to the duration of that stage of development, we may conclude that the later stages of the tooth replacement process were passed through rapidly. This is in line with the accepted view that *Dimetrodon* was the active carnivore of its day, requiring a constantly functional and efficient dentition.

The number of teeth per wave was not constant, but this could easily be a result of many variables such as age, state of nutrition, or season. *Dimetrodon limbatus* Cope, M.C.Z. 1403, had nine or ten teeth per wave,

while another specimen of the same species, M.C.Z. 1113, had only four or five. In this case, number 1403 was a dentary and 1113 a maxilla; however, there is no evidence to indicate a different rate between upper and lower jaw in any reptile, nor would much difference be expected.

Some of the sphenacodonts exhibit regional dental differentiation, at least of a primitive sort. In each upper jaw ramus of *Dimetrodon* for instance, there are a pair of well-marked canines. Occasionally both of these great teeth were functional, but usually they alternated so that while one, belonging to one alternately numbered series, was functional, the other, belonging to the other series, was being replaced. Thus, alternating tooth replacement with waves in opposite phases guaranteed that at least one of these important teeth would always be functional. Similar provisions are seen in many other reptiles, including the poisonous snakes.

Examples of the constant functioning of at least one canine were seen in the following specimens:

M.C.Z. 1907, *Dimetrodon* sp. A right dentary with the first canine intact and the second with a fairly large resorption pocket.

M.C.Z. 113, *D. limbatus*. A right maxilla with the first canine bearing a small lingual cavity and the second apparently freshly ankylosed.

U.M. 9732, *D. natalis*. A left dentary with the first canine intact and the second with only a shallow pit.

The dentition of *Dimetrodon* was different from that of *Ophiacodon* in several ways. The wave length was considerably shorter, therefore the space in which there were several alternate teeth in an unfused condition was quite short. An area in which there are several alternate unfused teeth is an area of weakness which can be rendered edentulous by the struggles of a vigorous and slow dying prey. Not only is the total length of each wave shorter, but the material on hand suggests, as we have seen, that the relative duration of the terminal stages is shorter, even when considered in relation to the total number of teeth being replaced.

SUBORDER EDAPHOSAURIA

Very little is known of the tooth replacement process in the edaphosaurs. The available material is usually poorly preserved, and teeth undergoing replacement appear only infrequently. Romer and Price (1941) remark that "we have noted . . . that the tooth replacement is of such a type that almost never is there seen a gap in the marginal series." They mention finding a few basal excavations in the teeth of *Edaphosaurus* jaws, but these are rare. The best material I have seen is a left lower jaw of *Edaphosaurus boanerges*, M.C.Z. 1531. This shows the presence of a distinct groove along the inner aspect of the tooth row, no doubt the site of the dental lamina in life. The teeth are set into fairly definite alveoli, and replacement probably occurs in the manner described in the introduction to the pelycosaur section. Three or four of the teeth in the specimen show distinct pits in the lingual side of their bases, apparently the site of development of the replacement teeth. One tooth is more clearly marked off from its alveolus than the others,

probably indicating that it had only recently become ankylosed. No regular sequence of stages of replacement can be detected and hence the presence of a wave-like pattern of replacement cannot be proven. There seems, however, to be a definite indication of an alternating pattern, since over a short series the alternate teeth are either less ankylosed than their neighbours or show basal pits.

Romer and Price (1940, p. 92) have also considered the probability of alternate replacement in edaphosaurs. "In numerous specimens of ophiacodonts and sphenacodonts a replacement of alternate teeth was obviously in process at the time of death. In edaphosaurs, owing to the seemingly rapidity of the replacement process, the evidence is not so extensive, but in several specimens of *Edaphosaurs* the presence of large resorption pockets on the inner side of alternate teeth indicates that the process was true of this group as well."

No replacement activity was seen in any specimens or illustrations of *Casea*. One specimen of *Mycterosaurus longiceps* Williston, C.N.H.M. U.C. 682, displays several well-preserved teeth in the upper jaw. Unfortunately, only the labial aspect of these teeth can be seen; information on the lingual side is therefore not available. However, such criteria as degree of ankylosis and relative height are considered, it is possible to detect definite waves of replacement passing cephalad along alternately numbered dental series. All of the evidence obtainable from the labial view, including the gaps in the series, agree with the common wave pattern. The wave length is about 4 teeth.

It is possible that the edaphosaurs had a shorter wave length than other pelycosaurs, and the significance of this has been discussed by Romer and Price (1940, p. 91) who believe it shows "either (1) that tooth replacement is becoming less frequent or (2) that there is no diminution in amount of replacement, but that the process is more rapid. The latter explanation is believed to be the more probable. As eaters of vegetable (or molluscan) food, the edaphosaurs would certainly require as much or more tooth replacement than the carnivorous members of the group."

From this brief survey of the pelycosaurs, we can state that tooth replacement occurred in discrete waves which progressed from posterior to anterior along alternately numbered tooth series and which were always out of phase with one another. *Ophiacodon* showed a long wave length, and consequently had many teeth undergoing replacement. *Dimetrodon* had a relatively short wave length. The scanty evidence indicates that the wave length may have been even shorter in some edaphosaurs. Both *Ophiacodon* and *Dimetrodon* show considerable intra-specific variation in wave length.

*Class Reptilia**Subclass Ichthyopterygia**Order Ichthyosauria*

Although large numbers of ichthyosaur skeletons are known, little interest has been shown in their dentition aside from morphological descriptions of individual teeth. Zittel (1890) briefly described the process of replacement of an individual tooth. The most detailed work on the anatomy of the head of an ichthyosaur is that of Sollas (1916). Sections were made of a 526-millimetre skull at one-millimetre intervals. The original plates, tracings, and even the grinding machine are still preserved, but the writer was unable, for financial reasons, to obtain prints of Sollas' sections, although they were generously offered by Mr. J. M. Edmonds of the Oxford University Museum. Romer (1948), in discussing the phylogeny of ichthyosaurs, noted that Triassic forms were thecodont, while post-Triassic forms had their teeth set in grooves.

On the surface, the dentition of an ichthyosaur does not present any obvious pattern. Most specimens are preserved with the upper and lower jaws closed firmly together, the teeth interdigitating and often not quite in line. Some teeth are not as large as others, probably indicating that they had assumed their places in the tooth row before reaching full size. To determine if there was any order behind this apparent chaos, the writer had serial frontal sections made of a fragment of the snout of *Ichthyosaurus* sp., R.O.M.Z.P. 339. Tracings from the peel sections (Fig. 10) show that replacement was occurring in many of the teeth.

The description of the method of replacement of an individual tooth given by Zittel (1890, p. 460) agrees with that found in our sections. The smallest replacement teeth were seen in positions J and L in section 'j.' These are less than one millimetre in diameter and lie closely applied to the old teeth. No obvious change has taken place in the associated old teeth at this stage. As the size of the replacement increases, a cavity appears in the base of the old tooth at the disto-lingual angle. This is seen in position E, section 'i'. Growth of the replacement tooth accompanies an increase in the size of

Fig. 10. Frontal sections through the left side of the snout of *Ichthyosaurus* sp. R.O.M.Z.P. 339. Both jaws are present, the teeth interdigitating.

the resorbed pocket, so that eventually most of the base of the old tooth is lost, the space being occupied by a half-grown replacement. This stage is seen in position 3, section 'b.'

As the base of the old tooth becomes resorbed, the new tooth moves closer to the centre of its definitive position. This process continues until the remains of the old tooth are completely gone and the new tooth has taken its place. Tooth F, section 'j,' is in this condition. The new tooth is fused to the jaw by the deposition of cementum which appears in the fossil as a buttress, a fine, radiating structure about the base of the tooth.

The small replacement teeth are often seen to lie with their long axes subparallel to the jaw margin, the tips pointing somewhat towards the centres of their predecessors, but this may be an artefact of preservation caused by maceration of the soft structures which held the replacements. However, it was seen both in the sections described here and in a specimen of *Ichthyosaurus longirostris* in which the lingual side of a tooth was prepared.

Analysis of the sections (Fig. 10) shows that an alternating pattern is present. Section 'j,' part of a dentary, shows a good replacement wave in the teeth labelled B, D, F, H, J, and L, distinct from another wave in teeth A, C, E, G, I, and K. A similar alternation is seen in section 'a,' part of the upper jaw. These waves are peculiar in that they appear to be moving from front to back, the reverse of the condition seen in most reptiles. For example, in section 'a,' teeth 1, 3, 5, 7, and 9 form a wave progressing caudad. Tooth 1 is intact and fused to the jaw. Position 3 contains a large replacement tooth lying within the remains of the base of the old tooth. Positions 1 and 3 also have very small replacement teeth, as shown in sections 'b' and 'c.' Tooth 5 is an old tooth with a pit containing a moderate-sized replacement, while 7 is similar but with a smaller pit and replacement. Tooth 9 is intact, with no evidence of replacement activity. Other series show waves identical to this one.

If this were the only ichthyosaur jaw known, we might be left in doubt as to whether or not this reversal of the usual back-to-front wave progression is typical of ichthyosaurs in general. Fortunately there are two skulls of *Cymbospondylus petrinus* in the Berkeley museum, both of which show the same pattern. Neither of these has the dentition perfectly preserved or prepared, but there is no question that replacement occurred in waves passing from front to back. This is best shown in the dentition of the upper left side in U.C.M.P. 9913, and also in several places in the jaws of U.C.M.P. 9950. The existence of the reversed pattern in three individuals representing two distinct families of ichthyosaurs strongly suggests that it is an ordinal character, and thus could be included in a description of the group as a whole. Examination of a large number of specimens will be necessary to establish this as a fact. Such a reversal is seen in the elapid snakes, and is confirmed there by a statistical study.

It would be futile to suggest any further phylogenetic significance for this dental anomaly. If the dentitions of many of the possible ancestors of the ichthyosaurs were known, they might provide a clue to their evolution,

but little is known about the subject. Romer (1948) discussed the available candidates for ichthyosaur ancestry, arriving at the conclusion that the most likely ancestor would be an anapsid close to the origin of the ophiacodonts. The ophiacodonts, however, show distinct back-to-front wave progression. If possible ichthyosaur ancestors are discovered in the future, it would be profitable to check their replacement pattern.

*Class Reptilia**Subclass Synaptosauria**Order Protorosauria*

Vaughn (1955) discussed the constitution of this order in connection with his description of *Araeoscelis*. Agreeing with Watson (1954) he said "The order Protorosauria has always been a trash basket; very few genera assigned to the group are seen as certainly allied one to another." Since this paper is not concerned with systematics, Romer's classification (1945) will be used unchanged. Specimens illustrating the dentition of protosaurs are rare, and information is available for only a few genera. Vaughn (1955) considered *Araeoscelis* to be a cotylosaur but, since we know little regarding the dentition, the change does not affect the present study.

The dentition of *Protosaurus speneri* was described by Seeley (1887) as consisting of rather simple cones which on surface view showed no evidence of tooth replacement. However, the (lingual?) surface of a maxilla was (accidentally?) removed, exposing "cavities like sockets, which may have been for successional teeth . . . the pits existed beneath the teeth which were in use. . . . No trace of successional teeth [was found] in any of these infra-dental spaces." This brief description suggests that the method of replacement of individual teeth may have been similar to that in *Diadectes*. The illustrations indicate that the material was too poorly preserved to show many details, and it is quite possible that cavities may have been produced by resorption near the bases, on the lingual side of the old teeth, for the admission of the young teeth. No evidence is available to indicate the sequence in which replacement occurred.

Tanystropheus longobardicus Bass. is well illustrated in Peyer (1937). In this figure (Abb. 102), pits lying in the bases of several teeth can be seen, at least one of which contains a well-developed replacement tooth. Apparently the replacement tooth is elaborated by the dental lamina at the base of the old tooth, and enters a cavity formed by resorption in the base of its predecessor. The cavity becomes enlarged as the size of the tooth increases. Peyer shows that the old tooth is reduced to a cap on the new

tooth, the old base becoming resorbed by increasing growth of the replacement. This cap may be shed as soon as it is loosened or retained by the soft tissues for a short period, as in *Alligator* in the Archosauria or *Tupinambis* in the Lacertilia.

In Peyer's (1937) specimen, a right maxilla with no specimen designation, at least two replacement waves can be distinguished. Tooth 2 is very small, having only recently erupted, while tooth 4 is nearly full grown and already partly worn. Numbers 6, 8, and 10 have obviously been in use for a relatively long period. Thus, the even-numbered series contains a wave of replacement proceeding from back to front.

In the odd-numbered series, teeth 1 and 3 appear moderately worn, while 5 is badly worn. A deep resorption pocket in 5 contains the crown of a young replacement tooth. The old tooth in position 7 has been lost, its place having been taken by a small replacement; tooth 9 is not fully erupted and is only slightly worn. Thus the odd-numbered series also demonstrates back-to-front waves of replacement passing along alternately numbered tooth series. This specimen is another example of the out-of-phase arrangement of the waves. Where the odd-numbered wave is just becoming established, the even-numbered series is intact. Similarly where the even-numbered teeth are being replaced, the odd-numbered ones are functional. At no place in the jaw are there two neighbouring teeth in advanced stages of replacement.

Peyer (1933) illustrated a left lower jaw of *Tanystropheus* with pointed, conical teeth. The order and method of replacement are the same as described for the maxilla above.

The dentition of *Trilophosaurus buettneri* was described and illustrated in excellent detail by Gregory (1945). This animal has a most unusual dentition, completely unlike any other seen in this study, though similar to the closely related (or congeneric) *Variodens* described below. Each tooth is transversely widened, with a chisel-shaped crown. Because of the peculiar nature of the replacement pattern, parts of Dr. Gregory's description will be quoted directly.

Almost every specimen shows a gap at some point in the dental series where a tooth is missing. . . . On the eroded sides of many of the jaws (both upper and lower) can be seen the crowns of successional teeth lying in the pulp cavities of their functional predecessors. The succession was vertical; as each tooth became worn or injured it dropped out and was rapidly replaced from below by the already formed replacement tooth. The gaps are interpreted as indicating the position of a tooth shed just prior to the death of the animal. The replacing tooth, not yet firmly attached to the bone, fell out, leaving a gap in the dental series. In all cases the alveolus thus left extends deeply into the jaw. . . .

In longitudinal section of the maxillary the developing crowns can be seen within the pulp cavity—a well-developed tooth beneath a tooth about to be replaced and rudiments of a second below that; beneath each of the other teeth is a single replacing tooth.

In a weathered lower jaw (No. 31025-108), in the pair of jaws numbered 31025-5, in the longitudinal section of a maxillary (No. 31025-105), and to a lesser degree in some other specimens, one may observe evidence of a regular order of tooth replacement. Beginning at the anterior end of the series the teeth were replaced one at a time, in a regular sequence posteriorly. . . .

The evidence for this hypothesis of orderly succession is found in the position of the crowns of the successional teeth beneath their functional predecessors. Beneath that tooth lying just behind the vacant alveolus, regardless of its place in the entire series, the successional tooth has grown well up into the pulp cavity and almost appears to have been pushing the functional tooth out. Each more posterior tooth has its successor less advanced and lower beneath its crown, so far as they are at all visible. Anterior to the gap, however, where the teeth had recently been replaced, the permanent teeth are firmly rooted with no trace of the successional tooth visible from the exterior.

The passages quoted clearly describe a pattern of replacement in waves passing cephalad along consecutively rather than alternately numbered teeth. The writer recently had the opportunity to study Dr. Gregory's material at the University of Texas, and can find no fault with his descriptions. The method of replacement of individual teeth is similar to that of *Diadectes*. The young tooth apparently arises in soft tissue lingual to its predecessor, and becomes associated with the formation of a pit in the wall of the latter. The pit perforates the pulp cavity and the young tooth enters and completes most of its growth there. Just before the loss of the old crown, the labial wall of the old tooth is also resorbed, thereby exposing the new crown both lingually and labially. Thus, a typical sequence along a tooth row, proceeding from front to back is (1) a fully mature tooth or series of teeth; (2) a young tooth, perhaps only partly ankylosed; (3) a vacant space representing the pre-mortem loss of an old tooth and the post-mortem loss of its replacement; (4) an old tooth containing the large crown of its replacement. This old tooth will probably have a labial as well as a lingual opening into the central cavity; (5) a series of old teeth (usually 2 or 3) with lingual pits decreasing in size towards the posterior.

The tooth replacement pattern of *Trilophosaurus* is unique, and certainly is different from the alternating pattern seen in most other reptiles. However, it can be explained by reference to the early embryonic dental development common to all vertebrates. The essential nature of the Zahnreihe was described in the captorhinomorph section above. If we consider that each potential tooth position produces, in sequence from front to back, only one tooth, then one Zahnreihe will be formed. Apparently, in *Trilophosaurus*, all of the teeth of one Zahnreihe have matured so as to make up the original dentition. This in turn is replaced by a second Zahnreihe developing from the same germinal material as the first, and again proceeding from front to back. As the individual teeth of the second Zahnreihe mature, they replace, from beneath the corresponding teeth, the first Zahnreihe. In

this way, there is a wave of replacement running along successive tooth positions from front to back, since the more anterior members of each Zahnreihe are older. This explains why, in the jaws of *Trilophosaurus*, there is a decrease in the size of the young replacement teeth as they are traced caudad. *Trilophosaurus* is unique among the reptiles in having a dentition composed of only one Zahnreihe, and replaced by a caudad wave passing along consecutive teeth. Such a system is found elsewhere only in the mammals where replacement occurs only once. In *Trilophosaurus* replacement was probably relatively frequent.

Robinson (1957) has described some *Trilophosaurus*-like material from the British Triassic. Two dentaries of *Variodens inopinatus* Robinson were illustrated and described, with remarks on the unusual form of the teeth. The method of replacement of individual teeth is similar to that of *Trilophosaurus* as described by Gregory (1945), but the regular sequential order seen in Gregory's specimens was not apparent.

Weigeltisaurus is known from its skull and skeleton, but its dentition is poorly known. Weigelt (1930) described the implantation as acrodont.

Vaughn (1955) described the osteology and relationships of *Araeoscelis*, but failed to find much evidence on tooth replacement. "Most of the specimens seem to have died with full sets of teeth, the few missing teeth apparently having been lost post-mortem . . . in all of the larger, more complete specimens the tips of almost all the teeth in a jawbone lie very nearly in a straight line. It seems doubtful if there was any ragged, wave-like replacement. Presumably, as in *Edaphosaurus* (Romer and Price, 1940) *Araeoscelis* had a very rapid mode of tooth replacement." The present writer can add nothing to this description.

Watson (1914) described the fragmentary skull of *Broomia perplexa*, adding that its affinities with known groups are not clear. Romer (1945) places it in the Araeoscelidae, but with a question mark. According to Watson, "The maxilla is not well shown, but in its anterior portion bears a single row of very closely set teeth which are wider from side to side than they are long. Posteriorly the teeth are small, separated and circular. The maxillary teeth seem to be thecodont and are very short and blunt, being directly opposed to those of the lower jaw." There is no description of the mode of replacement, but the fact that the teeth appear thecodont is significant, recalling the situation in *Protorosaurus* in which Seeley could see cavities beneath the teeth only when the lingual wall of the alveolus was removed. Further study of the actual specimen is needed before definite conclusions can be drawn.

All available descriptions and illustrations of other protorosaurs were studied, including those of *Kadaliosaurus*, *Macrocnemus*, and *Coelurosauravus*, but the results indicated that the dentitions were either missing or had not or could not be prepared.

It is difficult to arrive at any general conclusions on tooth replacement in the provisional assemblage which, following Romer (1945) is here termed the Protorosauria. *Protorosaurus*, *Tanystropheus*, and perhaps *Broomia* may have had a system of replacement similar to that in *Diadectes* or

Ophiacodon. Certainly in *Tanystropheus* the young teeth undergo much of their replacement in cavities resorbed in the lingual side of the bases of their predecessors, and the pattern of replacement is in waves passing cephalad along alternately numbered tooth series. The mammal-like sequence in *Trilophosaurus* is most unusual, and this genus is the only one seen in this study with a replacement pattern which is obviously not in agreement with that seen in reptiles generally.

*Class Reptilia**Subclass Synaptosauria**Order Sauropterygia*

A number of authors have referred to the dentition of sauropterygians, but there are few detailed descriptions in the literature. Edinger (1921) described the unusual method of replacement in *Nothosaurus*. Von Meyer (1855), Burckhardt (1894), and Jaekel (1905) noted the presence and possible significance of special alveoli in which the replacement teeth of nothosaurs develop. Erika von Huene (1944) described the nothosaur *Cymatosaurus*, but her description only served to amplify Edinger's previous one. Replacement of individual teeth in plesiosaurs has been described by Owen (1840) and Huene (1923) and several figures illustrate that the sequence in which their teeth were replaced was the same as in nothosaurs and in most other reptiles.

Edinger (1921) gives the best description of tooth replacement in *Nothosaurus*. The replacement teeth are always developed in the dentigerous bones in special, semi-permanent alveoli, one of which lies disto-lingual to each tooth. The ultimate size of the replacement alveolus is roughly proportional to the size of the tooth which it accompanies. Each is round or oval and the entire series forms a row lying subparallel to the row of tooth-bearing alveoli. Each is separated by a bridge of bone from the associated true alveolus. When replacement is about to occur, the replacement alveolus elongates towards the true alveolus. Presumably a zone of osteoclastic activity lies ahead of the replacement as it moves from the site of its origin to its definitive position. When the bridge of bone separating the two alveoli breaks down, the common outline appears like a distorted figure eight. The replacement alveolus may lie a considerable distance from the true alveolus, especially at the anterior end of the jaw, producing great elongation of the replacement alveolus during the migration of the tooth.

The replacement tooth apparently lies alongside the old tooth for a considerable period, since Edinger's illustration (Fig. 11) shows several pairs of confluent replacement and marginal alveoli. The old tooth probably becomes loosened by resorption of its base, permitting the replacement to

Fig. 11. Palatal view, anterior part of the jaws of *Nothosaurus juvenilis*. After Edinger.

enter its definitive position where it completes its growth and becomes ankylosed. The specimen of *Nothosaurus procerus*, illustrated by Huene (1956)* shows the same arrangement of replacement and marginal alveoli as in Edinger's *N. juvenilis*.

There has been some speculation regarding the true purpose of the replacement alveoli. It appears from the literature that in specimens examined by authors previous to Edinger the special alveoli did not contain replacement teeth, a common occurrence since the young teeth were retained only by soft tissue easily lost during fossilization. Von Meyer (1855) studied the foramina and mentioned that somewhat comparable foramina lie lingual to the teeth in crocodiles, but these are much smaller, more numerous, and not as regularly spaced as those in the nothosaurs. He recognized also that the replacement tooth in crocodiles arises close to the lingual wall of the root of the old tooth and does not arise in a separate distant alveolus. Edinger pointed out that nerve and vessel foramina in jaws of crocodiles are usually small and variable, while the unusual alveoli in *Nothosaurus* are large and constant in relation to the teeth. She also found replacement teeth in seven alveoli in *Nothosaurs*, thereby confirming their purpose as replacement alveoli. A similar phenomenon in the jaws of ornithischian dinosaurs is discussed in Edmund (1957).

Burckhardt (1894) also recognized a similarity between tooth replacement in crocodilians and nothosaurs. He remarked that the replacement tooth in the crocodile does not "eat its way" into the apical foramen of the old tooth, but, rather, is associated with resorbing of the lingual wall of the root. Although the replacement tooth in nothosaurs does not develop in the same site as in crocodilians, it does develop, like the crocodilian replacement, lingually and moves labiad to lie near the root of its predecessor where resorption of the root occurs.

Edinger's illustration of a small nothosaur, *N. juvenilis* Edinger (Fig.

11) shows that tooth replacement occurred in an alternate order, as in other reptiles. While the pattern of replacement is not clear in the premaxillae, it is obviously one of waves proceeding cephalad along the alternately numbered teeth in the maxillae.

Jaekel (1905) described a fine skull of *Simosaurus gaillardoti* H. v. Meyer from the upper Muschelkalk of Crailsheim which shows small alveoli lying lingual or disto-lingual to each tooth position in the illustrated upper jaw. There is clear evidence of alternate occupied and empty marginal alveoli at the rear parts of both maxillae. The right maxilla shows a typical alternating series with a wave progressing from back to front. Positions 6, 8, and 10 have moderate-sized replacement alveoli accompanying their functional marginal teeth. Tooth 12 appears to have a deep pit at its base, probably evidence of the labial migration of the replacement tooth and its alveolus. Positions 14, 16, and 18, are represented by empty marginal alveoli with no traces (or none illustrated) of replacement alveoli. The marginal alveoli in positions 20 and 22 bear teeth which appear randomly directed, as if perhaps not completely ankylosed *pre mortem*. These positions show no trace of replacement alveoli. The odd-numbered positions in this area are represented by functional teeth in the marginal alveoli, each accompanied by a moderate-sized replacement alveolus.

Another specimen of *Simosaurus gaillardoti* in the Tübingen collection from the Upper Triassic was described by Huene in 1921. In the discussion he noted the presence of alternating tooth replacement, and also briefly described tooth positions containing a wave of replacement progressing from back to front. This extended over several odd-numbered teeth in the premaxilla and maxilla of the specimen shown in von Huene's Plate II.

All stages in the process of tooth replacement can be seen in von Huene's specimen (1921, Plate II), permitting the entire sequence to be described. The new tooth probably develops on the surface of the dentigerous bone near the site of a replacement alveolus. It is not clear whether, after the previous replacement tooth has become functional, the replacement alveolus disappears or merely becomes so small that it escapes notice. As the replacement tooth increases in size it becomes associated with an enlarging replacement alveolus which begins migrating towards the true or marginal alveolus. In the third tooth position of the left premaxilla, the tip of a replacement tooth has migrated up the side of the bony swelling at the base of the functioning tooth. Eventually the two alveoli become confluent, the old tooth is lost and the new tooth assumes its definitive position. This process is almost identical with that in the ankylosaurs described below.

A further specimen of *Simosaurus*, designated as "property of Emil Roth, Reutlingen" was also described by von Huene (1921). This shows a long series of alternating occupied and unoccupied marginal alveoli in the upper jaw. Accessory alveoli were present alongside the ankylosed teeth, but apparently did not accompany the vacant alveoli. This agrees with the observation above that replacement alveoli are probably visible only when the replacement process is becoming advanced. In those positions where vacant alveoli are present, presumably the replacement teeth have only just

assumed their definitive positions, and therefore will not be replaced in turn for some time. The replacement teeth (i.e., those which will replace those now in the marginal alveoli, but as yet unfused) were probably quite small, lying only in soft tissue and not yet associated with the development of replacement alveoli. The replacement alveoli (called accessory alveoli by von Huene) which accompany the ankylosed teeth in the left upper jaw of the Reutlingen specimen increase in size towards the rear of the jaw, again indicating a back-to-front wave progression.

Erika von Huene (1944) described the skull of another nothosaur, *Cymatosaurus*. The alveoli are preserved, but are either empty or contain only broken bases. Accessory alveoli are present, as in the specimen above, but they are relatively larger, and many have joined with the true alveoli. This takes place first by a narrow neck, later by becoming widely confluent. No order of replacement could be observed in this specimen.

Owen (1840, p. 281) described the mode of replacement of individual teeth in "the Plesiosaur," but did not state which plesiosaur specimens he had, nor did he give their geological horizon.

The mode of succession of the teeth of the Plesiosaur differs from that of the Ichthyosaur in the growing tooth being developed in a cell at the inner side of the old socket, and affecting by its pressure the bone of the jaw, rather than the tooth about to be displaced. . . . notwithstanding the approximation of the crocodilian type which the teeth of the Plesiosaur make in their persistent pulp-cavity, there is not more than a single successional tooth in progress of development at the base of the tooth in use at any period; and the dentition of the Plesiosaur further differs from that of the crocodile, inasmuch as the new tooth, instead of emerging from the pulp-cavity of the old tooth, or even from the same socket, protrudes its apex through a distinct foramen at the inner side of the alveolus of its predecessor.

The last part of this quotation is particularly interesting since the process it describes is similar to that in the nothosaurs and in the plesiosaur specimen described by von Huene and discussed below.

Owen's description (p. 285) of "the pleiosaurus" from the Kimmeridgian is similar to that of "the Plesiosaur" quoted above.

The germs of the successional teeth are developed at the inner side of the bases of the old teeth, but do not penetrate these teeth; the apices of the new teeth make their appearance through foramina situated at the inner side, and generally at the interspace of the sockets of the old teeth. Here, therefore as perhaps also in the Pterodactyle, the growing teeth may be included in closed recesses of the osseous substance of the jaw and emerge through tracts distinct from the sockets of their predecessors; but this is an exceptional condition of the reproduction of the teeth in Reptiles.

The most detailed account of tooth replacement in a plesiosaur is that by von Huene (1923). He described the upper jaws of *Plesiosaurus brachypterygius* Huene showing all the stages in the replacement process.

As in *Nothosaurus*, there is a marginal tooth row on the premaxilla and maxilla, and a row of replacement alveoli lying lingual to the true alveoli and running sub-parallel with them. Each of the smaller alveoli, called accessory alveoli by von Huene, lies directly opposite and lingual to a functional or true alveolus. In the premaxilla, where post-mortem loss of teeth has not occurred, the accessory alveoli contain small, thin teeth, while the true alveoli have teeth in all stages of growth.

Von Huene recognized the fact that teeth developed in the accessory alveoli, and remarked that they were always small teeth, never attaining the size of those in the outer row. The fate of these small teeth is described by von Huene as follows (my translation): "In the specimen before me, the small teeth are to be observed in all stages of migration from the accessory, to within the true alveoli. This is seen in the maxilla, premaxilla and dentary." This process, as in the nothosaurs above, appears to be an extreme example of the condition in which a tooth begins development in one locality and completes it elsewhere. This was seen in *Diadectes* and is carried to its ultimate development in the sauropterygians and ankylosaurs, where a separate alveolus forms lingually to the true alveolus, through which the replacement tooth erupts, or in which it lies. As replacement takes place, the new tooth moves up and into its definitive position in the true alveolus.

Von Huene's specimen of *P. brachypterygus* is sufficiently well preserved, especially in the premaxillae, to indicate the sequence of tooth replacement. His sketch and photograph are not as clear and detailed as might be desired for this purpose, but the general plan can be made out. (This figure was reprinted in von Huene, 1956, as Fig. 437.)

In the right premaxilla, tooth 1 is missing, probably being lost *post mortem*. The old tooth at position 3 is still retained, but a small replacement lies close against its base in the same alveolus. The old tooth has been lost in alveolus 5, but the replacement, which is larger than that at position 3 has moved into the alveolus. The even-numbered positions in the same jaw both bear large intact teeth but each is accompanied by a replacement tooth, that of 4 being larger than that of 2. Thus, both series in the right premaxilla show a back-to-front wave progression.

Conditions in the left premaxilla are similar. Alveoli 2 and 4 contain partly grown replacement teeth, number 4 being about half-grown, number 2 about one-quarter grown. In the odd-numbered series, loss of the contents of the fifth alveolus has removed some of our evidence, but the replacement tooth was just moving in as the accessory and true alveoli had become confluent. Perhaps the old tooth in alveolus 5 was lost before the animal's death. The replacement for tooth 3 is still small and in its accessory alveolus and functional tooth 3 occupies the true alveolus.

The above account describes a dentition which closely resembles that of other reptiles. The alternation of odd- and even-numbered series is present, and replacement occurs in waves progressing from back to front. Also, the replacement teeth are developed lingually to the old teeth and come to lie alongside them, where resorption takes place. The only unusual

feature is that the replacement teeth are developed in separate alveoli and must migrate a short distance to reach their definitive positions.

Although the entire tooth replacement process in this specimen can be explained on the same basis as that of any other reptiles, von Huene, influenced by Bolk's distichy theory, gave a different explanation. This theory, as already noted, states that there are two morphologically distinct sets of loci for the development of the teeth on the dental lamina, one on its free margin, the other part way up its labial wall. According to Bolk's theory the first teeth produced by the buds which develop in the wall (termed the Exostichos) mature earlier than those from the free margin (the Endostichos), and the alternating arrangement of the two sets of loci are thus responsible for alternating replacement in the adult dentition. Edinger (1921) had discussed the possibility that the inner and outer rows of alveoli in *Nothosaurus* might be equivalent to Bolk's two odontostichi. Von Huene recognized in his plesiosaur the same arrangement of two rows of alveoli which Edinger had described for *Nothosaurus* and suggested a similar interpretation. The fallacy of Bolk's theory was discussed earlier and in general principles the method of tooth replacement in sauropterygians is no different from that of any other reptile. The two rows of alveoli do not represent two distinct tooth rows, but merely a row of functional teeth and a row of their replacements.

For the Placodontia, in which there is a strong tendency to develop pavement teeth, little information on tooth replacement is available. However, a specimen of *Placodus* described by Broili (1912) showed that replacement of individual teeth took place by vertical succession. The great, flat crowns had been lost from three positions in the skull revealing large replacement teeth beneath. The mechanism of replacement is unknown, but may be similar to that described for *Diadectes*.

Class Reptilia

Subclass Lepidosauria

Order Eosuchia

The typical eosuchians include a series of small primitive diapsids from the late Permian and early Triassic of South Africa, such as *Youngina* and *Eolacerta*. Unfortunately, published descriptions of these forms by Broom, Olson, and Camp yield no data of value regarding tooth replacement.

Other forms sometimes placed in this order are either aberrant or of doubtful position. *Champsosaurus*, of the late Cretaceous and Paleocene is included here by Romer (1945) essentially on negative grounds, since it is surely lepidosaurian but is not a member of the Squamata or Rhynchocephalia. *Petrolacosaurus* of the Pennsylvanian is regarded by Peabody (1952) as an eosuchian, but its position is doubtful (Watson 1954, Vaughn 1955, von Huene 1956). *Tanystropheus* and its relatives may be eosuchian derivatives but have been discussed under the Protorosauria.

The dentition of *Champsosaurus laramiensis* Brown is known from the figures of A.M.N.H. 981 and 982 in Brown's 1905 memoir. *Champsosaurus* ? *inflatus* Parks, R.O.M.Z.P. 699, shows the same general pattern. Examination of the lower jaws of the latter specimen gives some indication of the replacement process and pattern. Tooth replacement was active judging from the number of empty tooth spaces. Over a stretch of about fifteen alveoli, each odd-numbered one is empty. Then follows a region in which every alveolus is filled. Following this there is another stretch of alternating occupied and empty alveoli, but this time the even-numbered alveoli are empty. This arrangement demonstrates that waves of replacement were present, but does not in itself indicate the direction of progression of the waves.

A hint of the method of replacement of individual teeth can be gained by close observation of the alveoli and broken-off tooth bases. In certain bases, there is a definite pit formed by resorption in the lingual side near the rim of the alveolus. This may be shallow, affecting only the tooth substance or deep, involving bony ankylosing material and the margin of the alveolus.

This pit is probably the site of development of the replacement tooth. A sequence of teeth in the left lower jaw of *C. ? inflatus*, R.O.M.Z.P. 699, gives the order of replacement. The numbering begins at the anterior portion of the jaw.

Tooth number 7 has a small lingual pit, apparently not perforating to the pulp cavity. Tooth 9 is similar, but the pit is obviously larger and has perforated the wall of the tooth. Position 11 seems to show an even larger pit, and perhaps the crown has been lost *pre mortem*. Certainly the remains of the old base are very thin compared to those in the previous alveoli. Apparently resorption proceeds largely from within the tooth. In alveolus 11 there is almost no trace of the old base, and 13 is clean and smooth-walled. Presumably alveolus 15 contained a new tooth, since it contains a broken base only slightly ankylosed. Seventeen and 19 show progressively more ankylosing bone. A similar series was seen in alveoli 14 to 26. This series is obviously in opposite phases with the odd-numbered series. The sequence of replacement, with teeth in different stages of resorption, indicates that replacement was in waves, progressing from back to front.

Judging from the above, the replacement tooth developed in a trough between the base of the functional tooth and a narrow flange of the dentary running along the inner margin of the tooth row. As the replacement increased in size, a cavity was resorbed in the base of the old tooth and in the surrounding bony tissue, but we cannot tell whether or not the replacement lay within the pulp cavity of its predecessor. Finally the base of the old tooth was resorbed, mainly from within, the old tooth dropped out, the alveolus was cleared of traces of the old base, and the new tooth moved into its definitive position. Probably it underwent a considerable amount of growth before becoming ankylosed. This system leaves many alveoli with young teeth not fully grown or fused and, therefore, not completely functional. It is common among piscivorous creatures with many teeth, such as *Ophiacodon*.

Petrolacosaurus kansensis Lane, which may or may not belong to the Eosuchia, has been described by Peabody (1952) on the basis of a crushed, but fairly complete, skull and skeleton plus other fragments. His description of the dentition includes the following: "Irregularities in the length of teeth indicated active tooth replacement by the primitive method described by Romer (1949) whereby an 'odd and even' replacement is complicated by a 'wave' replacement running posteriorly." In the summer of 1960 Dr. Ted Eaton kindly permitted the author to examine recently prepared material including the lingual sides of several jaws. These revealed a tooth replacement mechanism similar to that described for *Iguana* in the example on page 20. A large proportion of the teeth showed pits on their lingual sides, and the arrangement of these clearly indicated the presence of overlapping cephalad waves.

Order Rhynchocephalia

Fossil specimens representing this order, in which the teeth are acrodont, are rare. There is only one living representative, *Sphenodon punctatus*, which because of its phylogenetic position has received considerable attention. Several authors have described its dentition (Gunther, 1875, Burckhardt, 1895, Baur, 1896, Howes and Swinnerton, 1901, and Harrison, 1901) and although they disagree on many details, it appears obvious that tooth replacement does take place at least during embryonic and early post-embryonic life. Gunther (1875) states that tooth replacement probably does not occur in older individuals, and if it does occur at all, it is only once after hatching, with replacement confined to the front of the jaws. A similar situation is seen in the acrodont lacertilian families Agamidae and Chamaeleonidae. Harrison (1901) described five generations of teeth produced in *Sphenodon* embryos, replacement occurring in a regular alternating pattern with no obvious indication of waves.

Most specimens of *Sphenodon* in which the teeth are not excessively worn show a regular alternation of larger and smaller teeth. This was illustrated by Harrison (1901) and is seen in specimen R.O.M.Z.P. R170 (not illustrated). It appears that these teeth represent two generations, the smaller teeth having been laid down earlier when the over-all size of the animal was smaller. If a young *Sphenodon* could be examined periodically by means of radiographs, interesting data on this problem might be obtained. At present, there is nothing to indicate whether or not the replacement occurred in waves.

The family Rhynchosauridae includes a series of Triassic rhynchocephalians usually with two dental specializations. The anterior parts of the jaws are edentulous with a well-developed beak, and the maxillary dentition consists of a number of antero-posterior rows of acrodont teeth. There are several descriptions of this dentition in the literature (von Huene 1938, 1939, 1944) but there is no evidence that tooth replacement occurred, at least in the adult. The teeth are all intact and thoroughly ankylosed, with no apparent replacement mechanism. A clue to the origin and interpretation of this type of dentition is provided by the primitive rhynchosaur *Howesia* from the lower Triassic of South Africa (Broom 1906). Here the jaws bear a series of diagonal tooth rows remarkably similar to those of *Captorhinus*. As suggested in the case of that genus, and as discussed in the embryological part of this paper, this pattern appears to be retention in the adult of an embryonic type of dentition, the rows identical with the Zahnreihen of Woerdeman (1921).

Class Reptilia

Subclass Lepidosauria

Order Squamata

SUBORDER LACERTILIA

Classification of the lizards has changed considerably in the last half century, and only recently has there been a lessening of the emphasis on soft parts as taxonomic characters. Cope (1900) proposed one of the earliest good classifications, recognizing teeth as being useful in the study of lacertilian evolution. The system proposed by Camp (1923) included many fossil forms and gained wide acceptance. Romer (1945) presented a system based partly on Camp and containing all of the determinable fossil genera described up to that time. His classification was revised by McDowell and Bogert (1954) and revised again by Romer in 1956. The latter classification will be used in this section.

Cope (1900) believed that all subsequent dentitions were derived from an ancestral acrodont type, but later workers, including Camp (1923) believe that pleurodonty is the more primitive condition. All modern lizards are either pleurodont or acrodont, although the Cretaceous mosasaurs were thecodont, undoubtedly a secondary development.

An important feature used by some authors in classification is the site of the developing replacement tooth and the effect of the replacement process on the old tooth. Tooth replacement is usually obvious in lizard jaws, most showing great replacement activity. The replacement teeth develop in the dental lamina, lying lingual to the bases of the functional teeth. In the Gekkonidae and Iguanidae the replacement tooth develops immediately lingual to its predecessor. As growth proceeds, a cavity is formed by resorption of the lingual wall of the old tooth, the size of the cavity corresponding to that of the replacement tooth. The replacement tooth undergoes most of its development within this cavity.

In contrast to the above method is that seen in the families Varanidae, Helodermatidae, Lanthanotidae, and in some members of the Anguidae. In these, the successional tooth lies disto-lingual to its predecessor, a position described as interdental by McDowell and Bogert (1954). No cavity is produced in the base of the old tooth for the reception of the replacement.

The latter merely continues to lie alongside (and behind) its predecessor until the old tooth is lost, then it enters the vacated tooth position, completes its growth and becomes ankylosed. The old tooth may or may not undergo some degradation during the final stages of replacement. In certain anguids, for instance *Anguis fragilis*, and in the varanids, there is some indication that the old tooth is attacked and rapidly degraded so that much of the tooth is destroyed before the remainder is shed. In *Heloderma* and *Lanthanotus* it appears that the old tooth is loosened and discarded with little destruction of tooth substance.

McDowell and Bogert (1954) mention these differences in replacement methods: "The teeth of the Anguinomorpha (roughly corresponding to Romer's Diploglossa) are nearly solid, without basal excavation, and are replaced alternately rather than successively. Tooth replacement is interdental, the replacement tooth lying behind, not beneath the older tooth. . . . (The teiids resemble the anguinomorphs in lacking basal excavations in the teeth, but their replacement is successive.)"

It is unfortunate that McDowell and Bogert used the terms alternately and successively in the above description. One gets the impression that only in the anguinomorphs does replacement occur in an alternate pattern. The term "successive" could be understood to mean that replacement occurs in each successive member in the tooth row, one after the other, which is certainly not the case. McDowell and Bogert seem to have chosen their terms without regard to the over-all picture of the tooth replacement process. No doubt they recognized that tooth replacement occurred along alternately numbered series, as shown by Bogert (1943). Because the use of their terms is misleading, the terms "varanid" and "iguanid" methods will be used here, since representatives of these two families clearly demonstrate the two typical methods.

As implied earlier in this discussion, members of the Varanidae, Lanthanotidae, and Helodermatidae, as well as all of the Ophidia have a fairly typical varanid replacement method, whereas members of the Gekkonidae, Iguanidae, and Pygopodidae have the typical iguanid method. The Leptoglossa and Anguioidea contain members which show a mixture of the two replacement methods. Most leptoglossans demonstrate the iguanid method, while most anguoids tend toward the varanid method.

In the Anguidae, several specimens were found to bear resorption pits in the bases of certain teeth. These cavities, when present, were always associated with teeth in an advanced stage of replacement and were found only on the disto-lingual angle of the old teeth. Several specimens of the genus *Gerrhonotus* demonstrate this point. *G. liocephalus*, R.O.M.Z.P. R57 (Fig. 12, e and f), *G. liocephalus*, A.M.N.H. 72638, and *Gerrhonotus* sp., A.M.N.H. 57821, all have pits as described above. *Celestus millipunctatus*, A.M.N.H. 63557, also an anguid, has unquestionable pits in a few teeth in the lower jaw, although none were seen in its upper tooth rows.

From the above discussion, we may conclude that some anguids have tooth replacement as in the Varanidae, with no pits in the bases of the old teeth, while in others there are well-marked basal excavations. None of the

Fig. 12. Jaws of various lacertilians.

- a. *Lepidophyma flavomaculatum*, M.C.Z. 38920, U.L. jaw.
- b. *Xantusia vigilis*, M.C.Z. 44313, L.L. jaw.
- c. *Xenosaurus grandis*, M.C.Z. 54307, U.L. jaw.
- d. *Pygopus lepidopus*, U.S.N.M. 56234, L.L. jaw.
- e. *Gerrhonotus liocephalus*, R.O.M.Z.P. R57, L.R. jaw.
- f. *Gerrhonotus liocephalus*, R.O.M.Z.P. R57, L.L. jaw.

Fig. 13. Drawings of lacertilian dentitions.

- a. *Heloderma suspectum*, R.O.M.Z.P. R87, L.L. jaw.
- b. *Anguis fragilis*, R.O.M.Z.P. R164, L.R. jaw.
- c. *Varanus flavescens*, R.O.M.Z.P. R71, L.R. jaw.
- d. *Tupinambis nigropunctatus*, C.N.H.M. 31279, partial L.R. jaw.
- e. *Sauromalis ater*, U.S.N.M. 29294, L.R. jaw. All are lingual view.

anguids studied had a large number of teeth with pits, and in no case was a replacement tooth found within a pit. Where present in the Anguidae both replacement tooth and pit are found in the disto-lingual side of the old tooth.

Among the leptoglossans, members of the family Teiidae show a trend towards the varanid interdental position of the developing replacement tooth. *Tupinambis nigropunctatus*, C.N.H.M. 31279 (Fig. 13d), *T. nigropunctatus*, C.N.H.M. 22393, and *Ameiva ? bifrontata*, A.M.N.H. 4847, demonstrate this. Wide invasion of the pulp cavity does not occur, but in many cases some resorption is seen in the disto-lingual angle of the tooth, as was also noted in some of the Anguidae. McDowell and Bogert (1954) recognized the similarity between certain anguids and certain teiids. In discussing the anguoids they say, "No less characteristic is the dentition, which although similar to that of snakes, is unique among the lizards, but is approached, probably as an example of convergence, by some of the Teiidae." These authors state (p. 129) in their definition of their infraorder Anguinomorpha (which includes the Anguidae and Xenosauridae) that "the teeth are without basal fossae for the replacement teeth." This definition, although generally sound, could be misleading. Basal pits are present in the genera *Xenosaurus* and *Gerrhonotus* but are present only in those teeth which are about to be replaced immediately. Only in *Xenosaurus grandis* (Fig. 12c) were the replacement teeth seen to lie within the cavities, but in several specimens of *Gerrhonotus* the replacement teeth lie very close to them, and may in life have lain at last partly within, possibly during the terminal stages of resorption of the old teeth. It is certain from this study that the clear-cut division proposed by McDowell and Bogert will not bear close scrutiny. Gans (1957), discussing the dentition of amphisbaenids, has also remarked on the same problem, and it appears to the present author that the whole matter should be thoroughly examined.

There is little discussion in the literature regarding the sequence of tooth replacement in lizards. Woerdeman (1912) made great use of embryological material, but, surprisingly, did not consider the dentition of adults. Parrington (1936) studied the dentition of mosasaurs and not only recognized an alternating system, but also described the presence of waves proceeding cephalad along the alternate series. Bogert (1943) recognized the presence of alternate tooth replacement in snakes and lizards, but was mainly concerned with the unusual front-to-back sequence seen in elapid snakes.

One of the best descriptions of lacertilian dentition is that of *Heloderma* in Bogert and Martin del Campo (1956), part of which is quoted in the section on Helodermatidae below. They were aware of the presence of an organized replacement pattern, but seem to stop short of recognizing its generality. "On the basis of the tabulations of vacant and occupied sockets in the *Heloderma* material at hand it cannot be ascertained whether succession is always from front to back. The presence of ankylosed teeth in contiguous sockets, however, points to the possibility that teeth are replaced

from back to front, as well as in the reverse order." Comparison was made between the condition in *Heloderma* and that in several other lizards, but no definite conclusions regarding replacement patterns were reached.

Brief mention should be made of the acrodont families Agamidae and Chamaeleonidae, which the writer has not studied in any detail. These groups undoubtedly developed from forms which had tooth replacement, but the living genera are characterized by complete or nearly complete lack of tooth replacement in the adults. Woerdeman (1919) reported that *Calotes*, an agamid, was the only reptile studied in which he could find no tooth replacement. However, Carlsson (1896) had studied earlier embryos and found that replacement did take place. Traces of the dental lamina persisted into the adult stage, but never again became functional. Apparently replacement occurs in the extreme anterior teeth of some agamids, even in later life, since *Amphibolurus barbatus*, A.M.N.H. 15161, shows replacement occurring as far back as the fourth maxillary tooth. The replacement in this specimen appears to be of the common alternating pattern described below for the iguanids, and the method of replacement of individual teeth was of the iguanid type.

Infraorder Iguania

As described in the preceding section, the lizards with typical iguanid tooth replacement include the Gekkonidae, Iguanidae, Scincidae, Lacertidae, Xantusiidae, and Cordylidae. The replacement process is known in considerable detail, the description by Leydig (1872) being typical. In these families with the iguanid type of tooth replacement, the tooth germ elaborated by the dental lamina lies directly lingual to the base of its predecessor. A cavity develops at this site, at first being only a shallow depression, but later exposing the pulp chamber. Growth of the cavity keeps pace with the growth of the replacement tooth, the latter having entered the cavity at an early stage. Eventually the old tooth becomes completely undermined mesially and distally as well as lingually, the crown is lost, and traces of the old base are resorbed. The new tooth is protected during much of its growth while the old tooth remains functional. By the time the old crown is cast off, the replacement has completed much of its growth and can assume a fully functional role in a fairly short time.

Material for the study of iguanid type dentition is abundant, and most of the jaws in museum collections could be used for the present study. In many cases hasty preparation has, as noted earlier, resulted in the loss of non-ankylosed replacement teeth, but in the iguanid type dentition, where the sizes of the resorption pits are proportional to those of the replacement teeth, the loss of replacement teeth does not affect the usefulness of the specimen for the preparation of graphs of replacement patterns. However, in the case of jaws with varanid type replacement, in which the size of the replacement tooth cannot be determined from the size of a resorption pit, loss of the replacement teeth made most specimens useless for this study.

The method of replacement is very similar in all iguanid type dentitions, therefore no detailed individual descriptions will be given. The replacement patterns of a large number of species are shown graphically. For various technical reasons, such as imperfections in some of the material, part of a jaw may have been omitted. Numbering, in all cases, begins at the anterior part of the section of the jaw used in the graph, and each graph illustrates a continuous series.

Family Iguanidae

Literally hundreds of specimens of iguanids were examined, both as skulls and as cleared specimens. It was easy to construct graphs of the replacement pattern, and a large number were analysed, all demonstrating the same regular pattern of replacement occurring in back-to-front waves. The example in Figure 4 is typical of iguanids in general, showing no apparent pattern on casual observation yet yielding a regular imbricating wave sequence when separated into alternate series. Figures 14 and 15 show stylized representations of the dentitions of a number of representative iguanid genera, all with the same pattern. Many more were studied but not illustrated.

The jaw of *Sauromalis ater*, U.S.N.M. 29294, shown in Figure 13e, at first glance appears to have an unusual replacement pattern. This jaw suggests that three series, rather than two, are present. Especially near the middle of the jaw there is a perfect recurring sequence of teeth in three stages: (I) with a small basal pit and replacement, (II) intact, and (III) in the process of ankylosis. Despite the triseriate appearance, when the jaw was subjected to graphic analysis (Fig. 14, c and d), the resultant pattern was that of waves passing from back to front along alternately numbered series, as in the other iguanids. Both of the upper jaws of this specimen exhibited a repetition of the three-stage sequence that was seen in the lower right jaw described above. The lower left jaw shows less of the triseriate pattern seen in the other three jaws, but analysis revealed the common wave pattern.

The general appearance of the graphs of replacement in iguanid lizards indicates that there are few teeth not undergoing replacement, and that each wave of replacement usually consists of many teeth. There was a considerable variation in the length of replacing waves, however; *Ctenosaura pectinata* for instance (Fig. 15, d and e), had many waves consisting of eleven teeth each, while four was the common count in *Sauromalis ater*. There does not appear to be any correlation between wave length and either the size of the animal or its total number of tooth positions.

The highly pleurodont attachment characteristic of the iguanid-like lizards lends itself to the presence of replacement teeth lying within lingual resorption pockets. Much of the area of attachment is on the labial, distal, and mesial sides, which means that the lingual side can be excavated with relatively little loss of strength. Thus, it is not surprising to see even newly replaced teeth already being prepared for replacement.

Several specimens of *Anolis grahami* and *Xiphocercus valenciennesii* were provided by Dr. E. E. Williams of Harvard. These were cleared, stained, and examined, yielding results identical with those of the skeletal preparations. They served to confirm the assumption that the replacement teeth were proportional to the size of the cavities in which they lay, and gave a picture of the replacement teeth *in situ*.

Fig. 14. Diagrams of wave-like tooth replacement in lacertilians.
a. *Anolis grahami* R.O.M.Z.P. R151, U.R. jaw.
b. *Basiliscus vittatus* R.O.M.Z.P. R27, U.R. jaw.
c. *Sauromalis ater* U.S.N.M. 29294 L.R. jaw.
e. *Amblyrhynchus cristatus*, A.M.N.H. 72806, L.R. jaw.
f. *Lacerta viridis* R.O.M.Z.P. R22, L.R. jaw.
g. *Lacerta viridis* R.O.M.Z.P. R21, L.R. jaw

Fig. 15. Diagrams of wave-like tooth replacement in iguanid lizards.

- a. *Iguana* sp. R.O.M.Z.P. R3 U.L. jaw.
- b. *Iguana iguana* U.S.N.M. 65840 L.L. jaw
- c. *Iguana* sp. R.O.M.Z.P. R2 U.R. jaw.
- d. *Ctenosaura pectinata* M.C.Z. 5020 U.L. jaw.
- e. *Ctenosaura pectinata* M.C.Z. 5017 U.R. jaw.
- f. *Basiliscus vittatus* A.M.N.H. 74615 L.L. jaw.
- g. *Anolis grahami* R.O.M.Z.P. R155 L.R. jaw.

Fig. 16. Diagram of wave-like tooth replacement in *Gekko gekko*, M.C.Z. 32235: a. L.L. jaw. b. L.R. jaw. c. U.L. jaw. d. U.R. jaw.

Infraorder Nyctosauria

Family Gekkonidae

Both the upper and lower jaws of an excellent specimen of *Gekko gekko*, M.C.Z. 32235, are shown graphically in Figure 16. Replacement of the numerous iguana-like teeth occurs in waves passing along alternately numbered tooth series, each wave passing from back to front. As shown in the graphs, twenty-five or more waves were present in the dentition of this individual. The regularity of wave length and form are well shown in this specimen, and at every point in each wave in the odd-numbered series the teeth are in

almost exactly the opposite phase to that of their even-numbered neighbours.

Uroplatus fimbriatus, A.M.N.H. 2235, has a well-preserved dentition almost identical with the *Gekko* above. The wave length is not as regular as in the previous specimen, but the same general pattern is obvious. In both specimens, replacement of individual teeth occurred exactly as in the iguanids.

Fig. 17. Diagrams of wave-like tooth replacement in lacertilians.

- a. *Xenosaurus grandis* M.C.Z. 54307, L.R. jaw.
- b. *Lepidophyma flavomaculatum* M.C.Z. 38920 L.L. jaw.
- c. *Lepidophyma flavomaculatum* M.C.Z. 38920 U.R. jaw.
- d. *Xantusia vigilis* M.C.Z. 44313, L.R. jaw.
- e. *Xantusia vigilis* M.C.Z. 44313, U.R. jaw.
- f. *Clidastes* sp. U.S.N.M. 11719, U.L. jaw.
- g. *Clidastes* sp. U.S.N.M. 11719, U.R. jaw.

Family Pygopodidae

Only one specimen representing this family was seen, *Pygopus lepidopus*, U.S.N.M. 56234, and the following description is based entirely on it. The preserved specimen was kindly loaned by Dr. D. M. Cochran and prepared by the writer so that all available dental details were preserved. The dentition is of the iguanid type (Fig. 12d) but it resembles that of certain members of the *Leptoglossa* rather than that of the *Gekkonidae*, with which the family is allied by Romer (1956) and McDowell and Bogert (1954). Definite pits are resorbed in the bases of the old teeth, but they are not as well developed as in the iguanids and gekkonids, and the replacement teeth apparently lie within these pits for only a short time. In no case was a tooth retained when resorption had proceeded more than one-third of the way up its lingual wall. This resulted in numerous gaps in the dental series in which only small replacement teeth were present. Tooth replacement

proceeded in a regular pattern of back-to-front waves, and few teeth were not undergoing replacement.

Infraorder Leptoglossa

The families of this group, with the exception of some teiids, are very similar to one another in the mode of replacement of individual teeth. The morphology of the teeth varies considerably among different genera, from sharp recurved cones through spatulate and bluntish cylindrical types to the almost biscuit-shaped crushers of the teiid *Dracaena*.

Family Xantusiidae

Two specimens of this family, *Xantusia vigils*, M.C.Z. 44313, and *Lepidophyma flavomaculatum*, M.C.Z. 38920, were loaned, with permission to prepare the skulls, by Mr. Loveridge of Harvard University. As shown in Figure 12, a and b, the dentition is typically iguanid, with extensive resorption of the bases of the old teeth. Although the teeth are cylindrical, as are those of many leptoglossans, the developing replacements lie within the cavities in the old teeth during a large part of their development. Several teeth were seen in which over two-thirds of the lingual wall of the old tooth had been removed, yet the crowns remained functional. Thus, in contrast to the condition in such a form as *Pygopus*, there are few gaps in the functioning tooth row. As indicated in Figure 17, the replacement pattern in the Xantusiids is that common to all typical lizards.

Family Teiidae

As mentioned in the introductory part of this section, the dentition of some of the teiids is similar to that of some of the anguids, while others are closer to the iguanid type. In *Ameiva ? bifrontata*, A.M.N.H. 4847, in *Tupinambis nigropunctatus*, C.N.M.H. 22393, and in *Tupinambis ? teguixin*, R.O.M.Z.P. R171, replacement is strictly by the iguanid method. With *T. nigropunctatus*, C.N.H.M. 31279, however, most of the replacement pits were found on the disto-lingual surface of the old tooth. This is a well-prepared specimen with most of the replacement teeth retained and lying in the cavities in their predecessors. Another specimen of *T. nigropunctatus*, C.N.H.M. 22392, shows a condition similar to this in the upper jaw, while the pits in the lower jaw teeth are lingual in position. Thus, the position of the resorption pockets can vary among genera, among species, and even between jaws in the same individual.

Callopistes flavipunctatus, C.N.H.M. 8452, had only a few teeth with resorption pits, these being lingual in position, and none extending more than one-third of the height of the old tooth. At numerous tooth positions the old teeth were lost, their places being taken by small replacements, leaving numerous functional gaps in the dentition. The common wave pattern of replacement was obvious in all four jaw quadrants.

Two skulls of *Dracaena guianensis* were available, U.S.N.M. 71729, which was prepared by the writer, and M.C.Z. 39800. The replacement pattern is essentially the same as that seen in the other lizards, replacement occurring in waves passing from back to front along alternately numbered tooth series. The dentition is heterodont, at least in the mature specimens studied, with the anterior teeth subconical and the cheek teeth modified into flat biscuit-shaped crushers. An individual tooth consists of a large crown divided from a well-developed base by a definite neck. The attachment is pleurodont, but processes from the dentigerous bones have grown up lingual to and between the teeth, resulting in a condition approaching thecodonty. This is most obvious in the smaller specimen, U.S.N.M. 71729.

The dental lamina lies in a definite groove lingual to the bases of the teeth. The first bony evidence of tooth replacement is a slight pit in the base of the old tooth well below the neck and situated directly lingual to the old tooth, between the interdental projections from the dentigerous bone. This pit becomes wider and deeper, the proportions being about the same as the section of the crown of the old tooth at that position, i.e., up to three times as wide as high. The developing crown of the replacement enters the pit at an early stage, the youngest preserved being a thin saucer in the crypt beneath the tenth left dentary tooth of the M.C.Z. specimen. Although this replacement is only about three-fifths of its definitive diameter and very thin, the pit in which it lies approaches the full diameter and height of a mature crown. Once the new tooth has become established beneath the old there is apparently little outward change in the latter for some time. The ninth and twelfth left dentary teeth in the M.C.Z. specimen bear large replacement teeth which appear to fill the space beneath the crown of their predecessors, yet the mouths of the cavities are the same size as those seen in teeth with very small replacements. The next stage in the replacement process is illustrated by the sixth right maxillary tooth of the M.C.Z. specimen. The old tooth has been lost, revealing a fully grown crown lying in the cavity in which it developed. There has been no elaboration of a base, but the crown appears complete and most of the neck is present. The corresponding tooth on the opposite side is in about the same stage, although not quite as advanced. The old tooth has been lost, but the neck of the replacement is just being laid down. Presumably the remainder of the replacement process, in which the crown is raised to occlusal level, is passed through rapidly, as no teeth were seen to be in this stage.

The most posterior left maxillary tooth in M.C.Z. 39800 (Fig. 18c) shows the mechanism permitting increase in tooth size during the growth of the animal. An old tooth with a crown 4 mm. across at its greatest width is being replaced with a new tooth whose crown measures 6.5 mm. The replacement has apparently entered the base of its predecessor in the manner described above but most of its growth has taken place outside the relatively small resorption cavity, a provision to avoid complete loss of the old tooth before sufficient growth of its larger replacement has occurred. Had the young tooth grown entirely beneath the old, the base of the latter would have been obliterated in the process.

Fig. 18. Dentitions of lacertilians.

a. *Tupinambis ? teguixin* R.O.M.Z.P. R 171.

b. *Amphisbaena caeca* U.S.N.M. 27549, part of the left lower jaw.

c. *Dracaena guianensis*, M.C.Z. 39800, occlusal view, posterior end of left maxilla.

d. anterior end of the above jaw.

It was stated above that the replacement pattern of *Dracaena* is essentially the same as that of other lizards. There is unquestionably a pattern of waves passing along alternately numbered tooth series. Most of the waves progress from back to front but there are a few exceptions, as shown in the graphic analysis (Fig. 19). Examination of the diagrams shows that several series retain the back-to-front wave progression, for example, in teeth 9, 11, 13, and 15 in the left maxilla of M.C.Z. 39800 or in teeth 1, 3, 5, 7, or 8, 10, 12 in the right dentary of U.S.N.M. 71729. However, other waves appear to be progressing from front to back or show a U-shaped curve similar to that seen in some of the elapid snakes discussed below. Examples of the U-shaped curve are the even-numbered teeth in the right maxilla and the odd-numbered teeth beginning at tooth 5 in the upper right jaw of M.C.Z. 39800. In still other instances, such as the anterior part of the left lower jaw of the M.C.Z. specimen, there is no discernable pattern.

The significance of these distortions in the usually regular pattern is not clear. A possible explanation is that there may have been a crowding out of some of the teeth during growth, the remaining teeth perhaps retaining their original synchrony. Such a crowding may occur in certain amphisbaenids (q.v.) and possibly in frogs (Gillette 1955).

Fig. 19. Diagrams of tooth replacement patterns in lacertilians.

- a. *Dracaena guianensis* M.C.Z. 39800 U.L. jaw.
 - b. *Dracaena guianensis* M.C.Z. 29800 U.R. jaw.
 - c. *Dracaena guianensis* M.C.Z. 29800 L.R. jaw.
 - e. *Dracaena guianensis* U.S.N.M. 71729 L.R. jaw.
 - f. *Dracaena guianensis* U.S.N.M. 71729 L.L. jaw.
 - g. *Anguis fragilis* R.O.M.Z.P. R166, L.R. jaw.
 - h. *Anguis fragilis* R.O.M.Z.P. R166, L.L. jaw.
 - i. *Anguis fragilis* R.O.M.Z.P. R165, U.L. jaw.
 - j. *Anguis fragilis* R.O.M.Z.P. R164, U.L. jaw.
 - k. *Aniella nigra* R.O.M.Z.P. R167, U.L. jaw.
 - m. *Aniella nigra* R.O.M.Z.P. R.168, L.R. jaw.
 - n. *Aniella nigra* R.O.M.Z.P. R168 L.L. jaw.
-

The jaws of *Tupinambis* ? *teguixin*, R.O.M.Z.P. R171, were carefully prepared by the writer to retain the replacement teeth. In this specimen (Fig. 18a) the replacement tooth lies directly lingual to its predecessor and comes to lie within a large pit in the old tooth. Replacement follows a fairly regular pattern but, as in *Dracaena*, there were a few irregularities. As shown in Figure 20, g and h, other specimens representing the same family (genera *Ameiva* and *Tupinambis*) exhibited a perfectly regular pattern.

Families Lacertidae, Cordylidae and Scincidae

In every specimen studied, replacement was by the iguanid method, with a cavity resorbed in the lingual wall of the old tooth. *Gerrhosaurus flavigularis*, A.M.N.H. 57404, a cordylid (not illustrated here), closely resembles a typical iguanid in the manner in which its teeth are replaced. The degree of involvement of the old tooth apparently varies within the genus, since this specimen showed numerous teeth with resorption cavities reaching over half the distance from base to tip, but *G. flavigularis*, A.M.N.H. 73606, showed none with this amount of resorption. Several good specimens of *Lacerta* (*L. viridis* and *L. ocellata*) in the collection of the Royal Ontario Museum showed numerous teeth with well developed lingual resorption cavities containing small replacement teeth, but all were less than half the height of the old tooth, and many positions contained replacement teeth only one-third to one-half of their ultimate size. The old tooth is retained until the replacement is much larger than in the *Callopistes*; consequently the resorption pocket in which it lies is larger, being more than half of the height of the lingual wall in a few teeth. *G. flavigularis*, A.M.N.H. 73606, is similar to A.M.N.H. 57404 described above, but the resorption pockets do not exceed half of the height of the old teeth.

C. giganteus, A.M.N.H. 62940, was the only good specimen of *Cordylus* seen. All of the replacement teeth have been lost, but because replacement was by the iguanid method practically the entire story can be

reconstructed. The dentition is reminiscent of that in *Lepidophyma*, a xantusiid. The rather cylindrical teeth show all stages of replacement, with the resorption cavities reaching over three-quarters of the way to the tip of the crown in some cases. It appears very probable that the young teeth lay in these cavities. The young teeth could grow to nearly full stature before the loss of their predecessors and hence required only a short time to complete their growth; thus in the macerated specimen there are only a few gaps in the functioning series, although most of the teeth were actively undergoing replacement. Replacement patterns of two skinks, *Tiliqua* and *Tribolonotus*, are shown in Figure 21, e and f, while *Eumeces* is shown in Figure 20, e and f. The cordylids are represented in Figure 20, a, b, c, and d, and *Lacerta* in Figure 14, f and g.

The families just described (Xantusiidae, Teiidae, Scincidae, Lacertidae, and Cordylidae) make up the infraorder Leptoglossa. Replacement is by the iguanid method and the replacement pattern is that of back-to-front waves as in most lizards. The differences between families and genera are merely in degree of resorption of the bases of the old teeth, and the resulting early or late loss of the predecessors.

Infraorder Diploglossa

Superfamily Anguoidea

Family Anguidae

Representatives of the genera *Anguis*, *Celestus*, *Gerrhonotus*, and *Ophisaurus* were studied, three specimens of *Anguis fragilis* and one of *Gerrhonotus liocephalus* being prepared by the writer. The method of replacement of individual teeth differs among genera and even within genera. As in the Teiidae, certain species tend towards the iguanid method, others toward the varanid method. Though discussed earlier, it should be emphasized that as far as tooth replacement is concerned the anguids tend to resemble the varanids and the teiids to resemble the iguanids.

In *Anguis fragilis*, the aspect of the dentition shown in Figure 13b is essentially that of the varanoid genera *Heloderma* or *Varanus* (Fig. 13a or c). In *Anguis* the replacement process begins with the growth of a replacement tooth disto-lingual to the old tooth, i.e., in the interdental position of McDowell and Bogert (1955). Growth of the replacement proceeds with no apparent structural change in the old tooth until the replacement is about half-grown, at which stage the old base is attacked, the resorption apparently progressing outward from within the pulp cavity. This resorption stage is probably passed through rapidly as it is rarely seen. The process of resorption is most fully expressed in the ninth tooth in the upper jaw of *A. fragilis*, R.O.M.Z.P. R165 (not illustrated), which has been almost completely excavated so that only a shell remains of the labial wall of the

Fig. 20. Diagrams of the wave-like tooth replacement in cordylid and scincid lizards.

- a. *Cordylus giganteus*, A.M.N.H. 62940 L.R. jaw.
- b. *Cordylus giganteus* A.M.N.H. 62940 L.L. jaw.
- c. *Gerrhosaurus flavigularis* A.M.N.H. 73607 L.L. jaw.
- d. *Gerrhosaurus flavigularis* A.M.N.H. 73607 U.L. jaw.
- e. *Eumeces laticeps* R.O.M.Z.P. R24, U.L. jaw.
- f. *Eumeces laticeps* R.O.M.Z.P. R25, L.L. jaw.
- g. *Tupinambis teguixin* A.M.N.H. 62537, U.R. jaw.
- h. *Ameiva bifrontata* A.M.N.H. 4847, U.L. jaw.

base. This is quite thin, being reduced to almost a reticulum of bony tissue, and the tooth appears to have been on the point of being shed. Such a complete resorption was seen in most snakes and in some varanids. As is shown in Figure 13b, the old tooth in *Anguis* is lost when the new tooth is about half-grown. No large replacement tooth in any anguid was seen at a position still occupied by an old tooth, and many vacated positions were filled by quite small replacement teeth.

In all anguids tooth replacement occurred in the common wave pattern, with wave progression always from back to front. No irregularities were noted. Examples of the pattern in *Anguis* are shown in Figure 19, with drawings of *Gerrhonotus* in Figure 12, e and f, and *Anguis* in Figure 13b.

Gerrhonotus liocephalus, R.O.M.Z.P. R57 (not illustrated), is an example of an anguid which shows a tendency towards the iguanid type of replacement. Pits develop in the bases of the teeth as replacement progresses, but they are not as large as those seen in the iguanids and seem to be smaller than the replacement teeth accompanying them. The pits and the replacement teeth were seen only on the disto-lingual angle of the old teeth and no replacement was seen to lie within a cavity.

The lower left jaw of R57 contains a replacement wave beginning at tooth 6, an intact tooth with no accompanying replacement. Tooth 8 is also apparently intact, but is accompanied by a replacement tooth about one-tenth grown, lying disto-lingual to the old tooth. About three-quarters of each of the distal and lingual walls of tooth 10 have been resorbed to about one-sixth of their total height. A replacement tooth, about one-fifth grown, lies against, but not within this opening. The old tooth has been completely lost in position 12, and a new tooth, about three-fifths grown lies, as yet unankylosed, in its place.

A similar series in the same jaw begins with tooth 9. This is intact but bears a very small replacement tooth disto-lingual to its base. Teeth 11 and 13 are similar to 9, but their replacements are progressively larger. The old tooth at position 15 has a resorption pit about one-fifth of its total height and confined to the lingual side of the base. The replacement tooth lies against the opening, but not in it. At position 17 the old tooth has been lost and the replacement tooth, about two-fifths grown, is not ankylosed.

The lower right jaw of the same specimen bears three complete waves of replacement, and parts of others. There are three vacant positions and six ankylosed teeth bearing distinct pits in their disto-lingual walls. This is in contrast to the condition in the lower left jaw in which five old teeth were lost and only two ankylosed teeth showed definite pits. It would appear that there is a considerable variation in the rate of attacking the old tooth. The wave length seems to be the same in both jaws and, if we can postulate the same rate of wave progression, the rate of final resorption and loss is the variable factor.

Fig. 21. Diagrams of wave-like tooth replacement in lacertilians.

a. <i>Gerrhonotus liocephalus</i>
A.M.N.H. 72638 incomplete,
U.L. jaw.	e. <i>Tiligua nigrolutea</i> M.C.Z. 1077
L.R. jaw.
b. <i>Gerrhonotus liocephalus</i>
A.M.N.H. 72638 incomplete,
U.R. jaw.	f. <i>Tribolonotus novaeguianae</i>
A.M.N.H. 6181 L.R. jaw.
c. <i>Gerrhonotus</i> sp. A.M.N.H.
57821 complete, L.L. jaw.	g. <i>Xenosaurus grandis</i> M.C.Z.
54307 L.L. jaw.
d. <i>Ophisaurus ventralis</i> 57871
U.L. jaw.	

Family Anniellidae

The only available useful material representing this family is the two skulls of *Anniella nigra*, R.O.M.Z.P. R167 and R168. These delicate skulls were specially prepared to retain their replacement teeth. Tooth replacement in this family occurs in a manner similar to that of *Anguis fragilis*. A shallow pit is excavated in the base of the old tooth, apparently followed by rapid resorption of the remaining part of the base and expulsion of the crown portion. No replacement tooth larger than one-third grown was seen to accompany an old tooth, indicating that the old tooth is lost while its replacement is still fairly small. The form of individual teeth is the same as in *Anguis fragilis*. The familiar pattern of back-to-front, out-of-phase waves seen in Figure 19 is typical of the many jaw rami studied.

Family Xenosauridae

The sole specimen retaining sufficient dental data for this study is *Xenosaurus grandis rackhami* M.C.Z. 54307 (Fig. 12c). This was loaned by Mr. Loveridge of Harvard and specially prepared by the writer. No cavities were seen in any of the forty teeth in the upper dentition, but three were found in the lower jaws at L.L. 18 and L.R. 7 and 18. Since only three teeth out of seventy-eight possessed basal pits, it must be concluded that the process of detachment of the tooth is passed through rapidly. No tooth over one-third grown was accompanied by its predecessor since the old tooth becomes undermined and lost at about the time its predecessor is one-quarter to one-third grown.

The three teeth with basal pits were accompanied by replacement teeth about one-third grown, and these lay within or partly within the resorption cavities. It appears that the teeth spend little or no time within their predecessors, and since the predecessor is lost when the replacement is still small, there are several gaps in the functioning dental series. Numerous teeth are accompanied by small replacement teeth, but their presence has produced no visible effect on the old teeth. In both jaws, the replacement teeth lie almost directly lingual to their predecessors, but are slightly distal to their mid-points. As shown in Figures 17a and 21g, the replacement pattern is the same as for most other reptiles.

Superfamily Varanoidea

Four families will be considered here, Helodermatidae, Varanidae, Lanthanotidae and Mosasauridae. No adequate specimens or photographs could be obtained to illustrate the other extinct varanoid families.

Family Helodermatidae

Despite the fairly large number of jaws preserved in museum collections relatively little was written previous to 1956 on tooth replacement in *Heloderma*. Odermatt (1940) described the dentition of *Heloderma*, but was

mainly concerned with an account of the detailed structure of individual teeth. He concluded that there was no apparent systematic arrangement. It seems obvious that Oudematt's material was imperfect, as are most ordinary skeletal preparations of *Heloderma*, since a large number of the teeth are not ankylosed and are usually lost during maceration. The work of Bogert and Martin del Campo (1956) will be discussed later.

A fine specimen of *Heloderma suspectum*, R.O.M.Z.P. R87, was prepared by the writer, producing a skull with practically all of the replacement teeth retained *in situ*, as in Figure 13a. The replacement teeth lie distolingual to their predecessors and two replacement teeth usually accompany each ankylosed tooth. Since there is little structural change in the old tooth as replacement progresses, a jaw from which all of the replacement teeth have been lost is useless for the present study. Therefore radiographs of the jaws were taken before maceration was begun, as a precaution against loss of valuable data. Similarly, Bogert and Martin del Campo used the clearing and staining technique, as shown in Figure 22a.

Heloderma exhibits the typical varanid method of replacement. The old tooth remains intact until the replacement tooth is about half grown, then is shed, apparently by detachment of its relatively intact base from the jaw. No trace of formation of basal pits was seen in any specimen studied. The new tooth enters its definitive position and remains unfused until growth and the elaboration of a base are completed.

The left lower jaw of *Heloderma suspectum*, R.O.M.Z.P. R87, is illustrated in Figure 13a. Positions 1 and 3 bear large replacement teeth, the older teeth having been shed. Numbers 5, 7, and 9 have become fused, and alongside teeth 1, 3, 5, 7, and 9 there are small replacement teeth increasing in size towards the rear. At positions 5, 7, and 9 there are very small replacement teeth representing a third generation.

In the even-numbered series, teeth 2, 4, and 6 are fused, although tooth 2 is apparently just becoming established. Tooth 8 is a large replacement. Replacements are present alongside 2, 4, 6, with number 8 being the first member of their wave to enter a functional tooth space. The second generation of replacements are present beside the primary replacements of teeth 4, 6, and 8. Thus the left lower jaw shows replacement proceeding in a wave-like manner along the odd- and even-numbered tooth series. The right lower jaw, and the upper jaws show exactly the same pattern (Fig. 23). Another specimen of *H. suspectum*, A.M.N.H. 73835 (not illustrated), while not as complete, shows the same order of replacement. Both this specimen and R.O.M.Z.P. R87 demonstrate that there is no break in the continuity of the wave pattern over the premaxilla-maxilla suture.

Bogert and Martin del Campo (1956) presented a drawing of the jaws of a cleared juvenile *Heloderma suspectum* (Fig. 22a). Bogert (1943) had previously noted the presence of alternate tooth replacement in other lizards and more especially in snakes. His remarks (1956, p. 100) on *Heloderma* are as follows:

Somewhat the same sort of tooth replacement mechanism is present in *Heloderma*, but our examination of the teeth in a juvenile

Fig. 22. Dentitions of *Heloderma* and *Varanus*.

- a. Drawings of the left upper and lower jaw of a cleared juvenile specimen of *Heloderma suspectum* in A.M.N.H. After Bogert and Martin del Campo.
- b. Tracing of radiograph of the lower right jaw of *Varanus salvator*, R.O.M.Z.P. R38.
- c. Diagram of part of the dentition of the lower right jaw of *Varanus komodoensis* A.M.N.H. 37912.

specimen of *H. suspectum* cleared and stained, in addition to several skulls, leaves doubt whether the teeth are replaced in regular succession from front to back. In the cleared specimen the right and left sides of both jaws are in the same condition. In the maxillae teeth are firmly ankylosed, counting from front to back, in sockets 2, 4, 6, and 8, with nearly mature teeth partly in place but not ankylosed in sockets 1, 3, 5, and 7. In the inner side of each ankylosed tooth there are two rudiments, one of which is barely discernible, consisting only of the pointed tip. On the inner side of the tooth that is moving into position but not yet ankylosed, only a single rudiment is present. It is intermediate in size between the two rudiments in position to replace the ankylosed tooth.

If we were to judge only by these maxillae, the situation is virtually identical with that encountered in many snakes. However, examination of the teeth in the lower jaw discloses teeth to be firmly ankylosed in sockets 1, 3, 5, 6, and 8, with unankylosed teeth present in sockets 2, 4, 7, and 9. In six additional skulls representing both species, perfect alternate succession is indicated in only about half of the series. That is, only odd-numbered or only even-numbered teeth are ankylosed in the maxilla, dentary, or premaxilla in but 17 bones of the 32 examined. In the other 15 bones the teeth of some contiguous sockets, more often near the middle of the series, were ankylosed.

There is, therefore, reason to doubt whether the teeth in any given series are replaced from front to back in two successions, at least with the precision that they are in the majority of snakes. Alternate explanations are possible: (1) either the replacement mechanism is in an early stage of its evolution and not yet perfected in *Heloderma*, or (2) a more complex mode of succession exists in lizards of the genus. On the basis of the tabulations of vacant and occupied sockets in the material at hand, it cannot be ascertained whether succession is always from front to back. The presence of ankylosed teeth in contiguous sockets, however, points to the possibility that teeth are replaced from back to front, as well as in the reverse order. In this connection it is of interest to note that Parrington (1936) found evidence of tooth replacement in mosasaurs, "starting at the back of the Jaw."

Bogert was correct in detecting a simple alternating pattern in the maxilla. There is no evidence of a gradient in this jaw at this stage. It is possible that tooth 7 would become ankylosed before tooth 5, and so on. In such a situation all of the replacement teeth may have reached a certain stage, which might be considered a resting stage, and although the anterior teeth have just attained that stage, the posterior teeth may be on the point of base elaboration and ankylosis.

The dentary illustrated by Bogert and Martin del Campo (Fig. 22a) provides an excellent example of back-to-front wave progression. The ankylosed teeth in positions 1, 3, and 5 are the oldest teeth in the odd-numbered series. The succeeding generation is represented by replacement teeth increasing in size from front to back. Of these, the three anterior ones

Fig. 23. Diagrams of the wave-like tooth replacement in *Heloderma suspectum*, R.O.M.Z.P. R87.

a. U.L. jaw. b. L.L. jaw. c. U.R. jaw. d. L.R. jaw.

lie disto-lingual to the ankylosed teeth, and numbers 7 and 9 have entered their definitive positions following loss of their predecessors. A third generation is present, the most anterior member lying disto-lingual to the replacement accompanying tooth 5. Others of this generation accompany the unankylosed teeth in positions 7 and 9.

In the even-numbered series, positions 2 and 4 are represented by loose replacement teeth, 4 being larger than 2. Teeth 6 and 8 belong to the same generation as the loose replacements at 2 and 4 but have become ankylosed. One small replacement tooth is present at each even-numbered position. Thus, only two generations are present in this series. The first tooth of a third generation would be expected, in time, to appear alongside the replacement tooth accompanying tooth number 8.

This specimen, therefore, strongly supports the regularity of the replacement pattern. It is unfortunate that Bogert's previous tooth studies dealt mainly with elapid snakes in which the waves of replacement move from front to back. He concludes correctly, however, that "it is evident that tooth succession [in *Heloderma*] is essentially alternate. . . ." The specimens also clearly indicate that the cephalad waves were present here, as in practically all lizards.

Family Varanidae

As with so many other lizards, the skulls of varanids in museum collections were usually found to be devoid of all teeth except those firmly ankylosed. After radiographs had been taken, a number of specimens in the Royal Ontario Museum collection were carefully prepared to retain their replacement teeth. Tooth replacement in typical varanids is well shown in the skeletal jaw of *Varanus flavescens*, R.O.M.Z.P. R71 (Fig. 13c), and the radiograph of the jaw of *V. salvator*, R.O.M.Z.P. R38 (Fig. 22b). In the latter, for instance, the development of a complete replacement wave can be traced through the even-numbered series. Tooth position 2 bears a fully functional, intact tooth accompanied by a disto-lingual replacement approximately half its definitive height. In position 4, the old tooth has been

lost and the replacement, still rather small and thin-walled is moving into its place. Tooth 6 is similar, but larger and a little more erect. No trace of a second replacement was detected. At position 8 the wall of the new tooth is considerably thicker, and the tooth is fully erect, but the ridges of bone which serve to anchor and buttress the tooth have not been laid down. This is consistent with the fact that the tip of the tooth has not yet reached its full height. A small replacement tooth has appeared disto-lingual to the tooth becoming established.

At position 10 the establishment of the new tooth is complete with the wall of maximum thickness, and the flaring, buttressed base well developed. The relative size of the replacement is about the same as in position 2, and thus we have reached the end of one complete cycle. Position 12 shows the beginning of a new wave, with loss of the old tooth and substitution of a replacement, just as in position 4 of the same jaw.

Similar replacement waves are well shown in Figure 13c and in other specimens studied. Until the replacement tooth reaches about half of its definitive height no changes are seen in the old tooth. At this point resorption starts and apparently proceeds rapidly, first attacking the base of the tooth disto-lingually, then involving the entire circumference. Only one tooth was seen in this advanced stage in the four jaws of R71. It has much the appearance of having been etched with acid, only spicules and thin buttresses remaining of the labial half of the base. When the tooth position has been vacated, the replacement tooth assumes its definitive position, increases in size, its base is produced, and it becomes ankylosed.

In the specimen *V. flavescens* cited above, and also in *V. salvator*, R.O.M.Z.P. R88, only one replacement tooth usually accompanied each functional tooth. The great carnivore, *V. komodoensis*, however, had especially good provision for the replacement of its sharp teeth. As many as five replacement teeth were seen lying *en echelon* behind and below the teeth in the lower jaw of *V. komodoensis*, A.M.N.H. 37912 (Fig. 22c). Except for the increased number of replacement teeth, the replacement pattern is the same as for other varanids.

Figure 24 illustrates the replacement pattern of six jaws of *Varanus* sp. All of the replacement teeth are shown, and in each jaw one replacement wave is traced by block symbols. These examples clearly illustrate how the basic replacement pattern can be detected only when alternately-numbered tooth series are considered.

Family Lanthanotidae

The only known representative of this family is the rare *Lanthanotus borneensis* Steindachner, described fully by McDowell and Bogert (1954). The teeth of *Lanthanotus* are similar to those of *Heloderma*, but they are not grooved. The replacement process in *Lanthanotus* is practically identical with that seen in *Heloderma* and is clearly of the varanid pattern. As in *Heloderma* the old tooth is shed without development of a basal pit, probably by resorption of the ankylosing bone.

Fig. 24. Diagram of wave-like tooth replacement in varanid lizards.

- a. *Varanus flavescens* R.O.M.Z.P. R71, L.L. jaw.
- b. *Varanus flavescens* R.O.M.Z.P. R71, L.R. jaw.
- c. *Varanus salvator* R.O.M.Z.P. R88, U.L. jaw.
- d. *Varanus salvator* R.O.M.Z.P. R88, U.R. jaw.
- e. *Varanus salvator* R.O.M.Z.P. R88, L.L. jaw.
- f. *Varanus salvator* R.O.M.Z.P. R88, L.R. jaw.

It is unfortunate, since this is the only prepared skull in North America, that in the specimen in the Museum of Comparative Zoology at Harvard University almost all of the unankylosed teeth were lost during preparation. Some of the loose teeth in the left dentary were retained, however, though partly obscured by a band of tough connective tissue.

In the odd-numbered series, tooth 1 has been broken off but the remains of the base indicate that an intact tooth was present. Tooth 3 is intact and is accompanied by a quarter-grown replacement. In the fifth position the old tooth is still intact, but the replacement is half-grown. Tooth 7 is similar, with the replacement about three-quarters grown. The ninth and eleventh positions are somewhat obscured, but apparently the old teeth are still retained. The replacement teeth remain hidden. Thus the odd-numbered series consists of a complement of old teeth accompanied in life by a series of replacements increasing in size towards the rear.

In the even-numbered series, replacement activity is more obvious. Tooth 2 is damaged, but is accompanied by two replacements, the larger about one-third grown, the other only a very small tip. In position 4 the old tooth has been lost, and a half-grown replacement is entering the vacated position. The sixth position bears a replacement about three-quarters grown, but with no trace of a base. Tooth 8 is practically full grown, its base flared out and almost complete, but not yet ankylosed. Tooth 10 is similar to tooth 8. The even-numbered series thus displays the loss of an old tooth and the almost complete establishment of a replacement generation.

Family Mosasauridae

The Mosasauridae is the only fossil lizard family for which adequate dental material is available. The teeth and jaws of these giants have been known for many years, yet the literature has few detailed descriptions of their dentition. Williston (1898 etc.), Osborn (1899), and several other authors of major papers on mosasaurs barely mention the existence of teeth. Marsh (1880) in describing tooth replacement in the bird, *Hesperornis*, compared its teeth with those of mosasaurs. Parrington (1936b) is the only modern author to describe mosasaur teeth in detail. He illustrated two fragments, one a dentary, the other a pterygoid, both of which showed not only alternation of elements of the odd- and even-numbered series, but also waves of replacement with the oldest teeth at the rear. His conclusions, though based on less complete material, are practically the same as those of the present writer.

Although there is a considerable degree of variation between species and genera of mosasaurs, they are similar in general anatomy and especially so in dentition. Large numbers of jaws were examined during this research, especially at the Peabody Museum at Yale University, the American Museum of Natural History, and the United States Museum. The following description refers mainly to the common genera from the Niobrara Cretaceous of Kansas. *Globidens* with its specialized dentition will be discussed separately.

Fig. 25. Dentitions of mosasaurs.

- a. *Clidastes* sp. U.S.N.M. 11719,
Linguo-occlusal view, left max-
illa.
- b. As above, right maxilla.
- c. *Globidens alabamensis*,
U.S.N.M. 6527, lingual view,
left maxilla.
- d. *Mosasaurus* sp. Y.P.M. 690,
lingual view, isolated tooth
from either L.L. or U.R. jaw.
- e. Unidentified mosasaur,
U.S.N.M. 4992, typical intact
tooth.
- f. *Clidastes tortor* U.S.N.M. 3765,
Fragment of right dentary with
lingual alveolar wall removed.

An individual tooth of a typical mosasaur is shown in Figure 25e. Most remarkable is the presence of a large bulbous base, clearly marked off from the enamel-clad crown. The shape of the crown varies interspecifically and often from one area of the jaw to another, but the differences are slight. The crown is usually somewhat compressed and recurved, but many teeth appear only slightly ovoid in section. Some teeth show a tendency towards the development of relatively sharp edges, especially on their rear margins. Implantation is thecodont, no doubt secondarily so.

Many loose teeth were seen to have cavities in their bases, as in Figure 25d, betraying the site of development of replacement teeth. It is impossible to find a jaw of a mosasaur which does not possess some teeth in the process of replacement and usually almost all teeth are in one stage or another of active replacement. The process of tooth replacement was probably as follows. A tooth bud developed on the dental lamina, which probably lay just labial to the tooth row and closely applied to the bases of the teeth. Once this young tooth attained a certain size, a resorption pit was formed between the base of the old tooth and the lingual alveolar wall, always at the disto-lingual aspect. Growth of the replacement tooth and the resorption cavity continued, widely involving both the base of the old tooth and the surrounding bone. In Figure 25f part of the lingual wall of a maxillary tooth position has been removed, revealing the size of the cavity occupied by the replacement tooth. In no specimen was more than the crown of the replacement seen in such a cavity. It appears that the old tooth was lost by

the resorption of the material cementing its base to the alveolus. The new crown, having reached its full size within the base of its predecessor, came to lie within the vacated alveolus and its bony base was elaborated there.

An excellent specimen, probably of a right maxilla, A.M.N.H. 127, labelled *Platecarpus coryphaeus* (not illustrated) shows several tooth positions in which fusion of the base to the alveolus is taking place. In the most anterior, the base is quite loose, lying like a ball in its socket. The next alternate alveolus is empty, the tooth having been lost, probably during handling, as shown by a mended break at this point. This loss indicates that the new tooth was lying quite loosely in its alveolus. The next tooth in the same series appears to be firmly attached to the jaw, but there is still a wide gap between base and alveolus all around the upper part of the base. In the next alternate tooth only a narrow separation persists, and in the final tooth in the series the base and alveolar wall are firmly united with no trace of separation. Synchronized with this increasing degree of fusion is an increase in the size of the pits formed by resorption in the bases of the new teeth. Development of a new replacement begins before the previous tooth has become completely ankylosed. The fifth, seventh, and ninth teeth in the series above show pits which are larger in the more posterior teeth.

Vacant alveoli occasionally seen in specimens are indicative of the stage in which the old tooth has been lost and the base of the new tooth has not been completed and ankylosed. In some jaws this process appears to occur rapidly over the interval of one or two teeth, while in others, such as the example above (A.M.N.H. 127), the process occupies a span of several tooth positions. *Clidastes tortor*, U.S.N.M. 3765 (not illustrated), has an interesting feature. An unfused tooth with a completed base is seen lying almost entirely out of its alveolus, apparently caught just before loss by a covering of sediment.

The size of the cavity in the old tooth is difficult to estimate by surface examination. As Figure 25f shows, there may be a completely formed crown lying largely beneath the old tooth, with only a few millimetres of its tip projecting. Therefore the degree of progress of replacement can be only roughly estimated by surface appearance. The apparent size of the resorption cavity and its contained replacement, the size and state of a new tooth in an alveolus, and the degree of fusion of tooth bases were used in constructing the graphs in Figure 17, f and g. These were prepared from especially good material and indicate that the pattern of tooth replacement in mosasaurs is identical with that of other lacertilians. Two replacement teeth were often seen in one cavity. In each case, however, the more distolingual tooth was smaller than the other, indicating that it was a third generation—a future replacement for the replacement. The presence of this third generation is shown in Figure 25, a and b. Since these smaller teeth are situated more superficially than the others, their size can be more accurately determined. The number of replacement teeth at each alveolus did not appear to be a generic or specific character.

One replacement series will be described in detail. Figure 25a illustrates the complete tooth row on the left maxilla of *Clidastes* sp., U.S.N.M. 11719, an exceptionally fine skull. In the odd-numbered series, tooth posi-

tion 1 is empty, indicating loss of a large replacement which had not become fused by the time of death. A small replacement was retained, however. The third tooth was retained, although incompletely fused and showing a wide channel between the base and alveolar walls. It had already developed a cavity for the reception of a replacement tooth.

Position 5 is occupied by a well-fused tooth with a cavity and replacement tooth somewhat larger than in 3. The replacement and pit in number 7 appear only slightly larger than in 5 on surface view, but were no doubt actually considerably larger. Position 9 contains a crown and part of the crushed base of a replacement tooth. Number 11 is similar, but the base of the replacement is much more fully developed. It has been crushed and resembles a crumpled paper bag. Apparently the base is formed first as a hollow shell, after which the remaining bony material is added to the inner side. Tooth 13 is a recent replacement with a well-formed base. It is not yet fused to the bone but already bears a moderate-sized pit and replacement. Tooth 15 is similar, but its replacement has been lost *post mortem*. Alveolus 17 is empty, indicating *pre mortem* loss of the old tooth and *post mortem* loss of its replacement. This series shows a complete wave, beginning with a small replacement in alveolus 1, leading up to complete fusion by position 15, and loss in 17. This shows perfect back-to-front wave progression in an alternately numbered dental series. Figure 17f shows this series in relation to the other waves in the jaw.

The dentition of *Globidens alabamensis* Gil. is known only from the illustrated left maxilla and a few isolated teeth. Gilmore (1912) described this specimen in detail, stating that "the germ teeth, as well as the comparative size of the cavities, show that the teeth increase in size from front to back."

The genus *Globidens* is characterized by the almost spheroidal shape of its tooth crowns. These are borne on bases similar to those of the other mosasaurs described above. Replacement takes place in exactly the same manner, every tooth in the type specimen showing a cavity formed by resorption in the disto-lingual angle of its base near the margin of the alveolus. Figure 25c shows the lingual side of the type maxilla, with replacement teeth lying in resorption pockets similar to those described for other mosasaurs. Position 1 is empty, the tooth probably being young and unfused. Tooth 3 is well fused, with a shallow basal cavity containing a small crown. Number 5 is similar, but the resorption cavity and the replacement crown are both larger than in tooth 3. The bases of teeth 7 and 9 have not been completely prepared, but appear to be in about the same condition as tooth 5. The resorption pockets have not been cleared out, and if replacement teeth are present they are obscured by matrix. The odd-numbered teeth show only a feeble increase in size towards the rear.

The even-numbered teeth demonstrate the growth and establishment of a new generation. Tooth 2 is similar to tooth 3 in having a small resorption pit containing a small replacement crown. Tooth 4 is similar, but with a larger pit and replacement. Tooth 6 is represented by a fully-formed crown lying deep in an otherwise empty alveolus. As described above, the base of a new mosasaur tooth is not elaborated until the old crown has dropped out.

Apparently the crown of the old tooth at position 6 had become lost *pre mortem* and the bulbous base of its replacement had not become elaborated before death. Position eight contains a firmly ankylosed tooth bearing a small disto-lingual pit, the contents of which are hidden. The base of this tooth is marked off from the dentary bone more clearly than are the bases of its neighbours, indicating that it is younger.

In many features tooth replacement in the mosasaurs resembles that in the Anguidae. The replacement tooth develops disto-lingual to the old tooth in both cases, and a pit is developed in the old base although in the anguids this is not occupied to any great extent by the new tooth. Both families share the common replacement pattern of waves passing cephalad along alternately numbered tooth series. Implantation is thecodont in the mosasaurs and the huge swollen bases are found in no other lizard family. Replacement in *Globidens*, despite the unusual shape of the crowns, was identical with that of other mosasaurs.

Infraorder Annulata

Family Amphisbaenidae

Six specimens from this family were examined, two of *Amphisbaena caeca* and four of *Rhineura floridana*. These were supplied as preserved specimens by Dr. D. M. Cochran of the Smithsonian Institution and the delicate skulls prepared by the writer.

The individual teeth are sharp compressed cones, well fused to the jaws when mature. In each case the aperture of the central canal is quite obvious at the base of the tooth and the process of resorption prior to the loss of an old tooth apparently begins at this aperture. *Amphisbaena caeca*, U.S.N.M. 27549, has several teeth in various stages of replacement, and forms the basis for most of the following description of the replacement process.

In a mature tooth of *A. caeca*, such as the sixth in either of the lower jaws of U.S.N.M. 27549, the aperture of the central cavity is oval, the long axis being perhaps one-sixth of the diameter of the tooth. As replacement progresses, a replacement tooth develops directly lingual to the aperture and, even when the replacement is still very small, the aperture becomes more nearly circular, and the lingual wall of the tooth around it is resorbed, forming a saucer-shaped depression. Resorption continues until over three-quarters of the lingual wall has been removed. Apparently the replacement tooth lies within this cavity during part of its development, although this is not shown in U.S.N.M. 27549. It is seen in tooth L.R. 5 of *Rhineura floridana*, U.S.N.M. 50960, where a replacement about one-quarter grown lies well within the cavity in its predecessor. Tooth 7 in the lower left jaw of U.S.N.M. 27549 is about to be replaced (unfortunately the replacement tooth has been lost). The old tooth has been completely undermined and is retained only by its labial attachment to the dentary, the lingual side being widely opened. Teeth 4 and 7 of the lower right jaw demonstrate the size of the replacement teeth which have been freed of the encumbrances of their predecessors, but which have not yet become ankylosed. They are respectively about three-quarters and one-half of their definitive sizes.

Many of the jaws of the amphisbaenids studied showed no signs of tooth replacement activity, and it is possible that the passage of a replacing wave may be an infrequent occurrence. It is also possible that tooth replacement may cease entirely after a certain age, but the writer has not found definite evidence to support this.

The sequence of replacement is, however, well shown in several jaws, and the lower right jaw of *Amphisbaena caeca*, U.S.N.M. 27549, will be described as typical (Fig. 18b). Teeth 1 and 3 appear to be intact, but the aperture of the central canal is somewhat larger and rounder in tooth 3, perhaps indicating the beginning of resorption. No replacement teeth are present at positions 1 and 3, but they could have been lost during preparation, since they would be smaller than grains of sand. Tooth 5 shows a definite "dishing-out" of the margins of the aperture, and a very small replacement tooth is present. The old tooth at position 7 has been lost and its place taken by a replacement about half grown and not yet ankylosed. Thus, there is a good series beginning with an intact tooth and leading up almost to complete replacement.

In the even-numbered series, tooth 2 has a small replacement tooth, perhaps one-eighth of its definitive height, lying against the opening of a somewhat enlarged aperture. Tooth 4 is a large replacement, about nine-tenths grown, but not yet ankylosed. Teeth 6 and 8 are fully mature with none of the signs of recent ankylosis and with small elongate-elliptical apertures in their bases. This series thus shows the latter part of one wave, together with the establishment of a new generation.

In the amphisbaenids studied, as in most other reptiles, tooth replacement occurs in waves passing cephalad along alternately numbered tooth series. It must be emphasized that the amphisbaenids are heterogeneous as far as their dentitions are concerned and some species are acrodont. A study of a large series of amphisbaenids will be required before details of their tooth replacement can be worked out. Recent work by Gans (1957) suggests that the regularity of tooth replacement described above may break down, at least in older specimens of *Amphisbaena*, possibly because of changes in jaw proportions in later life.

This survey of tooth replacement in the Lacertilia is necessarily superficial. The basic pattern of cephalad waves passing along alternately numbered tooth series is seen in all cases, with only a few irregularities, possibly caused by changes associated with growth. There is an interesting gradation between two extreme types of replacement, herein termed iguanid and varanid. In the former, the replacement tooth is early associated with a resorption in the lingual side of the base of its predecessor, and much of the replacement's growth occurs within the cavity so produced. In the varanid replacement method, the replacement tooth lies disto-lingual to its predecessor, and there is no resorption of a pit. The stage at which the old tooth is lost varies considerably, affecting the size of the replacement when it enters the vacated position. In mosasaurs, implantation is secondarily thecodont, the replacement tooth developing within the bulbous base of its predecessor. Because of the abundance and great diversity of material available, many years could be spent in more detailed study of this group.

Class Reptilia

Subclass Lepidosauria

Order Squamata

SUBORDER OPHIDIA

Unfortunately, only a very few fossil snake jaws useful to this study are known. However, the dentition of modern forms provides excellent material for the study of tooth replacement. Rather primitive living snakes are still abundant and may be studied along with more advanced species.

It was the author's original intention to present merely a brief survey of the snakes, with examples from the more common families. To this end, the excellent reptilian osteology collections of the Chicago Natural History Museum and the American Museum of Natural History were examined, and data on representative specimens recorded. Upon analysis, all snakes were seen to exhibit the common alternation of odd and even series, with most showing replacement occurring in waves progressing from back to front. However, the few specimens of poisonous snakes studied at an early stage of the investigation showed a reversal of the usual back-to-front progression.

In order to be able to make definite statements on these exceptions, a larger number of specimens, especially of the families Elapidae, Viperidae, and Crotalidae were examined. Mr. C. M. Bogert of American Museum of Natural History and Dr. R. L. Peterson of the Royal Ontario Museum, Life Sciences Division, kindly furnished several heads of *Crotalus* species. Dr. D. D. Davis of Chicago Natural History Museum loaned a fine *Bothrops atrox* head. Specimens of many genera of elapids were kindly loaned by Dr. Doris M. Cochran of the United States National Museum. These specimens, plus many preserved in the Royal Ontario Museum, Life Sciences Division, were carefully prepared by the author to retain as many as possible of the loose replacement teeth. Most snake skulls in museum collections had been prepared without this in mind, so that the only teeth remaining were those firmly fused to the jaws. X-ray photographs of some jaws were taken before they were reduced to skeletons by the author.

Several authors, Kathariner (1905), Tomes (1875, 1876), and Woerdeman (1921) have described in detail the processes of replacement of individual teeth and especially of the poison fangs in various snakes. The

only significant paper dealing with tooth replacement patterns in snakes which has come to the author's attention is that of Bogert (1943). In it he states that the fundamental method of fang replacement is the same in Viperidae, Crotalidae, and Elapidae, and is similar to the method of replacement of teeth in Boidae and Colubridae, and further suggests that this process is essentially the same as that seen in the platynotan reptiles. He also describes the general alternating pattern seen in all snakes and mentions specifically the front-to-back arrangement in an elapid but does not note the variations in this pattern.

Fig. 26. Dentitions of boid snakes.

- a. Lingual view of anterior part of upper right jaw of *Python regius*, A.M.N.H. 31921.
- b. Lingual view of right lower jaw of *Eunectes murinus*, R.O.M.Z.P. R41. The specimen has been macerated and stained.

The early development of snake teeth takes place in the soft tissue disto-lingual to the bases of the functioning teeth. In the palatine tooth rows, which will not be considered here, replacement occurs in an identical fashion, except that the teeth develop labially to the tooth rows. Implantation is pleurodont. The young teeth lie horizontally, i.e., parallel to the margins of the jaw bones, with their tips directed caudad. The base of the new tooth lies near the base of the old, or slightly posterior to it. Often several generations of replacement teeth are present (four or five are not uncommon), lying *en echelon* alongside the functioning tooth.

As the replacement tooth nears full size, the base of the old tooth begins

to show signs of resorption. The cementing bone on the outside of the base disappears and the tooth substance itself becomes resorbed. A tooth in an advanced stage of resorption is very weak, with the base, especially on the lingual side, being reduced to a reticulum of dentine. Finally the old tooth is lost and the remainder of the base is cleared away, leaving a fairly shallow pit in the jaw into which the replacement moves. The process of migrating into the functional position involves not only the movement of the base of the new tooth into the pit, but also the rotation of the whole tooth from its horizontal position to a nearly erect one. The replacement tooth usually nears full stature before assuming its functional position. The base flares outwards just before ankylosis, as is seen in the fourth position in the upper right jaw of *Python regius*, A.M.N.H. 31921, Figure 26a. This flaring and the deposition of a cementum-like substance establish the new tooth in the tooth row fairly rapidly. The tips of both loose and ankylosed teeth in most tooth positions are thus at nearly the same level.

Bogert (1943) briefly described the sequence of tooth replacement in the maxillae of a large series of elapids and concluded that replacement was uniformly from front to back. The present writer found the same situation in elapid maxillae but, since in most elapids these bones bear very few teeth, it was considered advisable to study lower jaws in which a much longer series was present. The following quotation from Bogert and Martin del Campo (1956) is the best description in the literature of the sequence of replacement of ophidian teeth, although it is based entirely on observations of elapids. "Bogert (1943) has described the mechanism of tooth succession in snakes, pointing out that ordinarily only the alternate teeth in any one series are ankylosed to the bone. Teeth move into position in vacant sockets where they become ankylosed at approximately the same time that the teeth in alternate sockets are shed. The teeth in any given series are replaced from front to back in two successions, one involving the even-numbered teeth and the other the odd-numbered teeth."

The method of replacement of poison fangs is not different from that of the other teeth. In most poisonous snakes (solenoglyphs and proteroglyphs) there are two adjacent tooth positions on the maxilla which bear the poison fangs. These are not newly evolved structures, but are merely the two most anterior members of the maxillary tooth row. Because of the specialization of the fangs the maxilla may be highly modified, so that the fangs are isolated from the other teeth in the series when these are present. Just as every alternate tooth on the other dentigerous bones is in opposite phase to its neighbours in the process of tooth replacement, so the poison fangs function alternately. If one fang is in function, the other fang (on the same bone) is usually being replaced. There is a brief interval when both fangs function. The excellent provision for replacement of fangs in the Crotalidae is shown in Figure 27 and will be described below.

The order in which the snakes will be considered, while based on the replacement patterns, is in agreement with the commonly accepted phylogenetic arrangement. The Boidae (= Boinae and Pythoninae), the Colubridae, and the Hydrophiidae, as will be seen, are characterized by simple

Fig. 27. Dentitions of crotalid snakes.

a. Lingual view, dentary of *Crotalus* sp. Specimen P-1.

b. Dorso-posterior view, bundle of replacement fangs, left jaw, *Crotalus atrox* R.O.M.Z.P. R30.

c. Labial view, functional fang and replacements, right side, *Crotalus adamanteus*, R.O.M.Z.P. R33.

back-to-front wave progression identical to that seen in the lacertilians. The elapids on the other hand often show a reversal of this scheme, with the waves progressing from front to back. Viperids and crotalids show some tendency towards the reversed wave pattern, but mainly show a flat gradient, i.e., all of the teeth in any alternate series are in about the same stage of development over an extended region.

The material will therefore be presented in three sections as follows: I: Boidae, Colubridae, Hydrophiidae; II: Viperidae and Crotalidae; and III: Elapidae. Specimens of the problematical genera *Typhlops* and *Leptotyphlops* in which the teeth were well preserved could not be found.

SECTION I: Families Boidae, Colubridae and Hydrophiidae

A jaw typical of this section is *Natrix maura* L., R.O.M.Z.P. R121, lower left jaw, shown diagrammatically in Figure 28b. Position number one is now empty but was in life occupied, or about to be occupied by a small replacement. Teeth 3, 5, and 7 are unankylosed replacement teeth forming a series increasing in size towards the rear. Teeth 9, 11, and 13 are members of the

Fig. 28. Diagrams of wave-like tooth replacement in snakes.

a. *Boa imperator* U.S.N.M. 59047

Left maxilla

b. *Natrix maura* R.O.M.Z.P. R121

L.L. jaw.

c. *Natrix maura* R.O.M.Z.P. R121

L.R. jaw.

d. *Natrix maura* R.O.M.Z.P. R121

U.R. jaw.

e. *Natrix maura* R.O.M.Z.P. R121

U.L. jaw.

f. *Hydrophis ornatus* R.O.M.Z.P.

R122 L.R. jaw.

Fig. 29. Diagrams of wave-like tooth replacement in boid and colubrid snakes.

- a. *Eunectes deschauenseei* U.S.N.M. 13454 L.R. jaw, odd-numbered teeth only.
 - b. as above, even-numbered teeth only.
 - c. *Farancia abacura* C.N.H.M. 22364 L.R. jaw.
 - d. *Acrochordis javanicus* A.M.N.H. 63955 L.L. jaw.
 - e. *Lyosophis bicincta* A.M.N.H. 60798 L.R. jaw.
 - f. *Python* sp. A.M.N.H. 36573 L.R. jaw.
 - g. *Eunectes murinus* A.M.N.H. 62559 U.L. jaw.
 - h. *Elaphe oxycephalus* A.M.N.H. 62576 L.L. jaw.
 - i. *Xenodon serverus* A.M.N.H. 62576 L.L. jaw.
 - j. *Natrix transversus* U.S.M.
 - k. *Python sebae* U.S.N.M. 29501 U.L. jaw.
 - l. *Eunectes deschauenseei* U.S.N.M. 13454 L.L. jaw.
-

same generation which have become fused to the jaw. The old tooth has been lost in position 15 and a young tooth, the first of another generation, is about to enter the space. Teeth 15, 17, and 19 form another series increasing in size towards the rear. Number 21 is becoming fused and 23 is functional. Thus in the odd-numbered series there are two nearly complete waves.

The even-numbered series is similar. The first three teeth are functional and number 8 is about to be shed. Teeth 10 and 12 are replacements of increasing size and 14 is becoming fused. The remainder of the even-numbered teeth are in the fused, functional stage. This series shows only one complete wave.

Another excellent specimen is illustrated in Figure 29b. While being macerated and stained, the lower right jaw of *Eunectes murinus*, R.O.M.Z.P. R41, showed the functional and replacement teeth particularly clearly. At most positions three generations of teeth can be seen, and the change from horizontal to near vertical as the replacement teeth assume their definitive positions is well illustrated.

At position 1 the old tooth is still present, but a large replacement is ready to take its place. The old tooth has been lost at position 3, and the large replacement has entered the space, although it is not quite erect, and of course not yet ankylosed. The remaining teeth in the wave, numbers 5, 7, 9, and 11 are all well ankylosed, and each is accompanied by two replacements, increasing in size towards the rear. At position 13, the old tooth has again been lost and the replacement has not yet assumed its definitive position. Teeth 15 and 17 are well established. Thus, in this series there is one complete wave of replacement followed by part of the subsequent wave.

The even-numbered series also shows a good wave, with loose replacements at positions 6, 8, and 10, increasing in size towards the rear of the jaw. Parts of the base of the old tooth are still attached to the bone at position 6, and to a lesser degree at 8, while position 10 bears a clean

Fig. 30. Diagrams of the dentition of viperid and crotalid snakes.

- a. *Lachesis muta* R.O.M.Z.P. R136 L.L. jaw.
 - b. *Vipera aspis* R.O.M.Z.P. R137 L.L. jaw.
 - c. *Vipera aspis* R.O.M.Z.P. R137 L.R. jaw.
 - d. *Vipera aspis* R.O.M.Z.P. R138 L.L. jaw.
 - e. *Vipera aspis* R.O.M.Z.P. R141 L.R. jaw.
 - f. *Cerastes cornutus* R.O.M.Z.P. R131 L.R. jaw.
 - g. *Cerastes vipera* R.O.M.Z.P. R142 L.R. jaw.
 - h. *Cerastes vipera* R.O.M.Z.P. R142 L.L. jaw.
 - i. *Trimeresurus monticola* R.O.M.Z.P. R132 L.L. jaw.
 - j. *Trimeresurus monticola* R.O.M.Z.P. R132 L.R. jaw.
 - k. *Trimeresurus wagleri* R.O.M.Z.P. R126 L.R. jaw.
 - l. *Bothrops atrox* C.N.H.M. 31161 L.L. jaw.
 - m. *Ancistrodon contortrix* R.O.M.Z.P. R127, L.R. jaw.
 - n. *Crotalus viridis* R.O.M.Z.P. R140, L.L. jaw.
 - o. *Crotalus viridis* R.O.M.Z.P. R135, L.L. jaw.
 - p. *Trimeresurus purpureomaculatus* R.O.M.Z.P. R129, L.R. jaw.
-

depression for the acceptance of its well-developed replacement. The remaining teeth in this series, numbers 12, 14, and 16 are well ankylosed.

The jaw described above demonstrated clearly not only the cephalad progression of replacement waves, but also the out-of-phase synchrony of the waves. The "leading edges" of the waves in the odd-numbered series are at positions 3 and 13, while the even-numbered series wave begins at position 6. All positions with loose teeth are flanked by ankylosed teeth, resulting in an efficiently functioning dentition at all times.

Figure 29a illustrates the dentition of the right dentary of *Eunectes deschauenseei*, U.S.N.M. 13545, with the teeth of the two alternately numbered series drawn separately. Both series show well-marked waves of replacement progressing from back to front. The replacing wave in the odd-numbered series is more advanced than that in the even-numbered series, as shown by the fact that the new generation has become established at position 15, while position 16 is still occupied by an old tooth, although accompanied in life by a large replacement which was lost during preparation. Similarly, the older generation in the odd-numbered series was well established at position 1, while in the other series ankylosis was only beginning at position 4. The L.L. jaw of the skull is analysed in Figure 29 l showing exactly the same arrangement of waves, passing cephalad, in opposite phases in the alternately numbered series.

Although the Hydrophiidae is considered a fairly advanced group phylogenetically, the tooth replacement pattern is apparently the same as for the colubrids and boids. A lower jaw of *Hydrophis ornatus*, R.O.M.Z.P. R122, is shown in the stylized diagram, Figure 28e. Each of the jaws of this specimen bears several replacement waves, each passing from back to front, the members of the two series being in opposite phases to one another. The

form of the teeth and mode of individual replacement does not appear to differ from other snakes of Section I. A large number of other boid and colubrid specimens were examined, all of which showed the typical replacement pattern described above. Selected examples are shown schematically in Figures 28 and 29.

SECTION II: Families Viperidae and Crotalidae

The replacement of individual teeth in the snakes of Sections II and III does not differ significantly from that in Section I. The distinction lies in the order in which the teeth are replaced. Boid, Colubrid, and Hydrophiid snakes, as we have seen, follow the common reptilian pattern of back-to-front wave progression. The viperids and crotalids, however, show at least a distinct flattening of the replacement gradient, i.e., the wave length tends to be longer, so that the more mature teeth are at the anterior part of the waves, and replacement appears to occur in front-to-back waves. This reversal of the usual reptilian sequence may be seen in such specimens as *Bothrops atrox*, C.N.H.M. 31161, Figure 30 l of *Trimeresurus purpureomaculatus*, R.O.M.Z.P. R129, Figure 30p. The dentitions of several other snakes representing Section II also are presented diagrammatically in Figure 30.

Examples of the flat gradient are seen in Figures 27 and 30. Specimen P 1 (Fig. 27) is a left dentary of *Crotalus* sp. with 9 tooth positions present. The odd-numbered tooth positions are occupied by advanced replacements, the older teeth having been lost. All of the replacements are in about the same stage of growth. The even-numbered teeth are all mature except for the most posterior (number 8) which is in the process of becoming ankylosed. This latter tooth gives the only indication of a replacement gradient in this jaw, pointing to a front-to-back wave progression. All of the odd-numbered teeth are ankylosed; all of the even-numbered teeth are in an advanced stage of replacement. There is a gentle replacement gradient from front to back, since tooth number two is beginning to become ankylosed, while the more posterior teeth are slightly smaller and less erect.

There is no obvious difference between the replacement patterns in viperids and crotalids. The replacement pattern in snakes of Section III will be compared statistically with that of the snakes in Section II in a later section.

The replacement of the great poison fangs of the crotalids and viperids follows the same pattern as the other teeth, i.e., they are replaced alternately just as are any other pair of neighbouring teeth. The axis of the tooth row in this region has rotated so that the bases of the teeth lie transversely to the long axis of the skull. Only two tooth position are present but at each there are a number of replacements lying above and behind the functioning fangs, enclosed in the soft tissue of the gum and tooth sheath. Usually only one of the pair of fangs in each maxilla is functioning at any one time, but occasionally both are present.

Figure 27b is a dorso-posterior view of the replacement fangs from the left maxilla of *Crotalus atrox*, R.O.M.Z.P. R30. The functional fang

Fig. 31. Dentition of *Micropechis ikaheka* U.S.N.M. 119520.

- a. Lingual view, lower left jaw.
- b. occlusal view, lower right jaw.

(shown in broken line) remained with the maxilla while the eight replacements were removed *en bloc*. The functional fang on this maxilla was the distal one. The mesial position was about to be filled with the large replacement marked "2" on the drawing. This tooth, almost completely formed but not ankylosed, will become the next functional poison fang on this maxilla. However, it cannot be said to "replace" the present functional fang (1) since it is not from the same germinal stock. In the sense in which the word "replacement" is being used in this paper, tooth 1 will be replaced by tooth 3, the next member of the tooth family in the distal position. Because of the laterally compressed nature of the fang apparatus, the replacement teeth lie close together but can be separated into the two families on the basis of size and arrangement. The narrow, deep orientation of the replacement bundle can be realized from a comparison of Figure 27, b and c.

The two fang positions function alternately, first left, then right, with a short period when both are in use. This guarantees that there will be at least one functional fang in each maxilla at all times. The number of replacement fangs (3 or 4 per position) is about the same as the number of ordinary teeth present at the dentary positions in the same animal. They are conspicuous mainly because of their great size. Loss of the old fang apparently occurs when the base becomes resorbed and detached, but the fang may be held in by soft tissue for a time. Ditmars (1933) states that the old fang is finally lost when the snake strikes its prey. The fang becomes embedded in the body of the prey and is, of course, swallowed at the same time.

SECTION III: Family Elapidae

The mode of replacement of individual teeth in the elapids is the same as was outlined for the snakes in Section I. As in the snakes in Section II, the replacement pattern of the elapids is not one of simple back-to-front

Fig. 32. Diagram of the dentitions of elapid snakes.

- a. *Notechis scutatus*, R.O.M.Z.P. R107, L.L. jaw.
 - b. *Notechis scutatus*, R.O.M.Z.P. R107, L.R. jaw.
 - c. *Notechis scutatus*, R.O.M.Z.P. R105, L.R. jaw.
 - d. *Micropechis ikaheka* U.S.N.M. 119520 L.L. jaw.
 - e. *Micropechis ikaheka* U.S.N.M. 119520 L.R. jaw.
 - f. *Bungarus ceylonicus* R.O.M.Z.P. R93, L.R. jaw.
 - g. *Bungarus ceylonicus* R.O.M.Z.P. R93, L.L. jaw.
 - h. *Bungarus candidus* R.O.M.Z.P. R89, L.R. jaw.
 - i. *Bungarus candidus* R.O.M.Z.P. R89, L.L. jaw.
 - j. *Pseudechis porphyriacus* R.O.M.Z.P. R117, L.L. jaw.
 - k. *Pseudechis porphyriacus* R.O.M.Z.P. R114, L.R. jaw.
 - l. *Pseudechis porphyriacus* R.O.M.Z.P. R104, L.L. jaw.
 - m. *Micrurus fulvius* R.O.M.Z.P. R109, L.L. jaw.
 - n. *Micrurus lemniscatus* R.O.M.Z.P. R103, L.L. jaw.
 - o. *Micrurus frontalis* U.S.N.M. 69256, L.L. jaw.
 - p. *Micrurus frontalis* U.S.N.M. 69255, L.R. jaw.
 - q. *Micrurus frontalis* U.S.N.M. 69257, L.R. jaw.
 - r. *Furina occipitalis* U.S.N.M. R97 L.L. jaw.
 - s. *Micrurus euryxanthus* U.S.N.M. 38044, L.L. jaw.
 - t. *Furina occipitalis* U.S.N.M. R109, L.R. jaw.
-

waves, but shows a considerable degree of flattening of the gradient, with a large proportion of the specimens studied showing front-to-back waves. Bogert (1943) has thoroughly described the upper jaw dentition of numerous elapids, and this will not be repeated here. The two drawings in Figure 31 illustrate the lower dentition of a fairly typical elapid, *Micropechis ikaheka*, U.S.N.M. 119520. The teeth are rather short and stubby compared to those of most snake groups, but the replacement teeth, as in all snakes, lie prostrate and well to the rear of their predecessors. From such well-preserved jaws the replacement pattern can be readily determined.

A fairly typical pattern is seen in the lower left jaw of *Bungarus ceylonicus*, R.O.M.Z.P. R93, shown in Figure 32g. In the odd-numbered series (stippled) the first six tooth positions (1 to 11) are filled by unankylosed teeth decreasing in size towards the rear. Thirteen and 15 are mature, intact teeth, while tooth 17 is just becoming ankylosed. This series is interpreted as containing the leading end of one wave progressing caudad in positions 1 to 11, and the trailing edge of an older wave, also caudally directed, in positions 13 to 17.

The even-numbered series in the same jaw is represented mainly by ankylosed teeth except at the posterior end where the second-to-last tooth is in the process of ankylosis, and the last is a medium-sized replacement. The ankylosed anterior teeth are accompanied by a series of replacement teeth decreasing in size towards the rear. Again, this is a pattern of waves passing cephalad along alternately numbered series.

It should be emphasized that this front-to-back wave progression along the entire jaw is not universal among the elapids. In many specimens it was seen in only the anterior of the jaws, and in many others the gradient was so flat that no wave direction could be detected, there being only a simple alteration of teeth in two stages of replacement. In some jaws the posterior part showed the back-to-front gradient characteristic of most reptiles, while the anterior had a front-to-back gradient. Various combinations of these types of gradients are seen in the stylized diagrams in Figure 32. In some jaws, replacement waves passing in both directions can be seen. In *Pseudechis porphyriacus*, R.O.M.Z.P. R117, the lower left jaw (Fig. 32j) has one wave passing caudad in the anterior part of that even-numbered series and cephalad in the posterior part of the same series.

At positions 2, 4, and 6 the old teeth have been lost, their positions being taken by replacements decreasing in size towards the rear. At position 8 the old tooth remains, but is being degraded and is accompanied by a small replacement. Teeth 10 and 12 are intact, though they have attendant small replacements. Positions 14, 16, 18, and 20 show a clear gradient increasing towards the rear. Thus in this series, there is a "U"-shaped gradient progressing in both directions from the centre of the jaw.

Numerous elapid jaws showed various combinations of different replacement patterns, including flat gradients and back-to-front waves, but the predominant pattern, especially at the anterior part of the jaws, was front-to-back progression. No correlation between species and any particular replacement pattern could be detected, although the fairly long series of specimens of *Micrurus* sp. all showed uniform front-to-back waves.

Forty-six jaws of Section III snakes, and twenty-eight of Section II snakes were examined. These seventy-four jaws provided 148 alternately numbered series, each with an anterior and posterior half, making a possible total of 296 individual pieces of information. Of these twenty-five were missing, damaged or otherwise indecipherable. The remaining mass of data was reduced to the percentages in the table below.

DIRECTION OF WAVE PROGRESSION IN DIFFERENT REGIONS OF JAWS OF SNAKES (*in per cent.*)

Direction	<i>Anterior part of Jaw</i>		<i>Posterior part of Jaw</i>	
	SECTION II	SECTION III	SECTION II	SECTION III
Front-to-back	34	68	37	46
Back-to-front	8	1	10	17
No apparent gradient	58	31	53	37

As shown in this table, the snakes of Sections II and III tend strongly away from the common back-to-front replacement pattern. Only a small fraction

of the specimens (average 9 per cent) show this common reptilian gradient, and it occurs more frequently in the posterior part of the jaw than in the anterior part. In Section II slightly more than half of the jaws achieved a flat gradient, while about a third (36 per cent) completed the transition to the reversed, front-to-back progression. In Section III more than half (57 per cent) attained the reverse gradient, with only a third retaining the flat gradient. In the anterior part of elapid jaws only one series in one specimen, representing less than 1 per cent of the sample, showed a back-to-front replacement pattern.

The snakes of Section I are generally conceded to be of simpler and probably more primitive structure. As expected, the dentition of this group most closely resembles that of the lizards, particularly the platynotan lizards from which they are generally believed to have descended. Replacement occurs in waves progressing from back to front, just as in the lizards. The gradient of replacement is more gradual than that of most lizards, but less gradual than that seen in sections II and III.

In those snakes with anterior fangs, a large proportion of the teeth in the jaws are replaced simultaneously and therefore do not function as efficient prehensile structures. However, the need for firm grasping teeth is not as great in the poisonous snakes as in those of Section I, since the prey is first killed by venom before being swallowed. A non-poisonous snake must have a firm hold on its prey before it can be subdued by crushing. The form of the teeth may also be correlated with this fact. In the majority of snakes of Section I the teeth are moderately long, recurved, fairly strong, and better adapted to grasping. Those of the elapids are usually shorter and not as pointed, and the viperids and crotalids tend to have longer but more slender teeth.

*Class Reptilia**Subclass Archosauria*

The archosaurs present an interesting study in the elaboration of many types of dentition from a single simple pattern. The order of presentation followed here, that of Romer (1945), shows the probable phylogenetic development of the subclass.

The early development of the archosaurs is poorly known, and fossil material with good dentition is rarer still. The earliest archosaurs are grouped in the Thecodontia, but although this group contains many familiar forms, most are represented only by scrappy material. However, the dentition of the thecodont group as a whole is sufficiently well known to describe the manner of replacement of individual teeth, and two well-preserved specimens give us the replacement pattern. As in most reptiles, replacement occurs in waves progressing from back to front along alternately numbered tooth series.

The specialized dentitions of the sauropods as well as the more orthodox dentitions of the theropods, pterosaurs, crocodilians, and birds are readily produced from the dentition of the thecodonts. Early in this study it was thought that adult crocodilians presented an exception to the regularity seen in other archosaur groups, but apparently this irregularity is merely attributable to age: in younger specimens the teeth are replaced with mathematical regularity. Röse (1892, 1893), Bolk (1912), and Woerdeman (1919 and 1921) used embryos of *Crocodylus* in their work on the rhythm of tooth replacement, and mainly because of these writers, crocodilians have become established in the literature as examples of regular alternate replacement. Because of the change from regular replacement in the young to irregular replacement in the adult, a large series was studied by the present writer.

Evidence concerning the dentition of the pterosaurs is very scanty. Alternating replacement was unquestionably present, as several specimens showed alternate empty and occupied alveoli. However, no specimen was found in good enough condition to show the presence of waves of replacement.

Compared with the ornithischians, there was little specialization of dentition in the saurischian dinosaurs. The carnosaurs retained the simple tooth of their immediate ancestors, the pseudosuchians. The dentitions of the sauropods were exceptionally weak, but show a few changes from the primitive conditions. Only in the Ornithischia was there a spectacular evolution which appeared both in the form of the individual teeth and in their arrangement. The sauropod dentition is a makeshift derived with little change from the carnivorous condition; the ornithopod dentition is an efficient mechanism far removed from that of its pseudosuchian ancestors.

Class Reptilia

Subclass Archosauria

Order Thecodontia

SUBORDER PSEUDOSUCHIA

Although restorations of such well-known genera as *Saltoposuchus* and *Euparkeria* are familiar, little is known about their dentitions. Only one pseudosuchian with reasonably complete dentition has come to the author's attention: an ornithosuchian, *Hesperosuchus agilis*, A.M.N.H. 6758, described by Colbert (1952). This rare specimen was found in a fragmentary condition, but a portion of the left dentary remained intact, permitting the study of a series of seventeen alveoli out of the twenty or so presumably present in life. Figure 33 shows the labial aspect of this jaw, the posterior part of which has been lost. Definite alternation is present, the odd-numbered teeth from 1 to 13 being fully grown, with smaller, even-numbered teeth between them. The last two teeth in the odd-numbered series, numbers 15 and 17, represent the beginning of a new replacement wave. Alveolus number 15 is empty; number 17 is occupied by a very small replacement tooth.

In the even-numbered alveoli, the teeth are in various stages of replacement, with the larger teeth towards the rear. Teeth 6 and 12 have been lost and number 16 is broken, but the remaining even-numbered teeth form a series with their size gradually increasing towards the rear, as in most other reptiles. Although it is difficult to tell without damaging this rare specimen, it appears that the replacement teeth lie directly lingual to their predecessors between the old teeth and the lingual alveolar wall. Perhaps some resorption of the old tooth takes place before its loss, but it is unlikely that the new tooth enters the pulp chamber of its predecessor, as in the crocodiles, for example. The arrangement may be a primitive one in the early archosaurs, as it is suggested to varying degrees in later archosaurs, such as pterosaurs, carnosaurs, and prosauropods.

SUBORDER PHYTOSAURIA

As in the Pseudosuchia, many specimens of phytosaurs have been described

Fig. 33. Partial left dentary of *Hesperosuchus agilis*, A.M.N.H. 6758, lingual view. After Colbert.

but good dentitions are rare. No doubt this is because the thecodont implantation relies on retention by non-calcified connective tissue, maceration of which leads to loss of teeth which would have been retained in forms with bony ankylosis. Of the many skulls examined, only one possessed a sufficient number of teeth *in situ* to permit analysis. It is, however, an excellent specimen giving us a clear picture of tooth replacement in the phytosaur group.

The type specimen of *Brachysuchus megalodon*, U.M. 10336A, was recognized by Case (1930) as unique in having an almost completely preserved dentition, but he concluded, "the arrangement and stage of development of the teeth are very irregular, showing that replacement was without order." The graphic analysis (Fig. 34, a and b) shows that Case was incorrect on that point, since there is a regular pattern of waves passing cephalad along the alternately numbered tooth series. In many cases, the

Fig. 34. Histogram showing the relative degrees of eruption of the teeth in the (a) lower right, and (b) lower left jaws of *Brachysuchus megalodon*, U.M. 10336A. Teeth are numbered from the symphysis. (c) Portion of the right lower jaw of U.M. 10336A from the thirteenth to the thirty-ninth tooth. Labial view.

young replacement teeth have been lost, but the series from 31 or 33 to 45 is remarkably complete. This pattern agrees well with the condition in Colbert's *Hesperosuchus* and with the dinosaurian descendants of the Thecodontia.

Figure 34c shows the superficially irregular appearance of the jaw, with individual teeth in many stages of eruption. The mode of replacement of individual teeth is not known with any degree of certainty. No changes could be seen in the old teeth *in situ* in the jaws examined, and the loose phytosaur teeth did not show notched bases or sides. The replacement tooth may have developed at least in part within the pulp chamber of its predecessor, as in the crocodilia, or may have been associated with a cavity resorbed in the lingual wall of the old tooth. Dissection of a phytosaur jaw will be necessary before this problem can be solved. In any case, the old tooth is apparently lost when its replacement is still fairly small, and much vertical growth is necessary before maturity. This makes possible the graph (Fig. 34) based on varying heights of eruption.

*Class Reptilia**Subclass Archosauria**Order Crocodilia*

The process of tooth replacement is probably more fully documented in the crocodiles than in any other group of reptiles. This is especially true of their embryonic dentitions.

That crocodilian teeth are replaced has been known for many years. Owen (1840) described the arrangement of functional and replacement teeth in the crocodile and compared the condition seen in the dental lamina of the embryo with that in the shark. Adams (1867), describing a visit to a haunt of crocodiles, wrote, "Quantities of deciduous teeth of various sizes were strewn along the slimy sides of the pond." Ditmars (1933) relates that often a dozen cast-off teeth were found each week in a pool in the New York Zoological Park containing five large alligators.

Excellent reviews of the literature on crocodilian dentition are given by Woerdeman (1919 and 1921) and Wettstein (1937), although the latter indicates that little progress has been made since Woerdeman's time. The works of Röse (1892 and 1893), Bolk (1912), and Woerdeman (1919 and 1921) are concerned entirely with the embryology of the dentition, and Bolk and Woerdeman proposed comprehensive theories based on these studies, explaining the phenomena associated with alternate tooth replacement. These will be discussed fully in the embryological section, with only the post-embryonic conditions described here.

Implantation in the Crocodilia is thecodont, although in immature individuals of at least some forms the teeth are set in grooves which are especially noticeable at the rear of the jaws. Because the teeth are held in by non-calcified connective tissue, fossil crocodilians are often found with all of the teeth missing. Of all the living reptiles, only the crocodilians possess a periodontal membrane. This was first reported by Owen (1840), who, with Röse (1893) and several later authors remarked that the relation of tooth to alveolus in the crocodile is more similar to that of mammals than of any living reptiles. It is very likely that this condition was shared by most, if not all, other archosaurs.

The youngest crocodilian (skull length 40 mm.) studied by the writer was *Alligator mississippiensis*, R.O.M.Z.P. R36, probably just out of the egg. Only the anterior teeth were set in definite sockets, those in the posterior half of each jaw lying in grooves which would later have become divided into individual thecae as discussed by Reese (1915). All teeth are held in by bands of connective tissue which lie between the teeth as well as on their lingual and labial sides. In very young crocodilians the bases of the teeth can be seen where this band is chemically removed, since a high lingual bony wall is not developed until later in life. The bases are widely open, and almost all bear signs of active tooth replacement.

The dental lamina in the late embryo lies in the groove in which the teeth are implanted, with tooth buds developing on its free margin. Woerdeman (1919) describes how the dental lamina breaks up into isolated groups of cells which retain the capacity to form replacement teeth. Presumably one of these cell groups is included in each alveolus as the groove is divided up to form individual thecae. A skull of *Caiman* sp., R.O.M.Z.P. R172 (skull length about 100 mm.), was examined to see if there was provision for the accommodation of germinal dental material and its products within the alveoli. In this specimen a few of the rear teeth in the maxilla and dentary were still set in grooves, the individual alveoli being as yet incomplete. Each tooth socket showed a definite pocket at the lingual side of the tooth, about 1 to 2 mm. deep and about the same diameter as the base of the tooth, which is certainly adequate for the purpose. Similar spaces were seen in other thecodont reptiles.

Teeth in all stages of replacement are clearly shown in the jaws of several young crocodilians in the R.O.M. collections. A typical specimen, *Alligator mississippiensis*, R.O.M.Z.P. R1, is shown in Figure 35b. The first indication of tooth replacement activity is the formation of a shallow pit in the lingual wall of the old tooth just above the base, as shown in Figure 36. In a more advanced stage, the pit becomes enlarged, perforates to the pulp cavity, then becomes confluent with the wide-open base of the tooth. Wettstein (1937) discussing young crocodiles, says that the perforation always begins on the lingual surface somewhat above the base of the old tooth. The isolated teeth shown in Figure 36 and the radiographs in Figure 37 illustrate the stages in the resorption of the lingual wall of the old tooth. The developing replacement tooth soon moves into the pulp chamber of its predecessor, completing a large part of its growth in that location. As the replacement tooth increases in size more and more of the base of the old tooth is resorbed. Eventually only a small part of the crown remains, appearing as a mere cap over the replacement tooth. Teeth in this stage are not uncommon, at least in younger animals.

A provision for the increase of size of the teeth to accompany the general growth of the animal is seen in many specimens. Radiographs of young individuals in which growth is rapid reveal that the crown of a replacement tooth developing within the functional tooth is larger than that of its predecessor. The crown of a replacement tooth develops within the body of the old tooth, mainly below the neck separating the wider base from

Fig. 35. Radiographs of crocodilian dentitions.

- a. Lower right jaw of *Crocodylus porosus*, R.O.M.Z.P. R10. Skull length 80mm.
- b. Upper right jaw of *Alligator mississippiensis* R.O.M.Z.P. R#1, skull length 68 mm.

the narrower crown. In this way the diameter of the replacement crown can become greater than that of the crown of the tooth within which it lies. The skull of *Alligator mississippiensis*, R.O.M.Z.P. R1 (Fig. 35b), shows, especially at its posterior end, a regular alternation of small older teeth and larger, younger teeth, just as was described for *Sphenodon*.

The process of regular tooth replacement is established long before hatching. Röse (1892 and 1893) and Woerdeman (1919) mention that many teeth are laid down by the dental lamina, although these are resorbed before eruption. They report that in very young (but hatched) crocodilians, teeth about to be replaced are almost completely degraded before being discarded. Wettstein (1937) described the process of replacement in young animals as being similar to that described above, where resorption of a part of the base permits the replacement tooth to enter the pulp chamber of its predecessor. The resorption spreads from the original perforation until the old tooth, together with its sheath, is thrown off as clumps of dentine. The process in older crocodilians is not so well known. Wettstein presumed that the teeth in the older crocodilians were not as severely degraded as those in the younger. Eleven jaws of older crocodilians, representing over 150 teeth,

Fig. 36. Teeth from a Pleistocene specimen of *Alligator mississippiensis*, U.S.N.M. 5995, showing successive stages in resorption of the base, lingual view.

Fig. 37. Radiographs of 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.

were studied by means of radiographs made by Dr. R. Zangerl at Chicago, and representatives of this series are given in Figure 37. In no case was a very large part of the old tooth resorbed before being lost. The radiographs of some of these adult jaws also show the openings in the bases of the old teeth through which the young replacement teeth entered the pulp cavities. These openings are usually circular but the proximal border of the opening soon becomes confluent with the margin of the apical opening. Very few teeth were seen to be without replacement teeth either alongside or within their pulp chambers.

The sequence of tooth replacement in the Crocodilia has been the subject of papers by several of the early dental embryologists. Röse (1892), Bolk (1912), and Woerdeman (1919) mention that replacement of the elements comprising an alternately numbered series occurs in a synchronized pattern long before hatching. The three authors agreed that all of the

teeth in each alternately numbered tooth series are replaced at the same time. The author did not prepare any crocodilian embryos to check on the work of the earlier microscopists, but made radiographs of about fifteen crocodilians of the genera *Alligator*, *Crocodylus*, and *Caiman*, with skull lengths ranging from 40 to 100 mm. These indicate that although simple alternation may have been present in the embryo, it tends to break down fairly early in life and often approaches randomness. In the posterior part of the upper right jaw of *Alligator mississippiensis*, R.O.M.Z.P. R1 (Fig. 35b), there is a fairly regular alternation of thin-walled, newly established teeth with older teeth containing advanced replacements in their pulp cavities. This same jaw also illustrates a fairly regular wave of replacement passing cephalad along the even-numbered series. Teeth 20, 18, and 16 are large, thin-walled teeth without replacements, indicating that they have only recently become established in their alveoli. Teeth 14, 12, and 10 form a series in which the old teeth have not yet become degraded and lost, but which contain replacements decreasing in size towards the anterior of the jaw. From tooth 10 forward, there appears to be little change in the status of the wave. A similar, but much gentler gradient in the replacement teeth can be seen in the odd-numbered series.

The alternation of older and younger elements seen in the posterior part of the above specimen is repeated in the lower right jaw of *Crocodylus porosus*, R.O.M.Z.P. R10, shown in Figure 35a. There is an indication of a wave passing cephalad in teeth 14, 12, 10, and 8, but the gradient is very gentle. In the odd-numbered teeth, on the other hand, there seems to be indication of a reverse wave, since teeth 9, 11, and 13, and probably also 15 are less well developed towards the rear.

Numerous other jaws of young crocodilians show different variations of the basic pattern. Frequently there are hints of either alternation or a wave-like pattern, but in many instances there is no recognizable order, the teeth in various stages of replacement appearing to be randomly distributed.

Radiographic examinations of the jaws of adult crocodilians at the Chicago Natural History Museum, some of which are illustrated in Figure 37, show no obvious pattern. A graphic plot (not illustrated) of the relative sizes of the replacement teeth showed what appeared to be a random distribution. Thus, it appears that there is a breakdown in the regularity of the replacement process. The embryologists describe regular alternation of uniformly developed dental elements in unhatched specimens; juvenile forms show some synchrony; teeth in the adults are apparently replaced in a random pattern. This is the only instance of such a breakdown in the archosaurs. It will be recalled that certain lizards showed a similar phenomenon, although for them there may be an entirely different explanation. The only reference to this irregular replacement is in Marcus (1931) and Hennig (1931) who used a fairly late embryo of *Caiman sclerops* and found that regular alternation was not apparent. From their illustrations the skeleton of an alternating pattern appears to be present, but some elements are not developing at the rate required to maintain synchrony. Further investigation of the problem would undoubtedly be well worth while.

A long-term project undertaken by the present writer involves the periodic radiographing of a series of live alligators. Close study of the crocodilians, the only living archosaurs, should provide information to assist in investigating their relatives the dinosaurs. One young alligator has been kept since December, 1954, and radiographs have been made every month. This animal was about one year old when the work began and showed only a slight increase in size during three years, despite a good appetite and plentiful food. The skull length in May, 1955, was 80 mm. Preliminary results indicate that there is a certain degree of synchrony present, especially at the mid-sections of the jaw rami, which becomes less regular anteriorly and posteriorly. The time required to replace a single tooth was between eight and sixteen months, with the average for thirty-five positions being slightly over twelve months. With a few exceptions, all of the teeth in any alternately numbered series were replaced within a four-month period. Similar results have been obtained using a larger alligator with a skull length of about 110 mm. and work has begun on an even larger specimen with a skull length of about 160 mm. The results of all of these studies will be published in detail in a paper dealing exclusively with crocodilian dentition.

Research in fossil crocodilians has proven unfruitful. Woerdeman used a partial left dentary of *Mystriosuchus stukelyi* Bronn, Teyler Mus. 2742 (Teleosauria, Mesosuchia), in which ten tooth positions are preserved. In the odd-numbered series, teeth 1, 5, and 7 are large and appear intact, 3 is about three-quarters grown, and 9 is half-grown. This series, therefore, shows the irregularity characteristic of the adults of later crocodilians. The even-numbered series is also irregular. At positions 2, 4, and 6, the old teeth have been lost and their place taken by small replacements, that in position 4 being the smallest. Tooth 8 has been dislodged and is lying loose near its alveolus. Tooth 10 is intact and fully grown. This series could be interpreted as showing a wave progressing caudad, but could also indicate a random distribution. At best, this specimen seems to agree with the adults of Eosuchians in not showing a regular pattern.

A second fossil specimen, possibly *Teleosaurus*, was sectioned by the writer. It consisted of a fragment from near the symphysis of the lower jaw and bore nine pairs of alveoli. Identification is uncertain, since the specimen, kindly supplied by the Museum of Comparative Zoology, Harvard University, was labelled only "No locality, Upper Jurassic Oolite." This is presumably the Upper or Superior Oolite, which is Upper Middle Jurassic, of which *Teleosaurus* is a characteristic genus. The size and general aspect of the specimen agree with this determination. Fourteen serial peel sections were made, roughly at right angles to the axes of the teeth, at about 1¼ mm. intervals. Representative sections are given in Figure 38. The odd-numbered teeth appear to be fairly well synchronized. Tooth 1, apparently near the symphysis, is accompanied by a very small replacement. There is a fine opening into the pulp chamber, but the replacement tooth has remained outside. Tooth 3 is nearer to replacement, with the tip of the new tooth just entering the pulp chamber. Tooth 9 is a younger tooth than the others and does not fill its alveolus. A small replacement is present, but has not yet

Fig. 38. A series of frontal sections through the symphyseal region of right dentary of an unidentified crocodilian, possibly *Teleosaurus*, R.O.M.Z.P. 1972. The Roman numerals indicate section numbers, there being 12 sections in all, each about 1½ mm. thick.

affected the old tooth. Thus, the odd-numbered teeth are all in the earliest stages of replacement.

The even-numbered teeth all appear to be in more advanced stages of replacement. Tooth 2 has recently assumed its definitive position, with its tip just visible in the first section. Number 4 is even younger, being still partly sheathed with the remains of its predecessor. A large replacement is present within tooth 6, and a large part of the base of the old tooth has been lost. Tooth 8 is similar to tooth 6, but not as far advanced. This even-numbered series indicates an excellent front-to-back gradient.

In this jaw, therefore, two replacement patterns are present, one a flat gradient in which all of the teeth are replaced at about the same time, the other a regular front-to-back wave. The replacement regularity here is much more pronounced than in the adults of the modern crocodilians in Figure 37, but it is impossible to draw any firm conclusions from this isolated specimen.

Clearly visible in Sections VIII, IX, and X (Fig. 38) are cavities extending lingually from the alveolus itself, obviously for the accommodation of the replacement teeth and their accessory tissues. This cavity was already noted in *Caiman sclerops* above, and in *Gavialis* by Cawston (1943). Similar cavities exist in the carnosaurs (q.v.) and are discussed in that section of this work.

From the evidence on hand we may construct a fairly clear picture of tooth replacement in the crocodilians. In the embryo, the basic alternating pattern common to all reptiles is established. The odd-numbered teeth and even-numbered teeth function as separate series, and all the teeth of one series are replaced at about the same time. There is little evidence, however, of a regular pattern of succeeding waves of replacement as was seen in most other reptilian groups.

In young and recently hatched individuals, the alternately numbered series functions as units but, as age increases, the order of replacement becomes less regular until in adult animals replacement seems to occur in a completely random pattern. Replacement teeth develop in pockets lying lingual to, but confluent with the alveoli. The small replacement tooth enters the pulp chamber of its predecessor through a hole resorbed in its lingual wall, or through an emargination of the base spreading out from this original hole. Growth of the replacement within the old pulp cavity is accompanied by increasing destruction of the old tooth, leading to eventual loss of the old crown. In a two- to three-year-old specimen of *A. mississippiensis* replacement of an individual tooth required about twelve months.

Two probably adult mesosuchians showed replacement patterns which were not quite regular, but which were possibly less irregular than adults of modern species. Because of the small sample, no definite conclusions could be drawn regarding a change in the regularity of the replacement pattern during geological time.

Class Reptilia

Subclass Archosauria

Order Pterosauria

The bulk of the pterosaur material is in European collections, and the writer has been forced to rely on the literature for information regarding their dentitions. This information is scattered, and on the whole not detailed. However, there is enough to provide a reasonably accurate picture of the gross aspect of the dentition and of the replacement process. An interesting semi-popular account of pterosaurs is given by Seeley (1901). Although the details are meagre, he does present a brief description of pterosaur dentition.

The teeth are all of pointed, elongated shape, without distinction into the kinds seen in most mammals and named incisors, canines, and grinders. They are organs for grasping, like the teeth of the fish-eating Crocodile of India, and are not unlike the simple teeth of some Porpoises. They are often implanted in oblique oval sockets with raised borders, usually at some distance apart from each other, and have the crown pointed, flattened more on the outer side than on the inner side, usually directed forward and curved inward. As in many extinct animals allied to existing reptiles, the teeth are reproduced by germs, which originate on the inner side of the root and grow till they gradually absorb the substance of the old tooth, forming a new one in its place. Frequently in Solenhofen genera, like *Scaphognathus* and *Pterodactylus*, the successional tooth is seen in the jaw on the hinder border of the tooth in use.

The most significant information in this description is that in different species of pterosaurs there may be two different sites for the appearance of the replacement teeth. In one type, the replacement develops on the lingual side of the old tooth. Little information is available regarding pterosaurs in which the replacement lies lingual to its predecessor, and the study of actual specimens by someone particularly interested in dentition will be necessary before a satisfactory account of tooth replacement in that group can be

written. Seeley (1901) mentions *Dimorphodon* as an example of this type, but gives no details. Owen (1840) refers to a paper by Münster (not seen) in *Nova Acta Nat. Cir.* (XV., p. 63): "In *Pterodactylus medius* the bases of the teeth have been stated (by Münster) to be hollow as in the case of the crocodile, and to contain the germs of their successors." This statement does not agree with the description below in which *Pterodactylus* is considered typical of the group which has the replacement teeth in a definitely distal position. Von Meyer (1856) does not illustrate *P. medius*, but illustrations of other species of the same genus (species valid today) show that at least some of them had the replacement teeth distal to the functioning ones.

The best illustrations, especially of German forms, are to be found in Von Meyer (1856). These lithographs present life-sized, accurate, and detailed representations of some of the best pterosaur material ever assembled. Von Meyer's descriptions in the text are concerned mainly with general morphology, but he is careful to distinguish between functioning and replacement teeth. In one instance, he takes his compatriot Goldfuss to task for expressing the dental formulae of certain specimens incorrectly by counting replacements along with functioning teeth.

A large proportion of the more completely preserved German pterosaur specimens show numerous replacement teeth. Differing from such forms as *Dimorphodon* in which the replacement teeth develop lingual to the old teeth, the Solenhofen genera have widely spaced alveoli with replacement teeth erupting either through new alveoli or directly into the functional alveoli, but always almost directly behind the old teeth. This type of replacement is seen in the genera *Rhamphorhynchus*, *Pterodactylus*, *Scaphognathus*, and probably several others. The exquisitely preserved specimen of *Rhamphorhynchus gemmingi* shown in Plate IX of Von Meyer (1856) is an excellent example of this type of dentition. Ten tooth positions are preserved in the upper jaw and in each, with the possible exception of the most posterior, the large functioning tooth is accompanied by a replacement lying directly behind it. In some cases the replacement is almost as large as the functioning tooth, indicating that the new tooth could move into the place vacated by its predecessor and become functional with little increase in size. The writer was unable to determine the sequence of replacement from the sizes of the preserved replacements. Stolley (1936) described a well-preserved specimen of *Rhamphorhynchus gemmingi* with replacements lying behind the functional tooth in most positions. The arrangement of the various sizes of replacement teeth indicates that replacement was occurring in two alternately numbered series, but the sequence of replacement could not definitely be determined. Replacement teeth 2, 4, 6, and 8 form a series increasing in size towards the rear, suggesting a wave proceeding cephalad, as in most other reptiles. In the odd-numbered series, tooth 1 has a very small replacement, while 3, 5, and 7 are all moderately large. This is in agreement with a back-to-front wave progression. However, the ninth position bears a small replacement which may or may not belong to a wave which was destined to replace the wave in positions 1, 3, 5, and 7. Tooth 11

has a fairly large replacement. Thus, the odd-numbered series appears to contain two waves, the more posterior one causing replacement of the first before it has become established. Alternatively, this may be purely a random distribution. We can only state that it does not disagree with the possibility that tooth replacement occurred in waves passing cephalad along alternately numbered tooth series.

Von Ammon (1884) described the dentition of *Rhamphorhynchus longicaudatus*. As in the specimen described above several replacement teeth were present but their arrangement, though indicating alternation, gave no hint of a wave pattern.

One of the strangest pterosaurs is *Ctenochasma* (Broili, 1936), a form with a highly specialized dentition. The number of teeth is considerably increased, each tooth being long, thin, and bristle-like. Tooth replacement apparently resembled that in *Rhamphorhynchus*, but there were probably two or three replacement teeth behind each functional tooth, all of the teeth, both functional and replacement, forming a brush or comb-like marginal series. From Broili's illustration it is difficult to determine any pattern, although some of the teeth near the rear of the jaws suggest that alternation was present.

The descriptions of pterosaur dentitions above serve mainly to illustrate our lack of concrete knowledge of the subject. We can be certain that tooth replacement took place, and that it probably occurred in an alternate arrangement. The site of development of the replacements appear to be different in different genera and species, but we have little evidence. Nor is there any definite proof of replacement occurring in a wave pattern. Special examination of a number of well-preserved specimens will be needed before definite conclusions can be reached.

*Class Reptilia**Subclass Archosauria**Order Saurischia*

SUBORDER THEROPODA

Infraorder Coelurosauria

Several well-preserved coelurosaurs are in the collections of the American Museum of Natural History representing the genera *Velociraptor* and *Coelophysis*. Descriptions of numerous coelurosaurs are to be found in the literature, but the specimens described in this section are the only ones with good dentitions to come to the author's attention.

As described earlier for the phytosaurs, the jaws of coelurosaurs bear teeth in all stages of eruption, permitting us to follow the sequence of replacement. The replacement teeth develop in pockets confluent with and on the lingual side of the alveoli, and with growth they become associated with an increasing resorption of the lingual wall of the old tooth. The old tooth is lost when the new tooth is about one-third grown. The mode of replacement is apparently identical to that of the carnosaurs, described in detail below.

Velociraptor mongoliensis, A.M.N.H. 6515, shows excellent cephalad waves of replacement in all four jaw quadrants. The right dentary (Fig. 39b) is particularly informative. Teeth 1, 3, 5 and 7 form a series increasing in size toward the rear, while 9, 11, 13, and 15 are fully mature members of the same wave. Alternating with these teeth is a similar wave at positions 8 to 16. The maxillae also show good waves of replacement. In the left dentary both of the alternately numbered series appear to be undergoing replacement. In the odd-numbered series, tooth 7 is missing, tooth 9 is erupted about half-way, and teeth 11 and 13 are of full height. This series is interpreted as the anterior end of a new wave. The old tooth is lost in both 7 and 9, and although the replacement tooth at position 9 is visible, that in 7 has either been lost or has not protruded far enough to become visible. Teeth 11 and 13 are the mature members of the same wave.

In the even-numbered series, tooth 2 is missing and no replacement is visible. Tooth 4 is not quite fully grown and is not in line with the other teeth, probably indicating that its base had not become completed *pre mortem*. Positions 6, 8, and 10 are occupied by mature teeth. The old tooth at position 12 has dropped out and the tip of a small replacement tooth can

be seen. Tooth 14 is perhaps half grown. Thus, in the even-numbered series in the left dentary, one wave was established, then in turn underwent replacement from the back.

Fig. 39. Diagrams of wave-like tooth replacement in coelurosaurs.
 a. Part of the right maxilla of *Coelophysis* sp. A.M.N.H. 7252.
 b. Right dentary of *Velociraptor* sp. A.M.N.H. 6515.

The other well-preserved coelurosaur, *Coelophysis*, is represented by several specimens in the American Museum of Natural History. Part of the right maxilla of a juvenile individual, A.M.N.H. 7242, is especially well preserved, and its dentition is shown graphically in Figure 39a. Tooth 1 is the last member of an old wave, and probably contains a fairly large replacement within its alveolus. The old tooth has been lost at position 3, revealing a replacement only half grown. Position 5 bears a large replacement, perhaps seven-eighths of its definitive size, and the teeth at positions 7, 9, and 11 are all fully grown. Thus, the series shows the end of an old wave and the complete establishment of a new one.

The even-numbered series shows a similar pattern, with teeth 2 and 4 old, but at least superficially intact. Tooth 6 is missing, indicating that it was lost, along with its replacement, either *pre* or *post mortem*. Tooth 8 is barely erupted, having just been freed from the remains of its predecessor. The tenth tooth is broken, but seems to have been less than fully grown. Tooth 12 is full size for its place in the jaw. In this jaw, the leading edges of the replacement waves seem to be fairly close together, i.e., the areas where replacement is active are not as well separated as in most reptilian specimens. Such a condition is not an anomaly, but is to be expected occasionally since biological processes are never mathematically precise. In most cases, however, similar phases of the replacement waves are well separated, as is shown by the other coelurosaur jaws described here.

Several other *Coelophysis* jaws were examined at the American Museum of Natural History, those with sufficiently well-preserved dentitions showing waves similar to those described for other coelurosaurs. The larger *Coelophysis* skulls, A.M.N.H. 7239 and 7240, both show good wave patterns.

From the study of the above genera, it is obvious that tooth replacement in coelurosaurs follows the common back-to-front wave pattern. This pattern was seen in the thecodonts, a group presumably ancestral to coelurosaurs, and will be seen in the carnosaurs, a group which apparently sprang from the coelurosaurs. The young teeth presumably develop in pockets within the alveoli, lingual to the bases of the old teeth, and lie in part in shallow pits resorbed in the walls of their predecessors.

Infraorder Carnosauria

Good carnosaur skull material is relatively abundant, so that information could be obtained not only from surface features, but from a specimen subjected to serial sectioning (Fig. 40). The carnosaurs resemble the coelurosaurs described above both in the method of replacement and in the recurved, compressed, and serrate form of the individual teeth. The process of replacement in a typical carnosaur, *Gorgosaurus libratus* is described by Lambe (1917) as follows:

The teeth replace each other from beneath, apparently as in the living Ghavial (*Gavialis gangeticus*) of India. In *Gorgosaurus* it is seen that the new tooth makes its appearance on the inner side of the base of the old tooth. The root of the latter is absorbed at this point, allowing the new tooth to enter its central cavity [see Figure 40]. With increased size, the growing tooth, through pressure exerted directly from beneath, ejects the old tooth, whose base has been weakened by further absorption. Even before a new tooth has grown sufficiently large to protrude beyond the margin of the alveolus a germ tooth may be formed, to be ready in turn to become functional.

Thus we find in a carnivorous dinosaur provision for a rapid replacement of teeth functioning in a single row, the mode of succession being identical, so far as we can judge, with that in the existing *Gavialis*. The inner face of the roots of old teeth are usually concave, and it is here that the tips of new teeth are first observed, pressing against the old ones they are later to replace. With the partial absorption of the root of an old tooth, the new one, by moving to the centre of the alveolus, directly beneath the old tooth, would gain a position more advantageous for pressure against the tooth, and at the same time make room for the formation of the succeeding germ.

The old teeth were lost alternately to some extent, a provision by nature by which large gaps in the dental series were avoided. This is well shown in the type specimen [Fig. 41 here] where the side teeth in full use seem to alternate regularly with the new ones incompletely protruded.

This last statement provides a key for estimating the relative age of each tooth in the jaw. The old tooth was lost when the tip of the new tooth was near the level of the alveolar wall. Several teeth in each wave seem to be

Fig. 40. Frontal section through the right maxilla of *Gorgosaurus libratus*, N.M.C. 8961.

Fig. 41. Right upper jaw of *Gorgosaurus libratus* N.M.C. 2120.
a. Occlusal view. b. Labial view.

less than full grown, so that a series which increases in size towards the rear of the jaw is always present. In the accompanying graphs the height of the replacement tooth is shown as a fraction of its possible height in its particular area of the jaw. When the sizes of these teeth are plotted on a graph, the resulting pattern is the same as that obtained for most other reptiles, i.e., the youngest teeth in each wave are to the front of the jaw.

Figure 41 shows the pattern in both dentary and maxilla of Lambe's type of *Gorgosaurus libratus*, N.M.C. 2120. In the right maxilla all the odd-numbered teeth appear intact, although a section or X-ray photograph would probably reveal the presence of replacement teeth. Tooth 2 is also superficially intact, although probably about to be shed. In position 4 the old tooth has been lost and the young replacement is just visible over the wall of the alveolus. Teeth 6, 8, 10, and 12 form a good series of increasing size and age. In the right dentary the condition is similar. The odd-numbered series shows the last part of one wave and the beginning of the next, and the even-numbered series contains almost a complete wave.

Numerous other specimens such as the famous skull of *Tyrannosaurus rex* Osborn, A.M.N.H. 5027 (Fig. 42d), show similar patterns. All four jaw quadrants of this specimen are illustrated in Figure 43. Osborn (1912)

Fig. 42. Dentitions of saurischian dinosaurs

a. *Proceratosaurus* (*Megalosaurus*) *bradleyi* Woodward. Restoration of skull. After Huene.

c. *Tyrannosaurus rex*, A.M.N.H. 973, Lingual view, left maxilla. After Osborne.

b. *Plateosaurus trossingensis*, A.M.N.H. 6810, L.L. jaw. After Brown and Schlaikjer. (Figure reversed)

d. *Tyrannosaurus rex*, A.M.N.H. 5027, left side of skull. After Osborne.

e. *Tyrannosaurus rex*, A.M.N.H. 973, transverse section through right dentary. The lingual side is on the right. After Osborne.

also figures the left dentary and maxilla of *T. rex*, A.M.N.H. 973. In the dentary of this specimen, not illustrated, teeth 3, 5, and 7 form an excellent series increasing in size towards the rear. Tooth 9 is missing. Tooth 11 is very small, indicating the beginning of a new cycle. Teeth 2, 4, and 6 are all full size, 8 is small, 10 is missing, and its replacement is also lost, and 12 is fairly large, but not fully grown. Both series thus show good replacement waves. The maxilla (Fig. 42c) provides a similar picture.

Tyrannosaurus rex, A.M.N.H. 5866, was described and illustrated (as *Dynamosaurus imperiosus*) by Osborn 1905. This specimen, like A.M.N.H. 5027 and 973, shows a clear picture of the wave pattern (Fig. 43f). Abel's (1927) illustration of *Proceratosaurus* (*Megalosaurus*) *bradleyi* (Fig. 42a here) and Gilmore's (1920) illustration of *Ceratosaurus nasicornis*, U.S.N.M. 4735, were both analysed graphically (Fig. 43) and confirm the wave pattern seen in other carnosaurs.

A jaw described originally as *Zanclodon cambrensis* Newton was re-described by von Huene in 1908, who considered it conspecific with *Plateosaurus cloacinus* Quenstedt. The specimen is well preserved and shows teeth in many stages of replacement. Two out-of-phase waves are present, with wave progression from back to front. The systematic position of the specimen is uncertain, but it is probably a carnosaur. *Zanclodon* is synonymous with *Teratosaurus*, and Schmidt (1928) places the specimen in the Carnosauria.

One of the most spectacular preparations showing tooth replacement in carnosaurs is the right maxilla of *Antrodemus*, Princeton University Museum 16554-9 (Fig. 44). The lingual walls of most of the tooth positions have been carefully removed, revealing the bases of the old teeth and the developing replacements. In every case where an old tooth is established, a well-defined cavity has been resorbed in the lingual wall of the base, this being partially occupied by the replacement tooth.

Numbering from the anterior of the maxilla, teeth 1 and 3 are well established and have resorption pockets and replacement teeth, that in 3 being larger than that in 1. At position 5 the old tooth has been lost, leaving a well-defined alveolus containing a replacement which would not be visible above the gum-line in life. At position 7 there is a small replacement projecting above the alveolar rim. The ninth alveolus bears a young tooth about half its definitive height. The eleventh and twelfth alveoli are damaged, but despite the loss of the tooth at this position, we can assume from the size of its replacement that it was at least as large, and probably larger than tooth 9. Thus, there is a clear-cut wave passing from back to front in the odd-numbered series.

There appears to be less replacement activity in the even-numbered series, with each tooth having resorption cavities and two generations of replacements, all of about the same relative size. In most positions in both series three generations of teeth can be seen.

This specimen was first mentioned in the literature by Stokes (1945) who wrote, "Although the potential number of teeth was evidently very high, replacement was not haphazard, but took place in a definite order.

1 3 5 7 9 11 13 15

a.

b.

c.

d. M

e.

f.

1 3 5 7 9 11 13 15 17 19

g. M

h.

i.

j. M

k.

l. M

Fig. 44. Lingual view, right maxilla of *Antrodemus* sp.
Princeton University Museum No. 16554-9.

Fig. 43. Diagrams of the dentitions of carnosaurian dinosaurs.

- a. *Gorgosaurus libratus*, N.M.C. 2120, right maxilla.
- b. *Tyrannosaurus rex*, A.M.N.H. 5027, U.L. jaw.
- c. *Tyrannosaurus rex*, A.M.N.H. 5027, L.L. jaw.
- d. *Proceratosaurus bradleyi*, N.M.N.H. 4680, L.R. jaw.
- e. *Teratosaurus suevicus*, left maxilla.
- f. *Tyrannosaurus rex*, A.M.N.H. 5866, L.L. jaw.
- g. *Gorgosaurus libratus*, N.M.C. 2120, L.R. jaw.
- h. *Tyrannosaurus rex*, A.M.N.H. 5027, U.R. jaw.
- i. *Tyrannosaurus rex*, A.M.N.H. 5027, L.R. jaw.
- j. *Proceratosaurus bradleyi*, B.M.N.H. 4680, U.R. jaw.
- k. *Megalosaurus bucklandi*, U.R. jaw.
- l. *Ceratosaurus nasicornis*, U.S.N.M. 4735, left maxilla.

Each tooth had next to it on either side, either a young tooth coming into use or an old tooth about to be shed. *Antrodemus* was theoretically never left with a gap of more than one tooth space on each maxilla and dentary at any one time, and each gap was flanked by functioning teeth of the next series. The process was continuous: excavations in the jaws have revealed three sets of teeth in addition to the two sets in use." The present author wishes to thank Dr. Glenn Jepsen of Princeton for permission to illustrate and describe this fine specimen.

To reveal more details in the carnosaur replacement cycle, a maxilla of *Gorgosaurus* sp., N.M.C. 8961, was sectioned and peels made (Fig. 40). The first (anterior) tooth is accompanied by a moderate-sized replacement which has not yet entered its pulp cavity. The third alveolus contains a single young tooth, probably elevated just slightly above the alveolar border. Tooth 5 is in about the same stage as tooth 3. The seventh tooth is larger than teeth 3 or 5 and has a small replacement lying near its lingual wall.

The concavity of the lingual wall, mentioned above by Lambe (1917) has developed in teeth 9 and 11, and the replacements for these teeth can be seen lying near these surfaces. The replacement for tooth 11 is much larger than that for tooth 9, but has not yet entered its predecessor's pulp cavity.

The thirteenth and last alveolus of the jaw contains a young replacement and part of the wall of its predecessor. The replacement corresponding to that in position 11 has entered its predecessor's pulp cavity and destruction of the old tooth has proceeded, so that only part of its labial wall remains at the level of the section.

The even-numbered series is equally informative. The contents of position 4 are disorganized but it seems clear that teeth 2, 4, and 6 represent replacements of increasing size lying in alveoli with no traces of either old teeth or other replacements at the level of the sections. No doubt replacement teeth were developing, at least in alveoli 4 and 6. In alveolus 8 a moderately advanced replacement has just invaded its predecessor's pulp cavity. A more advanced stage of this process is seen in tooth 10, in which about half of the old tooth at the level of the section has been absorbed.

Alveolus 12 contains a large replacement tooth, probably nearly full-grown. This is the first member of its wave to become functional. Thus, in both the odd- and even-numbered series in this jaw there are excellent waves of replacement proceeding from back to front.

In the frontal section described above, many of the alveoli appear to have had bony crypts in which the replacement teeth developed before migrating into their predecessors' pulp cavities. Cawston (1943) mentions a similar cavity in a sectioned jaw of *Gavialis gangeticus*. As in *Gorgosaurus*, this crypt lies lingual to the functioning tooth and contains the younger replacement teeth during their early development. With growth, the replacements apparently migrate towards the wall of their predecessors, leaving space for their own replacements to develop in the crypt.

The only good specimen representing this group available to the writer was *Plateosaurus trossingensis*, A.M.N.H. 6810. The excellent skull has been thoroughly prepared and shows several teeth in the process of replacement. In the left premaxilla (not illustrated) teeth 1, 3, and 5 are mature and full size. Teeth 2 and 4 are each about half-grown while tooth 6 is about seven-eighths grown. The even-numbered series thus shows part of the leading edge of a wave progressing cephalad. No obvious replacement is occurring in the odd-numbered teeth.

The lower left jaw (Fig. 42b) also shows several teeth being replaced. Almost all of the twenty-two teeth are fully erupted, with their tips at about the same level. However, many of the tips appear to be badly worn although others were fresh and still showed fine serrations. Neither the order nor the arrangement of these unworn teeth is random. Tooth 1 is fully grown but is broken. Teeth 3, 5, and 7 show increasing amounts of wear. At position 9 the old tooth is lost and its replacement is about half-erupted. This is the most anterior visible member of a new wave. Tooth 11 is fully erupted but shows very little wear, indicating that it is the first member of its wave to become mature. All of the succeeding odd-numbered teeth are worn, having been in function for a considerable time. This series thus contains the posterior end of one wave ending at tooth 7, and a succeeding wave with its leading edge at position 9.

In the even-numbered teeth in the same jaw there is a similar sequence. Teeth 2 and 4 are worn, but 4 bears a replacement tooth lying in a depression in its lingual side, the crown protruding about 5 mm. above the alveolar margin. It is difficult to tell if the base of the old tooth has been resorbed at this point. The situation is reminiscent of that in *Hesperosuchus*, in which the replacement probably lies in a depression in the old tooth, but in either case the replacement tooth may have been pushed into the old tooth by pressure during its entombment. It is conceivable that the inner surface of the pulp chamber of the tooth being replaced may have been resorbed, producing a thinner wall which could be more easily crushed. At position 6, the old tooth has been lost and its replacement is almost completely erupted, although its tip has not quite reached the occlusal plane. The succeeding teeth appear to be worn, but many of them are poorly preserved.

This jaw illustrates the manner in which waves of replacement are arranged so that neighbouring teeth at any point in the jaw are in opposite phases of replacement. One wave is passing along the odd-numbered series with tooth 9 at its head, and the even-numbered series has a wave beginning at tooth 4. From this study of one well-preserved skull, we can determine that the method of replacement of an individual tooth is similar to that described for *Hesperosuchus*, with the replacement tooth lying lingual to, but not within, its predecessor. Similarly, the sequence of replacement is the same as that seen in most other reptiles.

Despite the fact that skeletons of these dinosaurs are not uncommon, very few skulls are known, and skulls with good dentitions are rare indeed. Jahnensch (1935) illustrated several jaws of *Brachiosaurus brancai*, many of which showed complete tooth rows with no signs of replacement activity. In a few cases, however, replacement was evident by the presence of a few unworn teeth, not completely erupted, which were just entering the functioning stage. Jahnensch measured the degree of wear on the apices of the teeth of several jaws. A definite indication of alternate replacement was seen, with a suggestion of back-to-front wave progression. Because of the nature of the material and the type of measurement which had to be used, the picture was not as clear-cut as might have been desired, but there was no doubt of the presence of the same alternating tooth replacement as seen in the theropods.

One jaw of *B. brancai* illustrated by Jahnensch (Fig. 45b here), and probably belonging to Jahnensch's skull T-1, shows an excellent series of replacement stages. The odd-numbered teeth all appear to be in a fully functioning condition. Maxillary teeth numbers 2 and 4 represent the last teeth of an old wave, and teeth 6, 8, and 10 form a series increasing in size towards the rear. In most other specimens of Jahnensch's series young teeth appeared only rarely; presumably the end stages of the replacement process are rapid. In the illustrated specimen some unusual condition has caused premature loss of the old functioning teeth in alveoli 6, 8, and 10, permitting us to see the replacements which would ordinarily have remained hidden.

Fig. 45. Dentitions of sauropod dinosaurs.

- a. Section through the 4th maxillary tooth of *Diplodocus longus*. After Marsh.
- b. Reconstruction of the skull of *Brachiosaurus brancai*. The maxilla is from 'Schadel 1' of Jahnensch. After Jahnensch.

Details of the earlier stages of replacement are seen in Figure 45a, the well-known section of a *Diplodocus* maxilla by Marsh (1896). The large space in the bone on the lingual side of the base of the functioning tooth is the site of development of numerous replacement teeth, in this case five. Judging from the size of the largest replacement tooth, it is apparent that very little growth took place once the old tooth was lost and the new one assumed a functioning position. This agrees with the observation above that very few teeth of less than full size were seen in the well-preserved jaws studied. Although the dentition of the sauropod dinosaurs appeared weak, it obviously possessed an excellent replacement mechanism.

The method of replacement of individual teeth in the sauropods differs from that of their theropod ancestors since there is no indication that the replacement tooth grows within the old tooth, either in a resorption pocket or within the pulp chamber. Presumably the old tooth drops out, and the new tooth which has become fairly large, moves labiad into the vacated position, completes its growth and becomes functional. This is the method of replacement seen in those ornithischians without highly specialized dental batteries, and also in *Plateosaurus* described above. The order of replacement seems to be the same as that in the other dinosaurs.

*Class Reptilia**Subclass Archosauria**Order Ornithischia*

The evolution of the dentition of the Ornithischia is an interesting study in itself. Dental patterns vary from the simple conditions seen in hypsilophodonts or ankylosaurs to the great dental batteries of the hadrosaurs and ceratopsians. The relationships of the ornithopods as revealed by a study of individual tooth replacement methods and replacement patterns, agree closely with the phylogenetic arrangement accepted by most authors. Romer's classification (1945) will be used here. Three evolutionary levels can be distinguished in the dentitions of ornithischians.

(1) That seen in the Ankylosauria, Stegosauria, Hypsilophodontidae, and Troodontidae shows little basic change from the pattern seen in the thecodont ancestors. The form of the tooth has changed, the conical crown being replaced by an anteroposteriorly expanded cutting blade, and the replacement tooth is always found lingual to the old tooth, never within its pulp chamber. The teeth are more or less widely spaced, and each has a long cylindrical root set, in most forms, in an individual socket. *Geranosaurus* of the Upper Triassic of South Africa is very poorly known, but probably had teeth of this type.

(2) From these primitive forms, the trend was for a greater expansion of the leaf-like crown, resulting in an elongation of the enamelled triturating portion and a crowding together of the teeth, both horizontally and vertically. The number of teeth per vertical series, however, remained two, one functional tooth and its replacement. *Camptosaurus* of the Upper Jurassic is an example of this type, and such primitive ceratopsians as *Protoceratops* and *Leptoceratops* probably belong here as well.

(3) The culmination of this process of evolution is seen in the famous dental batteries of the Hadrosauridae and Ceratopsidae of the Upper Cretaceous. In these, the individual teeth became building blocks in a larger unit, with each tooth interlocked with its neighbours. The whole battery thus functioned as a single, complex, and highly efficient unit.

Material for the study of many groups, especially the earlier ones, is scarce, and in some cases altogether lacking. The geologically oldest genera for which adequate material is available are *Stegosaurus* and *Camptosaurus* from the Upper Jurassic. The next oldest are *Hypsilophodon*, and *Iguanodon*, which are lower Cretaceous. *Hypsilophodon* in many respects, including its dentition, actually appears to be more primitive than *Camptosaurus*. The dentition of *Stegosaurus* is not unlike that of *Hypsilophodon*, except that it is weaker and the teeth are smaller, less closely packed, and on (proportionately) longer and thinner roots. The vast majority of known ornithischians are from the Upper Cretaceous, at which time we find representatives at every stage in the evolution of the ornithischian dentition.

SUBORDER ORNITHOPODA

Family Hypsilophodontidae

The dentition of this family is adequately known for only two genera, *Hypsilophodon* and *Thescelosaurus*, and even for these we do not have a complete dentition, although individual teeth and short series are known. Swinton (1936) described the best available *Hypsilophodon* material and illustrated several jaw fragments. Unfortunately only a few replacement teeth remained *in situ*, insufficient to show the replacement pattern. The individual teeth are roughly similar to those of *Stegosaurus* in size and shape, differing from them only in details. Each has a cylindrical root bearing a laterally compressed crown with flutings and a crenate cutting edge.

Parks (1926) described an Upper Cretaceous dinosaur which he assigned to the genus *Thescelosaurus*. This was transferred to a new genus *Parksosaurus* by Sternberg (1940). The form of the teeth in this specimen is similar to that in *Hypsilophodon*. Unfortunately, this specimen, R.O.M.Z.P. 5202, is not well preserved, and is mounted in the exhibition gallery with its jaws firmly closed. Parks states that "there is distinct evidence, best shown on the right side, that the teeth arose alternately; shorter teeth with the crown diagonally worn down alternate with longer teeth in which the crown is practically intact."

The description of *Thescelosaurus edmontonensis* by Sternberg (1940) adds a few more details to our knowledge of hypsilophodont dentition. "Ten germ teeth are present in the left dentary, but no functional tooth remains in place. Nineteen loose teeth were found . . . near the left mandibular ramus end . . . there is no question that all belong to the same individual. Four of the loose teeth . . . resemble the premaxillary teeth of *Troödon validus*." The dentition illustrated in the evolutionary scheme (Fig. 46) is based on this specimen, N.M.C. 8537, but is not necessarily accurate in detail, since it is intended only to show the general aspect of the dentition and the replacement pattern.

An examination of the arrangement of the germ teeth in the left dentary of Sternberg's specimen indicates that the basic pattern was identical to that

seen in other ornithischian dinosaurs. Apparently only two teeth were present in each vertical series, one in use and a replacement lying lingual to it. In a few places it is possible to trace sequences over two or three alternately numbered tooth positions. In each case the more posterior teeth are more fully erupted than are the anterior ones; this is the condition seen at the leading edge of a replacing wave in most other reptiles.

The method of replacement of individual teeth is not known in any detail. Hulke (1882) described a jaw of *Hypsilophodon* as follows, "The successional teeth are evolved in cavities at the inner side and intermediately of those in wear." The writer assumes that the latter part of this statement to mean "between those in use." This description suggests that the condition is similar to that seen in the Stegosauria or Ankylosauria. In these the replacement teeth developed in pockets lying lingual to the true alveoli and probably continuous with them beneath the surface of the dentary. The replacements erupted through openings resorbed in the dentary somewhat lingual to the true alveoli, then migrated towards the alveoli, the temporary eruption openings finally becoming confluent with them. On the other hand, the replacement teeth may have erupted within the boundaries of the true alveoli, tight against the functional teeth. The latter method is the one illustrated in the evolutionary scheme (Fig. 46).

Since numerous intact detached teeth were found with the relatively edentulous jaw of *Thescelosaurus edmontonensis*, N.M.C. 8537, it appears that the teeth of this dinosaur were not retained by ankylosis but by soft tissue which, upon post mortem maceration, allowed the teeth to fall out. Probably old worn teeth were cast off by a loosening of this connective tissue, there being little or no degradation of tooth substance. The crown was worn down but the remainder of the tooth was probably shed relatively intact.

From the fragmentary remains of these three genera of hypsilophodonts we can tell that tooth replacement occurred in a pattern of waves passing cephalad along alternately numbered dental series. Implantation was thecodont and without ankylosis. Replacement probably involved discarding of the large root and the remainder of the crown with little degradation.

Family Iguanodontidae

The dentition is adequately known in only two genera of iguanodonts, *Camptosaurus* and *Iguanodon*. As shown in the dental evolutionary scheme (Fig. 46), the iguanodonts form an excellent transitional group between the hypsilophodonts and the hadrosaurs. The difference lies mainly in the form and method of retention of the teeth.

The crowns of iguanodont teeth (Fig. 6) are longer, thicker, and relatively narrower than are the leaf-like crowns of the hypsilophodont teeth. In arrangement and method of replacement they are identical. There are never more than two teeth in each vertical series. These are arranged in a perfectly alternating pattern, with a wave of replacement passing along each alternately numbered series in all specimens studied. This is seen in several

Fig. 46. Scheme suggesting possible lines of evolution in dental structures of ornithischian dinosaurs.

specimens of *Camptosaurus* illustrated by Gilmore (1909), such as Y.P.M. 1886, left dentary and left maxilla of *Camptosaurus* sp., and Y.P.M. 1884, left dentary of *C. medius*. The illustrations of *Iguanodon bernissartensis* Dollo and *I. atherfieldensis* Hooley (Fig. 47, a and c) also show excellent alternation and waves. It is surprising that Gilmore (1909) wrote, "None of the camptosaur jaws studied show the regular arrangement of teeth found in *Iguanodon* as figured by Dollo 1883."

The wave pattern in each indicates perfect back-to-front progression. The poorly preserved jaw of *I. atherfieldensis* described by Hooley (1925) and shown in Figure 47a shows only the younger members of each vertical series, but they illustrate the presence of waves even better than the well-preserved *I. bernissartensis* jaw in Figure 47c.

The teeth of hypsilophodonts are set in more or less discrete sockets. Those of iguanodonts are in such close contact that they tend to lie in a continuous groove, with probably only the roots in separate alveoli. The dentition of *I. bernissartensis* (Fig. 47c) superficially resembles that of a

Fig. 47. Dentitions of ornithopod dinosaurs.

- a. Lingual view, right dentary of *Iguanodon atherfieldensis*. After Hooley.
- b. Lingual view of left lower jaw of *Camptosaurus medius*, Y.P.M. 1886.
- c. Lingual view of left lower jaw of *Iguanodon bernissartensis*, individual 3A3, Royal Museum of Natural History. Belg. After Dollo.
- d. Transverse section through the jaws of a typical hadrosaurian dinosaur. After Lambe.
- e. Lingual view of the dental battery of *Corythosaurus* sp. R.O.M.Z.P. 1933.

hadrosaur, but close examination reveals that the teeth are independently affixed to the jaw. The development of a dental battery relies on the interdependence of all the teeth, so that each tooth is supported and retained by its neighbours.

Family Hadrosauridae

Probably the best-known example of dental specialization in fossil reptiles is that furnished by the hadrosaurian dinosaurs. They differ from their iguanodont ancestors in that the number of teeth per vertical series and the number of series per jaw are usually increased, and most important of all, the form of the teeth is modified so that each interlocks with its neighbours on all sides to form a single composite unit, the dental battery. In the hypsilophodonts and iguanodonts each tooth position is represented by only one functioning tooth and a single replacement. In the hadrosaurs up to six or seven teeth per position is not uncommon, and there may be fifty such series per jaw.

The simplest hadrosaurian dentition seen in this study was in *Bactrosaurus johnsoni*, a lambeosaur from the Iren Dabasu formation of Mongolia (Gilmore, 1933). These jaws, many of which were juveniles, possessed teeth of typical hadrosaur form united into an efficient dental battery. The number of teeth per vertical series was low—only two or three, and there were only between sixteen and twenty-three such series. In the iguanodonts, as we have seen, there may be roughly the same number of teeth in about the same arrangement. Usually in iguanodonts, such as *Iguanodon bernisartensis* there is a regular alternation of those tooth positions bearing one tooth with others bearing two teeth. Thus, if the odd-numbered positions have only one tooth per position, the even-numbered ones will each have two teeth. Each even-numbered position will be occupied by one tooth in use and one small replacement, whereas each odd-numbered position has a single advanced replacement. In this way, each odd-numbered tooth is surrounded by four teeth, an old tooth and a small replacement on each side. This is superficially the same as the arrangement in hadrosaurs. The main difference is that in the iguanodonts each tooth contributes little to the support of its neighbours. In contrast, in the hadrosaurs, the root of each tooth has developed an angular orientation to the long axis of the vertical series so that it is anchored not merely in the soft tissue of the alveolus but by contact with the other teeth. Often several generations of teeth are present at each position so that each tooth is held in place not only by the crowns and roots of the two teeth on each side, but by the crowns and roots of its predecessor and successor. This is partly shown in Figure 47d. Because of the mathematical precision of the alternation of elements in the odd- and even-numbered series, and the crowding together of individual teeth, the resultant pattern is a modified hexagonal mosaic. This is seen in the enamelled faces of the dentary teeth (Fig. 47e or Fig. 46) and also at the occlusal plane (not illustrated) where wear has ground sections across the functional crowns and the roots of other teeth whose crowns have been worn away. In Figure 47d it will be seen that two teeth in each vertical series are in use; one crown and the roots of at least one of its predecessors. The interlocking of the individual roots and crowns is so efficient that even the tips of the roots are retained.

If the teeth of a single, alternately numbered tooth series are traced along the jaw, this series will be seen not to lie parallel to the long axis of the jaw, but to slope occlusad towards the rear of the jaw (Fig. 47e). The more posterior members of each generation apparently developed and came into function before the more anterior members, thus forming a pattern of waves as in other reptiles. The difference here is that every tooth is worn down from above, practically to the tip of its roots, while in most other reptiles most of the tooth is discarded after a period of use. There is no loosening or resorption of the old tooth in the hadrosaurs. As the crown of a tooth is worn away, the crown of its successor is exposed and functions along with the remaining root of the old tooth. Practically every bit of every tooth is used up in the chewing process. This system is a most efficient one in the economical use of dental substance.

The left dentary of a juvenile of *Bactrosaurus johnsoni*, shown in Figure 46 is probably the smallest of the series described by Gilmore (1933, p. 61). "Study of the present series of maxillae and dentaries, most of which have full dental complements, showed clearly that in the Hadrosauridae the number of vertical tooth rows increases with the age of the individual from young to adult. In the smallest dentary of the series there are 16 rows; a little larger one shows 17 rows, and in the largest, supposed to be an adult, 23 rows can be counted. The smallest maxillary has 17 rows; a slightly larger one 18 rows, and the largest 28 rows. It is also observed that the teeth increase in size from young to adult. . . . There were probably never more than three teeth in any one vertical series in the dentary and not more than two in juvenile specimens. Never more than two teeth appear on the triturating surface of any one vertical row."

The presence of replacing waves is obvious in the illustrated dentary of *Bactrosaurus* (Fig. 46) in which the teeth of one wave are shown shaded. Another example is in *Mandschurosaurus monogoliensis*, A.M.N.H. 6551, figured by Gilmore (1933), but not illustrated here. This jaw of a small hadrosaurine form is similar to that of *Iguanodon* shown in Figure 47c, with most of the functional teeth lost and the alternately numbered replacements forming a step-like pattern increasing in size towards the rear. These, of course, are cephalad waves.

The Mongolian forms fit so well into an evolutionary scheme between the iguanodonts and the more familiar hadrosaurs that we must not forget that they are not necessarily ancestral to the well-known North American duckbills. The exact age of the Iren Dabasu formation is uncertain; it may be contemporaneous with the North American Oldman or Edmonton formations. For our purposes, however, *Bactrosaurus* and *Mandschurosaurus* may be considered as illustrating a stage in evolution passed through by the immediate ancestors of such forms as *Kritosaurus* or *Anatosaurus*. Gilmore (1933) sums up the situation as follows: "In composition, implantation and manner of succession, the teeth of *Bactrosaurus* conform fully to the usual arrangement in the Hadrosauridae." We must add that they differ from the common North American Upper Cretaceous forms only in the number of elements incorporated both vertically and horizontally into their dental batteries. They are definitely more advanced than the iguanodonts in that they have consolidated the individual teeth into a dental battery.

The possible number of teeth in a hadrosaur jaw has been the subject of much controversy. A statement frequently made in the literature is that there may be over two thousand teeth in the mouth of a hadrosaur. The writer has yet to see such a specimen or even a reference to the original statement. It was probably made in a popular article by an early collector or student. Cope (1883) described a lower jaw of *Anatosaurus copei* with 460 teeth, probably the highest count supported by a cited specimen. A left dentary of *Trachodon* sp., U.S.N.M. 4808, bears about 280 to 300 teeth, which is a higher than average count.

The total number of teeth in a complete dentition is often obtained by

counting the number of teeth in a dentary and multiplying by four. The inner alveolar wall of a hadrosaur dentary is very thin and often missing (Fig. 47d), thus revealing the enamelled surfaces of the teeth and making counting easy. In the maxillae the successional teeth are hidden so that it is impossible to tell the number of teeth per vertical series except by destructive preparation. Examination by the writer of a few broken maxillae suggests that there may be fewer teeth per vertical series in the maxilla than in the dentary. The same observation was reported by Gilmore (1933). Obviously, an accurate count of the total number of teeth in a hadrosaur is impossible without examination of sections of the maxilla.

Typical of hadrosaurian jaws is a row of near-circular foramina on the lingual side, running sub-parallel to the alveolar margin. The function and evolutionary history of these has been described by Edmund (1957). Dissection shows that the foramina lie directly opposite the bases of the vertical tooth rows, and there seems little doubt that they serve as routes either for the migration of very young teeth produced outside of the alveolus by the dental lamina, or for the admission of dentigerous processes of the lamina itself. A similar phenomenon is seen in several cases in which the bases of the teeth are set deeply into the alveoli but are not accompanied by the dental lamina. The connections between the lamina and the sites of later development of the teeth remain but the high lingual alveolar wall has grown around them, leaving the foramina.

Briefly, the dentition of the hadrosaurs is characterized by several teeth (usually three or more) in each vertical series, and a large number of vertical series per jaw. The teeth are packed closely together to form a compact dental battery, the shape of each crown and root being modified so as to interlock and retain practically every part of each tooth until it is worn away. There is no loosening or erosion of the base, merely a wearing away from the crown to the root. Alternation of teeth is maintained with mathematical precision because each element is firmly locked into a hexagonal mosaic. The plane of each horizontal series is tilted with respect to the long axis of the jaw, resulting in a pattern of back-to-front waves as seen in other reptiles.

Family Troodontidae (Pachycephalosauridae)

The only specimen of this family studied was a cast of the well-preserved skull of *Stegoceras validus*, no. 2 in the University of Alberta collection (Gilmore, 1924). Although the cast is of the highest possible fidelity, the fine details needed for this study are inherently lacking, and the illustrations of the original do not contribute any specific information not derivable from the cast. However, the cast of the right maxilla shows such features as size and the amount of wear and degree of eruption of the teeth, thus enabling us to determine the replacement pattern with reasonable certainty. Because the specimen was inadequate it is not illustrated here. However, in the evolutionary scheme (Fig. 46) a reconstructed dentition of *Stegoceras* is shown with the conditions of the teeth essentially the same as in the speci-

men. The replacement pattern is similar to that in the other ornithopods, with waves passing cephalad along alternately numbered tooth series.

The method of replacement of individual teeth is interesting, though not fully understood. The teeth are similar in form to those of the ankylosaurs and not unlike those of the stegosaurs or even the hypsilophodonts. Each tooth consists of a long cylindrical base or root, and an expanded, laterally compressed crown. A row of foramina is present on the lingual alveolar wall, running sub-parallel to the alveolar margin. Presumably the replacement teeth were formed in crypts behind these foramina.

Because of the inadequate material, no early stages in the replacement process could be seen. The crown of an advanced replacement was seen breaking through the inner alveolar wall at or near the base of an old tooth. Eruption through the inner alveolar wall occurs in the ankylosaurs and stegosaurs and may well occur in the troodonts as well. Probably the old tooth became loosened and dropped out once its successor's crown had erupted, permitting the replacement to enter the alveolus and become established. That growth continued for a while is shown by the presence of obviously unworn replacement teeth which have not reached the occlusal plane.

SUBORDER STEGOSAURIA

The dentition of *Stegosaurus* is remarkably similar to that of the hypsilophodonts and also has many points in common with the *Troodontidae* and *Ankylosauria*. It is generally believed that some of the hypsilophodonts are ancestral to the other three groups, and we can therefore consider this type of dentition as a retention of a primitive characteristic. Perhaps the mode of life or type of food readily available did not require the evolution of a very different type of dentition. Apparently the hypsilophodonts and troodonts filled similar ecological niches and hence did not require greatly different dentition. Moreover, it is likely that the Jurassic stegosaurs were replaced ecologically in the Cretaceous by the ankylosaurs.

Gilmore (1914) described the dentition of *Stegosaurus* as follows: "The teeth are held in distinct sockets. Those worn out or lost through accident are replaced by germ teeth developed in cavities within the jaw. Specimen U.S.N.M. 4934 shows quite clearly the relationship of germ and functional teeth [Fig. 48d here]. The crown of the germ tooth lies in the inside of the base of the functional tooth, the crown resting on the root of the old one, and as usual among the dinosaurs, ascends or descends according to whether it is in the upper or lower series. It appears that there are not more than two teeth in a vertical series."

This specimen, *Stegosaurus stenops* Marsh, U.S.N.M. 4934, is the only one known to the writer in which the dentition is adequately preserved. Even in it only about ten tooth positions are retained intact. Figure 48d, a right maxilla, illustrates the order of tooth replacement. Teeth 1, 3, 5, and 7 form a series increasing in degree of eruption toward the rear. Position 9 is now empty, but a replacement was about to enter the alveolus. Small replacements were developing alongside teeth 5 and 7 as well. Positions 2,

Fig. 48. Dentition in ankylosaurian and stegosaurian dinosaurs.

- a. Lingual view, right maxilla of *Edmontonia rugosidens* R.O.M.Z.P. 1215.
- b. Part of the left maxilla of *E. rugosidens* R.O.M.Z.P. 1215.
- c. Occlusal view, right maxilla of *E. rugosidens* U.S.N.M. 11868. After Gilmore.
- d. Lingual view, right maxilla of *Stegosaurus stenops* U.S.N.M. 4934. After Gilmore.

4, 6, 8, and 10 also show an excellent graded series, again with the younger members to the front. Thus, there was unquestionably an alternation of odd- and even-numbered teeth, with the waves of replacement proceeding from back to front.

Two excellent specimens of ankylosaurs are available for this study, *Edmontonia rugosidens*, R.O.M.Z.P. 1212, and ? *Euoplocephalus* sp., R.O.M.Z.P. 1930.

At first glance the dentition of the ankylosaurs seems to be as peculiar as the appearance of the animals themselves. The tooth rows are restricted to the narrow margins of the maxillae and dentaries, with only about fifteen tooth positions per bone. The teeth are simple in structure; a sub-triangular crown with a well-defined cingulum is borne on a long cylindrical root. A row of foramina herein called the replacement foramina lies about 6 mm. below the lingual alveolar border, with one foramen beneath each tooth (Fig. 48a and b).

Tooth replacement begins with the appearance of the crown of a young tooth in the cavity behind a replacement foramen. In the early stages the foramen is fairly small, about 2 to 3 mm. in diameter, the larger foramina being associated with the larger functional teeth. The replacement tooth develops within the lingual alveolar wall in a bony crypt lingual to the true or functional alveolus and possibly confluent with it, as in the carnosaurs. During the earlier stages at least, the growth of the young tooth is such that the base of the crown remains near the level of the foramen.

Eruption through the lingual alveolar wall usually takes place above the foramen and below the margin of the true alveolus. In one instance (the second tooth in Fig. 48b), a shallow but definite depression was seen at a point where the eruption of a crown was expected to occur, suggesting that osteoclastic action was taking place from the outside as well as from the inside of the cavity in which the tooth was developing. The tip of a crown appears at the opening thus formed, as shown in tooth 6 in Figure 48a. The opening thus formed will be called the eruption opening.

The replacement tooth within its special crypt, similar to the "accessory alveolus" seen in the plesiosaurs, continues to increase in size and moves towards the functioning position. Loss of the old tooth, probably from loosening of the connective tissue, takes place at this stage and the new tooth gains access to the functional alveolus by resorption of the bar between the eruption opening and the alveolus itself. The edentulous jaw of *E. rugosidens* in Figure 48c shows three positions in which eruption openings lie alongside alveoli, and also two positions (14 and 16) in which the openings have become confluent. There is some variability in the formation of eruption openings. In some cases the crown of the replacement erupts through the foramen itself rather than through a separate new opening in the alveolar wall (e.g. tooth 7, Fig. 48b).

That growth of the replacement tooth continues after it enters the alveolus is shown by the finding of obviously new teeth with their tips not half-way between the level of the alveolar margin and the occlusal plane. The wall of the alveolus is rebuilt externally to its resting stage, and at about this stage a new crown appears within the replacement foramen.

The pattern of tooth replacement seen in the ankylosaurs is the same as

that in other dinosaurs. In the right maxilla of *E. rugosidens*, R.O.M.Z.P. 1215 (Fig. 48a), there are obvious waves passing cephalad along alternately numbered tooth series. Position 1 bears an old, broken tooth and a small replacement is visible at its replacement foramen. Tooth 3 is also badly worn and is accompanied by a replacement larger than that at position 1. Tooth 5 is very badly worn, but its replacement has apparently erupted through the replacement foramen which in turn has become confluent with the alveolus. The crown of this replacement is nearly full grown. Position 7 is empty, the old tooth probably having been lost *pre mortem* and the new replacement lost *post mortem*. Tooth 9 has not yet reached the occlusal plane and is unworn. Tooth 11 is similar to tooth 9. Tooth 13 is somewhat older, but has not yet reached the occlusal plane. Positions 15 and 17 are empty, no doubt as the result of *post mortem* maceration.

The growth of another generation of teeth in the odd-numbered series can be easily traced. At position 5, there is no trace of a replacement foramen. At position 7 the lingual wall of the alveolus bears an emargination, indicating the point where it became confluent with the eruption opening. A very small replacement foramen is present, suggesting that at least in some cases this structure may be reduced during the replacement process and must be regenerated. There is a progressive increase in the size of the replacement foramina at positions 9, 11, and 13. Although the functional and replacement teeth have been lost at position 15, the replacement tooth has apparently erupted through an eruption opening, the latter, as suggested by its elongate shape, having become confluent with the replacement foramen. At position 17 the replacement tooth has obviously become functional following the loss of its predecessor. There is, however, no trace of the replacement foramen, suggesting that the replacement foramina may be produced when needed to admit germ teeth being budded off the dental lamina lying alongside the alveolar wall.

The even-numbered teeth in the same jaw also show a clear wave pattern. The teeth from positions 2 and 4, have been lost, but apparently they were advanced replacements which had not become well established by the time of the animal's death. Tooth 6 is almost unworn, although of full size. A very small crown can be seen through its accompanying replacement foramen. Tooth 8 is similar, but shows more wear and the replacement tooth and foramen are larger. Tooth 10 is almost identical with 8. Tooth 12 shows considerably more wear and its replacement has erupted through the lingual alveolar wall to make three openings here: the true alveolus, the eruption opening, and the replacement foramen. Tooth 14 is badly worn but its replacement is within the alveolus, the tip of its crown just above the alveolar margin. The base of the crown is visible through the replacement foramen. The margin of the alveolus shows a definite emargination where the eruption opening became confluent with it. Position 16 is similar to position 14, except that both the functioning and the replacement teeth have been lost, probably *post mortem*. The margin of the alveolus is being rebuilt, and the replacement foramen is apparently returning to a resting state.

To see the size and position of a replacement tooth more clearly, part of the lingual wall at position 4 of the left maxilla was removed (Fig. 48b). The replacement tooth, previously visible only through its foramen and through a small eruption opening, is revealed as a nearly full-grown crown. If the lingual wall could be removed along the entire jaw, it would reveal a tooth arrangement identical with that seen in, say, *Camptosaurus*, as in Figure 47b. *Camptosaurus* possesses the same number of tooth generations at each position, and shows the same wave pattern. The ankylosaurs therefore have a dentition basically the same as that of the hypsolophodonts or iguanodonts. The main difference is that in the ankylosaurs the teeth are somewhat more widely spaced and most of the growth of the replacement teeth occurs within the dentigerous bones.

From the material studied it is obvious that tooth replacement in ankylosaurs occurs in waves passing along alternately numbered tooth series. A tooth germ is produced by the dental lamina lying outside the lingual alveolar wall, and enters through a foramen or canal into a bony crypt probably confluent with the alveolus itself. With continued growth, the replacement tooth erupts, either through a new opening in the lingual alveolar wall, or possibly directly into the alveolus itself. The old tooth is discarded with little structural degradation, and the new tooth completes its growth and becomes attached to the jaw by non-calcified connective tissue.

SUBORDER CERATOPSIA

The evolution of the dental pattern in the ceratopsians apparently followed a course similar to that in the ornithopods. Unfortunately the early history of the group is unknown, but there are a few examples in which the ultimate stage of development has not been reached.

It has been suggested that *Psittacosaurus* and *Protiguonodon* (Psittacosauridae, Ornithopoda) are at least related to the ancestors of the ceratopsians (Romer, 1945) but these have already lost the teeth on the premaxilla, whereas *Protoceratops* which most authors consider to be a true ceratopsian, retained those teeth. The teeth of psittacosaurids are, however, of a type which could easily give rise to those of *Protoceratops*. The jaws of the psittacosaurids have not been completely prepared and therefore we do not have an exact picture of their dental arrangement. However, it is certain that they had not yet formed the individual teeth into the dental battery. There were only two teeth per vertical row, one functional tooth and one replacement.

The Ceratopsia is divided into two families, the Protoceratopsidae and the Ceratopsidae. These are distinguished by a number of characters, but the important one here is that the protoceratopsids, like the psittacosaurids, have not achieved a dental battery, while the ceratopsids have.

Only two genera of protoceratopsids are known, *Leptoceratops* and *Protoceratops*. The latter is represented by a large number of specimens of all ages. The lower jaw of the youngest known individual measures only 23 mm. (Fig. 49c) and has six alveoli, the two posterior ones being exposed

Fig. 49. Dentitions of ceratopsian dinosaurs.

- a. Right lower jaw of an unidentified ceratopsian from the Oldman of Alberta, R.O.M.Z.P., 1944 lingual view.
- b. Part of the dental battery of *Triceratops flabellatus*. The lingual alveolar wall has been removed. After Hatcher, Marsh and Lull.
- c. Right dentary of *Protoceratops andrewsi*, A.M.N.H. 6499. Lingual view.
- d. Left lower jaw of *Protoceratops andrewsi*, A.M.N.H. 6471. Lingual view with the lingual alveolar wall removed. After Brown and Schlaikjer.
- e. Single vertical series of teeth of *Triceratops flabellatus*. After Hatcher, Marsh and Lull.

by loss of their lingual walls. One of these alveoli bears part of an unerupted tooth, probably a member of the first functional generation to be produced by the young animal. A row of foramina lies on the lingual side of the dentary, one foramen at the base of each tooth position. When compared

with the size of similar foramina in adults, these are remarkably large, probably indicating an important function. The purpose of the foramina is seen at position 5, where the crown of a developing tooth lies immediately behind the foramen, apparently within a crypt or accessory alveolus as described in the ankylosaurs. Further preparation of the other foramina would probably reveal the bases of functional teeth or their developing replacements. The foramina are no doubt homologous with those seen in the hadrosaurs and ankylosaurs, and are almost certainly for the admission of germ teeth into cavities at the bases of the vertical tooth series. It is probable that the dental lamina lay along the lingual alveolar wall at the base of the teeth, as in most reptiles, and its products migrated through the foramina to take their place within the alveoli. The problem of these foramina in several groups has been discussed by Edmund (1957).

No replacement pattern could be discerned in the very small (23 mm.) jaw, A.M.N.H. 6499. It seemed obvious, however, that the more anterior teeth were laid down earlier, since tooth 5 (counting from the front) was not yet erupted. The four erupted teeth appeared to be of the same size but, because of their delicate nature, were not completely preserved.

A more fully grown specimen of *Protoceratops* is A.M.N.H. 6471, a left lower jaw of 230 mm. total length. Brown and Schlaijker (1940) have shown a dissected view of the dental chamber with part of the lingual wall removed (Fig. 49d). The arrangement is somewhat similar to that of *Camptosaurus*, the teeth lying in a fairly compact mass, but with no more than two teeth in each vertical series. Each tooth is single-rooted, with an expanded leaf-like crown. However, these authors mention that the teeth of *Leptoceratops*, which is also a protoceratopsian, are less advanced towards the bifid condition seen in the true ceratopsians than is *Protoceratops*. In the former both the inner and the outer surfaces of the tooth are smooth and in the latter there is a groove on the anterior and posterior surfaces into which the marginal portions of the crowns of the adjacent teeth fit.

The same specimen of *Protoceratops* shows the presence of waves in alternately numbered tooth series. The most fully erupted teeth in each series are at the rear, indicating a back-to-front replacement gradient, as in most other reptiles. Rather than being degraded from beneath, the teeth in ceratopsian dinosaurs, as in the hadrosaurs, move occlusad with age, and are worn away. The most occlusal teeth are thus the oldest, most worn teeth in each wave.

Leptoceratops gracilis is known from five skeletons, but the dentition is poorly preserved. As noted above, it is more primitive than *Protoceratops* in lacking any provision for interlocking of the teeth; it is more advanced, however, in having lost the premaxillary teeth. The manner of its occlusion, as described by Sternberg (1951), differs from that in other dinosaurs: "Due to the shape of the jaw and the breadth of the teeth, the lower jaw cannot go up past the maxilla and give a long shearing face on the teeth, but rather the dentary teeth are notched; and while the inner face (enamelled) forms a cutting edge, the tooth is worn down only part way, and the base of the broad fang root forms a shelf to stop the upper teeth. Thus,

Leptoceratops could not only shred but could actually crush his food." As in *Protoceratops* there is no indication of bifid roots such as are seen in the Ceratopsidae.

The best-preserved dentition of *Leptoceratops* is N.M.C. 6888, in which the lower jaws have been freed from the uppers and most of the teeth are retained. These jaws show well-defined waves passing cephalad along alternately numbered tooth series, as in *Camptosaurus*, and like that iguanodont they also have only two teeth in each vertical series. A single fairly large foramen is found at the base of each vertical series, and in several of the foramina in both jaws traces of small replacement crowns can be seen. Again this seems to confirm the function of these foramina as the route by which the germ teeth get to the hidden bases of the vertical series.

Apparently the teeth of *Leptoceratops*, like those of other dinosaurs, did not have bony ankylosis but relied on retention by non-calcified connective tissue. Many teeth have fallen from the jaws of the specimens, but although the crowns are often worn, there is no trace of degradation of the base. This was also seen in troodonts, ankylosaurs, and hypsilophodonts where similar intact loose teeth were found with skulls and jaws.

An interesting feature was seen in teeth 5, 7, 8, and 10 in the left dentary of N.M.C. 6888. The bases of the teeth have been exposed by loss of the lingual alveolar wall, and the crowns of the replacement teeth are seen to be against the bases of their predecessors about 12 to 14 mm. below the beginning of the crowns. At this point the bases of the old teeth appear to be excavated to receive the crowns, as in the iguanid lizards. Preservation is poor at this point, but there is no doubt that the bases have been hollowed out. Since this is the only occurrence of such a phenomenon I suggest that it may be an artifact caused by the solid crowns of the replacement teeth being crushed into the relatively soft, hollow bases of the old teeth during entombment.

One of the characteristics of the later ceratopsians is the development of a dental battery similar to that of the trachodonts. The ceratopsians, however, are distinguished by the presence of two-rooted teeth, as shown in Figure 49e. This results in a remarkably strong and well-integrated system, with each tooth straddling its own replacement with its roots and being held in by pressure on its concave sides by the crowns of its neighbours (Fig. 49b). The number of teeth in each vertical series varies, but in most species there are about four.

A comparison of the structure of the dental batteries of hadrosaurs and ceratopsians indicates that in the hadrosaurs the structure mainly responsible for anchoring the tooth is the root, and in the ceratopsians the crown is more important. In the hadrosaurs, the teeth in each vertical row are arranged in a diagonal fashion, as shown in Figure 47d. In the dentary, for instance, the enamelled surface of the crown is on the lingual side of the battery, and the apex of the root is on the labial side. The roots are elongate and are held in by interlocking with neighbours on all sides so that, even after the crown has been worn away, the root remains firmly attached to

the jaw and contributes to the area of the triturating surface. In the ceratopsians on the other hand, one tooth lies almost directly above the next, with its roots straddling the crown of its successor (Fig. 49e). When the crown has been worn away, there is little provision for the retention of the roots, and unless they were held in the connective tissue in life, they would readily be lost. This probably explains why the occlusal surfaces of most horned dinosaur jaws are very irregular (Fig. 49, a and d) and those of hadrosaurs are fairly level (Fig. 47e).

The writer has noted, however, that in some ceratopsian jaws, such as the well-preserved lower jaw of an unidentified Belly River specimen, R.O.M.Z.P. 1944, there may be a mechanism to partially prevent early loss of the roots. Thanks to the careful work of the technician, Mr. Ralph Hornell, small masses of bone overlying the junction of the crown of one tooth with the root of its predecessor were detected and carefully preserved (Fig. 49a). This bone appears grossly similar to the type of bone commonly involved in ankylosis of teeth in other reptilian groups, and in function provides a certain amount of union between the elements of each vertical series. As shown by the figure, no teeth in which the crown was worn away were preserved, but it is possible that some fragments of roots were retained in life by this method and lost *post mortem*. Since there was no mention of this unusual mechanism in the literature, the author searched for further instances of such bony union. In the excellent lower left jaw of *Triceratops serratus*, A.M.N.H. 970, a section of the lingual wall just forward of centre has been removed, revealing three or four vertical series, each containing three or four teeth. At each junction in the vertical series there were well-defined masses of spongy bone, as in Figure 49a. The same bone was also seen in *Monoclonius nasicornis*, A.M.N.H. 5351, on the lingual side of both lower jaws; in *Chasmosaurus belli*, A.M.N.H. 5402, on the labial side of both upper jaws; in *Triceratops brevicornis*, Y.P.M. 2148, on the lingual side of the lower left jaw; and in *Chasmosaurus russelli*, N.M.C. 8801, on the lingual side of a lower jaw. The dental battery of *Triceratops flabellatus* illustrated in Figure 49b shows the tips of the roots broken away in every case, as if some persistent material, perhaps the bone described above, had been removed during preparation.

The steps in the evolution of the ceratopsian pattern from that of the generalized thecodont pattern described below, are as follows. The regular alternation of elements of the odd- and even-numbered series was retained. Replacement continued to occur in waves passing along the jaw from back to front. The earliest ceratopsians exhibited an arrangement of teeth into a more or less compact mass, tending towards the formation of a true dental battery. Teeth were still single rooted. Teeth in the Ceratopsidae developed a bifid root which enabled them to straddle their replacements, giving greater strength to the dental battery. More teeth were retained per vertical series, each tooth being closely applied to its neighbours and to the preceding and succeeding members of its own vertical series, thus forming a compact dental battery.

Class Aves

The early toothed birds, although placed in a separate class, have many characteristics which indicate that they are in a sense merely highly specialized reptiles. One such characteristic is their dentition. Specimens of two genera of birds, *Archaeopteryx* and *Hesperornis*, are sufficiently well preserved to show this feature. Both have been thoroughly described and illustrated in the literature.

Perhaps the most famous fossil bird is the type of *Archaeopteryx lithographica* von Meyer in the British Museum. De Beer (1954), restudying this specimen, believes *Archaeornis siemensii* Dames, represented by a single specimen in the Berlin Museum, to belong to the same genus and species, i.e. cotypic. Dames (1884) described the dentition of both *Archaeornis* and *Archaeopteryx*, pointing out similarities and differences. By using more intensive preparation, radiography, and ultra-violet light photography, De Beer was able to describe many features unseen by Dames. De Beer unfortunately did not describe the dentition of the London specimen but his illustration of the right premaxilla (Fig. 50 here) shows the inner surface of the teeth in good detail. The Berlin specimen indicates the presence of six alveoli in the premaxilla, but De Beer's photograph suggests the presence of seven in the London specimen. Such variation is not uncommon among reptiles, and is probably not significant here.

As with *Hesperornis* described below, the teeth of *Archaeopteryx* resemble those of mosasaurs in possessing expanded, barrel-shaped bases. Replacement of individual teeth probably occurs in the same manner as in the crocodilians, as shown by the exposed lingual sides of the bases of the premaxillary teeth (Fig. 50). It is fortunate that in the separation of part and counterpart slabs, the main body of the maxilla went with one, while the lingual alveolar wall went with the other. This exposed the lingual side of the bases of the teeth, permitting the description of the replacement process.

The most anterior tooth lies loose in the matrix having apparently drifted out of its alveolus. The alveolus probably was damaged before consolidation of the matrix, as the premaxilla has been split into two relatively separate portions, the break passing through the first alveolus. This first tooth shows a definite pit near the apex on the lingual side of the base,

identical with the pit seen in mosasaurs (Fig. 25d). Two of the ankylosed teeth, in alveoli 4 and 6, show similar pits. Their bases are not exposed all the way to the apices because part of the lingual alveolar wall remains in this area. However, the degree of resorption appears to be about the same as that in tooth number one. Presumably the replacement tooth developed in the alveolus alongside its predecessor, its presence associated with the development of the pit. The young tooth may have entered the pulp chamber and completed its growth there, as in the theropods and crocodilians.

The distribution of teeth in this jaw agrees with the wave-like pattern of tooth replacement seen in the reptiles. Teeth 2, 4, and 6 are *in situ*, tooth 2 apparently intact as its base is almost completely exposed yet shows no resorption. Teeth 4 and 6 have pits, each extending about one-third to one-half of the length of their bases. This series could be interpreted as showing the anterior end of a back-to-front wave, with tooth 2 not yet attacked and 4 and 6 in the early stages of resorption. No replacement teeth were detected.

The odd-numbered series is also suggestive of a back-to-front wave, but is inconclusive. Tooth 1, lying loose, is probably in a fairly early stage of replacement, with only part of its base resorbed. It may have been about to be shed, as it had become loosened from the bone, but probably the teeth of birds (as of crocodilians) were not ankylosed. Positions 3, 5, and 7 are empty, and give no indication of the passage of a wave. It should be emphasized, however, that the above description is based only on a printed illustration, and further study will be necessary before definite conclusions can be stated.

Unfortunately, the Berlin specimen does not show any evidence which would indicate the presence of a wave pattern. It is only by a stroke of luck that the lingual side of the bases of the teeth of the London specimen are exposed.

The dentition of *Hesperornis regalis* Marsh is somewhat similar to that of *Archaeopteryx*. Marsh (1880) recognized that tooth replacement took

Fig. 50. Reconstruction of the premaxilla of *Archaeopteryx lithographica*. Modified after De Beer.

Fig. 51. A tooth of *Hesperornis regalis*, Y.P.M. 1206. After Marsh.

place and described the germ of a young tooth lying in a cavity on the inner side of the base of an old tooth. He describes the replacement process (p. 14), "As it, the germ tooth, increased in size, a pit for its reception was here gradually made by resorption. The old tooth at last became undermined and was expelled by the new one which occupied the same position. . . ." This is clearly shown in Figure 51 taken from Marsh (1880). The shape of the tooth is very similar to that of *Archaeopteryx* and is practically identical to that of a mosasaur (Fig. 25d). Marsh also recognized the similarity between the teeth of *Hesperornis* and those of a mosasaur, stating that the former resemble the teeth of the mosasauroid reptiles more than any other creature, not excepting the teeth of *Ichthyornis*. "In all their main features, the teeth of *Hesperornis* are essentially reptilian and no anatomist would hesitate to refer them to that class had they been found alone."

In contrast to those of *Archaeopteryx*, the teeth of *Hesperornis* are set in a continuous groove with only faint indications of sockets. Only a few teeth are retained in the known jaws, retention apparently being by means of soft tissue rather than by ankylosis. No series of teeth is sufficiently complete to indicate the sequence or replacement.

Gregory (1952) has shown on the basis of comparative osteology that the lower jaw of Marsh's *Ichthyornis dispar* is almost certainly not associated with the skeleton. His suggestion that the jaw belongs to a young mosasaur, *Clidastes*, seems reasonable although there are a few objections. As Gregory himself points out, no specimen of a mosasaur with such a small jaw has yet been reported. Also, it should be noted that the swollen tooth bases characteristic of mosasaurs are absent and that the replacement teeth are located centrally in the alveoli, not disto-lingually as in adult mosasaurs. These differences may be features of age but, as we have no corroborative material, further speculation on the identity of the specimen is unprofitable. The lower left jaw associated with *Ichthyornis dispar*, Y.P.M. 1450, is in fairly good condition, with twenty-one alveoli present. A definite back-to-front replacement wave is present in the odd-numbered alveoli.

On the basis of known material, we can tentatively draw the following conclusions regarding primitive avian dentition. The individual teeth resembled those of mosasaurs, with a sub-conical crown borne on a barrel-shaped swollen base. The replacement tooth developed in association with a pit resorbed in the lingual side of the base of its predecessor. In *Hesperornis*, the replacement tooth was seen to lie within this pit. Implantation of the teeth in *Archaeopteryx* was apparently thecodont. That of *Hesperornis* more closely resembled certain crocodilian or ichthyosaur specimens in which the teeth were set in a groove with only slight indication of division into alveoli. In the premaxilla of *Archaeopteryx* there was probably a regular alternation of replacement stages in the odd- and even-numbered dental series. The evidence is not sufficient to prove the presence of the replacement waves, but does not contradict their existence. On the basis of inheritance from a thecodont ancestor, they would be expected in the toothed birds.

Problems

Part II provided a description of the sequence and rhythm of tooth replacement for all reptilian groups represented by adequate material. Several general conclusions are evident. The most basic is that in nearly all forms replacement does not occur in a random fashion, but proceeds regularly within alternately numbered tooth series. In almost every reptilian jaw, it is possible to detect waves of replacement passing, usually from back to front, along the alternately numbered series. The sequence of replacement in the odd- and even-numbered series is synchronized so that at any point in the jaw, teeth of the two series are in opposite phases of replacement. Thus, a wave in the odd-numbered series always alternates with a wave in the even-numbered series. Many varied types of implantation and replacement of individual teeth were described and discussed, but despite such differences, the basic replacement rhythm prevailed. The purpose of this part is to discuss the origin of this rhythm phylogenetically and ontogenetically.

As stated above, waves of replacement pass from back to front along alternately numbered teeth in most reptiles. In a few instances, however, such as in the ichthyosaurs, the reverse is true. In the viperid snakes and in young crocodilians all of the teeth in a series appeared to be replaced at about the same time. In the elapid snakes the progression was often in both directions in the same jaw. What is the significance of these changes in the form of the replacing wave? Is the presence of replacement occurring in waves an advanced characteristic evolved from a system without waves? How far back in evolutionary history can we trace the presence of replacement waves passing along alternately numbered series? Is there a possibility that the phenomenon was acquired independently in more than one phylogenetic line?

Tooth replacement by the system described above apparently was present in one of the earliest known reptiles in which the dentition is adequately preserved, *Petrolacosaurus* (Upper Conemaugh, Pennsylvanian). It is also established in the cotylosaurian reptiles. Can it be traced

back beyond the amphibian-reptilian boundary? Is it found in either modern or fossil representatives of the other sub-reptilian vertebrates?

Bolk (1912 *et. seq.*) suggested that the alternately numbered tooth series were primitively separate, independent dentitions which later became combined into the apparently single dentition of modern reptiles. Studying embryos of various reptiles, he described separate sites of origin for these dentitions, and from these observations proposed his distichy theory to explain many of the phenomena of tooth replacement. A more critical examination of embryos as well as comparative studies on both modern and fossil material are necessary to test the validity of his theory.

The answers to these problems must come from various sources. The embryology of modern reptiles contributes a great deal to our understanding of the over-all patterns. Comparison of the embryos of reptiles with both embryos and adults of lower vertebrates reveal interesting similarities. Also, the examination of the dentitions of adults of lower vertebrates adds to our understanding of the phylogeny of reptilian dentition. No single line of attack gives the complete story in itself, but each contributes to the whole. Information from each will, therefore, be woven together to form what I believe to be a reasonable scheme explaining the facts presented in Part II.

Embryological Studies

Embryology is probably the most useful single field contributing to a general concept of reptilian dental history. The following account is necessarily brief, as this work is not primarily concerned with problems of dental embryology, but with the development of over-all patterns of replacement which function throughout the life of the individual.

The names of Bolk and Woerdeman are central in the study of embryonic tooth replacement. Bolk's many papers, the subjects of much controversy, have nevertheless publicized the nature of tooth replacement and the problems connected with it. Woerdeman amplified and corrected much of Bolk's work and placed at least the reptilian section of tooth replacement studies on a sounder footing. His reviews of the literature are also very useful. The following section is a combination of embryological description and historical review based on the findings of these authors.

Reptilian marginal teeth are developed on narrow strips of epithelium lying lingual to, and sub-parallel with the jaw margins. In the embryos of many species, the first teeth are produced directly on the surface of the oral epithelium, although in others formation of teeth is delayed until the area has been opercularized and invaginated. A fold or operculum overgrows the tooth field from the lingual side outward (Fig. 2b), resulting in an invaginated fold lined by mucous epithelium which becomes the dental lamina, or "Zahnleiste" of the German literature. Because the area covered by the operculum is the only tissue with the capacity to produce tooth buds, only the labial limb of the dental lamina produces teeth.

Hertwig (1874) described the anlagen of placoid scales and shark teeth, showing how the latter arose on the labial side of an epithelial lamella which had become invaginated from the surface. Later he showed that a similar structure produced teeth in amphibians.

Many early authors believed that the first teeth were formed by one dental lamina and the replacement teeth by another. Leche (1893) and

Levy (1898), in thorough researches later confirmed by Bolk (1912) and Woerdeman (1919 and 1921), demonstrated that only one dental lamina was present.

There are many references in the literature to the similarity between the arrangement of teeth in the dental lamina of sharks and that in other animals. Similarly, several authors have mentioned the development and arrangement of teeth on the surface of the oral epithelium before the invagination of the dental lamina occurred. Owen (1840) described the regular arrangement of teeth in sharks. Laaser (1900 and 1903) described the development of tooth anlagen on the oral epithelium in young selachians and termed the area where this occurred the "ausseres Zahnepithels." Röse (1892, a and b) mentioned finding the same stage in the crocodile, and named the rows of tooth buds the "placoid Anlagen." These early anlagen were resorbed before birth. Hertwig (1874) reported similar tooth buds on the surface of the oral epithelium in urodeles, thus showing that the early teeth are formed in a similar manner in many diverse groups of vertebrates.

Woerdeman (1919), following the researches of Röse and Bolk, remarked that the crocodile shows shark-like characteristics on one hand but mammal-like characteristics on the other. The site of early development and the pattern in which the shark's teeth are arranged is identical to that in the crocodilian embryo, but the form and mode of implantation of adult crocodilian teeth are mammal-like. De Terra (1911) had arrived at similar conclusions after reading Röse's (1892) description of crocodilian embryos. Röse (1894) described "placoid Anlagen" in embryos of *Vipera* sp., the early dentition of which closely resembled that which he had seen in crocodiles. Levy (1898) saw the same condition in other snakes. Thus there are many instances in which the first teeth are laid down in a shark-like pattern. In his summary, Woerdeman (1919) concluded that in many reptiles early teeth are laid down directly on the surface of the jaw but never attain maturity. The functional dentition is produced by the same tissue after it has been opercularized and invaginated to form the dental lamina (Fig. 2).

Another important series of observations is concerned with the site of origin on the dental lamina which produces the later teeth. Levy (1898) said that the teeth of the second and following dentitions do not all arise in the same place on the dental lamina. Röse (1893) believed that the second arises at the insertion of the dental lamina, and the third on its free margin. Further, he says that the teeth which originate on the free end of the lamina alternate with those from the angle between the lamina and the oral epithelium, i.e., the fixed margin of the lamina. This observation was a very significant one, since it was used by Bolk in support of his distichy theory. Similarly Harrison (1901, a and b), describing *Sphenodon*, wrote that "after the embryonic dentition is laid down, two different kinds of teeth are formed." He stated that one originated on the free margin of the dental lamina and in that location was not calcified. The second kind was found on the wall of the lamina and had received dentine. The teeth of the two kinds alternated regularly, so Harrison believed that "it is difficult to

avoid coming to the conclusion that we are here dealing with two dentitions." He termed these "alternating series."

If we consider that the first anlagen are laid down on the free surface, and are later covered by an operculum, it is easy to see why some of the anlagen would be nearer the free margin than others. The more advanced teeth are those which have moved labiad on the surface. The labiad movement becomes an occlusad one when the odontogenic strip is invaginated. Therefore the older anlagen which had moved labiad on the surface are now found near the fixed margin of the dental lamina. As these are more fully developed, they are more completely calcified. This results in the condition which was reported by Röse, Harrison, and others.

Bolk's (1912 and 1913) description of the dental lamina of an embryo of *Crocodylus porosus* is similar to that by Röse (1893 and earlier). Some of the tooth anlagen lie on the free margin of the dental lamina, others are on its labial wall (Fig. 3). Bolk named these two sites terminal and parietal respectively. In the specimens studied, these two kinds of anlagen alternated regularly along the lamina.

Figure 3, from Bolk (1912), illustrates a series of transverse sections through a dental lamina. Sections a, c, e, and g represent the blank parts of the lamina between developing teeth. Sections b and f represent buds growing on the free margin of the lamina. Section d represents a bud growing on the labial wall. This pattern is repeated along the length of the lamina. The upper drawing presents a reconstruction of a portion of a dental lamina made from such serial sections and the small letters on this stereogram indicate the plane of the sections used.

In discussing the fate of these anlagen, Bolk concluded that the teeth from the parietal site become the first functional tooth row; further, that the teeth from the terminal site do not replace those from the parietal, but come to lie between those in the functioning tooth row, the teeth of the first set then being replaced by others developed at the same site as were their predecessors.

Thus the complete dentition, according to Bolk's interpretation, is formed by elements developed at two different sites, arranged in an alternate fashion. In Bolk's terminology, a tooth family consists of all the teeth produced at one tooth position, either at the terminal or parietal level. Each tooth represents one generation of one family. Later Bolk termed all of the teeth produced by one generation of all of the families at one level (i.e., parietal or terminal) an odontostichos. Those from the terminal site he called endostichos, those from the parietal, exostichos.

The functioning dentition, according to Bolk, is composed of the alternating elements of two odontostichi, one endostichos and one exostichos. This condition he termed a "Scheinmonostichismus," i.e., an apparent monostichy, the result of the combination of two odontostichi, and really constituting a distichic dentition. Bolk described the same condition in other reptiles and considered distichy to be a general phenomenon in the production of reptilian dentition. He further suggested that there was probably an ancestral form in which the two odontostichi remained separate in adult life. Such a form has yet to be demonstrated (see below).

Although Bolk is generally credited with the discovery of the principle of alternating tooth replacement, it should be pointed out that almost all of the conclusions he reached were in the literature before 1912. Röse (1893) described the alternating position of developing tooth buds. Loomis (1900) described the presence of alternating replacement in adults of fish, amphibians, and reptiles, and Friedmann (1897) described the alternating nature of developing replacement teeth in the pike. Friedman's illustration of the order in which teeth are replaced is identical with that of Bolk. Similarly Harrison (1901, a and b), described the same phenomenon in *Sphenodon* embryos.

Bolk's main contribution was to bring together the accumulated data both from the literature and from his research, and to weld it into a theory which called attention to the problems of dental embryology and phylogeny. His many controversial papers were invaluable in encouraging research and publication either in support or criticism of his work. Bolk's later works went on to describe the probable evolution of mono- and didelphian dentitions on the basis of his distichy theory, but made no further contributions applicable to the present problem.

A student of Bolk's, Martin Woerdeman continued his work on reptiles, at first agreeing closely with his professor, later modifying certain of Bolk's conclusions. Most of the embryos used by Bolk and other early authors who worked on the distichy problem had been fairly well advanced ones. Woerdeman used embryos in all stages, including those showing the first appearance of the dental lamina and its products. The dental lamina is developed first at the anterior end of the jaws and progresses caudad. Similarly, the first teeth to appear are produced at the anterior end of the lamina.

Differing from Bolk, Woerdeman (1921) described the development of teeth as follows: "Zwei bildungsstätten für Ersatzzähne, wie Levy annimmt, oder parietale und terminale bildung, wie Bolk beschreibt, konnte ich nicht auffinden. In den von mir untersuchten fallen war immer der freie Zahnleistenrand die einzige bildungsstelle," that is, the teeth are formed only on the free margin of the dental lamina, not at two different positions. Marcus (1931) studying both gymnophionans and crocodiles, came to the same conclusion, "Der Unterschied von exostichaler und endostichaler Zahnanlage existiert nicht. Samtliche anlagen sind zunächst terminal und werden dann exostichal."

As noted above, Bolk was not the only author to claim that there were two sites for the development of tooth anlagen. Röse (1892, a and b), Harrison (1901, a and b), and Levy (1898) described the same phenomenon. These authors, however, mentioned that the "endostichial" buds were usually less developed than the "exostichial," and it is surprising that Bolk did not find this observation a serious impediment to his distichy theory. He recognized that as an endostichial bud developed, it migrated up the labial wall of the dental lamina and increased in size and degree of calcification. Similarly he realized (and illustrated) that at a single tooth position there could exist simultaneously an "endostichial" bud as well as an older tooth part way up the labial wall of the lamina. Bolk apparently never actually

saw in his specimens the beginning of the development of a bud on the labial wall of the dental lamina; the very young anlagen he described were seen only on the free margin of the dental lamina. As Marcus said, there is no doubt that each bud is at first endostichial and then migrates upward during development to become exostichial.

The scheme of development of the dentition described by Woerdeman differs in one other essential aspect from Bolk's theory. The latter described his odontostichi as being formed of a number of teeth in the same stage of development, produced at the same time, either at the free margin or on the labial wall of the dental lamina not both. An odontostichos so conceived thus consists of members of the same generation of several tooth families. A complete dentition, according to Bolk, consists of several odontostichi lying parallel to the jaw margin with the elements of the most labial odontostichos alternating with those of the odontostichos immediately lingual to it. The elements of the third odontostichos lie behind those of the first and become their replacements; similarly, elements of the fourth lie behind those of the second and act as their replacements. Thus, elements of the first endostichos are replaced by those of the next endostichos; those of the first exostichos are replaced by those of the next exostichos. The fallacy of this concept will be discussed in detail below.

Woerdeman's reconstructions of the development, through time, of embryonic reptilian dentitions showed that even more basic than Bolk's odontostichi was the development of series of teeth which came off the dental lamina in waves, rather in parallel rows as described by Bolk. These waves, according to Woerdeman, proceeded from front to back, the first element appearing on the free edge of the dental lamina at the anterior end of the jaw. This is illustrated in Figure 52a. As illustrated in Figure 2, the earliest anlagen of the teeth are formed at the free margin of the dental lamina or its equivalent. As each anlage increases in size and maturity, it migrates towards the fixed margin of the lamina.

At this point it may be convenient to think of some sort of impulse, perhaps of a chemical nature, which passes caudad along the free margin of the lamina. As it passes each definitive tooth position, an anlage is generated. Thus, there are two "vectors" at work, one being the migration of the anlage towards the fixed margin, the other the caudad movement of the hypothetical impulse. In this way a "Zahnreihe" as described by Woerdeman in 1921 is produced. Each Zahnreihe consists of a number of teeth, the most anterior being the farthest from the free margin and naturally the oldest. At the other end is the anlage closest to the free margin and, of course, the youngest. As shown in Figure 52a, once the formation of one Zahnreihe is well under way, a second one is begun. The first indication of this is the initiation of a second anlage at position 1, budded off the same germinal stock which produced the first anlage. The key to the entire synchrony of tooth replacement lies in the time at which the second Zahnreihe is laid down. Graph (4) in Figure 52a shows a second anlage being produced at position 1 just slightly after the first anlage was produced at position 3. That is, the Zahnreihen are spaced a little over two tooth positions apart. Presumably the rate of advance of the hypothetical impulse

Fig. 52. Stages in the production of a typical lower vertebrate. In each case, the anterior is to the left.

a. the sequence of production of tooth buds to form the Zahnreihen.

b. the completed dentition consisting of numerous Zahnreihen.

c. the diagrammatic appearance of the above dentition. One replacement wave is shown in black.

causing initiation of anlagen at each tooth position is constant. Keeping these facts in mind, one can see how the entire dentition is built up (Fig. 52b).

In life, Zahnreihe after Zahnreihe is produced, each following the next caudad along the jaw. At each tooth position there is a constant stream of dental elements passing occlusad from their origin as anlagen at the free margin of the dental lamina to become functional teeth near the attached margin. All of the teeth at any one tooth position, from the earliest anlagen to the functional tooth, are the products of one clump of cells. The products of this clump of germinal material make up a tooth family, as accurately described by Bolk (1912). The new anlagen are budded off from this germinal material and as they move occlusad the germinal material remains at the free margin of the lamina, where, periodically, it will give rise to new anlagen.

Figure 52b illustrates diagrammatically the arrangement of Zahnreihen in the dentition of a typical lower vertebrate. What is the effect on the functional dentition of the temporal and spatial arrangement of Zahnreihen discussed above? Since it was stipulated when composing Figure 52 that the spacing between Zahnreihen is about two-and-a-quarter tooth positions apart, it seems likely that the more mature elements in the occlusal region will not be in a particularly orderly arrangement. Figure 52c illustrates in stylized fashion the actual appearance of the dentition produced in Figure 52, a and b. The arrangement of the most mature teeth at each tooth position appears to be random. However, when we consider the principle of alternation and examine only every second tooth in the dentition, the familiar pattern of cephalad waves at once becomes obvious. Thus, this mechanically derived model has produced, from the observed embryological origin of the dentition, exactly the same pattern of replacement as was seen in practically every group of lower vertebrates. Compare this for instance with the dentition of *Iguana iguana* in Figure 4. In Figure 52 the length of each wave is nine spaces and in Figure 4 the length is seven. Otherwise, in arrangement of waves, direction of wave progression, etc., they are identical. It will also be noted that, in the model, a wave in the odd-numbered series must always be followed by one in the even-numbered series, and vice versa. This again is exactly what was observed in nature.

Variations in the length of the replacement waves, as observed in actual specimens, can be duplicated exactly with the model. The example in Figure 52 was constructed using a spacing between Zahnreihen of 2.25 tooth spaces, resulting in replacement waves of nine teeth each. At 2.5 spaces each wave contains five teeth, and at 3.0 spaces only three teeth.

In the ichthyosaurs, and frequently in the elapid snakes, the replacement waves progress from front to back. This does not require any radically different organization. By specifying a spacing between Zahnreihen of less than 2.0 tooth spaces, the resulting replacement waves run from front to back. At a spacing of 1.75, the waves have five teeth each, and at 1.5 spaces they have three teeth. Thus, by varying the spacing between Zahnreihe initiation on one side or another of 2.0, all wavelengths and directions can

Fig. 53. Stages in the production of dentition in which there is simple alternate tooth replacement.

be produced. The closer the spacing is to 2.0 the longer will be the wave produced.

What of simple alternate replacement? The work of Bolk, Röse, and others has become solidly entrenched in the literature, and Bolk's distichy theory is still accepted in some circles. The mistaken conception of distichy has been discussed earlier, but should be examined here in relation to the concept of Zahnreihen. To produce simple alternate replacement, it is necessary only to specify a spacing between Zahnreihen of 2.0 tooth positions. Such a dentition is built up from the first anlage in Figure 53. The functional dentition produced consists of a recurring sequence of the two most mature members of a number of successive Zahnreihen. Thus, the most mature member of each will be fully functional while the second most mature member of each will be in an earlier stage of the replacement cycle.

In this way an assemblage of elements is built up identical to that described by Bolk as being typical for lower vertebrates. The odontostichi (exostichi and endostichi) are plainly discernible, yet it is obvious that they are not the basic units making up the dentition, but are only secondarily derived from a fortunate synchrony in the production of the Zahnreihen. There is, of course, only one site for the production of tooth buds, i.e., the free margin of the dental lamina, and thus the terms endostichi and exostichi are meaningless. Furthermore, odontostichi, or at least the regular odontostichi described by Bolk are present only when regular alternate replacement is taking place. When the common pattern of wave-like replacement prevails (Fig. 52) there are no odontostichi.

Fig. 54. a. A wax plate reconstruction of part of the dental lamina of *Varanus chlorostigma*. After Woerdeman.
b. Analysis of the above.

Figure 54 is a portion of a dental lamina of a fairly typical lower vertebrate. The tooth buds on the lingual side of the lamina project bell-like, those near the attached margin being naturally much larger than those on the free margin. Three tooth families are present. Figure 54b presents the analysis of this preparation, according to both Bolk and Woerdeman. The arrangement of elements suggests that simple alternate replacement was present, but the area represented is so short that it is impossible to be sure. Figure 55, modified after Woerdeman, illustrates the arrangement of Zahnreihen and tooth positions which produce simple alternating replacement. The important fact to note is that all the features of Bolk's distichy system can be readily derived from one laid down by the production of Zahnreihen. There can be no doubt that the dentitions of the lower vertebrates are based on Woerdeman's Zahnreihen. One fact is still somewhat in doubt, however. As noted earlier, numerous authors mentioned that in the embryos they

studied simple alternate replacement was the rule. However, in the large series of adult lower vertebrates studied here, simple alternation was rare indeed. How can these conflicting observations be reconciled? There are two possible explanations. It is possible that the initial few Zahnreihen are laid down, as in Figure 54, 2.0 spaces apart; then later in life the spacing increases (or decreases as the case may be), to produce waves. The other explanation is that these workers, using tedious sectioning methods, may have investigated only relatively short series of teeth. An examination of a short series, especially if the replacement waves were rather long, could indicate a picture similar to that in Figure 54, where there are only three tooth families with three members each. It will be realized from this that an author might easily be inclined to postulate a scheme of simple alternation. This aspect of the problem requires more research before definite conclusions can be reached. It seems certain, however, that the scheme of Zahnreihe production and synchrony as shown in Figure 52b is the one prevailing in most adult lower vertebrates. It would also appear that the scheme of development of the dentition shown in Figure 52a is the correct one and is more logical than postulating a change from simple alternation occurring after the first appearance of teeth and before maturity.

Fig. 55. Woerdeman's conception of the arrangement of elements in the dental lamina of a typical lower vertebrate.

As noted earlier in this paper, Woerdeman stated that tooth replacement proceeded from front to back. It was observed in the survey section, however, that replacement occurs in waves passing (usually) from back to front, along alternately numbered tooth series. We must remember that Woerdeman was concerned almost entirely with embryos. If we agree that one Zahnreihe is indeed replaced by another Zahnreihe, and that these, in effect, move from front to back, then Woerdeman is quite correct. However, most of our observations are on adult animals with actively replacing dentitions and hence in nearly every case the replacement waves proceed from back to front.

As mentioned previously, the dentitions of all lower vertebrates can be divided into two main types both of which are laid down ontogenetically as

Zahnreihen. The most common type of dentition consists of a single marginal row on the premaxilla and maxilla in the upper jaws, and on the dentary in the lower jaws. Only mature teeth enter this row, and at the conclusion of their active life they are replaced by fresh teeth from alongside (lingual) or beneath. In contrast to this is the type of dentition in which all of the teeth in each Zahnreihe, once produced, reach maturity and are ankylosed and retained throughout life. This was seen in the jaws of the cotylosaurs *Captorhinus* and *Labidosaurikos*, in certain rhynchosauroids, and is common in many fish. The first Zahnreihe produced is ankylosed, then a second is added lingual to the first, then a third, a fourth, and so on. *Pleuronectes platessa* (Fig. 56a) is, as Vorstman pointed out, an excellent example of this type. Another is the angler fish, *Lophius piscatorius*. Skeletal jaws of this fish often have six or more Zahnreihen, each with twenty or more teeth. Cleared specimens of *Esox lucius* and *Alma calva* prepared by the writer show the same pattern which has also been described or figured by Friedman (1897) and Schnakenbeck (1936).

Fig. 56. Diagrams of the arrangement of dental elements in fish. All are occlusal views of left lower jaws. After Vorstman.

a. *Pleuronectes platessa*, 7 cm. specimen showing numerous Zahnreihen.

b. *Esox lucius*, 7 cm. specimen. The Zahnreihen are connected by heavy broken lines.

c. *Salmo salar*, 2.4 cm. specimen.

The dentitions of most of the chondrichthyes are of the multiple row type. Jaws of sharks, rays, etc., show many rows of teeth of various forms, yet all are laid down in a pattern which is very similar to that in Figure 53 (6). Furthermore, there is usually a synchrony so that the teeth in the rows alternate with one another as in Figure 53 (6), thus producing a hexagonal pattern. This is especially well seen in many rays, where the teeth have become short hexagonal prisms.

In most cases, animals with multiple rows of teeth (i.e., ankylosed

Zahnreihen) show no apparent synchrony of Zahnreihen production. However, there are some cases which are on the borderline between the single and multiple row conditions. This was especially noted in fish, for example in the genera *Salmo* and *Salvelinus*. In many fish not only are the most mature members of each Zahnreihe ankylosed and functional, but also several of the less mature members are often functional, frequently held in by tough connective tissue. However, there is often a condition close to an alternate replacement pattern. Figure 56c shows this clearly. A number of Zahnreihen are present in this young fish, but their arrangement is such that there is regular alternation in the tooth row between older and younger teeth. In older fish, the number of teeth in the tooth families and Zahnreihen increases, and more of the teeth are functional, but there is still a fairly well established alternate replacement pattern, occasionally showing a back-to-front wave-like progression, just as in the reptiles. Vorstman (1922), from whose paper Figure 56 is taken, showed that a marginal tooth row with alternation can be produced by the fortunate spatial arrangement of Zahnreihen. This is exactly the situation developed in the mathematical model (Fig. 53). Vorstman, relying mainly on earlier literature, considered simple alternation to be the common adult condition and thus did not derive the condition seen in Figure 52.

Before leaving this consideration of Zahnreihen, the dentition of the mammals should be reviewed briefly. Mammals are diphyodont, i.e., there is only one wave of tooth replacement which passes caudad along successively numbered teeth in each jaw ramus. The more posterior teeth are not replaced at all, and are apparently members of the first (i.e., lacteal) dentition. This arrangement of teeth seems to be identical with that seen in the earliest stages of the development in the lower vertebrates. Consider Figure 52a, graph 8, in which the first Zahnreihe is complete, and the second is about half laid down. This is remarkably similar to the mammalian condition. The lacteal dentition is composed of the first members of the first Zahnreihe. Before the more posterior (i.e., molariform) teeth come into use, the anterior members of the first Zahnreihe are replaced by the anterior members of the second Zahnreihe. The eruption of these coincides with the eruption of the so-called permanent molars, which in reality are the more posterior elements of the first Zahnreihe. In man, therefore, the lacteal dentition, consisting in each quadrant of two incisors, one canine, and two premolars, plus the molars of the permanent dentition, are the teeth of the first Zahnreihe. The permanent incisors, canines, and premolars are the teeth of the second Zahnreihe. The more posterior members of the second Zahnreihe are virtually never developed. Very rarely the anterior elements of a third Zahnreihe may develop: a few cases of replacement of the so-called permanent incisors have been reported, but these are rare.

In Part II the peculiar dentition of *Trilophosaurus* was described on the basis of the Zahnreihe concept. As in the mammals, the entire first marginal tooth row is formed of the matured elements of one Zahnreihe. These teeth are replaced in sequence from anterior to posterior by the elements of the second Zahnreihe. This is the only case in which a "mammalian" pattern of

tooth replacement was seen in any group other than the mammals themselves. Since it is not difficult to derive the pattern from the general embryonic arrangement it is not surprising that it has appeared at least twice in vertebrate history.

From this consideration of dental embryology it will be seen that the Zahnreihe is the most basic unit in the formation of any dentition. In some cases many Zahnreihen mature and are retained throughout life; their individual teeth are never replaced. In other cases only a single marginal row of teeth exists, but it is made up of the more mature members of a number of Zahnreihen. From a modification in the sequence of production of Zahnreihen all of the variations in replacement patterns seen in the lower vertebrates can be produced. These include the direction of wave progression, differences in wave length, and simple alternation or a wave pattern. The considerably reduced dentition of the mammals is also based on Zahnreihen. The Zahnreihe appears to be a constant embryological feature of the vertebrates and one with great flexibility, permitting the relatively simple evolution of many far-reaching modifications.

Phylogenetic Studies

Two approaches are available for this aspect of the study: palaeontology, and comparative study of modern forms. The previous chapter proved that alternating tooth replacement with a posterior-anterior wave pattern was general throughout the reptiles. It is necessary to examine the sub-reptilian forms to find how far down the phyletic series this pattern became established.

Seymouria baylorensis is generally considered as being very close to the amphibian-reptilian boundary, so that a study of its dentition seems particularly pertinent. As with so many crucial forms, the available material is rare and fragmentary; however, two specimens have come to the author's attention as showing significant features. The right maxilla of *S. baylorensis*, M.C.Z. 1083, was preserved with the lower dentition in place, pressed against the lingual surfaces of the upper teeth. This occurrence has prevented post-mortem loss of some of the replacement teeth, as shown in Figure 57. The anterior end of the fragment is damaged and difficult to interpret, but two waves of replacement can be distinguished clearly in the remainder. Tooth 5 has a shallow excavation in its lingual side near the base with the remains of a small replacement tooth lying partly within the excavation. Tooth 7 is similar to tooth 5. Position 9 is vacant except for traces of an old base; obviously the old tooth was lost and its replacement not ankylosed *pre mortem*. Tooth 11 is obviously a new tooth just becoming ankylosed, lying almost loose within its space. There is a wide separation between the labial side of the tooth and the jaw, a space filled in by bone in the more mature teeth. Teeth 13 and 15 are apparently well ankylosed and do not seem to be undergoing replacement.

In the even-numbered series, position 2 is represented by the base of an old tooth which apparently was being degraded prior to replacement. Tooth 4 is a young tooth just becoming ankylosed, as is tooth 11 above. Teeth 6, 8, and 10 appear to be mature, being well ankylosed and showing no signs of resorption. Tooth 12 bears a small pit in its base, and a small replace-

ment tooth about 2 mm. long lies in the pit. Tooth 14 is deeply excavated, with about half of its lingual surface removed. No doubt a large replacement tooth occupied the space in life. Thus, in this specimen there are at least two waves of replacement passing cephalad along alternately numbered tooth series, just as in the typical reptiles.

Fig. 57. Lingual view of part of the maxilla of *Seymouria baylorensis*, M.C.Z. 1083.

A second specimen of *S. baylorensis*, M.C.Z. 1085, is represented by fragments of the two lower jaws and part of the right upper jaw. In the right lower jaw fragment, tooth 1 is apparently young, the deposition of cementing bone being incomplete and leaving a definite groove between the bone and the base of the tooth on the lingual side. Tooth 3 is similar, but more advanced towards complete fusion with the dentary. Teeth 5, 7, and 9 are completely fused. Tooth 9 bears a definite excavation on its lingual side at the junction with the bone. Lying within this is a bell-shaped structure about 1 mm. high which is apparently a small replacement tooth. Position 11 is occupied by a rather disorganized structure which may be the remains of a small tooth about one-quarter grown. Tooth 13 is in place, but not completely ankylosed, and 15 is firmly fused. Thus, there is a series running from incompletely ankylosed teeth at the anterior end of the jaw, through a stage of resorption and loss back to ankylosis again.

A similar series is seen in the even-numbered teeth in the same jaw. Teeth 2 and 4 appear to have resorption pits in their bases. Position 6 bears what appears to be a young tooth about one-third grown. Tooth 8 is incompletely ankylosed, and 10 appears to be completely fused. Number 12 has a basal pit, probably the beginning of another cycle of replacement. The remainder of the jaw is obscured by ironstone matrix.

The right upper jaw fragment of M.C.Z. 1085 bears similar evidences of tooth replacement, including several teeth with basal pits, and one good back-to-front sequence was noted. The lower left jaw of M.C.Z. 1085 also shows the same type of replacement. Tooth 13 has a small pit, 15 is missing, and 17 is only partly ankylosed. Teeth 21, 23, and 25 show a similar sequence. From these descriptions, it is obvious that tooth replacement in *Seymouria* is quite similar to that in many reptiles, for example the sphenacodonts. The teeth are labyrinthodont, closely resembling those of *Trimerorhachis* in size and form. However, the method of replacement is decidedly different from that seen in any palaeozoic amphibian—further

evidence suggesting strong reptilian affinities. Romer placed *Seymouria* in the Amphibia in 1945, but transferred it to the Reptilia in 1956.

It is unfortunate that most of our knowledge of tooth replacement in amphibians is based largely on the Rhachitomi. The anthracosaurs, which presumably contain the ancestors of the reptiles, are not well known dentally. Several jaws of the Permian embolomere *Cricotus* were examined, including U.M. 9754 and M.C.Z. 2060. Both specimens showed discrete waves of replacement, but it was difficult to make out the details in most cases. In the lower left jaw of M.C.Z. 2060 there are several replacement waves. At the anterior end of some of these waves the teeth are obviously younger than their neighbours. The most conspicuous wave is in the even-numbered series from numbers 26 to 36, in which teeth 26 and 28 are shorter and less well fused than the others. Similarly, in the odd-numbered series, teeth 35 and 37 are obviously younger than teeth 39, 41, and 43, again indicating a back-to-front wave progression.

The labyrinthodont amphibians unquestionably show a regular alternating pattern. Our best information comes from the common rhachitome *Eryops megacephalus*. Numerous nearly complete jaws of this animal are available, although in most cases only the bases of the ankylosed teeth are retained. By close examination of the better material it is possible to determine certain stages in the tooth replacement process.

Bystrow (1938 and 1944) described changes in the structure of the labyrinthodont tooth during its life, indicating that resorption occurred from within the tooth before it was shed. Teeth which have only recently come into function can usually be distinguished by their incomplete ankylosis. By using such criteria it was possible to establish the fact that replacement occurred in waves progressing from back to front. A fragment of the right maxilla of *Eryops megacephalus*, M.C.Z. 2197, shows a good back-to-front sequence over a fairly long interval. Similarly the symphyseal area of the left lower jaw of *E. megacephalus*, A.M.N.H. 4662, shows an obvious back-to-front pattern. A right maxillary fragment of *Trimerorhachis* sp., A.M.N.H. 4585, is similar. The skull of *Acheloma cumminsi* Cope, U.C. 481 in C.N.H.M., has a well-preserved upper left jaw. Two waves are present, one in each alternate series. The anterior tooth of each of these waves is obviously young and incompletely ankylosed.

Although only a few specimens showed the probable direction of wave progression, many showed the presence of the waves themselves. In each alternately numbered series there were groups of occupied tooth positions separated by intervals of several empty tooth positions. In *Eryops* the number of ankylosed teeth per wave was usually about eight, followed by an interval of about six empty positions. When good material of fossil amphibians was available, this arrangement was almost always seen. The following rhachitomes showed the presence of discrete waves. *Eryops megacephalus*: A.M.N.H. 4183, both left jaws; A.M.N.H. 4313, lower right; M.C.Z. 1905, lower left; M.C.Z. 1900, lower left, lower right; M.C.Z. 1583, upper left; M.C.Z. 1485, lower right; *Trimerorhachis* sp.: U.M. 16031; *Cacops* sp.: U.M. 3417.

Two well-preserved metoposaurs which show regular alternate replacement with a definite pattern are *Buettneria bakeri*, U.M. 13944, and *B. perfecta*, U.M. 7475. These species have been assigned by Colbert and Imbrie (1956) to *Eupelor fraasi jonesi*. As in *Eryops* described above, obviously younger teeth at the anterior end of the waves indicate a back-to-front wave progression.

Modern amphibians were also studied, but although they showed the presence of alternating tooth series with waves of replacement passing along them, they were rarely as regular as the reptiles. In some specimens, such as *Amphiuma tridactylum*, C.M.N.H. 24950, for example, the derived graph (not illustrated) is practically identical to that of most lizards. Specimens of *Cryptobranchus alleganiensis* studied at the Palaeontological Museum of the University of Michigan showed good alternation, but the replacement waves showed many irregularities. Several specimens of *Rana catesbeiana* in the Royal Ontario Museum were also studied, yielding results similar to those for *Cryptobranchus*.

Gillette (1955) found similar irregularities in the shape of replacement graphs made from cleared preparations of adult *Rana pipiens*. He described "gentle distortions of a continuous sort" as well as sharp discontinuities. The discontinuities affected both functioning teeth and their developing replacements. Gillette says,

A detailed discussion of the distortions and discontinuities is beyond the scope of this paper, which is confined to the description of the basic rectilinear pattern of correlation which is approximately true for any short segment of the dentition. The distortions and discontinuities, however, are not haphazard but occur in characteristic ways and places. A preliminary examination of these lawful irregularities indicates that they are phenomena associated with the long-term past history of the dentition as a whole, involving the increase in individual size of succeeding teeth, the growth of the teeth-bearing bones, and the orderly addition of new tooth-positions to existing rows.

In correspondence with the writer (August 23, 1955), Dr. Gillette indicates that he intended to publish on the causes of these lawful irregularities. He said, "I came to the conclusion that the break sites were caused by failure of development of tooth germs at the break sites. . . . Since successive generations of teeth are larger in individual tooth size and since the teeth are ankylosed to the maxillary bone, they cannot shift in position rapidly enough to make room for the larger teeth. Hence the teeth became crowded and at each site of greatest crowding a germ is suppressed, and with it all of its successors. The loss of tooth numbers that this causes is more than made up for by the addition of teeth at the ends of rows."

This explanation may be correct, but in the gekkonid lizards the teeth are also small and numerous and a great deal of growth takes place, as in the frog, but their replacement pattern is quite orderly. However, a similar explanation was proposed by Gans (1957) to explain irregularities in

amphisbaenid lizards. Further study of the problem is necessary. Woerdeman (1921) used embryos of only a single amphibian, the caecilian *Gongylus ocellatus*, the dentition of which developed in exactly the same manner as did that of typical reptiles. A similar study of an amphiumid or ranid would probably yield interesting results.

This survey of the fossil and modern amphibia has demonstrated that alternating tooth replacement with a wave pattern was present not only in the embolomeri but also in many other labyrinthodonts as well as in most modern amphibia. To trace the pattern further down the evolutionary series, sections were prepared of a dentary of *Eusthenopteron foordi*, a representative of the rhipidistian crossopterygii, generally believed to be close to the ancestry of the later tetrapods. The specimen is being described in detail in a separate paper (Edmund (1960)), but its general characteristics deserve mention here. As in the rhachitomous labyrinthodonts, it is possible to distinguish old and new teeth by the condition of their inner walls and degree of ankylosis. In two tooth positions very small loose replacement teeth were preserved. The graphic analysis of this jaw (not illustrated here) showed the same replacement pattern as in the typical reptiles. Several cephalad replacement waves followed one another along the jaw. Thus, the well-established pattern seen in reptiles and amphibians can be traced to the origin of the tetrapod stock in the Upper Devonian.

The crossopterygians are part of the bony fish stock, and before searching farther in geological time, a brief survey of some modern bony fish will be presented. Several teleost fish were seen to have fairly regular alternation of teeth on the jaw margin. As Vorstman showed (Fig. 56 here) the correct arrangement of Zahnreihen and tooth families produces simple alternation in several fish. Loomis (1900) was intrigued with the regularity of the alternate replacement seen in his Kansas Cretaceous fish, mainly *Protosphyraena*. He described the dentition of these fish and then compared it with that in many other vertebrates. From this study he postulated a general case (Fig. 1) remarkably similar to that of Woerdeman (1922) (Fig. 55 here).

An interesting paper (Evans and Deubler 1955) on replacement of pharyngeal teeth in cyprinid fishes indicates that even in this location replacement follows a wave pattern, as in the marginal tooth rows of lower tetrapods. Unfortunately, the authors were not aware of the basic principle of alternation, and in their statistical analyses sought to determine the order of replacement in the entire dentition. In re-analysing their material, it is possible to show that most of their patterns can be resolved into series of short, overlapping waves. For example, Figure 58, which is taken from their paper, clearly shows that two waves follow each other along the 5-tooth arch. Tooth 1 in stage a is an old tooth about to be replaced, as shown by the progressively increasing replacements at the same position in stages b to e. Tooth 3 in stage 1 is a very small replacement which has just come to occupy a position vacated by an old tooth. Its increase to a full-sized functional tooth (as in 2-1) is shown in stages 3b to e. Tooth 5 in stage a is advanced over tooth 3, and becomes a mature tooth by stage d. Thus, in

Fig. 58. Hypothetical stages in a typical replacement cycle, from Evans and Deubler, 1955.

the odd-numbered series, there is an obvious wave from left to right, as is clearly shown in stages b, c, or d. It is only in stages a and e that the wave is not well demonstrated owing to the extreme shortness of the tooth row which does not permit the demonstration of a series of successive waves. Similarly, the even-numbered teeth show their wave progression in stages a, b, d, and e. The problem of tooth replacement in both marginal and pharyngeal dentitions of fish is a fascinating and complex problem demanding more attention. Dr. Evans is continuing his work on pharyngeal teeth, and the present writer wishes to thank him for making his original material available for study.

The jaws of *Sphyræna barracuda* were radiographed and show excellent alternation of both functional teeth and tooth germs (not illustrated). Superimposed on this simple alternation is a wave pattern similar to that seen in the elapid snakes, i.e., from one area of the jaw to another the waves show not only back-to-front progression but also the reverse. Owen (1840) remarked that the dentition of *Sphyræna* was very similar to that

of *Crocodylus*, an observation made apparently independently by Loomis (1900). Jaws of several modern teleosts in the Museum of Comparative Zoology, Harvard University, were examined by the writer and excellent alternation was seen in several including *Salvelinus namaycush* and *Salmo salar*.

Alternate tooth replacement is thus present in two distinct phyletic lines, the Actinopterygii and the Choanichthyes, both of which presumably had a common origin very far back in Chordate history. It has been demonstrated above that the Chondrichthyes have a similar dental pattern. The early history of the evolution of fish is not at all well known, but it is obvious that the history of a dentition formed by the production of Zahnreihen must extend back to an ancestral form common to both the Chondrichthyes and the Osteichthyes.

Thus, we can trace the pattern of tooth replacement from the mammals through the reptiles and amphibians to a point, possibly in the Middle or Lower Devonian, where it apparently arose in some ancestral fish. This is a record of the process of evolution acting for three hundred million years on a simple basic design.

Summary

Although the emphasis of this investigation centres on the reptiles, it is obvious that the amphibians, fish, and mammals cannot be excluded from consideration. Two main types of dentition are noted. The less common consists of a band or pavement of teeth composed of a number of rows of teeth lying sub-parallel to the jaw margin. No replacement of these teeth was seen. The second type of dentition is composed of a single marginal row, the teeth of which were replaced periodically throughout life. A wave of replacement, usually cephalad, in the odd-numbered series was followed by one in the even-numbered series. Only rarely were all of the teeth in an alternately numbered series replaced at the same time. Examples of both the simple marginal-rowed type and the multiple-rowed type were found in various lines in the fish, amphibians, and reptiles.

Embryological studies showed that all vertebrate dentitions are laid down on the dental lamina in a series of Zahnreihen, as described by Woerdeman. The marginal dentitions are made up of the more mature members of a number of successive Zahnreihen. The temporal and spatial arrangement of the Zahnreihen determines such features as the number of teeth in each replacing wave and the direction of the wave's progress. A graphic model was constructed which could, by simple adjustments, produce dental patterns identical with those of practically every vertebrate possessing a marginal tooth row.

The various types of marginal dentitions are basically the same, but differ in such features as tooth form, mode of replacement, site of development of the replacing tooth, mode of attachment to the jaw, etc.

The type of dentition which consists of a number of sub-parallel rows of teeth is also derived from Zahnreihen. In this case, all or most of the teeth in each Zahnreihe mature, are ankylosed, and are retained until the death of the individual, and Zahnreihe after Zahnreihe is produced to keep up with the growth of the animal's jaws. This multiple Zahnreihe type of dentition is a secondary feature which has arisen independently in several lines.

The dentition of the mammal consists of the products of one and part of a second Zahnreihe. The anterior teeth are replaced by the members of the partial second Zahnreihe, while the posterior, "permanent" teeth are the posterior members of the first Zahnreihe. The dentitions of most reptiles and amphibians and of the crossopterygian fish are remarkably similar in their basic features. The Chondrichthyes and Teleostei also have an essentially similar type of dentition. Fossils of all of these phyletic lines, dating back in some cases to the Devonian period, indicate that the principle of a dentition composed of Zahnreihen is almost as old as the vertebrate structural plan itself.

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