Amphibia-Reptilia 1, 19-27 (August 4, 1980)

Amphibia-Reptilia

The Dentition of the European Glass Lizard *Ophisaurus apodus* (PALLAS, 1775) (Reptilia, Sauria: Anguidae), with Notes on the Pattern of Tooth Replacement

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Abstract. The description of individual teeth, the dentition as a whole, and the main features of tooth-bearing bones in *Ophisaurus apodus* is given. The tooth replacement is rather different from that described for non-mammalian vertebrates (the wave replacement of alternate teeth). The wave of replacement affects adjacent teeth, not even and odd teeth separately. In some periods of the life none of the teeth are replaced which suggests that replacement is not continuous in time. As a result the posterior set of teeth becomes permanent and much worn in aged specimens.

Introduction

The outlines of the cranial osteology of *Ophisaurus apodus* are known especially from the paper of FEJÉRVÁRY-LÁNGH (1923) which is a careful but rather static description. Little is known, however, on the dentition in different stages of ontogeny. The only attempt to show the mode of tooth replacement in the genus *Ophisaurus* was made by EDMUND (1960). Some brief notes on cranial osteology and tooth shape were given by MESZOELY (1970). In spite of this lack of knowledge, many fossil ophisaurs were described in the past, mainly on the basis of dentition and tooth-bearing bones.

The present author, during his paleontological excavations at the Lower Miocene locality Dolnice near the town Cheb in western Bohemia, found many fragments of tooth-bearing bones which undoubtely belong to representatives of the family Anguidae. For a proper interpretation of this material, a need for further knowledge on available recent species arose.

Material and Methods

For the purpose of this study skeletons were used showing different stages of tooth replacement. Some of the skulls were carefully prepared in such a way that soft tissue with teeth in early stages of development was preserved. However, where soft tissue with tooth buds was absent, the stage of successive tooth development was deduced from the degree of tooth base resorption.

The following material was used: Four specimens from the osteological collections of National Museum, Praha (NMP – 23583, 22069, 22070, 22071), one specimen from the osteological collections of the Department of Paleontology, Faculty of Natural Science, Charles University, Praha (DP FNSP 6448), and seven specimens borrowed from private collections of RNDr J. Klembara and MUDr V. Seichert.

The following tooth attributes were evaluated: (1) Tooth shape. (a) Tooth shape in both labial and lingual views. (b) Tooth profile in mesial or posterior view. (c) Nature of tooth upper termination (if with pointed or blunt crowns etc.). (d) Nature of tooth lower termination (the outline of tooth bases, the degree to which the individual teeth are affixed to the wall of the dentary and to its lingual shelf, the degree of basal resorption etc.). (2) Tooth number. (3) Distance between adjacent teeth. (4) Size of adjacent teeth. (5) Inclination of teeth from the crista dentalis (both in lingual and mesio-posterior views). (6) Proportional size of the exposed part of the tooth above the level of the crista dentalis ("crown" of some authors) in comparison with the part of the tooth which is attached to the bone ("root" or "base" of some authors) in lingual view. (7) Ratio between the height of the seventh tooth above the crista dentalis and the height of mandible in the same level.

Further characters refer to the tooth-bearing bones: dentary, maxilla and premaxilla. (8) Nature of the sulcus dentalis. (9) Presence or absence of the spina splenialis. (10) Number of foramina pro rami nervorum alveolarium inferiorum on the dentary (syn. foramina dento-facialia according to HÜNERMANN 1978), and number of foramina pro rami nervorum alveolarium superiorum on the maxilla (syn. foramina supralabialia according to OELRICH 1956). (11) Ratio between processus nasalis premaxillae and processus maxillaris premaxillae (both measurements were taken from the cross-section of the midline through the crista dentalis premaxillae).

Special attention was paid to the character: (12) Tooth replacement.

For recording informations on ratio of the tooth bearing bones and other parts of the skull some proportionality indices are given. The basic measurement to which all others are referred is the width of the parietal bone at the level where the lateral margins of this element begin to diverge into processus supratemporales (LtP – latitudo ossis parietalis). This part of parietale is easily visible also in non-articulated skulls in anguids, if caudal osteoderms are removed. Other measurements taken were the length of the crista dentalis of dentary (LCD – longitudo cristae dentalis; it cannot be taken as identical with the maximal length of the dentary in some anguids, especially *Ophisaurus*), and the length of the maxillary (LM – longitudo maxillae, which only slightly differs from the length of the crista dentalis maxillae). From this measurements indices LtP/LCD and LtP/LM were counted. For comparison with the actual size of an animal the following measurements were taken: the length of cranium (LCr) which is the distance between the anterior-most and posterior-most points of cranium in median line, and the length of mandible (LMd) which is the distance between the anterior-most point near the symphysis to the posterior tip of the processus retroarticularis.

The osteological terminology generally follows that of FEFÉRVÁRY-LÁNGH (1923), and the dental terminology that of EDMUND (1969) and PEYER (1968).

Results

(i) Description of Dentition and Tooth bearing Elements

Dentary – Generally agreed that two types of teeth occur in *Ophisaurus apodus:* (1) A slightly asymmetrical conus without pointed apex, with the free part above the level of the crista dentalis relatively slender, and the basal part considerably swollen lingually; (2) Blunt-crowned, robust crushing teeth which are more spherically shaped both from lingual and occlusal view. Both these types of teeth possess radially striated crowns. This striation, if well developed, ends on the straight circumdental boundary. Crushing teeth are undoubtely worn and reach the stage of degeneration in some specimens; the shape is irregular, crowns are very low and sometimes it seems that two adjacent teeth are fused. The striation is absent in such cases. Different kinds of transition between both types of teeth in the single tooth row may occur: either a sudden boundary between two adjacent teeth when both of them are typical representatives of the two types described above, or the transition may be very gradual so that typical representatives of both types are at the opposite ends of the tooth row. Whatever type of transition occurs on one side, the same exists contralateral; likewise opposite maxillae are similar. In some specimens, a small additional tooth localized rather lingually from the main tooth row was observed on the boundary between the seventh and eighth tooth which suggests that the tooth row may be extended by additions here.

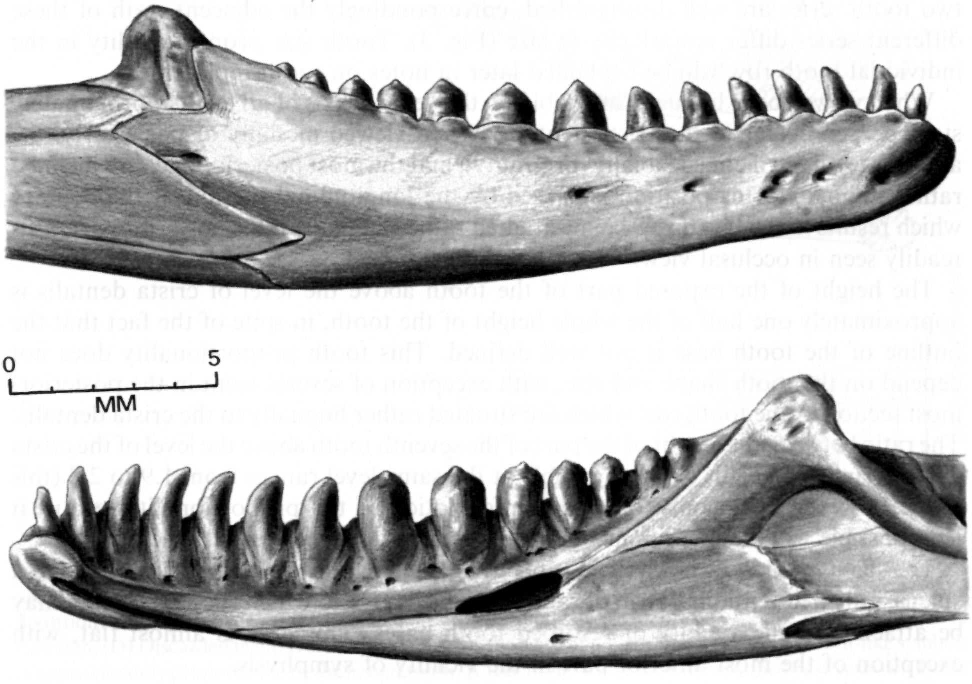

Fig. 1. Right lower dentition of Ophisaurus apodus (Klembara's collection No 6). The upper termination of teeth in the posterior set is rather anomalous. Drawings by I. Kolebaba

Pleurodonty is not developed to such a degree as, for example, in Iguanidae, Scincidae and Lacertidae; the inner aspect of the dentary to which tooth bases are affixed is not vertical, but sloping. The outlines of tooth bases are not well developed. The degree of basal resorption ranges from little depressions without connection with tooth pulps to large cavities which occupy almost the whole bases of teeth. The number of teeth ranges from 12 to 16 in the single tooth row and it can differ by one in the opposite ramus of mandibulae. However, young successive teeth are sometimes more numerous in the same area which suggests that some mature teeth (those which are elongated mesio-posteriorly) arose by fusion of two or more successive teeth (suspected and found occasionally in *Lacerta* – COOPER, in litt.). In the anterior part of the dentary, teeth are separated by a distance which approximately equals one half of the tooth width in the level of the crista dentalis. However, the space between the first and the second tooth may be larger. The blunt posterior teeth, if not yet at the stage of degeneration, are standing close each other. Both height and width differences between two adjacent teeth are only slight in the anterior series. Of course, the first and the last tooth of this series differ considerably, but the size changes along the series are gradual. In the posterior series, if teeth are not degenerated yet, the situation is similar as for gradual changes in the height. Both height and width, however, considerably but gradually decreases posteriorly here, so the posterior-most tooth is small and the first or the second tooth of this series is the largest, while in the anterior series the reverse situation occurs.

This is the case of the gradual shape transition between two types of teeth. But if the two tooth series are well distinguished, correspondingly the adjacent teeth of these different series differ remarkably in size (Fig. 3). Tooth size proportionality in the individual tooth row will be explained later in notes on tooth replacement.

When viewed both lingually and labially, the vertical axis of all teeth approximately stays perpendicular to the crista dentalis. When viewed mesially or posteriorly, the anterior teeth are inclined labially (prodonty), and the most posterior ones are inclined rather lingually. This position is caused by the longitudinal torsion of the dentary which results in the tooth row being situated rather lingually in its posterior part, as is readily seen in occlusal view.

The height of the exposed part of the tooth above the level of crista dentalis is approximately one half of the whole height of the tooth, in spite of the fact that the outline of the tooth base is not well defined. This tooth proportionality does not depend on the tooth shape and size, with exception of several teeth in the posterior-most section of the tooth row which are situated rather lingually to the crista dentalis. The ratio between the height of the part of the seventh tooth above the level of the crista dentalis and the height of the mandible at the same level ranges from 1.9 to 2.8 (this index, however, serves only for general information on this proportionality because it is impossible to take measurements in the exactly same view in all specimens).

The sulcus dentalis is not well developed. Below the tooth bases there is, instead of a sulcus, only a longitudinal strip of rather wrinkled bone to which successive teeth may be attached in the vicinity of resorbed tooth bases. This area is almost flat, with exception of the most anterior part in the vicinity of symphysis.

The spina splenialis, although poorly developed in some specimens, is constantly present. The number of foramina pro rami nervorum alveolarium inferiorum ranges from 4 to 6. This number can be considerably different in left and right dentary (4 and 6 respectively).

Maxillary—The maxillary dentition shows the exactly same features as were described in the dentary. When evaluating both maxillary and premaxillary dentitions together it is necessary to state that tooth size in the anterior series of maxillary teeth gradually decreases up to the most anterior tooth, but the premaxillary teeth grow in size again in the direction to the median line. The number of foramina pro rami nervorum alveolarium superiorum is mostly 4 (sometimes also small 5th is present). The number of teeth is 10–14.

Premaxillary—It is the unpaired element, its teeth generally corresponding to the most anterior dentary teeth including striations and other characters. There are slight differences in size between median and lateral ones. The number of teeth is 7 or 9; the odd tooth is situated towards the median line. The ratio between processus nasalis and processus maxillaris ranges from 1.4 to 1.6

(ii) Notes on Tooth Replacement

At first, it is necessary to say that the two tooth types described above do not reflect different stages of tooth history. In all specimens conical teeth are in the front of the tooth row and the blunt teeth are in the posterior part of it. Teeth are laid down in the lamina dentalis which can be seen on carefully prepared jaws as a slight transparent

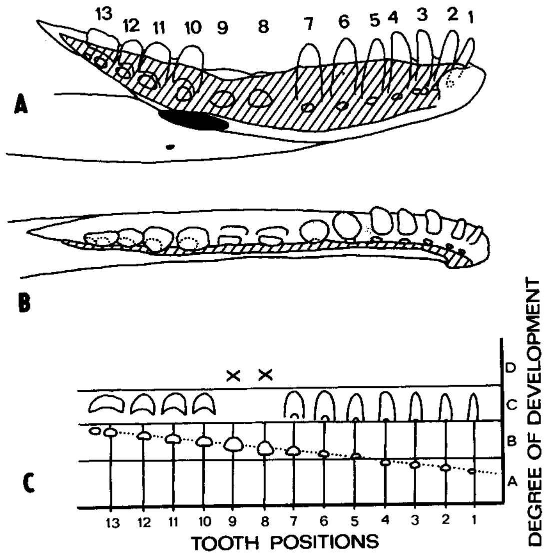

Fig. 2. Left mandible of Ophisaurus apodus, NMP 22071. A—lingual view. B—occlusal view. The shaded area represents the extent of soft tissue of the dental lamina. C—diagram to show stages in the ontogeny of a dentition: (A) Tooth buds on the lamina dentalis, (B) Successive teeth attached to the bone, (C) Teeth in function, (D) Discarded teeth. Dotted line represents the wave of replacement. The size of tooth-like symbols is approximately proportional to the actual tooth. A functional tooth with the resorbed base is shown by the symbol with closed arch-like base; a tooth with beginning of basal resorption by the symbol with open arch-like base

band of tissue lining the lingual wall of the tooth bearing bone. Histologically, the lamina dentalis is a specialized part of oral epithelium (COOPER 1965, EDMUND 1960, 1969). At the beginning of tooth formation the tooth bud is firmly connected with the lamina dentalis. As the developing tooth increases in size it moves occlusad on the labial wall of the lamina. The lamina, including replacement teeth, is often lost during maceration of the skeleton. The lingual side of tooth bases of functional teeth become rather concave which is the more obvious the larger the successive tooth is. The old teeth can be shed already at this stage when the successive teeth are not yet firmly attached to the bone. However, in other *Ophisaurus apodus* specimens one can observe that old teeth remain until the stage when successive teeth already are firmly ankylosed to the bone. Therefore, at certain times, at least in some parts of the tooth bearing bone, two tooth rows exist: the lingual one consisting of small but well ankylosed successive teeth, and the labial one consisting of functional teeth (see Figs. 2 and 3). The bases of the old teeth become resorbed to such a degree that more or less large openings are broken into the tooth hollows. Successive teeth gradually move into these cavities and old teeth are then shed.

The successive teeth develop in front of the posterior half of the old teeth, but not in the interpositions. In the case of teeth with bases extended mesio-posteriorly, two small successive teeth are situated in front of them on the lamina dentalis. It suggests that these prolonged teeth develop by fusion of at least two successive teeth of the same generation.

In some specimens examined, however, no successive teeth were observed and also no other evidence of tooth replacement was found. It suggests that at some periods of the life none of the teeth are replaced, and that tooth replacement cannot be continuous in time.

A rather more complicated problem is the explanation of the mode of tooth replacement. In some specimens (for example NMP 22071, Fig. 2) it seems as if the replacement does not proceed in regular waves as successive teeth are observed along the whole tooth row, and their proportional size in comparison with the functional teeth in the same tooth position is approximately the same, that is, the most robust functional teeth which are situated in the middle of the tooth row are accompanied by the largest successive teeth. However, further details can be observed which considerably illuminate this situation. Four anterior-most successive teeth are still firmly attached to the dental lamina without any connection with the bone. The next five successive teeth in the middle section of the tooth row are already attached but not firmly ankylosed yet to the bone. The positions of three of them are on the bottom of space between the lamina dentalis and bases of functional teeth, the positions of remaining two of them are already in the row of functional teeth (see Figs. 2 and 3). The most posterior successive teeth are ankylosed already and are hidden completely in the resorbed cavities of old teeth. One can conclude that in the specimen NMP 22071 the wave of replacement involves all teeth in the tooth row and that it is impossible to differentiate the tooth row into odd and even sets (cf. EDMUND 1960). This can be deduced from the facts that the wave of replacement influences adjacent teeth gradually from the rear to the front without any interruption, and that two adjacent teeth are shed. The orgin of this diastema is not due to a chance because the same gaps in the same positions also occur contralaterally and in both maxillaries. But why the

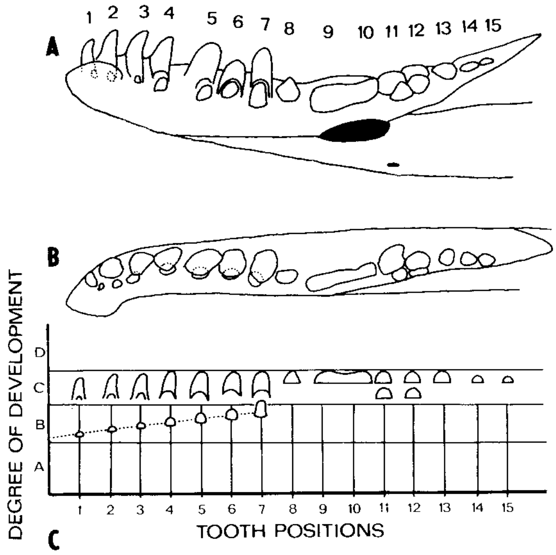

Fig. 3. Right mandible of Ophisaurus apodus, NMP 23583. Permanent functional teeth are shown by a symbols with straight bases. Other explanations are the same as in Figure 1

posterior-most teeth are not shed instead of the eight and nineth ones? The possible answer on this question is offered by the specimen NMP 23583 (Fig. 3). In this case only seven anterior teeth show the wave of replacement with successive teeth in a high degree of development. The situation confirms the above statement that the wave of replacement goes through adjacent tooth positions. The posterior half of the tooth row, however, consists of highly degenerated teeth which are present as rudiments of formerly well developed teeth and which do not show any marks of the next tooth generation.

The explanation can be given that the posterior half of the tooth row consists of teeth which are regularly affected by waves of replacement in the younger individual, but which become permanent after achievement of a certain age. It can be deduced from the following fact that the permanence or replacement of teeth in the posterior set is dependent on the individual age: it is known that the number of teeth in the tooth row is usually greater in old than in the young specimens (EDMUND 1969). Therefore, the specimen NMP 23583 with the tooth row consisting of fifteen tooth positions (Fig. 3) is older than specimen NMP 22071 with only thirteen tooth positions. The situation observed in specimen NMP 22071 can be taken as transitional between the stage with tooth replacement including the posterior segment of the tooth row, and the stage with fully permanent teeth in this posterior part. This transitional nature is indicated by the fact that teeth in the posterior segment of the series which will be regularly replaced in the future (teeth at position 8 and 9; see Fig. 2) are shed instead those which become perhaps in next generation permanent ones.

(iii) Biometrical indices

LtP/LCD 0.41–0.48	LtP/LM 0.41–0.59
LCr (in mm.) 36.4–44.8	LMd (in mm.) 35.5 44.5

Discussion

There is a basic disagreement in the above results on *Ophisaurus* in comparison with the general statement of EDMUND (1960) who noted (p. 78): "In all anguids tooth replacement occurred in the common wave pattern ... No irregularities were noted". The reason would be caused by the fact that this author generalized results of examination of only one *Ophisaurus* specimen *(O. ventralis)* out of many representatives of this genus. The difference may be expressed as two points: (1) In *Ophisaurus apodus* it is impossible to differentiate the tooth row into odd and even sets in which the waves of replacement alternatively occur. In other words, the wave of replacement affects adjacent teeth. (2) Posterior teeth undergo replacement only in young and subadult individuals; as the individual achieves older age the replacement is restricted only to the anterior section of the tooth row, and posterior teeth become permanent.

Another of EDMUND's statements (1969), however, confirms these two conclusions indirectly. He notes for example (p. 134) that the usual, regular, wave-like pattern may be lacking in some groups, or that replacement rythm may be restricted to a certain segment of dentition. According to this author, the explanation may lie in the suppression of one or two adjacent tooth matrices to accomodate a single larger tooth. Such a suppression was observed also in *Ophisaurus apodus* (NMP 23583, 22071). COOPER (personal communication) observed in *Lacerta* replacement of two adjacent teeth by one larger successor. But as a tooth with an elongated base mesio-posteriorly is always the result, one is forced to take this only as an anomaly. It is not likely that teeth along entire jaw have arisen in this way, neither blunt-crowned nor conical ones.

As for replacement differences at the anterior and posterior tooth row segments: MILES (1967), COOPER, POOLE and LAWSON (1970) and some other workers conclude that the length of life of anterior teeth is found to be shorter than that of posterior teeth, and that (MILES 1967, ex EDMUND 1969, p. 135) "... it is possible to predict a condition where replacement is almost too slow to be observed posteriorly but still occurs anteriorly". EDMUND (1960) in his diagram of tooth replacement in *Ophisaurus ventralis* also confirms this suggestion: none of the posterior-most six teeth show basal resorption and four posterior-most teeth do not show any mark of tooth replacement. The tooth replacement considerably slows down with age also in *Lacerta viridis* (ROČEK, in press), and is suppressed completely in old specimens of *Agama agama* (COOPER, POOLE and LAWSON 1970). It can be supposed that this phenomenon is not uncommon within reptiles.

Another disagreement may be found when comparing the above results with statements of McDOWELL and BOGERT (1954) on the migration of successive teeth. They say that one of the especially characteristic features of anguinomorphs is that the successive tooth arises in the interdental position, behind, not beneath, the older tooth, and it is forced to migrate in a rostral occlusal direction. This is not the case in *Ophisaurus apodus* as may be seen from the Figures 2 and 3. The successive teeth develop in front of the functional teeth or rather in front of its posterior part in the case of large middle teeth. Successive teeth in interpositions were not found.

Acknowledgements. I thank Dr. J. Klembara and Dr. V. Seichert for the loan of specimens from their private collections, as well as Dr. I. Heráň, Curator of the osteological collections of National Museum, Praha. Special credit is extended to Dr. J. S. Cooper and Dr. D. F. G. Poole, Dental School, University of Bristol, Great Britain, who supplied me with many helpful remarks on the manuscript.

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Received: October 29, 1979