# Museum of Comparative Zoology

CAMBRIDGE, MASS. January 31, 1957 NUMBER 70

# "ANGUIMORPH" TOOTH REPLACEMENT IN AMPHISBAENA ALBA LINNAEUS, 1758, AND A. FULIGINOSA LINNAEUS, 1758 (REPTILIA: AMPHISBAENIDAE)

# By CARL GANS

In the course of an investigation into the status of the acrodont amphisbaenids it proved necessary to prepare the skulls of some related forms. When cleaning the mandible of a female specimen of *Amphisbaena alba* Linnaeus, 1758, it was noted that six to eight teeth were in the process of being replaced, while two or three others had only recently moved into position, and were as yet but imperfectly fused to the dentaries. The replacement teeth appeared to lie interdentally, between, rather than below, their predecessors.

McDowell and Bogert, in their recent revision of the anguimorph lizards (1954, pp. 102, 104, fig. 30), have stated that "alternate" tooth replacement was restricted to this group, all other lizards possessing "vertical" replacement. The amphisbaenids are generally considered to be Scincomorpha (Camp, 1923, p. 296) and if the distinction between an anguimorph and non-anguimorph pattern is as clearcut as McDowell and Bogert suppose, the occurrence of a pattern descriptively alternate would thus be unexpected here. For this reason and because certain other aspects of dental replacement in these forms seem worthy of special attention, it appears desirable to describe the female specimen mentioned above, as well as two specimens of A. fuliginosa Linnaeus, 1758, in which a similar replacement pattern was noted, in the hope of stimulating further research into these matters.

# The mandibular dentition of Amphisbaena alba

Figures 1 to 5 show labial and lingual views of the mandible of an adult (body length 440 mm.; length of mandibular ramus 15 mm.<sup>1</sup>) female specimen (MCZ 54299) from "Brazil." This had been cleaned by dissection following controlled applications of full strength commercial bleach to selected portions of the soft parts.



Fig. 1. (Upper) Amphisbaena alba. Lingual view of right mandibular ramus of MCZ 54299.

Fig. 2. (Lower) Amphisbaena alba. Labial view of same mandibular ramus as Figure 1.

<sup>1</sup> The length of the mandibular ramus has been selected as a convenient indicator of the total length of the specimen and is hence abbreviated as lmr.

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The first part of this description covers the general aspect of the dentition and applies equally well to the female cited and to larger specimens listed below. The description of the replacement pattern and of individual or possibly ontogenetic variation follows upon this.

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The dentition is weakly pleurodont, the height of the dorsal margin above the lingual shelf on which the teeth rest barely



Fig. 3. Amphisbaena alba. (MCZ 54299) Sketch of lingual view of right mandibular ramus showing location of the replacement teeth.

equaling the width of the tooth base. There are eight teeth on each side; the third is largest, the fourth, fifth, sixth, and seventh are slightly smaller, while the second, eighth, and first are progressively smaller in that order. All of the teeth are curved, this being most noticeable near the tip, and the curvature is directed medially and slightly caudad. There is a rotation in the tooth alignment so that the planes of curvature of the individual teeth do not lie parallel to one another. The teeth are of oval crosssection with the long axis lying in the plane of curvature.

The base of the fully formed tooth is hollow, the pulp cavity extending two-thirds of the total height of the tooth. About midway up the tooth the diameter of the cavity contracts so as to continue upwards as a thin cylindrical tube.

There is no tooth-bearing shelf as in a typical pleurodont dentition; instead, a ridge of bone (Fig. 6) rises to the projecting dorsal margin of the dentary between each two adjacent teeth (where replacement teeth are present this ridge is hollowed out to afford lodgement for the pit of the new tooth). Consequently

the base of each tooth is almost entirely surrounded by bone, to which it is ankylosed by a ring of cement. The lowest exposed point lies on the lingual aspect and careful, but thorough, preparation shows here a single round foramen.<sup>1</sup> The foramen leads into the pulp cavity and presumably carries its vascular and nerve supply. A line extending to the level of the tip of the interior cavity is visible on the lingual side. Inspection along the lingual aspect of even the smallest cap-shaped tooth germs reveals a slight scalloping so that this line may be formed during



Fig. 4. *Amphisbacna alba*. Lingual view of the left mandibular ramus of MCZ 54299.

tooth development by the fusion of the anterior and posterior portions. Several of the skulls showed longitudinal cleavage of the teeth along this line, which coincides with the long axis of the oval tooth cross-section.

Various stages of tooth replacement are shown in MCZ 54299. In the subsequent description of it and other specimens, L and R will stand for left and right mandibular ramus, and the number following this for the particular tooth or alveolus counting from front to back.

At L-7, R-3 and R-4 the replacement tooth is but a small hollow conical shell, thicker at the top than at the sides, its lower edge somewhat excavated on the lingual side. It lies in a small and deep depression in the dentary in line with the posterior edge

<sup>1</sup> These foramina, as shown in Figure 6, are of a larger specimen, which could be cleaned completely without danger of dislodging the firmly fused teeth.

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of the tooth it is replacing. As a result, this pit lies on the ascending ridge directly between the tooth to be replaced and the one posterior to it. Even at this stage there is already some erosion into the base of the tooth being replaced.

L-4 and L-5 show a slightly more advanced stage with progressive erosion into the precursor and an increase in size of the enamel cap of the new tooth.

In R-8 the replacement tooth has reached approximately onethird of its final height, though its tip is still below the level of the projecting dorsal margin of the dentary. It has, however, destroyed almost half of the base of the tooth lying above it.



Fig. 5. Amphisbaena alba. (MCZ 54299) Sketch of lingual view of left mandibular ramus showing location of the replacement teeth.

At R-6 the tooth has just moved into its final position, its predecessor having been pushed out at some prior stage. It is still only loosely held in place by struts of cement, and appears slightly smaller, and thinner-walled than its neighbors. Its dark appearance is due to the contents of the large, soft-tissue-filled pulp cavity being visible through the translucent walls. This may indicate that the build up of the internal dentine layers is not completed until after the tooth is finally cemented into place.

The heavier enamel and more opaque, shell-like appearance of L-3 may indicate a more advanced stage of development. It is, however, still darker than its neighbors, and its base is still far from fused to the dentary. Its slightly cocked position seems to indicate that it is not fully aligned as yet.

All of the replacement teeth except the last two lie freely in the soft tissues and show no fusion to the dentaries.

Another interesting point is that the alveolus formation appears to start in the interdental ridge and only begins to extend into the base of the precursor tooth as growth takes place. No pits or alveoli were found at the base of any tooth that was not undergoing replacement.

Though the replacement pattern is interdental it differs from that described by Camp (1923, p. 329, fig. H) for *Gerrhonotus s. scincicauda* (Skilton), 1849 (and from that seen in a skull of the same form in the MCZ). In this specimen there is no trace of cavity or alveolus formation and the replacement tooth appears



Fig. 6. *Amphisbaena alba*. (MCZ 32257) Dorsal view of tip of mandible, to show interdental bone ridges, basal foramina, and fusion lines.

to lie always in the layer of tissue next to the bone. *Gerrhonotus* s. scincicauda is also definitely pleurodont and does not possess the interdental ridge that produces what is almost a sub-thecodont condition in *Amphisbaena alba*.

The pattern in *alba* is actually closest to that of the snakes (Bogert, 1943, p. 327 ff.). Here the replacement occurs in pairs, alternate teeth being replaced, while those between them are functional. This results in the characteristic tooth – alveolus –

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tooth – alveolus succession of the prepared dentate bones of the snake skull. *Amphisbaena alba* differs from this in that at each locus only one replacement tooth appears to be present at a time, and that this erodes its own pocket into the interdental ridge.

Four Amphisbaena alba skulls and mandibles from museum collections were available for comparison (MCZ 4031 - Brazil, lmr = 23.5 mm; MCZ 32256 - Surinam, lmr = 20 mm; MCZ 32257 — Brazil, lmr = 22.5 mm; AMNH 73233 — no data, lmr = 17 mm). In only one of these was any soft tissue still present along the lingual aspect of the dentary, but in this as in the others there was not the slightest indication either of replacement teeth or of eroded areas in the interdental ridges which might have lodged replacement teeth. This lack of evidence of tooth replacement may perhaps be related to the fact that all of the skulls were larger (see lmr above), and hence probably belonged to older specimens. The tip of one of these lower jaws is figured (Fig. 6) and illustrates not only the basal foramina previously referred to, but also the interdental bone ridges and the strong cementing of the tooth bases. The complete absence of evidence of replacement activity in these adult specimens, contrasted with the large number of teeth undergoing almost simultaneous replacement in the above described smaller specimen, may indicate that the ability to replace the teeth is lost in the adults.

It is interesting to observe that there is no evidence for the replacement of maxillary or premaxillary teeth in any of the skulls of A. alba examined.

# The mandibular dentition of Amphisbaena fuliginosa

All available dried amphisbaenid skulls were examined for evidence of tooth replacement. Only two medium-sized specimens of *Amphisbaena fuliginosa* (MCZ 2154 — South America, lmr-8mm; MCZ 7799 — Riobamba, Ecuador, lmr-8 mm; listed by Zangerl 1944, p. 426 as specimens A and B) demonstrated a discernible tooth replacement pattern.<sup>1</sup>

Figures 7-10 show lingual views of two of the mandibles of

<sup>&</sup>lt;sup>1</sup> A very clean skull of *Rhineura floridana* Baird, (1858) (Gainesville, Florida) from the collection of Walter Auffenberg also reveals that some sort of tooth replacement occurs in this form. Since there are many reasons such as overcleaning, etc., which might explain the absence of tooth replacement evidence in any given specimen, no useful purpose would be served by listing the names or numbers of specimens examined with negative results.

A. fuliginosa. The dentition is again pleurodont, with the lateral shelf slightly higher than the width of the tooth base. The teeth appear to lie in a slight trench formed between the lingual shelf and the ascending face of the dentary. This trench is crossed by only faint and occasional ridges.

There are seven teeth or large alveoli in each of the four



Fig. 7. (Upper) Amphisbaena fuliginosa. (MCZ 2154) Lingual view of left mandibular ramus.

Fig. 8. (Lower) Amphisbaena fuliginosa. (MCZ 7799) Lingual view of right mandibular ramus.

mandibular rami. However, the broken tooth spacing of the somewhat macerated mandible of one of the specimens (MCZ 7799) (Figures 8, 10) leads one to suspect that we are dealing with a row of eight teeth. The third and fourth teeth are again the largest, with numbers five, six and two equal to each other and slightly smaller, while seven and one are smallest. In other aspects the mandibles closely resemble those of A. alba though the cementing of the teeth is not quite as solid.

Three replacement teeth are visible in each of the mandibular rami of MCZ 2154 and two or three in each of MCZ 7799. These



Fig. 9. (Upper) Amphisbaena fuliginosa. Sketch of mandibular ramus shown in Figure 7 to show locations of replacement teeth.

Fig. 10. (Lower) Amphisbaena fuliginosa. Sketch of mandibular ramus shown in Figure 8 to show locations of replacement teeth.

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again lie clearly interdentally and the general pattern of the dentition is very similar to that previously described for A. *alba*. The largest replacement tooth, the precursor of which is still in position, is but slightly higher than the dorsal margin.

However, there is one item apparent in these jaws that cannot be seen in the specimen of A. alba, where the erosion always takes place on the posterior edge of the tooth undergoing replacement. In A. fuliginosa there are several instances of teeth eroded on the front only or on both front and rear. This is the case in R-5 and L-7 of MCZ 2154, as well as in R-3 and R-4, and possibly L-4 of MCZ 7799. Both in R-5 of MCZ 2154 and in R-3 of MCZ 7799 the developing anterior replacement tooth is considerably larger than the tooth that is eroded. The anterior tooth has thus eroded itself an alveolus wider than that of its precursor. The general spacing indicates that what is involved here is a rearrangement, respacing or perhaps a change in the tooth number, possibly due to the growth of the mandible.

Both sets of upper jaws show evidence of tooth replacement, with alveoli present above both maxillary and premaxillary teeth. As far as can be seen from the skulls, which are somewhat overcleaned for this purpose, the replacement proceeds alternately as described above. The only complications are due to the different alignment of the various teeth which make terms like "alternate" and "vertical" very difficult to apply here.

# Discussion and Summary

# In Amphisbaena alba and A. fuliginosa:

The teeth are pleurodont in that they lie against the lingual side of the dentary on a low shelf.

A ridge rises between each two teeth. This character, which gives the dentition a sub-thecodont appearance, is most strongly expressed in older or larger individuals.

The teeth when fully grown have a pulp cavity extending through more than two-thirds of their total height, and are fused to the dentary by a heavy layer of cement around their base. Vascular supply reaches the pulp cavity by a foramen located on the ventral edge of the tooth's lingual aspect.

Tooth replacement is alternate, with the developing tooth lying in a deep pit close to the posterior edge of its precursor. During growth it erodes away the posterior aspect of its precursor and sometimes the anterior face of the tooth next in line. The latter feature may provide for rearrangement or change in number of teeth. As the mandible lengthens and the individual teeth increase in size, it becomes possible for the replacement teeth to realign themselves (thus extending the length of the tooth row, and maintaining or increasing the interdental gap), rather than being restricted to entering the exact alveolus vacated by their precursor. Shortly after the new tooth extends higher than the dorsal margin it either displaces the tooth above it or the latter breaks away due to the dissolving of its base.

When initially entering the alveolus the new tooth is dark and has but a thin coating of enamel. Internal dentine deposition appears to continue until the tooth is well cemented into place.

In Amphisbaena alba there is evidence that tooth replacement either becomes rare or stops altogether beyond a certain size. If the function of the replacement were related to the provision of larger teeth, this phenomenon might result from a flattening of the growth curve with age.

None of the skulls of A. alba examined showed any evidence of tooth replacement on maxillaries or premaxillaries.

Both taxonomically and in a descriptive sense these results modify the simple picture presented by McDowell and Bogert. It is hoped that this brief note will stimulate supplementary investigation of this problem in every family and genus of the Squamata. This seems particularly desirable since even a cursory inspection of the lizard skeletons in the MCZ shows such divergence in the patterns<sup>1</sup> of tooth replacement that clearly they cannot be described in terms of just two categories — anguimorph or non-anguimorph.

 $^1$  Some of these patterns have previously been referred to in the literature (e.g. Camp 1923, p. 329, fig. H).

I wish to acknowledge the aid of the following friends, who read the manuscript and commented thereon: Walter Auffenberg, Charles M. Bogert, Tilly Edinger, Gordon Edmund, Richard van Frank, Arthur Loveridge, Samuel B. McDowell Jr., M. Graham Netting, Neil D. Richmond, and Ernest E. Williams.

This paper was completed while working under a National Science Foundation Predoctoral Fellowship.

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