Tooth Replacement in the Red-backed Salamander, *Plethodon cinereus* [1]

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ABSTRACT The developmental cycle of the teeth in *Plethodon cinereus* is analyzed on morphological grounds using alizarin preparations. All the stages in development do not occupy the same proportion of the life cycle time. Functional teeth and germs at an early stage in development occupy a large proportion of the life cycle time, whereas the processes of tooth shedding and ankylosis occur very quickly. The time during which any locus does not bear a functional tooth, and is therefore a non-functional locus, is reduced to a minimum. *P. cinereus* has a basic pattern of tooth replacement which is consistent with *Zahnreihen* which are 2.0 tooth spaces apart. Variations in the replacement pattern are common and these are produced by relatively small fluctuations in the spacing of the *Zahnreihen* around the "mean" of 2.0. Localized disturbances which produce breaks in the replacement pattern and cause waves to cross also occur. These may be due to the failure of tooth germs to develop, the fusion of tooth germs, or may be the result of the inherent variability in a complex biological system. This variability causes individual tooth germs to develop too slowly or too quickly and hence assume an "abnormal" position thus causing breaks in the replacement pattern. Tooth replacement may be controlled by an intra-local mechanism(s) rather than by stimuli which travel along the jaw.

Replacement of teeth throughout life (polyphyodonty) is a characteristic of lower vertebrates and the pattern of replacement revealed by the arrangement of functional teeth and non-functional buds varies from species to species. Edmund ('60) recognized two features of tooth development which could be controlled by some intrinsic regulating mechanism to product characteristic patterns of replacement:

1. The time interval between the successive "stimuli" initiating tooth development. He visualized such stimuli passing caudad along the dental lamina and producing a tooth germ at each locus in turn; and 2. the rate of development of individual tooth buds.

The total cycle of tooth development and replacement (Life Cycle Time, see Lawson, '66) may be conveniently divided into stages on morphological grounds, and it has been noted that a tooth germ does not necessarily spend an equal amount of time in each stage (Gillette, '55; Goin and Hester, '61; Lawson, '65b, '66). A bud may pass rapidly through some stages and more slowly through others.

Edmund ('60) used the term *Zahnreihe* to describe the teeth and tooth germs produced by a single "stimulus" at any moment in time. Graphically the *Zahnreihen* are oblique lines connecting teeth in adjacent loci (see figs. 4–7). The number of teeth in any *Zahnreihe* is determined by the rate of tooth production relative to the rate of resorption. If the rate of resorption is greater in one species than in another the *Zahnreihen* of that species will contain fewer teeth, assuming that the rates of production are similar.

The term replacement waves was used by Edmund ('60) for the rows of teeth, in alternate loci, that are produced by successive stimuli. Each tooth in a *Zahnreihe* is a member of a different replace-

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ment wave. He demonstrated that when the interval between successive stimuli is 2.0 tooth spaces then the replacement waves are of infinite length and run parallel to the longitudinal axis of the jaw, i.e., the teeth in each wave are all of the same age. He further showed that if the interval between stimuli is increased to 2.5 tooth spaces the waves become slanted, and the age of the teeth in any wave increases in a posterior direction. If the interval is increased to 3.0 tooth spaces the slope of the waves increases further and the age difference between adjacent teeth becomes greater. If the interval between stimuli falls below 2.0 then the direction of the replacement waves is reversed, in which case the oldest tooth in any wave is the most anterior. Few workers have used Edmund's method to describe tooth replacement in lower vertebrates and only three others have analyzed tooth replacement phenomena in amphibians in any detail. Gillette ('55) worked with *Rana pipiens;* Goin and Hester ('61) studied *Hyla cinerea;* and Lawson ('65b, '66) used *Hypogeophis rostratus* and *Rana temporaria.* No analysis of this type is available for urodeles. Therefore, the primary object of this paper is to present data concerning the pattern of replacement in the salamander *Plethodon cinereus.*

MATERIALS AND METHODS

The fourteen specimens of *Plethodon cinereus* used in this study were collected at Indiana Dunes State Park in Porter County, Indiana, on May 21, 1966. There were nine females and five males. All were sexually mature, as determined by gonad development and the snout-vent length criteria established by Sayler ('66). Measurements were made from the tip of the snout to the posterior angle of the vent after fixation.

The salamanders were fixed in 10% neutral formalin and stored in 70% ethanol. The specimens were then placed in a mixture of 3% H_2O_2 and 2% KOH for several hours, then into a solution of trypsin in a sodium tetraborate buffer after a soaking in distilled water to remove the KOH. When nearly translucent, the specimens were stained with alizarin red-S and cleared in a graded series of glycerin solutions. They were stored in 100% glycerin. The mineralized parts of the skeleton and teeth, with exception of the enameloid, were stained in deep pink-red. The enameloid [2] remained transparent, and usually colorless, but could sometimes be seen as a clear yellowish-brown layer capping each cusp of the tooth. In addition to the above material, two adult *Gyrinophilus porphyriticus* were used in the investigation of parasphenoid dentition.

Gillette ('55) stated that maceration in KOH could result in loss of teeth and recommended prolonged treatment in alcohol, followed by clearing in oil of wintergreen. However, clearing techniques involving KOH and glycerin were used by Stewart ('58), Goin and Hester ('61), and Lawson ('65b, '66), who reported no significant loss of teeth or germs. The KOH-glycerin technique was therefore considered suitable for use in this study. It is not likely that any developing teeth were lost during treatment since the tongue and tissues of the mouth would tend to hold them in place, and the mouths were not opened until the clearing treatment had been completed. The mature, ankylosed teeth could be removed with forceps, but only through the application of considerable force.

To establish criteria for defining developmental stages, all tooth buds and some ankylosed teeth of a mature female were removed, embedded in glyecrin jelly, and examined under a dissecting microscope.

Dentition of Plethodon cinereus

No significant differences were found between the tooth buds and teeth of the maxilla as compared with those of the mandible or vomer. The premaxillary teeth and tooth buds of the five males showed the characteristic monocuspid state noted by Noble ('31) and Stewart ('58) in plethodontid males; with this exception, there were no differences in morphology between teeth and tooth buds of opposite sexes. The teeth were left intact in the jaw in the remaining specimens.

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[2] Considerable confusion exists as to the structure and embryological origin of the hard outer covering of the teeth in lower vertebrates. Poole ('68) suggested that the term *enameloid* be used to describe this material in fishes and amphibians.

The teeth of *Plethodon cinereus* are located in three groups: (1) along the dentary bone of the lower jaw and the premaxillary and maxillary bones of the upper jaw (*marginal teeth*); on the posterior part of the vomer and on the medial one-half of the pre-orbital process of vomer (*vomerine teeth*); and (3) in two patches below the parasphenoid bone (*parasphenoid teeth*). The last group is derived embryologically from the extension of the vomerine tooth row; they are essentially posterior vomerine teeth. Each parasphenoid patch consists of several rows of teeth with one or two rows of replacement buds along the lateral border and teeth undergoing resorption along the medial border (fig. 1).

Tooth replacement

On the basis of cleared and stained material (see materials and methods), it was possible to divide the developmental cycle of the teeth of *Plethodon cinereus* into seven stages (see fig. 2):

(a) Calcification of the tooth bud beginning; bud very small, at its farthest distance from the occlusal margin, and may be lying on its side at right angles to the long axis of the ankylosed tooth anterior to it; lingual and labial cusps of nearly equal size.

(b) Bud somewhat larger and closer to the occlusal margin; lingual cusp somewhat larger than the labial.

(c) Bud elongated; enameloid cap sometimes seen as a yellowish-brown layer on tip of cusps; lingual cusp much larger than labial; tooth parallel to axis of ankylosed tooth.

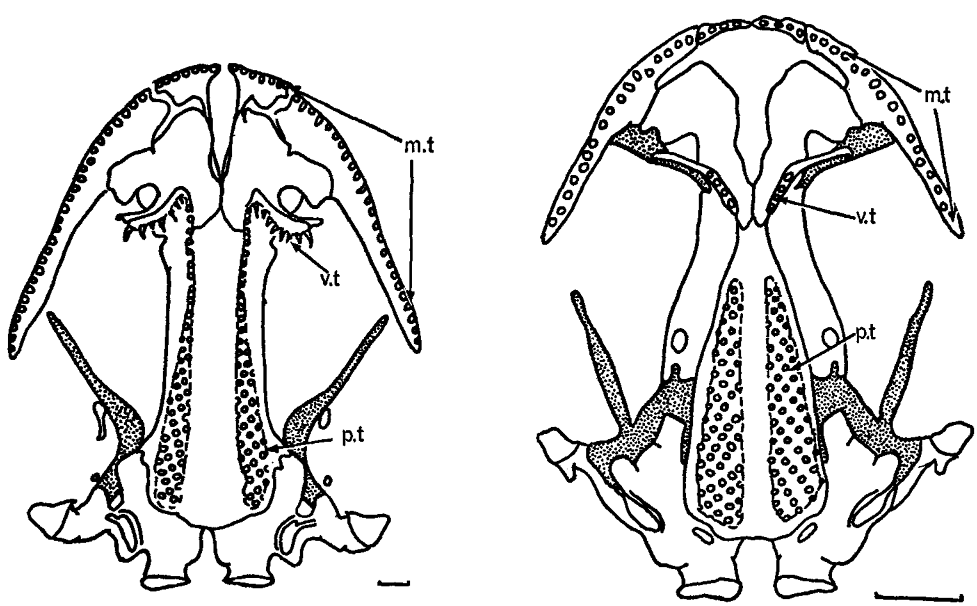
(d) Tooth moving into an empty socket and beginning to form a pedicel which is as yet uncalcified.

(e) Pedicel calcifying from above downwards (a dark red ring adjacent to the fibrous band is characteristic of this stage).

(f) Mature ankylosed tooth.

(g) Crown lost; pedicel absent or almost completely eroded.

The process of erosion of the pedicel in *Plethodon cinereus* is apparently very rapid since one rarely sees a tooth in which the pedicel is partly eroded. Usually all that



G. porphyriticus P. cinereus

Fig. 1 Ventral view of the skulls of *Plethodon cinereus* and *Gyrinophilus porphyriticus*. m.t., marginal teeth; p.t., parasphenoid teeth; v.t., vomerine teeth. Scale 1.0 mm.

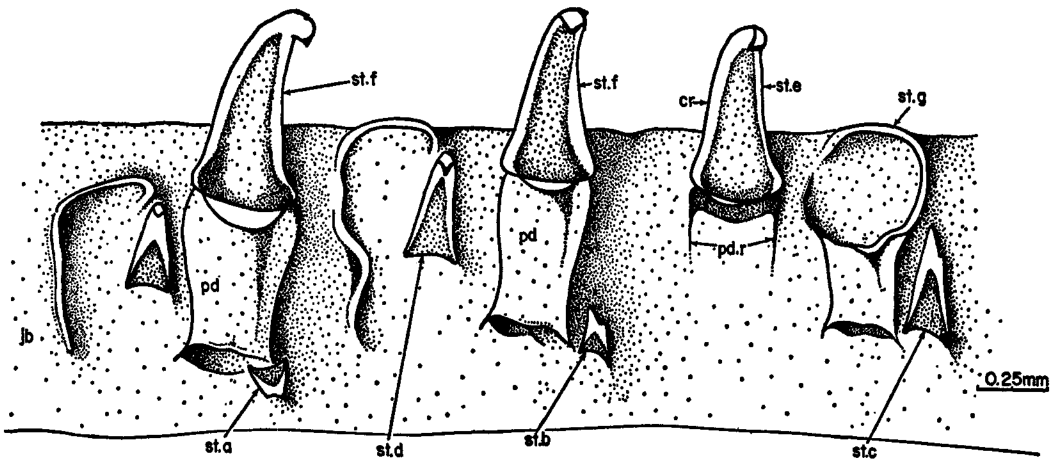


Fig. 2 Lingual aspect of the lower jaw of *Plethodon cinereus* showing the stages in tooth development and erosion. cr, crown; jb, dentary; pd, pedicel; p.r., pedicel rudiment; st. a, through st.g. states a-g in life cycle of the tooth.

is visible is an empty space containing remnants of the anterior wall of the pedicel. It is not clear whether the crown of the tooth is lost first, after a weakening of the fibrous band connecting it to the pedicel, or whether the entire tooth is shed. In *P. cinereus* the crown is missing from the tooth at one or two loci in three different specimens while the pedicel is still intact. In remaining animals, however, a few pedicels at various loci show some indication of erosion along the posterior wall while the crown is still attached. This is also true of some loci in the three specimens with missing crowns. The evidence therefore suggests that loss of the crown before erosion of the pedicel begins is an accidental occurrence in *P. cinereus* and that resorption of the posterior wall of the pedicel is normally the first step in loss of the tooth. Rose ('68) reports a similar situation in *Amphiuma tridactylum*. After the crown is lost, the lateral and lastly the anterior wall of the pedicel begin to erode, leaving a shallow depression at the site of the former tooth. The replacement tooth is generally moving into this depression as the anterior wall of the pedicel is being eroded.

The process of tooth erosion occurs in a similar manner in anurans (Gillette, '55; Lawson, '66), in the caecilian *Hypogeophis rostratus* (Lawson, '65a,b), and in most reptiles (Edmund, '60, '69). In these forms, however, there are usually more pedicels in the early states of erosion along the tooth row, indicating that the process occurs less rapidly than in *P. cinereus.*

Analysis of tooth replacement in marginal and vomerine tooth rows

Graphs of the replacement patterns of the mandibular, maxillary (including the premaxillary teeth), and vomerine dentitions of each specimen were constructed by plotting the state of development of each tooth and tooth germ against its position in the jaw (locus). The tooth loci were numbered from the anterior midline towards the end of each tooth row. The number of teeth in each stage of development was tabulated and calculated as a percentage of the total number of teeth. This percentage was taken as an indicator of the relative duration of each stage (fig. 3; see also Goin and Hester, '61; Lawson, '65b, '66).

It is apparent from figure 3 that the developmental stages are not of equal duration since it follows that those stages which have a relatively long duration will be found most often whereas those which occupy a relatively short period of time will not be found so frequently. The tooth bud forms and develops through stages a and b relatively rapidly and these two

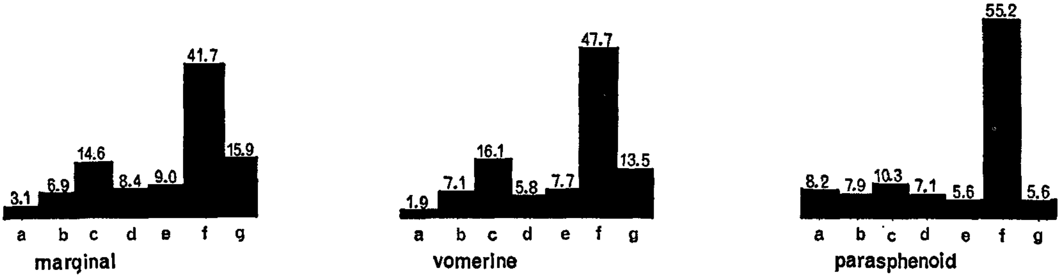


Fig. 3 Histograms showing the frequency of stages a-g in *Plethodon cinereus.*

stages account for 10% of the total life cycle time in the marginal teeth and 9% in the vomerine teeth. Stage c is of much longer duration and occupies 14.6% of the time in the marginal teeth and 16.1% in the vomerine teeth. The process of moving the tooth into position and ankylosis is rapid (17.4% in the marginal teeth and 13.5% in vomers) whereas the functional tooth occupies a major portion of the life cycle time (14.7% in marginal teeth and 47.1% in the vomerine teeth). The process of tooth erosion occupies from 15.9% of the life cycle in the marginal teeth to 13.5% in the vomers.

Figure 4 indicates that there is a good deal of variation in the pattern of tooth replacement in *P. cinereus.* This variation involves the number of teeth in each replacement wave, the direction of the waves and the spacing between the *Zahnreihen.* Figure 4a shows a specimen in which the replacement waves are discreet, run parallel to the longitudinal axis of the jaw and in which the *Zahnreihen* are approximately two tooth spaces apart. In figure 4b the replacement waves are again parallel to the jaw margin but cross each other. The spacing of the *Zahnreihen* is again around 2.0 tooth spaces. Figures 4c through 4f show replacement waves which run from anterior to posterior and *vice versa* and the spacing of the *Zahnreihen* varies from slightly more than 2.0 to slightly less than 2.0. It seems to us that the changes in the pattern of tooth replacement can largely be accounted for by variations in the spacing of the *Zahnreihen* on either side of 2.0 (see Discussion).

Analysis of tooth replacement in parasphenoid patches

Although tooth patches are a common feature in the dentition of lower vertebrates no previous attempt has been made to analyze tooth replacement in such areas. *Plethodon cinereus* has well developed tooth patches which contain several rows of teeth (figs. 1, 8). The teeth are separated from the parasphenoid by connective tissue and their bases are fused thus forming a relatively solid tooth mass. New teeth are added laterally and teeth are shed medially. The stages in tooth development and erosion are similar to those of the marginal and vomerine teeth. Unfortunately the parasphenoid patches in *Plethodon* are large and complex and therefore make analysis difficult. It was therefore decided to examine a simpler parasphenoid dentition to provide a basis for the study of the more complex one in *Plethodon.* The dentition chosen was that of *Gyrinophilus porphyriticus* since in this species each vomerine tooth row is extended posteriorly and then expands into a parasphenoid patch (fig. 1). Thus it affords the opportunity to trace the gradual transition from a single to multiple rows of teeth.

Tooth replacement on the vomer of *Gyrinophilus* involves *Zahnreihen* which are approximately 2.7 tooth spaces apart and replacement waves which contain four teeth on average (fig. 7). Hence the succession of teeth is similar in general nature to that of the marginal teeth of other lower vertebrates (including *Plethodon*) and involves well defined waves of replacement. In the parasphenoid patches of *Gyrinophilus* the number of rows of functional teeth is increased so that a single tooth family may contain up to six teeth (including both functional teeth and developing germs). The pattern of tooth replacement in the patches is similar to that of the anterior vomerine tooth row and there is a gradual transition between the two which involves no interruption of the sequence of replacement. The *Zahnreihen* remain approximately 2.7 tooth spaces apart. Additional waves of replacement in the parasphenoid patches are produced by the retention of successive generations of functional teeth in individual loci. The specific number of such generations determines the number of tooth rows and the ultimate shape of the parasphenoid patch. Figure 7b is constructed on a theoretical basis using *Zahnreihen* 2.7 spaces apart and in which successive generations of teeth are retained rather than shed. The results obtained are entirely consistent with those of the specimen.

The tooth patches in *Plethodon* are similar to those of *Gyrinophilus* and contain several rows of functional teeth. Initial examination of the tooth patches shows that the teeth are arranged in a number of well defined rows. However, it is difficult to decide whether the rows slope anteriorly or posteriorly and which teeth are members of the same tooth family. Analysis of tooth replacement was undertaken by placing each tooth graphically without any assumption regarding direction of tooth rows or the position of tooth families. Figure 8 indicates that tooth replacement is essentially alternate and the waves of replacement run parallel to the longitudinal axis of the tooth patch. The tooth families are oriented approximately

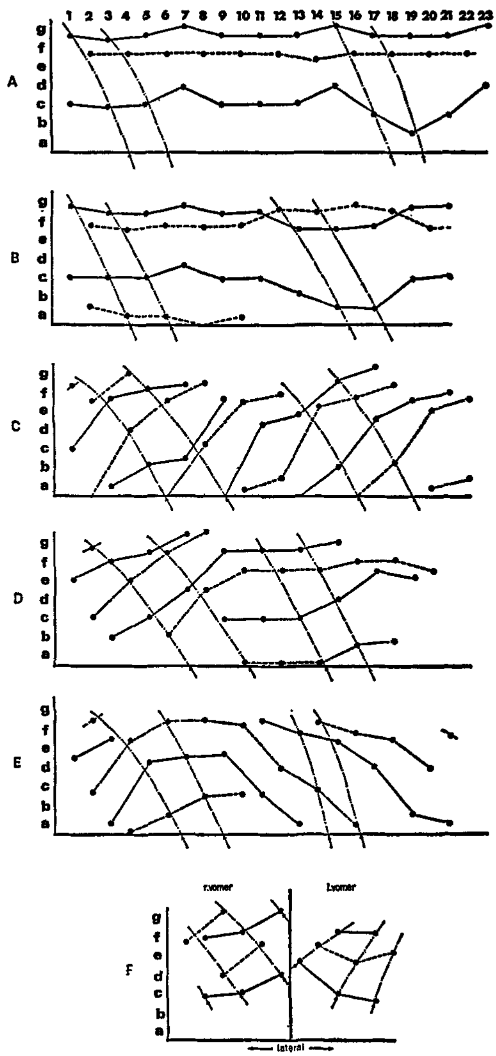


Figure 4

Fig. 4 Tooth replacement patterns in the marginal and vomerine teeth of *Plethodon cinereus*. a-g are stages of the tooth life cycle. 1–23 are tooth loci. The teeth and tooth germs are solid circles. Replacement waves connecting teeth in odd numbered loci are solid lines and those for even numbered loci, broken lines. The bases of the *Zahnreihen* are indicated by arrows.

Fig. 4a Replacement waves parallel to the jaw margin. *Zahnreihen* 2.0 spaces apart. Alternate replacement.

Fig. 4b Replacement waves parallel to the jaw margin but with cross-over of waves. *Zahnreihen* 2.0 spaces apart. Alternate replacement.

Fig. 4c Waves running from posterior to anterior along the jaw. *Zahnreihen* approximately 2.6 loci apart.

Fig. 4d In the anterior part of the jaw the waves of replacement run from posterior to anterior (*Zahnreihen* approximately 2.5 spaces apart). In the posterior part of the jaw replacement is roughly alternate with *Zahnreihen* 2.0 spaces apart.

Fig. 4e Replacement waves run from posterior to anterior in the anterior part of the jaw (*Zahnreihen* approximately 2.7 spaces apart). In the posterior part of the jaw the direction of the replacement waves is reversed as the spacing between the *Zahnreihen* falls below 2.0.

Fig. 4f Vomerine replacement waves traveling in medial to lateral direction. *Zahnreihen* more than 2.0 spaces apart.

at right angles to the patch and contain up to five teeth. The *Zahnreihen* are 2.0 tooth spaces apart. The only assumption which was made in the construction of figure 8 was that the "stimuli" which initiate tooth development (and hence control the slope of the *Zahnreihen*) travel posteriorly along the lateral border of each patch. The dentition of *Gyrinophilus* suggests that this is likely to be the case. However, if the stimuli ran in the opposite direction (postero-anterior) this would alter the orientation of the *Zahnreihen* but would not change the pattern of tooth replacement which would remain alternate (see fig. 8).

An important feature of the parasphenoid dentition in both *Gyrinophilus* and *Plethodon* is that there are very few teeth which are undergoing erosion. This suggests that the final stages of erosion are extremely rapid which ensures that at any moment in time the parasphenoid has a relatively complete battery of functional teeth.

DISCUSSION

1. *Crossing of replacement waves* (see fig. 4b)

The existence of breaks in the replacement waves where successive waves cross each other poses a problem, since according to the *Zahnreihen* concept the replacement waves must always remain discreet. Gillette ('55) suggested that such breaks are the result of the failure of certain tooth germs to develop. He indicated that these failures would be most likely to occur where severe overcrowding of dental units was an important feature of the growth of the jaw as a whole. There is no doubt that the failure of tooth germs to develop would produce the type of break which actually occurs (see fig. 4b). Figure 5a shows, in theoretical terms, the result of such a failure. It should also be noted that if two adjacent germs fail to develop, then no cross over of waves would occur (fig. 5b), and such occurrences (if they happen in reality) would produce no break in the replacement waves. Gans ('57) has used a similar argument to account for the irregularities he found in *Amphisbaena*. Edmund ('60) suggests that

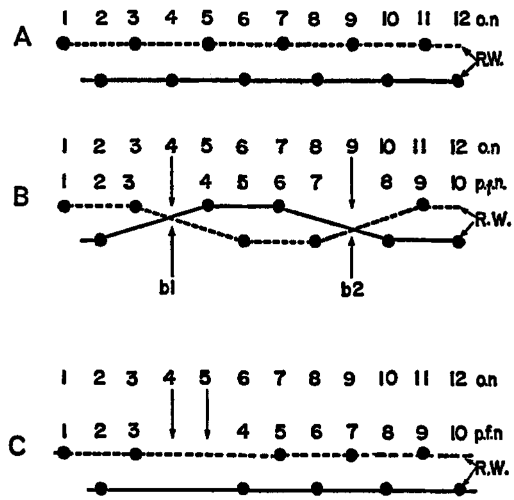


Fig. 5 Cross-over of replacement waves produced by tooth germ failure.

Fig. 5a "Normal" alternate replacement with waves running parallel to longitudinal axis of jaw. *Zahnreihen* 2.0 spaces apart.

Fig. 5b Germs at loci 4 and 9 fail to develop, producing breaks at b1 and b2 and the cross-over of replacement waves.

Fig. 5c Germs in adjacent loci 4 and 5 fail to develop. The sequence of replacement is unaffected.

Fusion of tooth germs rather than germ failure would produce similar effects. o.n. original number of locus, p.f.n. post-failure (or post-fusion) number, R.W. replacement waves.

this explanation is not likely to be correct, since in the gekkonid lizards which have numerous teeth, and would hence have similar overcrowding problems, the replacement pattern is orderly. We do not have, and it is difficult to see how one could obtain any firm evidence of germs failing to develop.

A second possibility is that the cross over of replacement waves could be accounted for by the *fusion* of adjacent tooth germs. The net result would be the same as those produced by dental failure. We have seen no evidence that such fusions occur in the dentition of *P. cinereus*, but Cooper ('63, '66) reports fusion of tooth germs in the lizard *Lacerta viridis* and the slow worm, *Anguis fragilis*.

It may be, however, that the cross over of replacement waves is due to variations in the growth rate of individual teeth. It seems to us that in such a complex system teeth will develop either too rapidly or too slowly and hence assume an "abnormal" position producing distortions in the replacement waves. We feel that such variations are to be expected and it would require only small fluctuations in the growth rate of individual teeth to produce the effects described.

We are unable to say which of the above possibilities is the most feasible and there is no reason why they could not all occur at different times or even simultaneously in the life of a given animal.

2. *Variations in replacement waves and Zahnreihen*

Considerable variation in the disposition and direction of the replacement waves in *P. cinereus* has been described (see fig. 4). Such variations may present some difficulty in an interpretation of the overall process of tooth replacement in this species. However, we are inclined to believe that the mechanism of replacement in the marginal, vomerine and parasphenoid teeth in this species is essentially one which involves (a) *Zahnreihen* which are 2.0 tooth spaces apart and (b) replacement waves which are of infinite length and run parallel to the jaw margin, i.e., alternate replacement. It is important to realize that small variations in the spacing of *Zahnreihen* on either side of 2.0 will produce relatively massive changes in the pattern of tooth replacement. For example, if the spacing is lowered from 2.0 to 1.9 then instead of the replacement waves running parallel to the jaw margin, long gently sloping waves which run from the *front* to the *back* of the jaw are produced. If on the other hand the spacing of the *Zahnreihen* changes from 2.0 to 2.1 then long waves run from *back* to *front* of the jaw. Figure 6a–c shows the effects, in theoretical terms, produced by the variation of the spacing of *Zahnreihen* on either side of 2.0. It is clear that the figures constructed on a theoretical basis clearly resemble those actually taken from the specimen (see fig. 4). It is important to note that a shortening of the spacing between successive *Zahnreihen* would tend to increase the rate of tooth replacement and an increase in the distance between *Zahnreihen* would have the opposite effect. Thus, modification in *Zahnreihen* spacing provides an immensely variable mechanism for alternating the pattern and rate of tooth replacement. We are unable to say whether the variations seen in *P. cinereus* are selected modifications in the mechanisms which control tooth succession or whether they are random variations around the "mean" of 2.0.

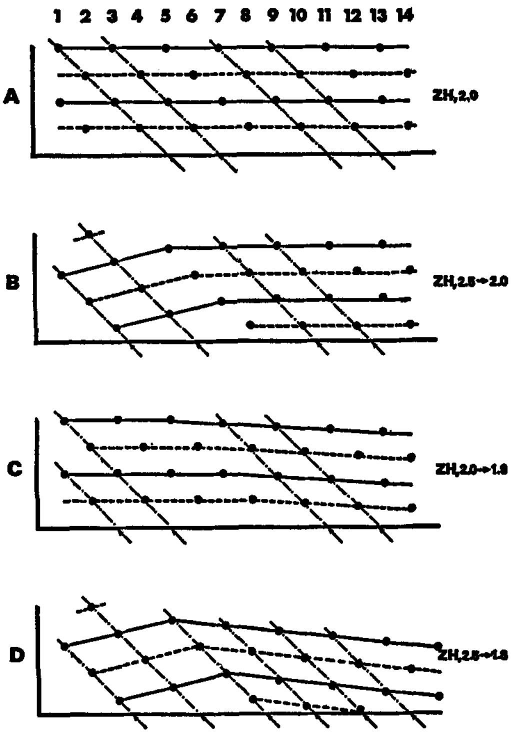


Fig. 6 Theoretical variations in replacement waves produced by alteration in *Zahnreihen* spacing.

Fig. 6a *Zahnreihen* 2.0 spaces apart. Alternate replacement.

Fig. 6b *Zahnreihen* spacing changes from 2.5 to 2.0

Fig. 6c *Zahnreihen* spacing changes from 2.0 to 1.9.

Fig. 6d *Zahnreihen* spacing changes from 3.5 to 1.8.

Compare 6a with 4a; 6b with 4d; 6c, d with 4e.

3. *Control of tooth replacement*

The *Zahnreihen* concept is based on the assumption that tooth production at successive loci is initiated by some "stimulus" which progresses along the jaw from anterior to posterior. It should be emphasized that such stimuli are hypothetical and no biochemical, physiological or cytological

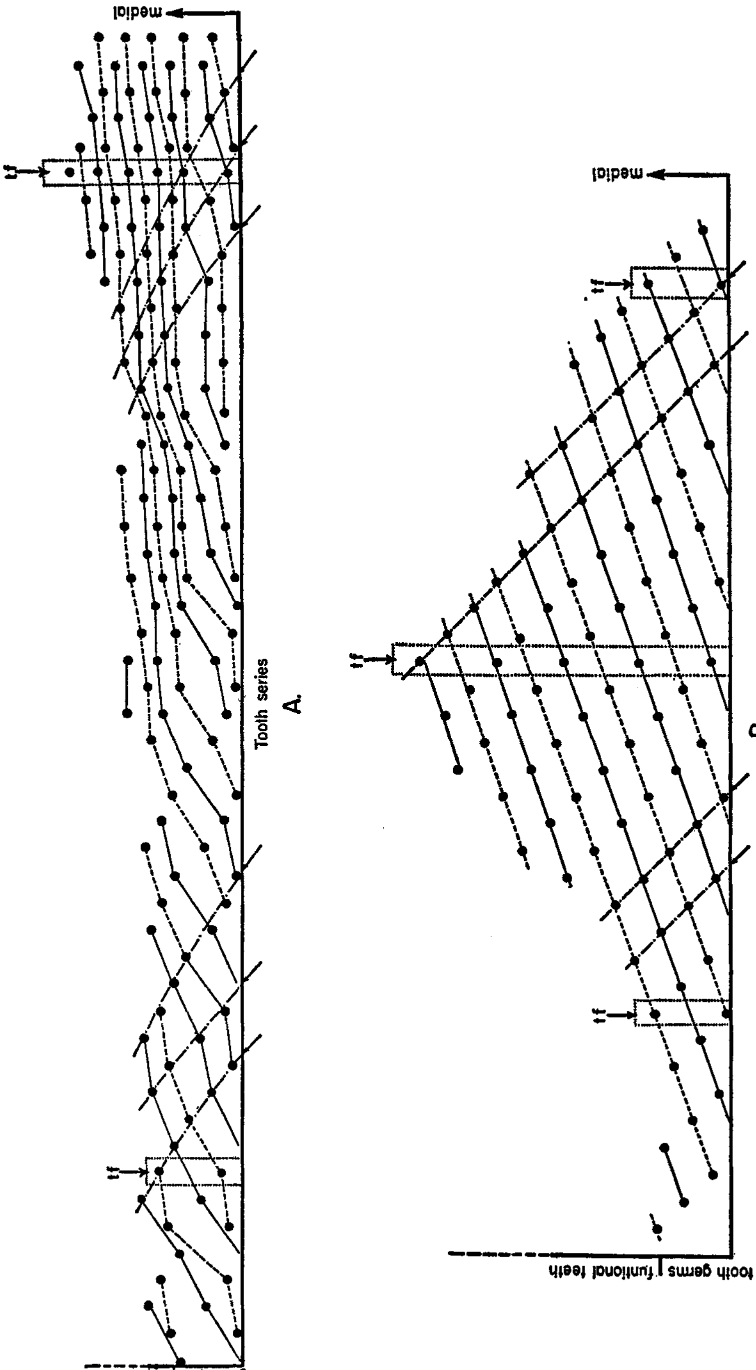


Fig. 7 Tooth replacement in *Gyrinophylis porphyriticus.*
Fig. 7a Graphic analysis of vomerine and parasphenoid teeth. *Zahnreihen* approximately 2.7 tooth spaces apart. Replacement waves running from posterior to anterior.
Fig. 7b Theoretical analysis generated by using *Zahnreihen* 2.7 spaces apart and varying the number of functional teeth retained in individual loci. t.f. tooth family.

evidence either supports, or denies, their existence.

Gillette ('55) pointed out that the erosion of a tooth pedicel is usually correlated with the development of a replacement tooth. He took this as an indication that the developing tooth initiates and controls the erosion of the functional tooth at the same locus. He also felt that the presence of a tooth germ at any locus might inhibit the formation of a bud at the locus immediately posterior to it, and that this inhibitory effect would persist until the anterior germ reached a certain stage in development. At this time the inhibition would be removed and the more posterior germ would be allowed to develop. He correctly pointed out that this would produce a similar effect to that of moving stimuli. There are two features of the dentition of *P. cinereus* which indicate that the mechanism suggested by Gillette does not operate, at least in this species. In some of the marginal teeth, erosion is taking place without the presence of a visible tooth germ. Secondly, in the posterior part of the parasphenoid tooth patch there are several rows of functional teeth between the one undergoing resorption and the replacement bud. Any effect of the replacement bud on the erosion would be expected to involve the nearest mature tooth. However, in this case the teeth closest to the tooth germs are not undergoing erosion and are in fact the most recent ankylosed. The teeth which are being eroded are therefore separated from the germs by several rows of functional teeth.

In the absence of experimental work on the control of tooth replacement it is only possible at this time to speculate on the mechanism(s) involved. It may be that the tissues capable of forming teeth and which constitute the embryonic dental field may be "pre-timed" to produce buds at a given sequence as the field becomes progressively differentiated. The timing process could be the consequence of concentration gradients within the presumptive dental tissue and might also involve inductive processes produced by the invasion of cells derived from the neural crest. Once the initial sequence of tooth production has been established it can readily be maintained by an intra-local

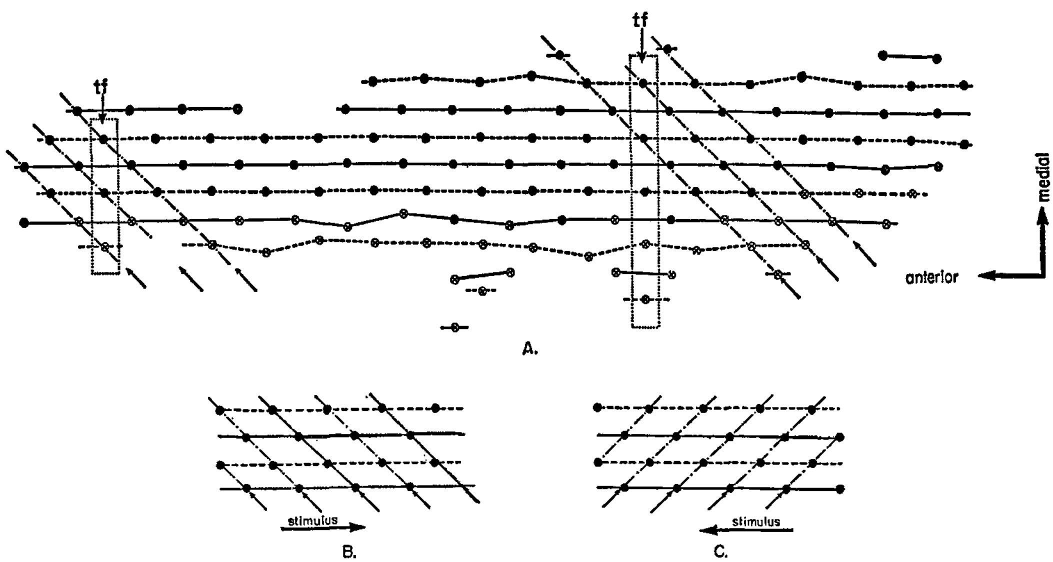


Fig. 8 Tooth replacement in parasphenoid patches of *Plethodon cinereus*. Functional teeth are solid circles and tooth germs (stages a-c) are open circles with crosses.

Fig. 8a Graphic analysis of replacement in parasphenoid patch.

Fig. 8b Theoretical analysis with *Zahnreihen* 2.0 spaces apart. Stimuli moving from anterior to posterior along the lateral margin of the patch.

Fig. 8c As for 8b, but with direction of stimuli reversed. t.f. tooth family.

mechanism which does not involve moving stimuli. The mechanism(s) probably involves the repression of the developing tooth by the functional tooth until such time as the functional tooth starts to fall out, at which time the replacement germ develops rapidly and fills the space left as the mature tooth is shed. We think that there are no stimuli which pass along the jaw and initiate tooth production. Nevertheless rows of teeth (and tooth germs) produced by some developmental mechanism correspond in position to Edmund's *Zahnreihen*. Characterization of such rows remains a useful conceptual device, facilitating comparisons within and between groups.

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