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Department of Paleontology, Charles University, Praha

INTRASPECIFIC AND ONTOGENETIC VARIATION OF THE DENTITION IN THE GREEN LIZARD LACERTA VIRIDIS (REPTILIA, SQUAMATA)

Zbyněk ROČEK

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Abstract: Eleven specimens of *Lacerta viridis* Gray, 1845 are examined to evaluate intra-specific and ontogenetic variation of individual tooth shape, general pattern of dentition, mode of tooth replacement and related features of the tooth-bearing bones: dentary, maxilla and premaxilla. Both number of tooth sites and rate of tooth replacement correlate with age, as indirectly ascertained by size of individual specimens. Tooth replacement is synchronous in left and right tooth rows except for posterior-most sections.

INTRODUCTION

Nearly all comparative anatomical studies of reptiles, although including a wealth of detailed information, omit evaluation of intraspecific and ontogenetic variation. When the paleoherpetologist requires detailed descriptions of the skeletal elements of contemporary species in order to taxonomically interpret fragmentary fossil material he often meets with failure because these studies have not paid any attention to the variability of the skeleton. This is certainly the case for studies of lizard dentition.

The earliest comparative studies, for example, Owen (1840—45), of reptilian dentition were simply descriptive. Only recently has the phenomenon of reptilian tooth replacement and development been elucidated; however, many groups remain unstudied. Edmund (1969) gave a general description of the dentition of the lizard family Lacertidae, including tooth counts for 12 species belonging to eight genera. Cooper (1963) carried out a comparative study of the dentition of species in the genus *Lacerta*, but these details are not readily available as this is an unpublished doctoral thesis. He did however publish some of the information on tooth replacement sequences and rates of this genus (Cooper 1965). Edmund (1960) studied the mode of tooth replacement in two specimens of *Lacerta viridis* and presented the data in the form of an odontogram.

The objective of this paper is to describe the dentition of one species, *Lacerta viridis,* paying special attention to intraspecific and growth related variability in the mode of tooth replacement. This information may be useful for an evaluation of the taxonomic status of several different morphologically distinct fossil *Lacerta* spp. which I have obtained from a Lower Miocene site at Dolnice, near Cheb in western Bohemia (Roček, in preparation).

MATERIAL AND METHODS

Eleven specimens of *Lacerta viridis* from the osteological collections of the National Museum, Praha (NMP), were examined (14/60 : 2, 14/60 : 3, 14/60 : 10, 14/60 : 13, 14/60 : 16, 23592, 23596, 23599, 23607, 23609, 23668). The length of the mandibles and tooth counts suggest that the animals were not only fully matured, but at least some of them represent old large lizards. In some specimens preparation had been carried out in such a careful manner that replacement teeth were well preserved. Where successive teeth were absent, the stage of tooth development was deduced from the degree of tooth base resorption.

For tooth description similar characters were evaluated as in a previous paper (Roček, 1980). Replacement waves were drawn as diagrams similar to those utilized by Edmund (1960, 1969). Dental terminology follows Peyer (1968) and Edmund (1969); bone nomenclature follows Fejérváry-Lángh (1923).

To ascertain the size and the relative age of each specimen the length of the mandible from the anterior-most point near the symphysis to the posterior tip of the processus retroarticularis and the length of the crista dentalis are listed.

RESULTS

(1) Description of individual teeth, the dentition as a whole, and the main features of tooth-bearing bones.

Dentary — Most of the teeth in a tooth row may be characterized as bicuspid, with the smaller cusp always mesial. Both cusps may be developed to a different degree: the smaller cusp may be only a rudiment in the form of an indistinctive process on the edge inclined mesially, or it may be strongly developed with both cusps separated by shallow groove on the lingual surface of the crown. Bicuspidity is the original feature because some young successive teeth are already thus terminated. Several anterior teeth, however, are bluntly chisel-shaped, mostly assymetrically with the edge slanting mesially. A limited number of posterior teeth may be tricuspid with a small third cusp distal to the main cusp. This additional cusp is situated lower than the anterior one, and it is also less prominent from the tooth outline. If the mesial cusp is separated from the main cusp by a groove on the lingual surface of the crown, then the distal cusp is separated in the same way regardless of its prominence. The transition between the tooth types mentioned is always gradual.

When comparing these attributes with the size of the lizard, we can conclude that there is no correlation in the occurence of tricuspid teeth. In the largest specimen (length of mandible 30.1 mm), only the twenty eighth tooth on the left dentary possessed a small third distal cusp (total number of teeth in this tooth row was twenty nine). On the other hand, in the specimens with mandibular lengths of 24.0 mm and 21.8 mm, the posterior four teeth were clearly tricuspid. These teeth may also occur individually in the middle section of the tooth row.

The general shape of a tooth is cylindrical in lingual view, that is, the width of the crown is approximately equal to the width of the base. Teeth are rather swollen lingually. This convexity, however, does not reach as high as the tip of the tooth. In some specimens this feature is not well expressed. Besides, in the case of the posterior-most teeth, the lingual surface is usually straight.

Teeth are typically pleurodont with the bases attached laterally to the almost vertical wall of dentary. The foramina more or less follow the line of attachment. Between two adjacent teeth there is only one row of foramina. Such which the bone and the tooth meet) is covered by cement-like tissue ("attachment bone" according to Peyer 1968). Where such tissue is lacking but adjacent teeth are present, a row of tiny foramina can be observed in the vertical wall of dentary. The foramina more or less follow the line of attachment. Between two adjacent teeth there is only one row of foramina. Such a perforation is quite common in fossils where attachment bone is naturally lacking due to the fossilization.

The number of teeth is a character which is undoubtely dependent on the size of animal (see Tab. 1), therefore probably on its age. One may conclude that the larger an animal is, the higher number of tooth positions it possesses. Therefore, it is impossible to characterize the species only by one tooth count. In the examined specimens the number of tooth positions range from 22 to 30.

Anterior teeth are close to each other. The space between adjacent teeth becomes gradually larger in the middle and posterior sections of the tooth row up to one half of the tooth width, and rarely even more. Gaps between adjacent teeth, however, need not be regularly enlarging; some irregularities are caused by slanting of the perpendicular axis mesio-distally in some individual teeth.

The size of adjacent teeth is not an important character because it is influenced by the process of tooth replacement.

Teeth are mostly perpendicular or slightly inclined to the crista dentalis posteriorly or very rarely anteriorly. In some specimens, however, irregularities occur concerning either individual teeth or groups of them. Teeth may be considerably inclined distally, with the lower part of their bases in a normal position. In one specimen, a few teeth were observed, inclined, however, anteriorly. Two adjacent teeth with quite opposite inclination may also occur. Usually, small teeth in the anterior-most section of the tooth row are slightly inclined labially (prodonty). The free part of a tooth above the level of crista dentalis represents approximately $^1/_4$—$^1/_3$ of the whole tooth height.

The sulcus dentalis is well developed along the entire tooth row. The number of foramina pro rami nervorum alveolarium inferiorum (syn. foramina dento--facialia according to Hünermann 1978), or of the little depressions instead of foramina, range from four to seven only. The number is the same in both halves of the mandible or differs by only one or two.

Maxillary — The teeth on the maxillary are similar to those on the dentary, however, they are rather more inclined distally which is especially visible in a labial view. The anterior-most tooth is always smaller than the lateral-most teeth of the premaxillary, regardless of the process of tooth replacement. The number of teeth does not depend on the size of an animal so much as in the case of mandibular dentition (see Tab. 1). Tooth counts range from eighteen to twenty.

No correlation with size in the number of foramina pro rami nervorum alveolarium superiorum (syn. foramina supralabialia according to Oelrich 1956) was observed. Their counts range from four to six and they can differ by one in both maxillaries. Sometimes they are developed only as rudimentary depressions, however, they also may be multiplied into two rows (only the openings of the lower row were taken into account). In one specimen, a large opening standing out of the usual row of foramina was observed. It may be, however, considered anomalous because it did not occur on both maxillaries.

Premaxillary — Tooth position caunts are given in the Tab. 1. Like in the dentary, a correlation between the size of a lizard and tooth position counts is quite obvious. An odd tooth always stands in the median line, even in specimen NMP 23592 with 10 teeth which are distributed assymetrically (4 and 5 on either side of the odd tooth). Their shape appears fang-like (similar to the anterior-most tooth of maxillary), and they are never inclined labially.

(2) Tooth replacement

The first developmental stages of successive teeth are connected with the lamina dentalis (cf. Edmund 1960, 1969) which is sometimes retained in carefully prepared skulls. Soon, however, the developing tooth bud moves from the lamina to the bone, close to the lower marginal part of the mature tooth base. In such a stage a firm attachment does not exist either with lamina or with the bone. As the developing tooth increases in size, base of the old tooth becomes correspondingly resorbed. Therefore, it is possible to deduce the degree of successive tooth development from the degree of basal resorption.

The mature tooth begins to be resorbed at the lower part of its base, from the postero-lingual margin. First, only a slight depression on the tooth base is visible. The depression becomes gradually deeper which results in its connection with the tooth pulp cavity. The following stages can be described simply, as a cylinder which is open at its lower end, which owing to progressing resorption becomes shortened. The resorption can reach various degrees; in extreme cases only a shell of the tooth tip may be shed.

The successive teeth develop first within the depressions in the bases of the old teeth, and later in their cavities. The small developing tooth is attached only to the vertical wall of dentary, not to the dental groove. It is open at the lower end and resembles an inverted cup.

This attachment is not quite firm because some successive teeth can be found at this developmental stage which are strongly inclined lingually or in other directions. This weak attachment to the dentary during the initial developmental stages of the successive teeth may cause irregularities concerning the inclination of the teeth described above. A developing replacement tooth quickly attains its definitive shape. Its upper termination may either have the shape of an asymmetrical cone or be typically bicuspid.

When lower jaw dentitions are analyzed (see Fig. 1) by separating the teeth into odd and even numbered series, most specimens display several waves of replacement in each series. While in young specimens the waves of replacement are numerous and short, the number of waves of replacement is reduced and the number of teeth per replacement wave increases in older specimens. Moreover, in larger specimens the number of intact teeth and some irregularities in the mode of replacement remarkably increases. In other words, the speed and regularity of replacement is greater in young animals and slows down considerably with age. It is quite probable that still older lizards possess at least some permanent teeth which do not undergo replacement.

At first sight, the pattern of replacement appears very similar in both halves of the mandible. For example, the posterior-most waves in specimens NMP 14/60 : 10, 23607, 14/60 : 2, 23609, 14/60 : 3, and 23599 look almost identical regardless of the fact that both halves may differ in tooth number. These specimens display regular tooth replacement. Surprisingly, there is a peculiar contrast between right and left posterior-most sections of the tooth rows. If in one mandibular half the posterior-most wave belongs to an odd numbered series, the corresponding wave on the opposite side belongs to an even series. The waves of replacement in the anterior sections near to the symphysis, however, always belong to the same numbered series, either an even or odd numbered series.

Tab. 1. Biometrical attributes of the tooth-bearing bones of *Lacerta viridis*.
Measurements are in mm. Specimens are ordered according to mandibular length

	Nat. Mus. Praha Collection Number	Length of Right Mandible / Length of Left Mandible	Length of Crista Dentalis of Right Dentary / Length of Crista Dentalis of Left Dentary	Ratio Between Both Measurements	Number of Tooth Positions		
					Dentary	Maxilla	Premaxilla
1.	23668	30.3 30.1	14.8 14.5	2.04 2.07	30 29	20 20	11
2.	23596	29.9 29.8	14.5 14.5	2.06 2.05	27 29	20 20	11
3.	23592	29.7 29.7	13.4 13.2	2.21 2.25	25 24	18 18	10
4.	14/60 : 10	28.1 28.4	18.0 18.1	1.56 1.58	26 26	20 21	9
5.	23607	25.9 25.8	12.8 12.8	2.02 2.02	26 26	19 19	9
6.	14/60 : 13	25.2 25.4	12.2 12.5	2.06 2.03	24 25	19 26	9
7.	14/60 : 2	24.9 24.9	11.8 12.0	2.11 2.07	26 25	18 18	9
8.	23609	23.8 24.0	11.5 11.8	2.06 2.03	22 25	19 20	9
9.	14/60 : 3	22.1 22.1	10.7 10.9	2.06 2.02	25 24	19 19	9
10.	14/60 : 16	21.9 21.8	10.5 10.7	2.08 2.03	24 24	18 19	9
11.	23599	21.2 21.3	10.5 10.7	2.01 1.99	24 23	19 19	9

DISCUSSION

The above results demonstrate that tooth counts which are usually given as one of the most important dentitional characters for taxonomic diagnosis are clearly dependent on age. Studies of dentitional ontogenetic variability are sorely needed. Therefore, at least one size measurement, for example body length, skull length or at least length of mandible must accompany the tooth count.

Characteristic tooth shape occurs both in small and large specimens. However, my observations indicate that teeth may be abraded to such a degree that tooth crowns are bluntly terminated in large specimens of *Lacerta lepida* (length of mandible 50.0 mm). In such case cusps were absent although young specimens of this species possess distinctly bicuspid and tricuspid teeth. *Lacerta viridis* may attain even larger sizes than any of the specimens included in my sample, and in such cases teeth may become permanent and exibit different degrees of abrasions.

The general pattern of replacement occurs by the usul method (Cooper 1965). Edmund (1960, Fig. 14) published two diagrams of the lower right jaw dentitions of *Lacerta viridis,* with 22 and 24 tooth positions respectively. In spite of a slightly different interpretation of the waves of replacement, Edmund's results approximately correspond with those reported in this paper, including the fact that there are some intact teeth in anterior section in the larger specimen (cf. Fig. 1).

The odd — even alternation of posterior opposite waves of replacement in left and right jaw halves has never been described for lizards. Tooth replacement is synchronous in opposite jaws but not quite symmetrical. Edmund (1969, p. 137) notes only that "replacement rhythm may or may not be synchronous on both sides of the mounth" and that "only rarely was synchrony seen between the dentitions on the two dentaries".

Little attention was given to the tooth replacement of the upper jaw dentition but apparently, on the basis of macroscopical observations, that the premaxillary-maxillary suture is not an impediment for the replacement rhythm on the upper jaw despite the fact that Cooper described a clear break in the lamina dentalis at this boundary for *Lacerta* (Edmund 1969). However, Edmund (op. cit.) also mentioned that some lizard specimens show uninterrupted waves crossing this suture.

The number of foramina in the labial wall of the dentary and/or maxillary probably is not reliable taxonomic character because of the relatively large variation among specimens and even between jaws in individual specimens (see differences between right and left jaws). In some cases they are represented only by shallow depressions or scars, and sometimes additional openings may occur. Fejérváry-Lángh (1923) expressed some doubts on the relevance of this character for comparative studies.

SUMMARY

(1) Teeth are primarily bicuspid; premaxillary and anterior maxillary teeth are bluntly fang-like or canini-form; tricuspid teeth may occur in the posterior sections of tooth rows. Tooth shape is not dependent on age with the probable exception of the oldest specimens where permanent teeth may be abraded.

(2) The number of tooth positions depends on the size of the lizard (which is correlated with its age), observed in both maxillae and dentaries as well as in the premaxilla. Therefore, it is impossible to characterize the species by average tooth count; a range of counts and mandibular lengths must instead be given.
(3) Teeth are replaced by replacement waves which operate separately as odd and even numbered tooth series within a single tooth row. The speed and regularity of the replacement is greater in young lizards and slows down considerably with age.
(4) The waves of replacement are synchronous on both sides of the mouth, and are symmetrical in anterior sections of tooth rows. However, in the middle and posterior sections the symmetry is broken; the corresponding left and right replacement waves belong to different tooth replacement series.

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The figures 1 and 2 will be found at the end of this issue.

Author's address: Dr. Zbyněk Roček, Department of Paleontology, Faculty of Natural Science, Charles University, Albertov 6, 12843 Praha 2, Czechoslovakia.

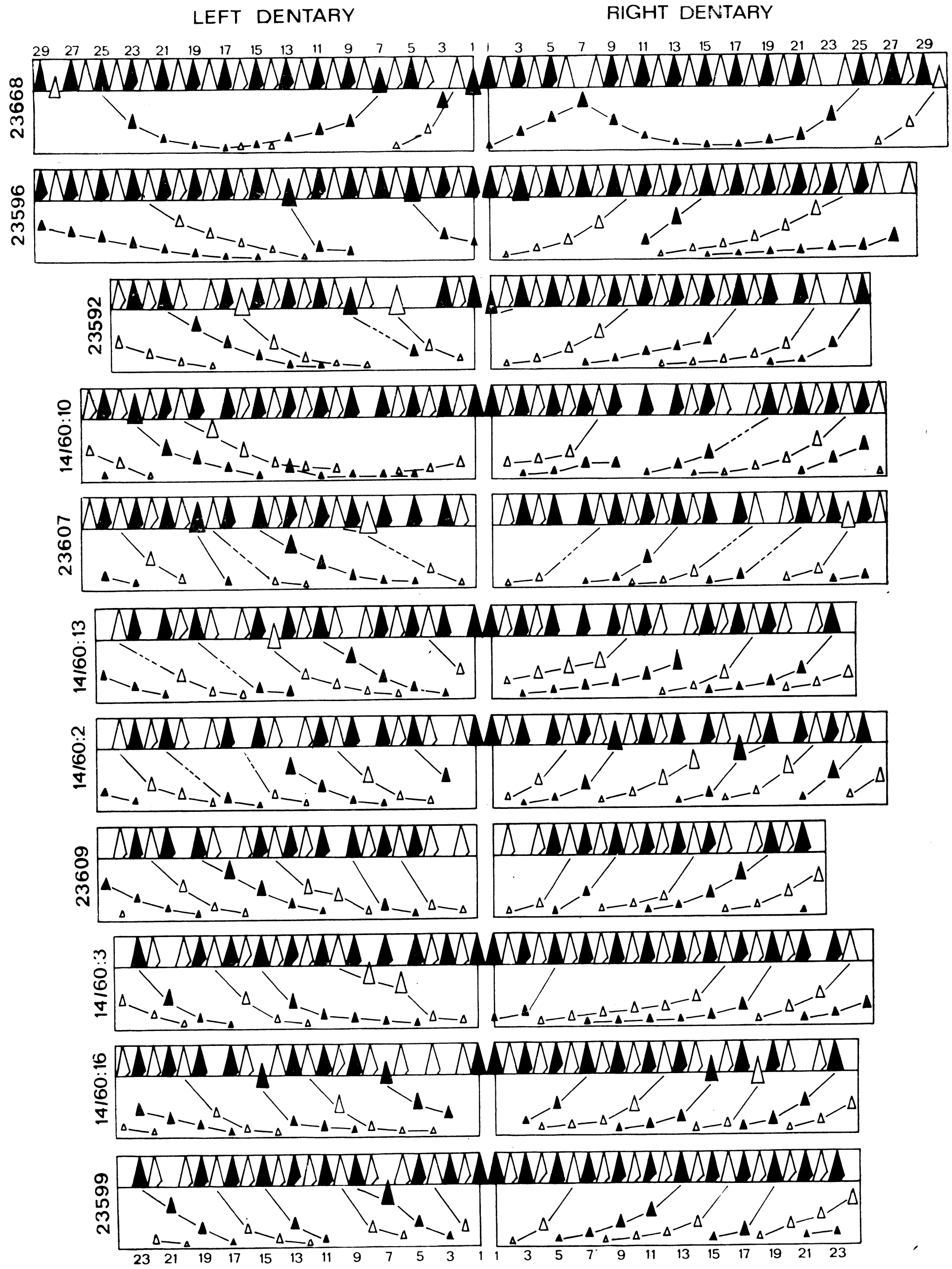

Fig. 1. Stereo-odontograms illustrating the functional dentition and the mode of tooth replacement. Specimens are ordered according to length of the mandible. National Museum Praha collection numbers are on the left margin of each diagram. The size of the tooth-like symbols are approximately proportional to the actual teeth, The symbols in the area between the two upper lines are functional teeth. Where basal resorption of the old tooth occurs, it is depicted by a bite out of the symbol; other symbols represent intact teeth. The small symbols below the middle line are developing teeth. Odd-numbered series of teeth are shown as solid black; even-numbered series are white.

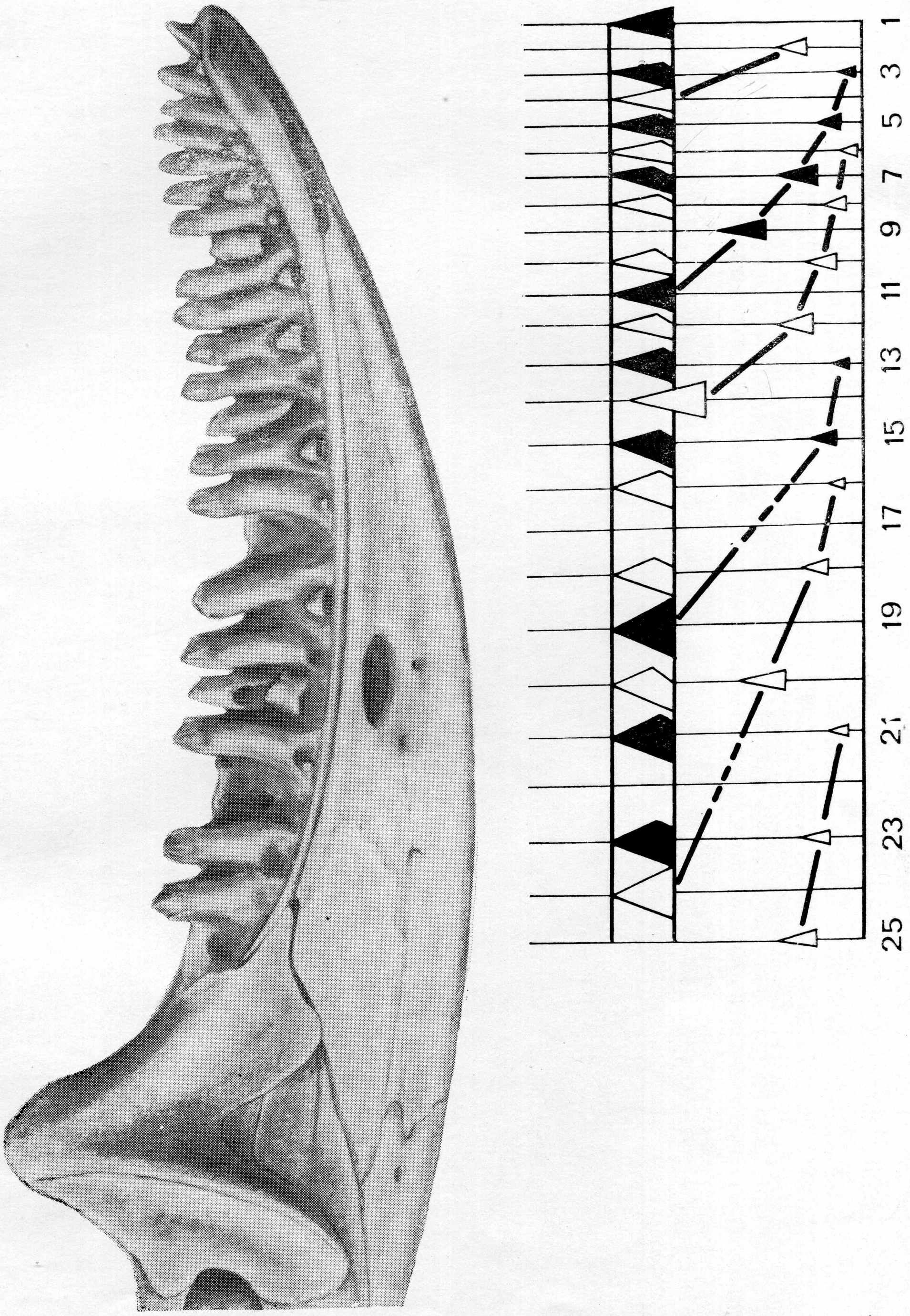

Fig. 2. Left lower dentition of *Lacerta viridis,* NMP 14/60 : 13, with the diagram of the wave-like alternative tooth replacement. For explanations see Fig. 1. Drawing by I. Kolebaba.