

The Late Cretaceous lizard *Pleurodontagama* and the origin of tooth permanency in Lepidosauria

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The sinuous double-row dentition of *Pleurodontagama aentigmatodes*, the Late Cretaceous Mongolian relative of the Acrodonta is a possible initial stage of evolution of tooth permanency in the Acrodonta. The reconstructed ontogenetic development of this dentition is considered as a model of evolutionary events that resulted in tooth permanency. The acceleration of the posteriad growth of jaws, that occurred at the origin of the Acrodonta, was probably followed by both peripheral and interstitial growth of the dental lamina. Created by the interstitial growth, the interdental spaces were not large enough to allow for the inclusion of the subsequently developed teeth into the main (labial) tooth row. Their blockage resulted in the eventual total blockage of tooth replacement. The requirements of the precise occlusion resulted in a reduction of the redundant lingual tooth row of the *Pleurodontagama* type. The dentition subsequently changed into a one-row permanent type increasing by a sequential addition of teeth. The patterns of dentition in the sphenodontidans and the varanoids may also result from evolutionary changes of skull proportions via the differential growth of jaws and consequent adjustment of the dental lamina.

Key words: *Pleurodontagama*. Squamata, Lepidosauria, tooth replacement.

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Introduction

Associated with the type of dentition commonly named acrodont type, permanency of at least a part of a tooth row is characteristic of the agamid and chamaeleonid group referred to as Acrodonta (Estes *et al.* 1988) and of the trogonophid *Amphisbaenia* (Gans 1960) as well as of the Sphenodontida.

The present paper is concerned with the case of development of tooth permanency in the Late Cretaceous Mongolian lizard *Pleurodontagama aenigmatodes* Borsuk-Białynicka & Moody, 1984 and its implications on the evolution of tooth replacement processes in the *Lepidosauria* as a whole.

Pleurodontagama is a primitive acrodontan relative (Borsuk-Białynicka & Moody 1984). It comes from the middle Campanian Red Beds of Khermeen Tsav, Gobi Desert. Because of its subpleurodont tooth implantation and a putative successional replacement of some teeth, *Pleurodontagama* was originally considered as a side branch rather than a link in the evolutionary line of the Acrodonta. According to the present reinterpretation, the *Pleurodontagama* dentition is regarded as an illustration, at least, of an initial stage of the evolutionary process leading from continuously replaced to permanent dentition. In my opinion, this dentition is explicable in terms of adjustment of the tooth replacement process to the pattern of jaw growth as proposed by Osborn (1973, 1974) and supported by Westergaard (1980, 1986).

Abbreviations of institutions: ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland; PIN – Paleontological Museum of the Russian Academy of Sciences, Moscow, Russia; IVPP – the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

Material

Pleurodontagama aenigmatodes is known from only two specimens. The first one is the holotype (ZPAL MgR-III/35). It is a fairly complete skull with both mandibles from the Late Cretaceous Red Beds of Khermeen Tsav (?middle Campanian according to Gradziński *et al.* 1976; Jerzykiewicz & Russell 1991), Gobi Desert, Mongolia. The second one is a left mandible (IVPP V10039) with a postdentary part missing. It comes from the Late Cretaceous Djadokhta Formation (slightly older than the Red Beds of Khermeen Tsav; Gradziński *et al.* 1976) of Bayan Manduhu, Urad Houqi, Inner Mongolia. This specimen belonging to the collection of the Dinosaur Project (China-Canada-Alberta-Ex Terra) has been mentioned but not illustrated by Gao Keqin & Hou Lianhai (1995). Two genera of primitive acrodontan lizards, *Priscagama* Borsuk-Białynicka & Moody, 1984 (ZPAL MgR-III/32) and *Flaviagama* Alifanov, 1989 (PIN 3143/101) from the Late Cretaceous (?middle Campanian) of the Gobi Desert, both of them closely related to *Pleurodontagama*, have been used for comparisons.

Lizard tooth replacement patterns and mechanisms

Our knowledge of tooth replacement phenomena in vertebrates lower than mammals begins as early as Owen's (1840–1845) papers. The regular alternation of functional teeth with those being replaced had been recognized by the turn of the 19th century, along with the embryological

background of the replacement. In particular, the embryological concept of the dental lamina was presented by Harrison (1901) and further developed by Bolk (1912, 1922). The dental lamina produces tooth families, consisting of series of replacements which successively occupy tooth positions throughout animal's life.

Bolk (1912, 1922) considered all the replacements within one horizontal series (one odontostichos in the terminology of this author) as simultaneously developed. In contrast, Parrington (1936) and Edmund (1960) demonstrated wave-like sequence of tooth development along the jaws in reptiles.

In most lizards the teeth are pleurodont, i.e. attached to the lingual surface of the jaw. This is just the type of dentition to be the subject of replacement. In the Acrodonta, the replacement process is almost fully suppressed, while the dentition, known as the acrodont type, tends to be shifted from the lingual side to the margin of the jaw.

Two methods of replacement of pleurodont teeth, the iguanid and the varanid method, have been recognized by Edmund (1969; see also McDowell & Bogert 1954). In the iguanid method, the replacements come directly from the lingual side of the functional teeth and are received into their bases before they shed off. In the varanid type the replacements come from the posterolingual side of the functionals, are thus interdental, and replace the functionals only after their shedding off. The intact functionals may thus coexist for some time with almost fully grown replacements.

Edmund's (1960) Zahnreihe Theory assumed some sort of impulse passing along the dental lamina to produce the regularity of tooth replacement pattern. In contrast, Osborn's (1973) Tooth Family Theory suggested that the replacement control is transverse rather than longitudinal with respect to the dental lamina. The mechanism depends on two factors: the growth of the tooth bearing elements and inhibitory action of developing teeth. Basically the same mechanism has been postulated by Westergaard's (1986) Tooth Position Theory. But, the latter author questioned the existence of clearly demarcated tooth families and tooth generations (Edmund 1960; Osborn 1973), and stressed the importance of differential jaw growth in the development of dentitional patterns, the latter idea having been foreshadowed by Osborn (1973).

According to these authors (Osborn 1971, 1973, 1974; Westergaard 1980, 1986; see also Gillette 1955), tooth buds generate around them a morphogenetic field in which any initiation of the next generation buds is inhibited. It is shown by the fact that they usually form separate units. Hence, the dental lamina have a potential to promote production of younger teeth only when situated at a certain distance from the existing tooth buds (outside their inhibitory zone), and among others within the spaces produced by interstitial growth of the jaws. The inhibitory potential of particular teeth tends to dissipate with age. This allows for initiation of subsequent tooth generations and for their shift towards the predecessors to be replaced. The temporarily changing inhibitory potential of tooth buds

has been proposed by Osborn (1974) as the main control of the regularity of tooth replacement.

According to the model of tooth replacement presented by Osborn (1973, 1974), two types of growth: an interstitial growth of embryonic tooth bearing elements and a posterior or apical growth (tip growth of Osborn 1973) of the tooth bearing bones contribute to produce the eventual regional variation of the tooth row pattern. A dental determinant, which is the first tooth bud to be initiated in the embryonic jaw, separates the two main regions of the cheek dentition of lizards. The anterior one grows interstitially in embryos. In the posterior one the tip growth prevails. This regionality is very often, but not always, obliterated in adults owing to the above mechanism of temporarily changing inhibitory influence of the tooth buds (Osborn 1974).

Studies on the embryonic development of dentition in lizards (Osborn 1971, 1973) and in *Sphenodon* (Harrison 1901) strongly suggest that the phenomenon of tooth alternation is a direct consequence of the interstitial growth of tooth bearing elements via a corresponding increase of the dental lamina. Westergaard (1986) negated the regularity in tooth alternation, except for *Sphenodon* dentition. But, the tooth alternation understood as an opposition to a direct sequence is supported by the results of the same author (Westergaard 1986) and demonstrated by earlier authors in different vertebrate groups (Reif 1976 in sharks; Berkovitz 1977 in teleosts; Oeder 1906 in anurans; Woerdeman 1919 in crocodiles). The interstitial growth produces the intermediate tooth sites between the existing teeth for the forthcoming ones, the latter being by obligation younger than the former. Different patterns of dentition develop at this early phase of embryonic development and depend on the relations between the volume of new sites and the sizes of teeth, which enter them. In the iguanid type dentition, the spaces between the earliest mineralized teeth of the embryo (whether drawn apart by interstitial growth or appearing as spaced) fit the sizes of the next teeth to develop. The resulting one-line, closely spaced tooth row is the subject of a directly successional tooth replacement.

The portion of dentition posterior to the determinant uses to appear in a sequential manner which is consistent with the tip growth of jaws characteristic of posthatchlings. A strict correspondence between the rate of growth of tooth bearing bones and that of tooth bud production by the dental lamina results in the development of a closely spaced one-line dentition. It may be the subject to a directly successional replacement. Any disturbance in this correspondence would inevitably lead to a disorder in replacement processes and consequent modification of the tooth row.

In the varanid type dentition, the interdental spaces are large enough to allow for the interdental position of the replacements. I would argue that the dependence of two subsequent generations of teeth is reciprocal. Not only the functionals control the development of replacements (by gradual vanishing of their inhibitory zones in ontogeny) but the development of replacements may accelerate a resorption of functionals by means of some

mechanical and/or physiological mechanisms. The displacement of the former may probably cause a delay in shedding off the latter. This is a good initial stage in the development of an actual blockage of replacement, which still does not occur in the varanids.

As shown by Edmund (1960) and by different authors thereafter, many groups of Autarchoglossa (Scincomorpha and Anguimorpha see e.g., Estes *et al.* 1988) show a mixture of replacement methods referred to as the intermediate method. In the Anguinae, representing the typical intermediate tooth replacement, actually transitional to the varanid type (Rieppel 1978; Estes *et al.* 1988), both localization of pits and resorption rate are variable even within an individual (Rieppel 1978). The interdental position of the replacements is followed by the changes from lingual to posterolingual position of resorption pits. The latter changes correlate with the increase in variability of resorption rate, that either match or not that of developing replacements.

Any other example of coexistence of the arrested functionals and accelerated replacements results from a disturbance of a strict coupling between subsequent tooth generations. It may be conceived in terms of either changes in a rate of hormonally controlled dissipation of inhibitory potential or a changing distance between functionals and replacements, which also bears on this potential. The first case is here exemplified by the double row dentition of *Crotaphytus cristatus* (ZPAL R-I/44, Fig. 4) in which a position of replacements remains directly lingual to the functionals, but the resorption pits do not match the size of growing replacements. Both the varanid and the intermediate type of replacement originated as an effect of evolving distances between tooth sites.

The varanid tooth replacement method has clearly been derived from the iguanid method via the intermediate one. The dentition of the Acrodonta has, too, derived from the pleurodont continuously replaced teeth. However, the intermediate stage of the latter transition series remains unknown.

Robinson (1976) suggested a correlation between the growth pattern of the tooth bearing bones and a precise occlusion in the acrodont dentition of *Uromastix*, and its lack in that of *Sphenodon*. But, she did not discuss the problem of the mechanism involved in the development of a permanent dentition from a replaceable one. Given the specialization of acrodont dentitions in extant lizards and *Sphenodon*, and difficulties in studies of embryological development of dentition (but see Harrison 1901; Cooper *et al.* 1970; Cooper & Poole 1973; Robinson 1976), the paleontological documentation of the early representatives of groups having acrodont dentition (the Acrodonta and Sphenodontida) is crucial to understanding of this evolutionary process. The most primitive sphenodontidans, Jurassic *Gephyrosaurus* (Evans 1980) and Triassic *Diphydontosaurus* (Whiteside 1986), and the most primitive acrodontan relative, the Cretaceous *Pleurodontagama* (Borsuk-Bialynicka & Moody 1984), are, thus, of special interest.

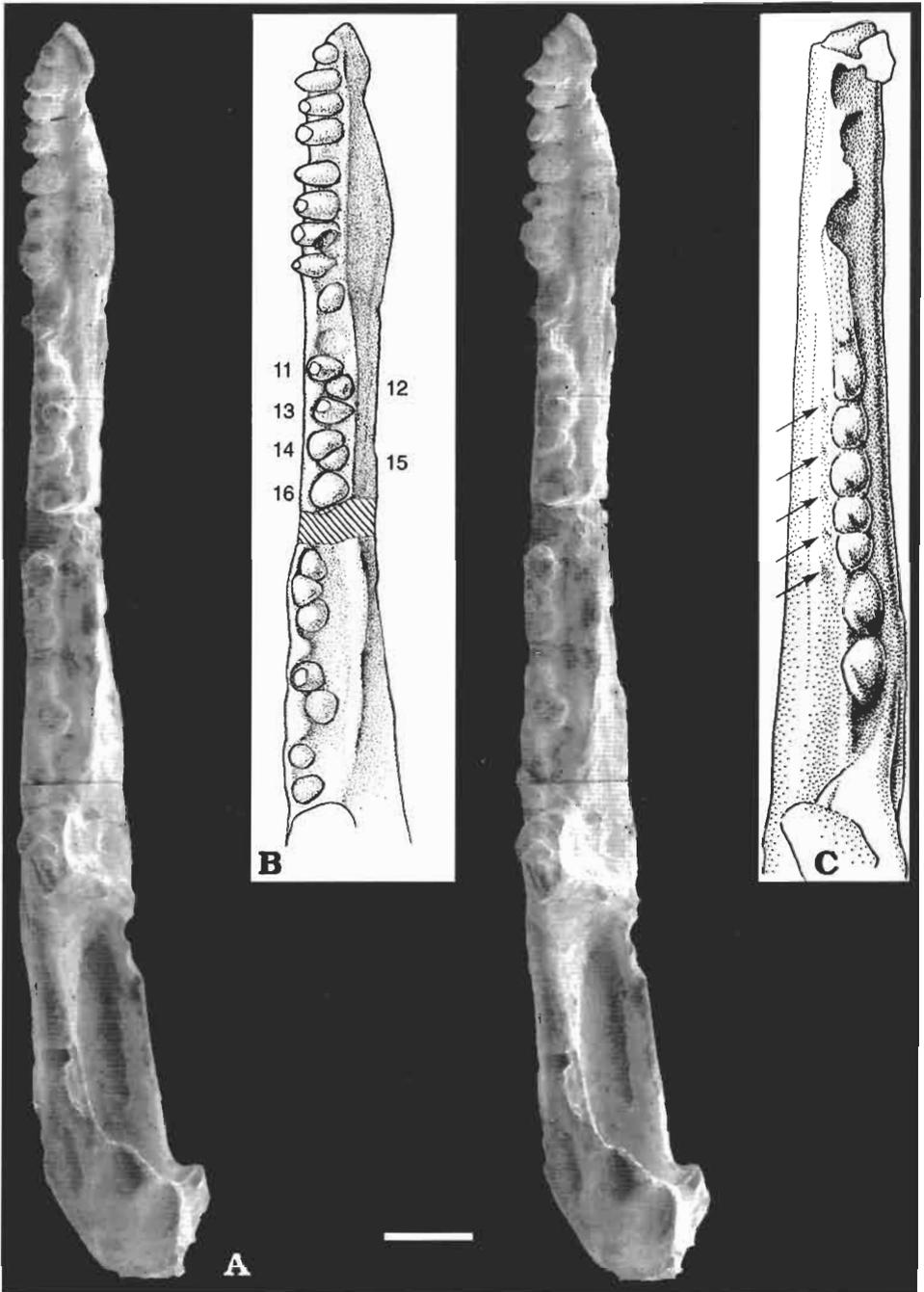


Fig. 1. **A-B.** *Pleurodontagama enigmatodes* Borsuk-Bialynicka & Moody, 1984. Late Cretaceous Red Beds of Khermeen Tsav (?middle Campanian). Left mandible of ZPAL MgR-III/35 in occlusal view. **A.** SEM stereo-pair. **B.** Drawing of the tooth row of the same. **C-E.** *Priscagama gobiensis* Borsuk-Bialynicka & Moody, 1984. Same horizons and locality. Left man-



dible of ZPAL MgR-III/32. **C.** Drawing of the specimen in occlusal view. **D.** SEM stereo-pair of the same. **E.** Lingual view of the same. Numerals in **B** refer to tooth count of the middle section of the mandibular tooth row. Arrows in **C** refer to traces of maxillary tooth bites. Scale bars are 2 mm.

Redescription of the dentition of *Pleurodontagama*

The dentition of *Pleurodontagama* is slightly heterodontous and displays a regionally differentiated pattern.

Not only the anteriormost series is discriminated from the rest of each tooth row, but also the cheek series is roughly divided into two parts, more distinctly so in the mandibular dentition. Only the left side of the lower dentition is accessible for studies in occlusal aspect. The right side of the upper dentition is badly damaged in the anterior section.

The teeth of the anteriormost series make up about one third of the tooth row in both upper and lower jaw. The much better preserved mandibular teeth are pleurodont, narrowly conical in shape and directed slightly labiad with their tips. They bear wear facets in terminal or slightly labial positions. In contrast, the teeth of both lower and upper 'cheek series' are implanted less deeply at the lingual side, more consolidated with the jaw bones, and inclined linguad with respect to the anterior series to be subperpendicular to the occlusal plane (Figs 1A, 2A). Wear facets are rarely preserved in the 'cheek series', most of the apices being damaged.

The poorly preserved anteriormost series of the upper dentition encompasses from two to four premaxillary teeth (not to be seen in figures) and about five anterior maxillary teeth. It is separated from the remaining dentition by a break of the maxilla. The twelve to thirteen upper teeth, which follow (Fig. 2A–B), produce a one-row-battery of subpleurodont teeth. The regionality is hardly expressed in this series, but the remnants of two teeth smaller than the rest and fused with each other (Fig. 2B: 1 and 2) may belong to a hatchling dentition, the distal part of which has been destroyed by a break of the proximal one replaced by the tooth numbered 3 in the Fig. 2A–B. The teeth 3–6 are spaced. Still, beginning with the fourth one, the teeth tend to loose their individuality at the bases, particularly so the teeth of the posterior half of the series (6–9) which are more crowded than the anterior ones. There are no traces of replacement process except for one tooth situated lingually between the sixth and the seventh tooth. The latter tooth has been resorbed at its lingual side but remains completely fused to the jaw by its labial wall. The replacement has probably been retarded at this site and the tooth row quasi permanent. Still some traces of replacement are to be seen at the same position of the right tooth row. The posteriormost left upper teeth (10–13) preserve their individuality, but are arranged in a lingually convex arch instead of a straight line usual in the agamids. I would suggest the teeth 10 and 13 originated as spaced while the teeth 11 and 12 developed subsequently in between.

The mandibular dentition (Figs 1A–B, 3A) consists of about 22 teeth and 4 empty tooth positions. The number of anterior pleurodont teeth ranges from eight to ten. The last two of them are subject to resorption and/or damage. In the middle section of the mandibular tooth row, six teeth (Fig. 1B: 11–16) are crowded within four tooth positions. The teeth

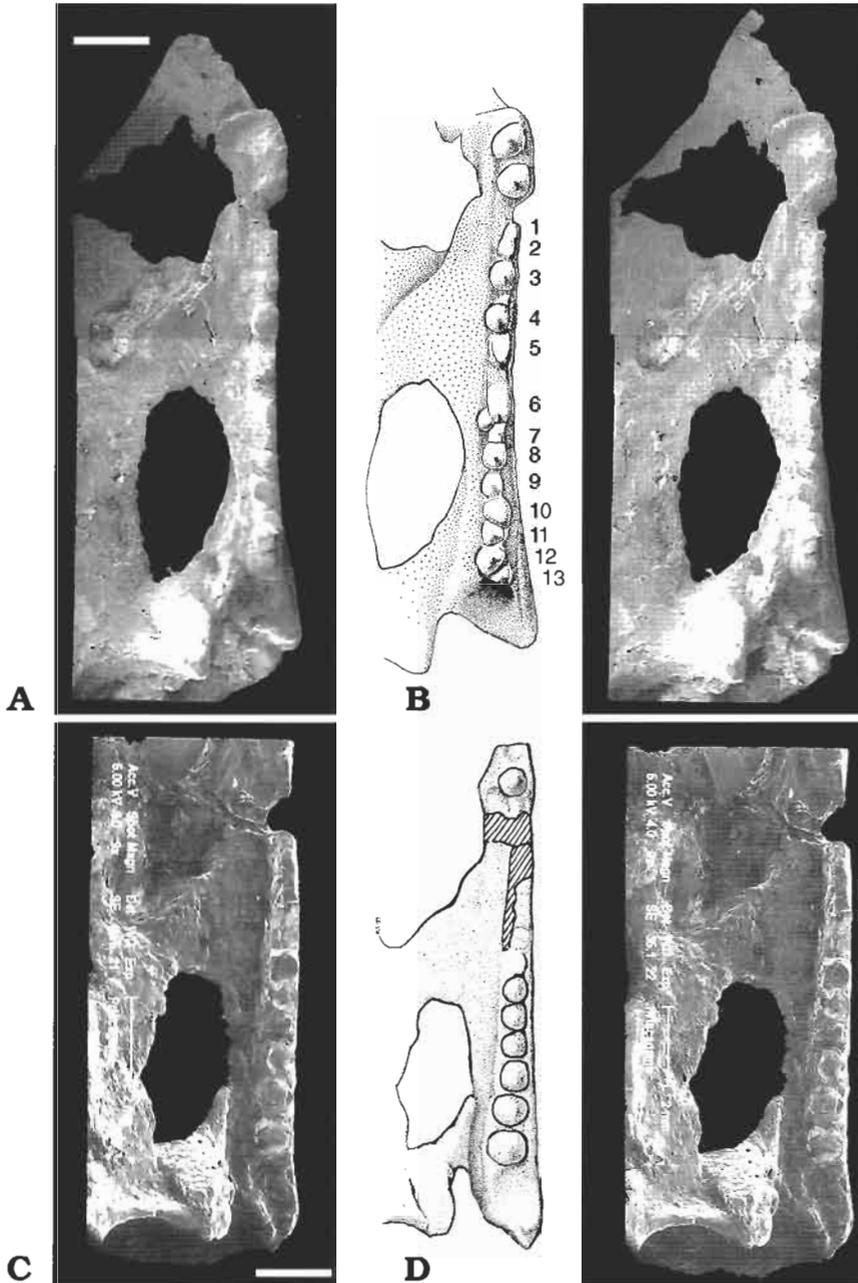


Fig. 2. **A-B.** *Pleurodontagama enigmatodes* Borsuk-Bialynicka & Moody, 1984. Late Cretaceous Red Beds of Khermeen Tsav (?middle Campanian). Left upper jaw of ZPAL MgR-III/35 in occlusal view. **A.** SEM stereo-pair. **B.** Drawing of the tooth row of the same. Numerals refer to tooth count of the middle section of the mandibular tooth row. **C-D.** *Priscagama gobiensis* Borsuk-Bialynicka & Moody, 1984. Late Cretaceous Red Beds of Khermeen Tsav (?middle Campanian). Left upper jaw of ZPAL MgR-III/32 in occlusal view. **C.** SEM Stereo-pair. **D.** Drawing of the tooth row of the same. Scale bars are 2 mm.

of this section are all broadly conical in shape but differ in size and position (Fig. 3A). The 11th and 14th are as labial as are those of the anterior section, the 13th and 16th being more lingual, whereas the 12th and 15th are clearly interdental and smaller in size. The smaller and more lingual cones are fused to the body of the larger and labial cones so as to lose their individuality. The series displays, thus, a double-row-structure and occupies the whole width of the broad dental shelf of which the first series occupies just a labial strip (Fig. 1A–B). This section of the lower dentition is situated within the limits of the superior process of the maxillary and occludes with the middle series of the maxilla.

The posteriormost series, separated from the middle one by a break in the mandible with an empty tooth position situated on it, consists of about seven teeth occupying nine tooth positions (18–26). The series is located in the labial part of the dental shelf but has a sinuous pattern, the teeth being alternatively more lingual or more labial (Fig. 1A–B). Empty tooth positions left by shed teeth or resulting from damage, are partly invaded by what appears to be bone of attachment characteristic of the acrodont dentition (Robinson 1976; Estes *et al.* 1988).

Ontogeny of dentition in *Pleurodontagama aenigmatodes*

Compared to a typical iguanid dentition as illustrated by Edmund (1960: figs 4, 14–15), the dentition of *Pleurodontagama* is characterized by a dramatic fall of the rate of tooth replacement. The replacement still proceeded in the anterior sections of the jaws, but almost completely ceased in both upper and lower 'cheek' series. Still, more than one generation of teeth have been developed, all of them cemented to the jaw, either to the labial wall or to the bottom of the tooth furrow, more strongly than usual. Some of the teeth are fused with each other.

In this dentition, the tooth alternation affected mainly a position of tooth series with respect to the labial wall of the jaw, and mainly the mandibular dentition. The more lingual of the alternating series is considered younger than the labial one on the basis of this position. The lingual series may be regarded as a row of replacements shifted to the interdental positions between the functionals. Given a posthatchling age of the studied specimen (ZPAL MgR-III/35), most of the jaws, and particularly their parts underlying the orbit, along with corresponding parts of the mandible, increased at the periphery (tip growth of Osborn 1973). This method of size increase of the tooth bearing bones implies a sequential method of growth of the dentition. Still, the existence of the interdental spaces suggests that the dental lamina was the subject of interstitial growth. The latter was most probably a way for dental lamina to keep up with the increased rate of posterior growth of the jaw bones. The full correspondence between the rates of these growing parts of jaws has temporarily been destroyed by the evolutionary change that was occurring.

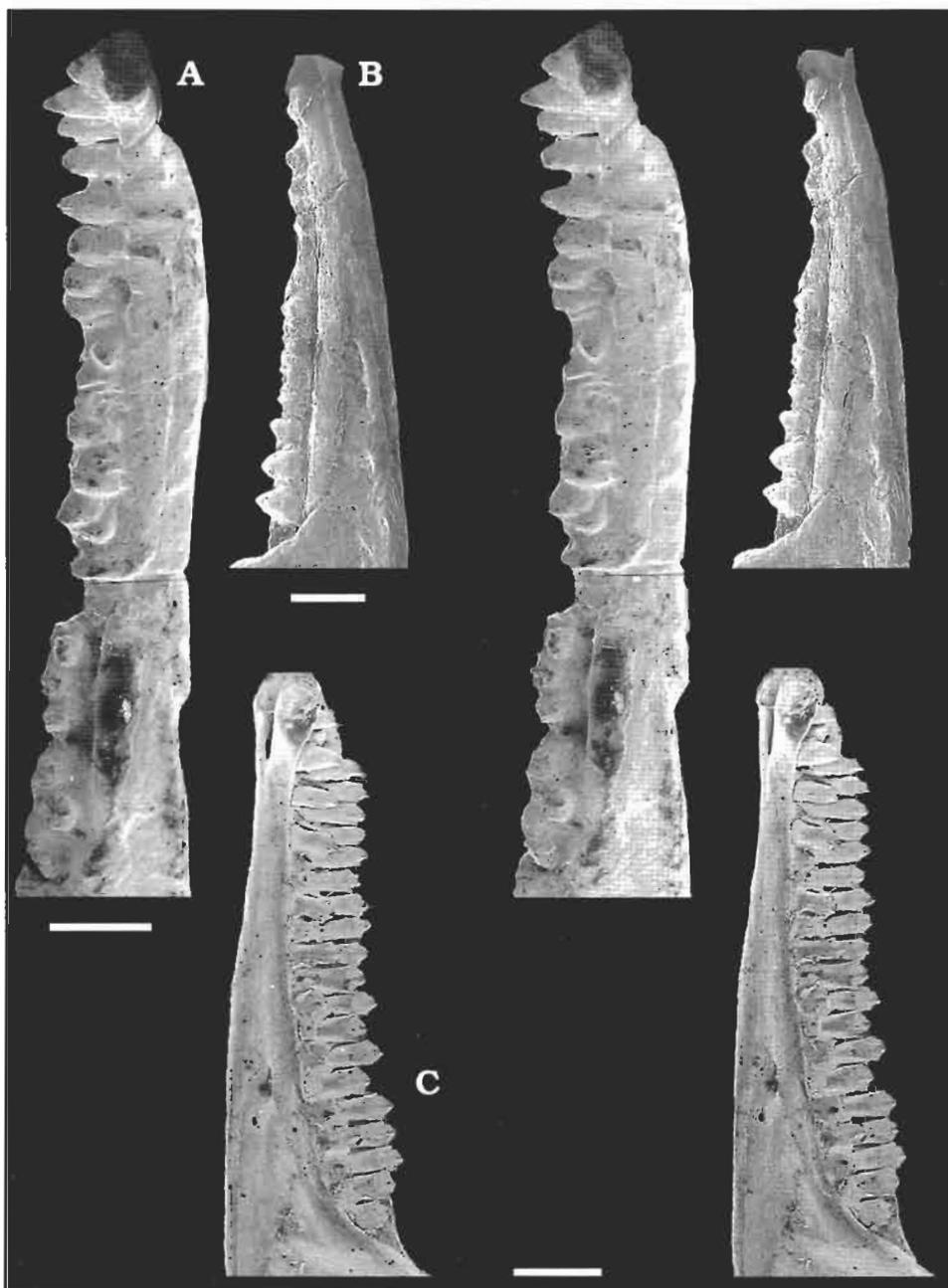


Fig. 3. **A.** *Pleurodontagama aenigmatodes* Borsuk-Białynicka & Moody, 1984. Late Cretaceous Red Beds of Khermeen Tsav (?middle Campanian). Left mandible of ZPAL MgR-III/35 in lingual view. SEM stereo-pair. **B.** *Priscagama gobiensis* Borsuk-Białynicka & Moody, 1984. Late Cretaceous Red Beds of Khermeen Tsav (?middle Campanian). Left tooth row of ZPAL MgR-III/32 in lingual view. SEM stereo-pair. **C.** *Corytophanes cristatus* (Merrem). Right mandibular tooth row of ZPAL R-I/44. Recent. Lingual view. SEM stereo-pair. Scale bars are 2 mm.

It is obvious that the lingually and interdentially situated tooth buds would have come to the labial sites to produce the alternative tooth row of this dentition (as they do in embryonic dentitions — Osborn 1971; Harrison 1901), if these sites were large enough to accommodate them. But, they were not. Hence, because of purely mechanical reasons these tooth buds have been arrested at the more lingual positions, some of them (the 12th and 15th lower teeth, Fig. 1A–B) arrested also in growth. The blockage could have been extended on to the development of subsequent generations of tooth buds and on resorption of the functionals, thus on the whole replacement process. The lack of replacement teeth directly lingual of the functionals probably accounts for a suppression of resorption of the latter. This was a possible mechanism of the development of permanency, though the important selective agent behind its development was probably a strong bite adaptation of the Acrodonta.

The interpretation of the ontogenetical development of the upper dentition is just the extension of that of the mandibular tooth row. The state of maxillary tooth row is considered more advanced than that of the lower one in the almost total absence of younger generation teeth. Still, the teeth of the posteriormost upper series, more crowded than allowed by a short section of the jaw they occupy (Fig. 2A–B), are supposed to include some younger generation teeth developed interdentially. The reduction of the redundant lingual teeth may mean that they either disappeared with the blockage of replacement or have been mounted in the eventual tooth row. The alternating pattern of tooth development would thus have turned (with some changes in tooth sequence) into the regular sequential pattern known in a typical permanent dentition of the Acrodonta. The latter evolutionary change probably reflects a trend towards a precise occlusion.

The fusion of some neighbouring teeth (Figs 1A–B, 3A) mentioned above, resulted from pushing together the corresponding buds prior to their mineralization. Acceleration of some replacements due to their interdental position (i.e. to their independence from the rate of development of predecessors) may be a possible reason for this deviation from the standard replacement rule.

The lingual inclination of the upper 'cheek' series as a whole is reminiscent of the agamids and most probably results from the development of a precise occlusion in these lizards. Though precise occlusion cannot be excluded in *Pleurodontagama*, there is no unequivocal evidence.

Exactly the same ontogenetic mechanism is here proposed for the development of the varanid dentition. The interdental position of replacements is correlated with the increased size of interdental spaces, i.e. relatively widely spaced functional teeth. The adaptive type of the Varanidae consists of a totally preorbital position of the jaws (McDowell & Boggert 1954). It remains to be explained why a similar agent, the intensification of bone growth, brought about such different results as tooth permanency versus varanid type replacement.

Discussion

It is a commonplace that the shape of teeth and pattern of dentition reflect particular dietary habits, but the actual relations between them are difficult to trace (Lundeilus 1957; Hotton 1955; Capel-Williams & Pratten 1978; Throckmorton 1976, 1978). Both tooth permanency and hypertrophy (and/or molarization) may be considered in terms of strong bite adaptation. Tooth form and size may be variable at a specific level and even in ontogeny of an individual (Estes & Williams 1984), the tooth molarization being scattered about different lizard families (teiids, varanids, anguids as well as iguanids, lacertids, xantusiids according to Estes & Williams 1984). In contrast, the tooth permanency, when present, is stable at about the family level and its development probably reflects much deeper genetic changes. The tooth molarization and/or hypertrophy affects, as a rule, the posterior parts of jaws, without affecting the basic skull proportions as characteristic for the family in question (see Estes & Williams 1984). In contrast, the tooth permanency is associated with a posterior shift of the jaws to underlie the orbit as demonstrated by Robinson (1973) and supported by a frequency distribution of a respective index in lizards (Borsuk-Białynicka 1986). The only factor in common which probably contributes to the development of both permanency and molarization is a decrease of the distance between a modified part of dentition and a mandibular joint acting as a fulcrum (McDowell & Bogert 1954; Robinson 1973). Powerful and long lasting teeth may evolve by simple deceleration of tooth replacement, and particularly so in the posterior part of the jaws. But, the exact mechanism of the development of the permanency may be related to the changes in style of growth of the tooth bearing elements associated with changing skull proportions.

It is widely accepted and assumed herein that the squamatan ancestor had a dentition continuously replaced, as it is the case among the majority of vertebrates other than mammals, and pleurodont as in most lizards. This assumption seems to be true in spite of the fact that tooth permanency is a rule in both Sphenodontida (which is a sister group of the Squamata) and the Acrodonta (which probably derived very early from the common squamatan stem, the Iguania being a sister group of the remaining lizards; Fig. 4). The dentition of the most primitive sphenodontidan *Gephyrosaurus bridensis* Evans, 1980 (Fig. 5A) from the Early Jurassic of Wales, which is pleurodont and replaced in the iguanid method (Evans 1985), demonstrates that tooth permanency of the Sphenodontida evolved independent from that of the Acrodonta. *Gephyrosaurus bridensis* displays a type of dentition (Fig. 5A) most common within the Lepidosauria as well as outside this taxon, and thus, may readily be regarded as ancestral for the whole lepidosaurian group (as already suggested by Evans 1985). That of *Pleurodontagama aenigmatodes* (Fig. 5B) may be considered as a type transitional to the acrodontan dentition, whereas that of *Diphydontosau-*

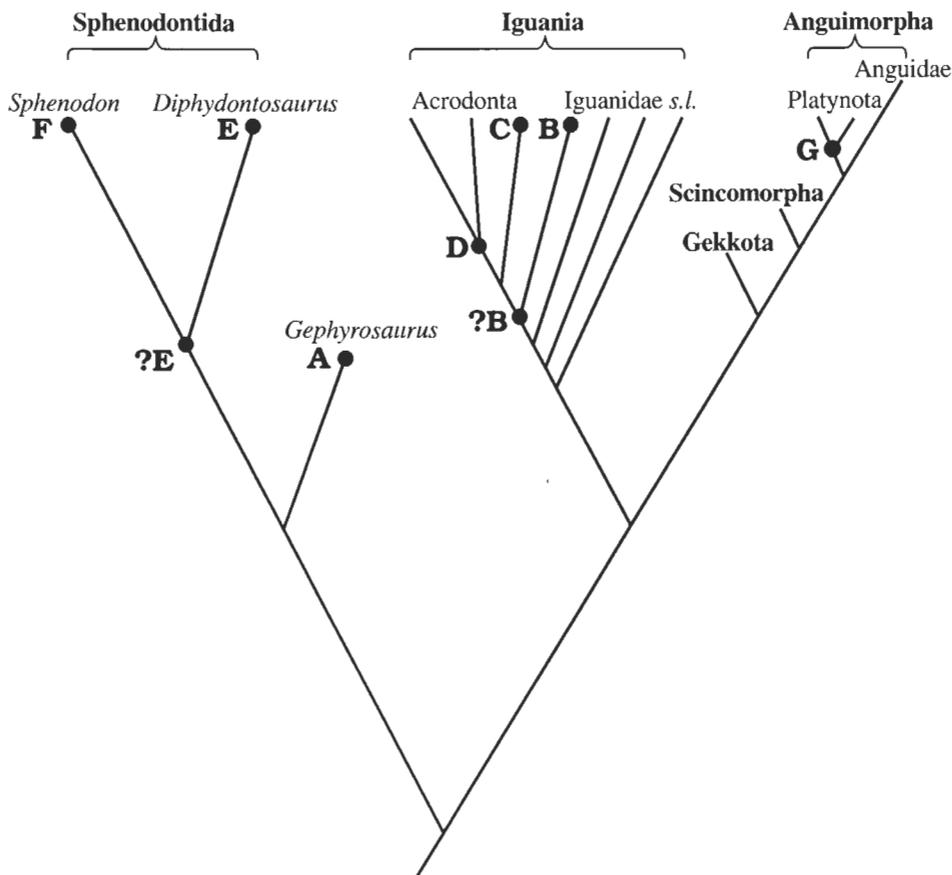


Fig. 4. Cladogram, compiled mainly after Evans (1988) and Estes *et al.* (1988), depicting phylogenetic relationships within the Lepidosauria with dentition character states plotted on it. The letters refer to Fig. 5 and denote the states of dentition of particular taxa. The letters provided with question marks denote possible novelties at the particular nodes of the cladogram.

rus avonis Whiteside, 1986 (Fig. 5E) from the Late Triassic of England, as the earliest stage of sphenodontidan type permanency.

Priscagama mongoliensis (Figs 1C–D, 2C–D) and *Flaviagama dzerzhinskii* (Alifanov 1989), the representatives of the priscagamines (Borsuk-Białynicka & Moody 1984) other than *Pleurodontagama aenigmatodes*, display a one-row 'cheek' series of dentition. This is the next step in the evolution of the acrodontan type permanency. In both genera, the teeth are arranged in a straight line, there being no signs of a sinuous pattern in the tooth rows. The rudiments of younger generation teeth have probably been lost, one-row dentition being the important element of a precise occlusion (given the association of the latter with the tooth permanency; Robinson 1976). The upper tooth row is inclined lingually in *Flaviagama dzerzhinskii* and less so in both *Priscagama mongoliensis* and *Pleurodontagama aenigmatodes*. In

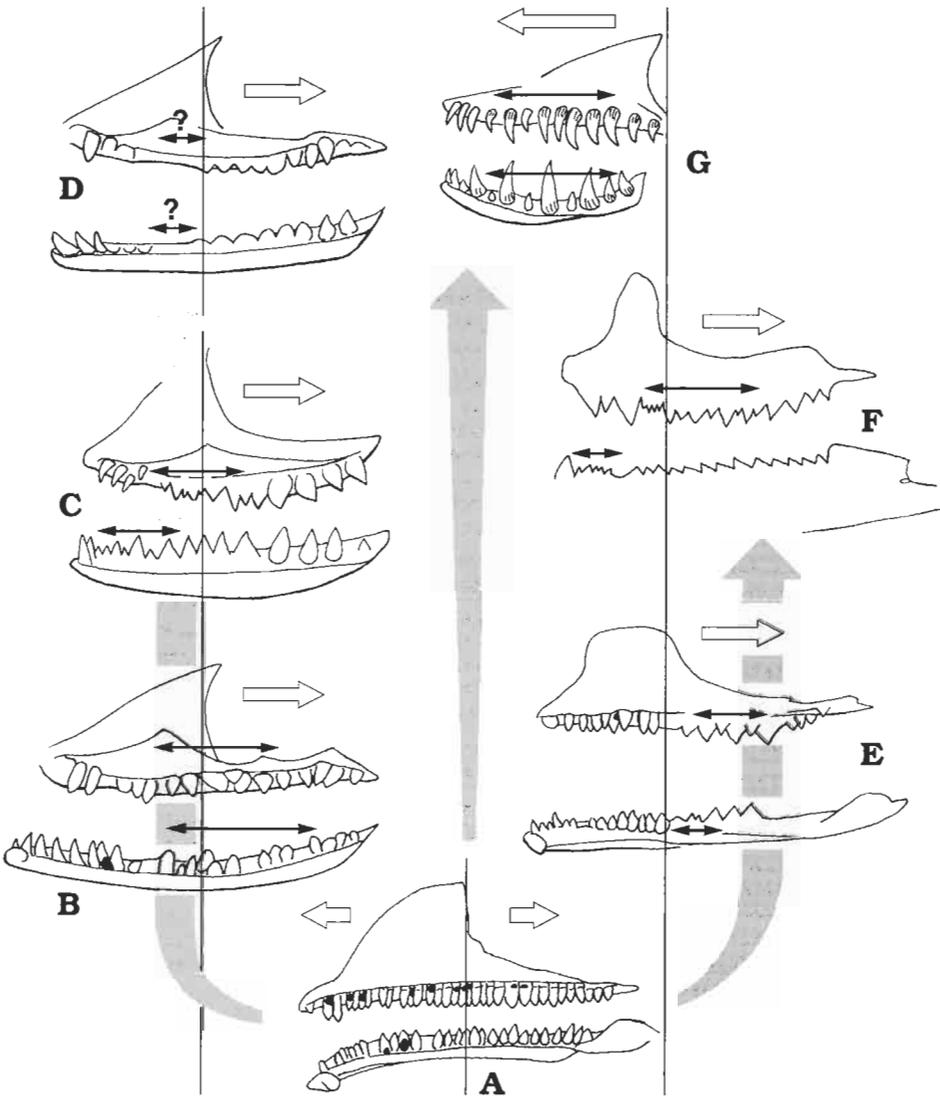


Fig. 5. Possible transformation series of dentitions in the squamates and sphenodontidans — schematic drawings of dentition types based on: **A.** *Gephyrosaurus bridensis* Evans, 1980. Early Jurassic, Wales (after Evans 1985); **B.** *Pleurodontagama aenigmatodes* Borsuk-Bialynicka & Moody, 1984. Late Cretaceous, Gobi Desert (ZPAL MgR-III/35); **C.** *Flaviagama dzerzhinskii* Alifanov, 1989. Late Cretaceous, Gobi Desert (PIN 3143/101); **D.** *Priscagama gobiensis* Borsuk-Bialynicka & Moody, 1984. Late Cretaceous, Gobi Desert (ZPAL MgR-III/32); **E.** *Diphydontosaurus avonis* Whiteside, 1986. Late Triassic, Wales (after Whiteside 1986); **F.** *Sphenodon punctatus* (Gray, 1872). Recent, New Zealand (after Robinson 1976); **G.** Varanid type according to *Varanus niloticus* Linnaeus, 1758. Recent (ZPAL R-1/31). All but *Sphenodon* in lingual aspect. Not to scale. Shaded arrows show the directions of evolutionary transformations of dentition types. Vertical lines denote the level of the anterior border of the orbit. Double-arrow-lines indicate the regions of interstitial growth of the dental lamina; hollow arrows denote the main growth tendency (the direction and rate of growth) in a phylogeny of a given group.

both *Flaviagama dzerzhinskii* and *Priscagama mongoliensis*, but not in *Pleurodontagama aenigmatodes*, this inclination is associated with traces of the maxillary tooth bites left on the labial surface of the mandible (Fig. 1C–D), as a univocal evidence of a precise occlusion.

In all the above priscagamines, there are some remnants of hatchling dentitions, very much damaged in *Pleurodontagama aenigmatodes* (Fig. 2A–B), strongly worn in *Priscagama mongoliensis* (Figs 2C, 3B) and best developed in *Flaviagama dzerzhinskii* (Fig. 5D), the latter species being represented by a juvenile (PIN 3143/101), the only specimen known (Alifanov 1989). This specimen demonstrates the method of jaw growth that is mainly posteriad in the dentary and both posteriad and anteriad in the maxilla. The remnant hatchling dentition of the maxilla which is the subject of replacement by large pleurodont teeth in its anterior section, is thus shifted backwards to lose the occlusive contact with its lower counterpart. This style of growth is reminiscent of the adult *Sphenodon* (Robinson 1976). Robinson associated this situation with the lack of precise occlusion in this genus. This explanation may not be valid in the case of *Flaviagama* having the precise occlusion already developed (see above).

In *Gephyrosaurus bridensis* (Fig. 5A) the teeth are closely spaced and arranged in one row all over the jaws, except for just some slight irregularities (Evans 1985: figs 5A, 7C) in the posterior jaw section. The increase of tooth bearing elements probably occurred mainly posterior to the dental determinant and thus proceeded by the tip growth. The teeth have been replaced in a directly successional method the rate of replacement decreasing in the posterior part of the jaws (thus with age).

In the Sphenodontida the tooth alternation affects mainly tooth sizes (Fig. 5F) instead of position. It has already been noticed by Harrison (1901), that the embryonic dentition of *Sphenodon* combines the teeth of two distinct tooth generations, the second and the third. The latter teeth instead of displacing the earlier ones come to alternate with them. The method of development of eventual tooth row in *Sphenodon* is basically the same as that described by Osborn (1973) in *Lacerta*, and thus, may be considered universal in *Lepidosauria* at least. As differing from the here advanced interpretation of the *Pleurodontagama* dentition, Harrison considered the smaller teeth as belonging to the older generation rather than to a rudimentary younger generation held up in growth. This is in conflict with his own observation (Harrison 1901) that the larger teeth have lost their original contact with the dental lamina whereas the smaller ones have not. If it were true, the situation would differ from that in *Diphydontosaurus* in which 'the base of smaller teeth of the alternating series is always placed on the lingual side of the ventral margin of the maxilla' (Whiteside 1986: p. 389) and thus the smaller teeth are probably younger and held up in size and position. Perhaps, the size relations between the alternating generations may be inverse in prehatchling and posthatchling stages, only alternation being a rule valid throughout the ontogeny.

The same type of tooth alternation is also known in *Clevosaurus* (Robinson 1973), *Homoeosaurus* (Whiteside 1986) and *Diphydontosaurus* (Whiteside 1986). So far considered as characteristic or even synapomorphic for the Sphenodontida (Whiteside 1986: p. 406), it has also been demonstrated in *Flaviagama* (Alifanov 1989: fig. 1; see also Fig. 5D herein), and may be conceived in terms of interstitial growth of the dental lamina.

Diphydontosaurus avonis Whiteside, 1986 (Fig. 5E) presents the first known stage of development of tooth permanency in the Sphenodontida. The tooth alternation is demonstrated just in a part of dentition underlying the orbit, most probably posterior to the dental determinant (*sensu* Osborn 1973), the more anterior jaw section being occupied by a row of 17 pleurodont teeth replaced in a directly successional manner. No hatchling dentition is preserved in the adult. The tooth alternation in *Diphydontosaurus avonis* may have resulted from an intense posterior growth of jaws followed by the interstitial growth of the dental lamina that tended to keep up with the growth of the bones. Subsequent generations of teeth found their place within the interdental spaces produced by this growth, their replacement and growth being blocked under a selective pressure of a strong bite adaptation. Demonstrated by Whiteside (1986: fig. 33) a possible anterior shift of the superior process of the maxilla in the evolution of the Sphenodontida (i.e. the elongation of the posterior process), implies a corresponding anterior extension of a style of the posterior part of dentition. It means that some features of the posthatchling growth (the regular tooth size alternation in the case of the Sphenodontida) extended onto the earlier phases of the ontogeny. They were eventually adopted by the hatchling, while being gradually substituted by a new style (a regular sequential growth) in the rear parts of jaws. Almost the whole maxillary and corresponding mandibular dentition became permanent.

A correlation between skull proportions and a type of tooth replacement in the varanoids, both unique in lizards, suggests an evolutionary association of these characters similar to that of the Acrodonta and Sphenodontida. Still, in the Varanoidea, the evolutionary shift of the jaws proceeded in the opposite direction, the eventual position of the maxilla and dentary being entirely preorbital. According to McDowell & Bogert (1954, see also DeBraga & Carroll 1993), a selective agent behind this evolutionary shift was the advantage of the platynotan skull proportions for a grasping snap. The displacement of the jaws must have involved an intensification of the anteriorly directed growth. This could have resulted in a loss of a strict coupling between the volume of the tooth sites and size of teeth that are to occupy them, and consequently in the interdental position of replacement teeth.

The earliest representative of the stem-platynotan group *Parviraptor estesi* Evans, 1994 from the Middle Jurassic and Early Cretaceous of England as well as from the Late Jurassic of Portugal, displayed an essentially anguimorphan (Evans 1994: p. 38), but rather intermediate than varanid type, dentition. The only one resorption pit preserved in the

holotype in a distolingual position suggested an interdental development of replacements. As shown by Evans (1994: text-fig. 5), the most posterior part of the maxilla could have underlain the anterior angle of the orbit. Still, the process of anterior displacement of the maxilla was already under way as suggested by the shape of the palatine and a disposition of its jugal and maxillary processes (Evans 1994: text-fig. 10A).

The evolutionary shift of jaws with respect to the rest of the skull corresponds to a directional growth of jaw bones. It may be speculated that it proceeded much more freely when directed distally than proximally. It produced a varanid type of tooth replacement differing from the iguanid type just by the posterolingual position of replacement and by the associated modification of tooth resorption. However, much more information on the embryonic development of the varanoid dentition is needed before a more conclusive hypothesis concerning its origin could be proposed. On the other hand, these are just the restrictions of the posterior growth of jaws which account for a disturbed regularity of the tooth replacement at the early phase of phylogeny of those groups that eventually developed the acrodont dentition.

Conclusions

Tooth permanency probably results from two reasons which interfere with each other. The biomechanical requirements of a strong bite adaptation may have been a direct selective agent that promoted a retardation of replacement and mainly so in the posterior jaw quadrants. They may have also acted indirectly by accelerating the posteriad growth of jaws that affected the tooth replacement process resulting in its eventual blockage.

The kind of relations between a differential jaw growth and tooth replacement processes is hypothesised as follows.

Each case of tooth alternation, whether in size or in localization, may be considered in terms of interstitial growth of jaw structures that produce and accommodate teeth. The growth of tooth bearing elements is transmitted onto the eventual pattern of dentition via the dental lamina, the organ responsible for tooth production. The jaws of the posthatchling lizards may only grow at the peripheries (Hall 1978; Herring 1993). The dental lamina has to follow their size increase, but, in contrast to bones, it is capable of the internal expansion.

The differences in intensity of growth, between particular parts of the dental lamina seem to be critical for the development of different patterns of dentitions.

The modification of growth should have occurred parallel in the evolution of the Acrodonta and in that of the Sphenodontida in connection with the posterior displacement of jaws in those groups (Robinson 1973, 1976). The proximally directed jaw growth in both the Acrodonta and the Sphenodontida, to an eventual suborbital position, is very much con-

strained by the bones which articulate with the jaws from behind, as well as by soft parts of the head that require some spaces in that region. The half rate interstitial growth of the dental lamina is here proposed as a mechanism of evolution of tooth permanency, by means of holding up the development of replacements wedged in the interdental spaces too narrow for them. However, the primary reason for the development of permanency is the biomechanical requirements of a strong bite adaptation. The interstitial growth of the dental lamina posterior to the dental determinant was just transitional in the phylogeny of those groups that developed permanency. This type of growth has been replaced very early by the apical growth and a sequential tooth bud development.

A selective pressure acting upon the double-row dentition of *Pleurodontagama* type may have caused reduction of the replacements, thus stimulating a development of the eventual one-row dentition. A selective agent responsible for this reduction would be the importance of the one-row dentition for the development of both precise occlusion (given its association with tooth permanency demonstrated by Robinson 1976), and propalinal action characteristic of at least modern sphenodontids (Whiteside 1986).

In contrast, the acceleration of antero-lateral growth is here postulated for the varanoids. As demonstrated by McDowell & Boggert (1954), the varanoid skull adaptation consists in a totally preorbital position of the jaws. The distally directed growth of varanoid jaws is quite free and results in a widely spaced dentition with the replacements shifted to the interdental spaces.

The sinuous double-row dentition of *Pleurodontagama* presents, thus, a short evolutionary event trapped in the paleontological material which has a potential to elucidate the mechanism of development of different types of lepidosaurian dentition.

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Późnokredowa jaszczurka *Pleurodontagama* a powstanie uzębienia permanentnego u Lepidosauria

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Streszczenie

Przedmiotem pracy jest interpretacja uzębienia najprymitywniejszego rodzaju i gatunku agamidów — *Pleurodontagama aenigmatodes* Borsuk-Białynicka & Moody, 1984 z późnej kredy Mongolii. Naprzemienny, dwuseregowy układ tego uzębienia zinterpretowano jako przejaw braku koordynacji między procesem wzrostu i wymiany uzębienia w ontogenezie z jednej strony a procesem wzrostu samych szczęk, stanowiących miejsce osadze-

nia tego uzębienia, z drugiej strony. W oparciu o tę interpretację zaproponowano model powstawania uzębienia permanentnego w filogenezie Acrodonta, stosując go następnie do wyjaśnienia pochodzenia uzębienia permanentnego Sphenodontida oraz waranidowego typu wymiany zębów u Anguimorpha.

Podstawowe założenia prezentowanego modelu to (1) związki między zróżnicowanym wzrostem kości a wymianą zębów proponowane przez Osborna (1971, 1973, 1974) i Westergaarda (1980, 1986) oraz (2) istotność zmiany kształtu szczęk dla powstania linii ewolucyjnej Acrodonta (Robinson 1973, 1976; Borsuk-Białynicka 1986). Zmiana ta polegała na podsuwaniu się szczęk pod oczodoł, co miało związek ze wzmacnianiem zgryzu u Acrodonta w porównaniu z ich iguanidowymi przodkami. Przesunięcie takie zachodzić musiało drogą intensyfikacji wzrostu tylnej części szczęki, czemu siłą rzeczy towarzyszył podobnie ukierunkowany wzrost listewki zębowej. Międzyzębowe (zamiast bezpośrednio dojęzykowego względem zębów funkcjonujących) położenie kolejnych pokoleń zębów świadczy o tym, że wzrost listewki zębowej zachodził nie tylko na peryferiach, lecz także wewnątrz jej tkanki (interstycjalnie). Zahamowanie wielu zębów na pozycjach dojęzykowych prezentowane przez pleurodontagamię świadczy o niewydolności tego wzrostu w stosunku do wielkości tworzonych zębów. Zgodnie z proponowaną hipotezą, takie właśnie niedopasowanie tempa wzrostu szczęki do tempa wymiany doprowadziło do zablokowania wymiany i powstania uzębienia permanentnego charakterystycznego dla agamidów, a także kameleonów.

Podsunięcie szczęk pod oczodoł charakterystyczne dla Sphenodontida wiąże się także ze swego rodzaju naprzemiennością uzębienia (dotycząca przede wszystkim rozmiarów zębów), a także z zablokowaniem wymiany. Zjawiska te dotyczyły pierwotnie (u *Diphydontosaurus avonis* Whiteside, 1986, późnotriasowego przedstawiciela Sphenodontida) tylnej, a więc najsilniej rosnącej części szczęk, później całego uzębienia. W oparciu o zaproponowany tu model można przypuszczać, że intensywny wzrost szczęk w kierunku ku przodowi od oczodołu, uważany za charakterystyczną cechę Platynota (McDowell & Bogert 1954) spowodował charakterystyczną, naprzemienną wymianę zębów, zwaną typem waranidowym (Edmund 1960). Kierunek tego wzrostu (na zewnątrz czaszki zamiast ku oczodołowi i stawowi szczękowemu) pozwolił na swobodne mieszczanie się zębów kolejnych pokoleń w jednym szeregu i na międzyzębowe położenie zawiązków.