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THE EARLY PHYLOGENY OF ANGUIMORPHA AS IMPLICATED
BY CRANIOLOGICAL DATA

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The problem of homology *versus* analogy of different craniological character states shared by Anguimorpha and Scincomorpha is analyzed. Only two character states, if any, may be tentatively considered as synapomorphies in both taxa. These are: low, tubular skull shape and broad, flat frontals. Other craniological features displaying similar states in both infraorders are regarded as parallel structures. Morphoclinical sequences of states of different craniological characters are proposed. The derived pattern of tooth replacement is regarded as the earliest and the most important achievement of the anguimorphan lizards which is probably the only autapomorphy of this infraorder. A certain pattern of the brain case is regarded as synapomorphic in the Platynota and Diploglossa, the two superfamilies that probably do not cover the range of the infraorder.

Key words: Sauria, craniology, cladistics.

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INTRODUCTION

The present paper is an attempt of an analysis of some problems concerning the early phylogeny of Anguimorpha and their relationships to other Sauria. Camp (1923) regarded Anguimorpha as a sister group of Scincomorpha and created a common taxon Autarchoglossa to include both of them. Camp's concept has long been considered valid and was supported by Underwood in 1971 but has been shaken by more recent data (Estes pers. comm.). However, the evident similarities between the representatives of both groups as regards craniological features as well as difficulties in discrimination between the primitive representatives of them demand some elucidation. It seems interesting to consider the problem from the point of view of the distribution of craniological character states with the assistance of cladistic methods of Henning as presented

by Shaeffer *et al.* (1972) and Hecht (1976). The main ideas of this paper have been developed during the studies on the Late Cretaceous anguimorphan lizards from the Gobi Desert described elsewhere (Borsuk-Białynicka in press).

Studying this material I had the opportunity to examine about a hundred of extant lizard skulls from different infraorders of Sauria.

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Abbreviations:

- HUB Zoological Museum of Humboldt University, East Berlin
MCZ Museum of Comparative Zoology, Harvard University, Cambridge
ZIN Zoological Institute, USSR Academy of Sciences, Moscow
ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw

DETERMINATION OF POLARITIES

The following skull features are presumed to have achieved their derived states at the early stage of phylogeny of Anguimorpha or still earlier: the type of dermal skull covering; the characters of the brain case such as the alar process of the prootic, the brain case wall and the sphenoccipital suture; some characters of the dentition and the overall shape of skull or, more precisely, of the maxillary segment of skull.

On the basis of the commonality principle (Hecht 1976) as well as the ontogenetic premisses, the irregular incrustations of different shape varying from tubercles to ridges separated by branching and anastomosing furrows or pits (pl. 2: 1) are regarded as a primitive type of the osteodermal skull covering (fig. 1.1). The ontogenetic development of this type of incrustation implies two transformation series passing from this type of sculpture towards the osteodermal armour consisting either of small elements or of solid plates (fig. 1.3' or 3 correspondingly).

A long, anteriorly extended alar process (fig. 3.2' and pl. 1: 2a) of the prootic is shared by all the Diploglossa and all the Platynota (comp. Rieppel 1980), the Late Cretaceous genera, known to date, included (Borsuk-Białynicka in press). The same is true of the prootic crest directed to the dorsal corner of the paroccipital process resulting in the narrowness of the posterior part of the recessus vena jugularis in ventral view. This

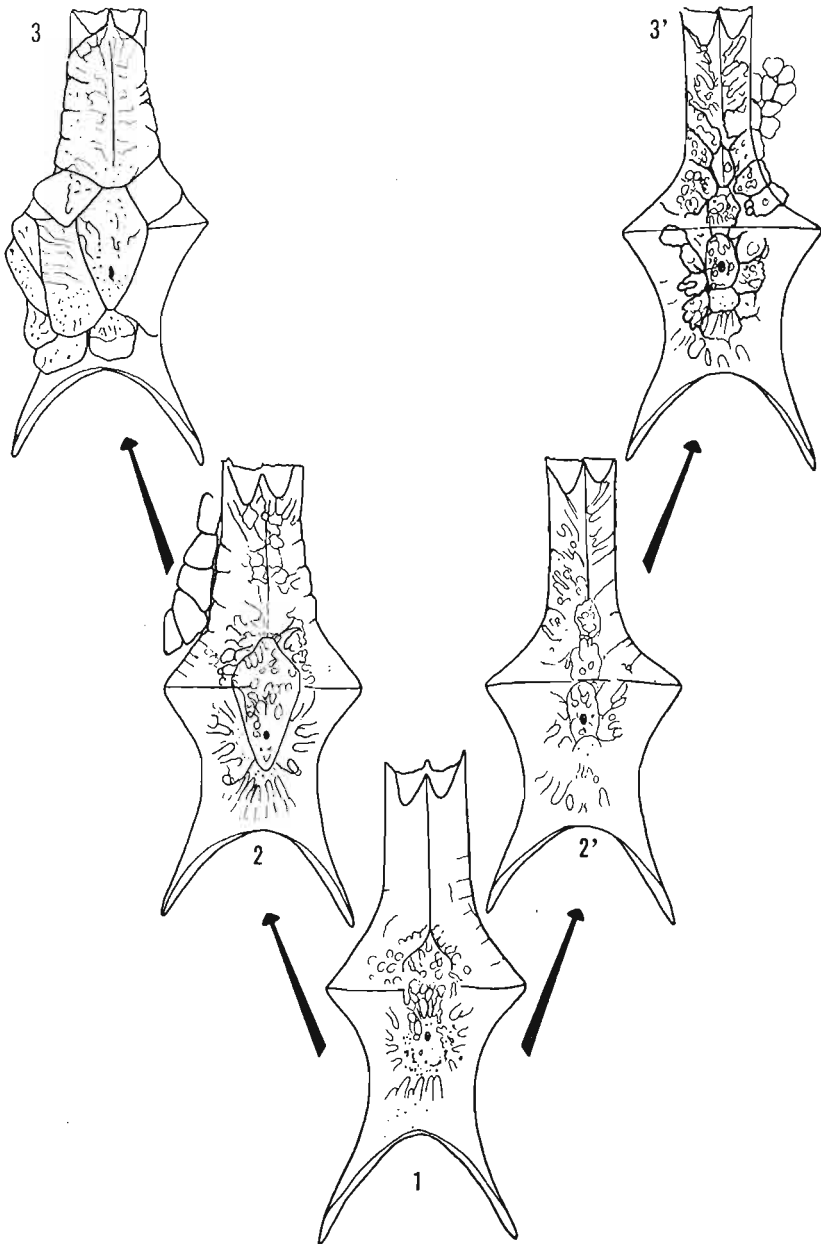


Fig. 1. Transformation series of states of osteodermal skull covering leading from a primitive state (1) to a derived shield pattern (3) and from the primitive state (1) to a derived small element pattern (3'), via hypothetical intermediate states (2) and (2').

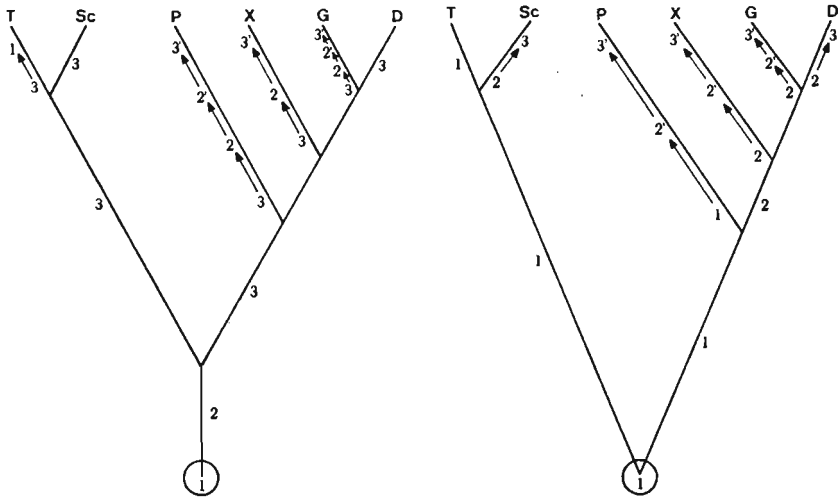


Fig. 2. Cladograms illustrating the rate of development of derived states of the osteodermal skull covering in two infraorders of Sauria, Anguimorpha and Scincomorpha. *Left* early appearance of the derived states, *right* late appearance of the derived state. *D* main diploglossan stem; *G* Glyptosaurinae; *P* Platynota; *Sc* remaining Scincomorpha; *T* Teiidae; *X* Xenosauridae. Explanations to numbers as in fig. 1.

can be briefly called a narrow type (fig. 4B) in contrast to the broad type (fig. 4A), characterized by the prootic crest extending to the ventral corner of the paroccipital process. As a result, the paroccipital process has a broad, triangular ventral surface instead of a ventral ridge present in the narrow type (comp. pl. 1: 1b, 2b). The broad type of the jugular recess is typical of the Late Cretaceous teiids exemplified by *Macrocephalosaurus* and *Erdznetesaurus* (Sulimski 1975, pl. 21: 1c and pl. 23: 1d). The character states contributing to this type are difficult to assess, but the structures displayed by many other Scincomorpha and Iguania as well as by nonsaurian diapsids, such as *Prolacerta* (Gow 1975), seem to be closely similar to the broad type while differing from the anguimorphan narrow type. On the basis of such a distribution of states of this character within the range of Sauria and in the outgroups (commonality principle) I suggest that the broad type of the jugular recess is primitive in Sauria whereas the narrow type is derived.

Correlated with the broad type of the jugular recess, the lack of the alar process is also presumed to be primitive. The alar process is a supplementary ossification of the brain case which may be, at least theoretically, very susceptible to changes. However, its correlations with other craniological features makes it more stable in fact. Each of the infraorders may be characterized, allowing for a certain amount of variability, by its own type of the alar process (fig. 3) which is probably uniquely derived for it. The most likely state of the brain case characteristic of

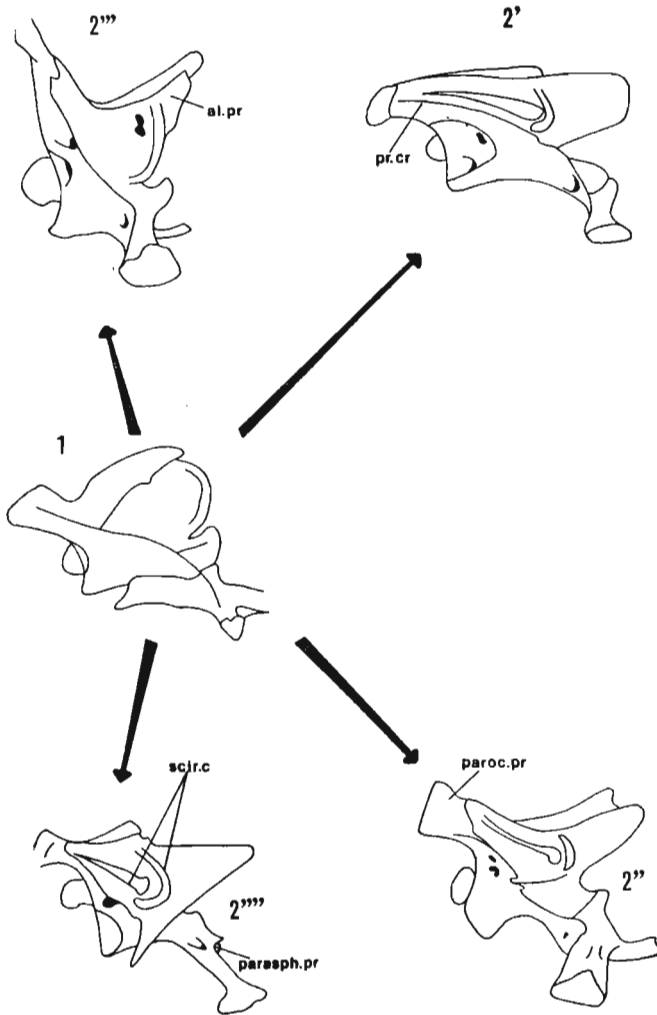


Fig. 3. Transformation series of states of brain case wall leading from a primitive state without the alar process (1) to different derived states of: anguimorphan type (2'), scincomorphan type (2''), iguanian type (2'''), and gekkotan type (2'''). *al. pr* alar process; *parasph. pr* parasphenoid process; *paroc. pr* paroccipital process; *pr. cr* prootic crest; *scir. c* semicircular canal.

the common ancestor is the one without any alar process (fig. 3.1). However, the type of the alar process of Anguimorpha is similar to that of Scincomorpha thus suggesting their common origin. Whether they are derivable from the common ancestor already displaying an extensive alar process and are, thus, homologous or have they developed in parallel from the ancestor having no trace of this process (see p. 39 and fig. 6), is a question closely related to the essential problem of this paper.

The state of the sphenoccipital suture directly depends on the shape of the parasphenoid that partly overlaps the ventral surface of the ba-

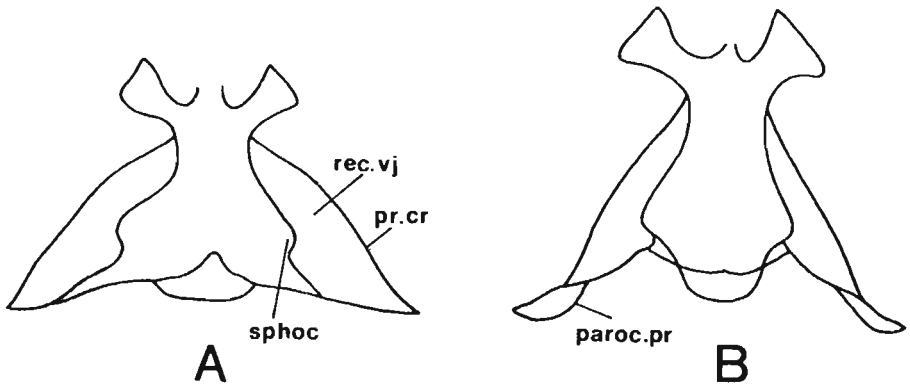


Fig. 4. Two states of recessus vena jugularis as demonstrated by ventral aspects of the brain case. A broad type; B narrow type. *paroc. pr* paroccipital process, *pr. cr* prootic crest, *rec. vj* recessus vena jugularis, *sphoc* — sphenoccipital tubercle.

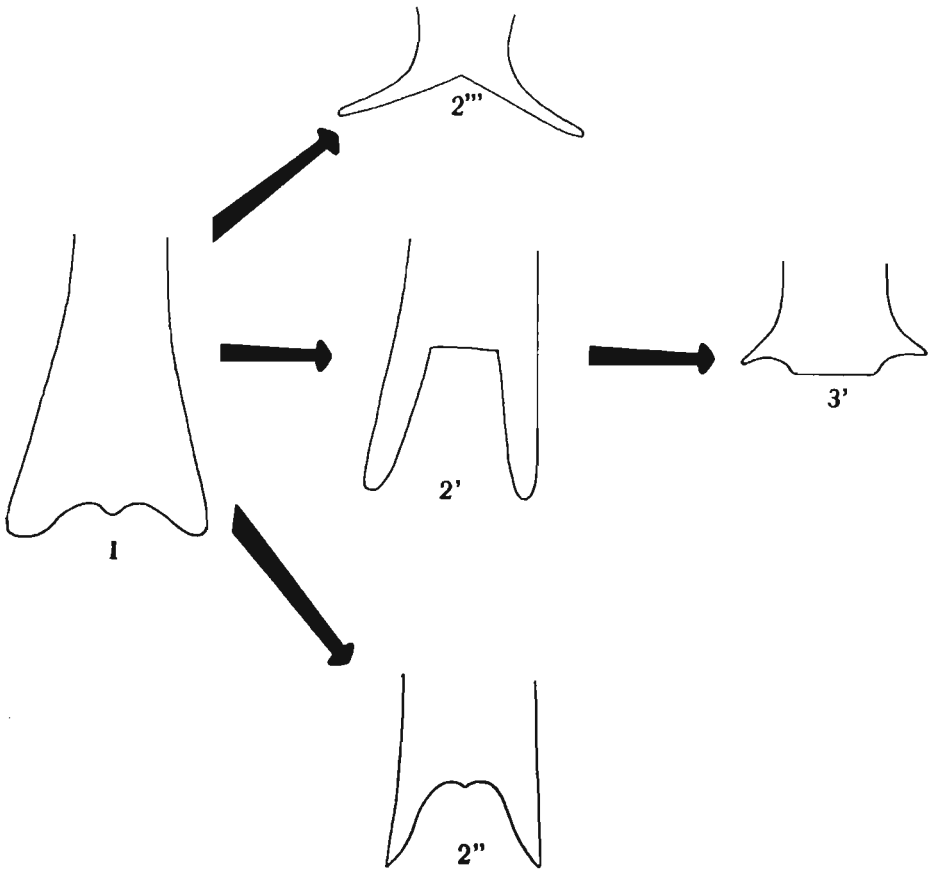


Fig. 5. Transformation series of the parasphenoid and the sphenoccipital suture leading from a primitive state (1) via a derived anguimorphan state (2') associated with a trapezoidal sphenoccipital suture, to the most derived shortened type (3') characteristic of *Varanus* and *Lanthanotus*. 1 to 2'' and 1 to 2''' other transformation series. 2'' scincomorphan type, 2''' iguanian type.

sioccipital. The most common structure of this bone within Sauria is that with a shortened parasagittal part and posteriorly extended lateral parts. Characterized by a transversal parasagittal part and posteriorly divergent lateral parts, a trapezoidal type of sphenoccipital suture (fig. 5.2'; comp. pl. 1: 2b) is shared by the Diploglossa and the Platynota in contrast to Iguania displaying the angular type of suture (fig. 5.2''; pl 1: 1b). A proposed morphocline (fig. 5) of the parasphenoid leads from a long type considered primitive for diapsids according to Gow (1975) *via* the derived trapezoidal type to the most derived shortened type. Here again the problem arises whether the type of sphenoccipital suture present in Anguimorpha is homologous or parallel to that of Scincomorpha.

The morphocline sequence of the tooth replacement patterns, proposed by Rieppel (1978) leads from the primitive, directly successional iguanid tooth replacement *via* the intermediate pattern exemplified by the Diploglossa, to the specialized varanid or alternate method of tooth replacement in the platynotans. This transformation series may be compared exclusively with the anguimorphan part of phylogeny since Scincomorpha do not usually exceed the primitive state of this sequence.

CORRELATIONS BETWEEN CHARACTERS; THEIR DEPENDENCE ON FUNCTIONAL CAUSES

The following correlations of the craniological characters are suggested. The eventual pattern of the osteodermal skull covering is, in my opinion, dependent on the pattern of the epidermal scale covering of the skull roof bones to which it tends to adhere in the ontogeny. The scale covering appears earlier in the ontogeny than the osteodermal covering does and its pattern is probably due to the skull roof bones as the large and flat frontals provoke the development of the large scale covering whereas the narrow and uneven frontals favor a small scaling (see Bor-suk-Białynicka in press).

The proportion of the posterior part of skull probably affects the brain case characters such as (1) the angle between the axis of the supraoccipital and that of the brain case floor, (2) the shape, size and direction of the alar process of the prootic, the function of which is to bridge the gap between the skull roof and the brain case wall, and (3) the shape of the sphenoccipital suture. The long and low skull favors a long, anteriorly directed alar process, whereas the skulls with short and high posterior parts have the alar processes small and directed upwards or none. Shortening of the parasphenoid in the phylogeny causes the corresponding shortening, i.e. a transition into the derived shortened type (see above), of the sphenoccipital suture, its eventual shape depending on the rate of this process.

I suppose that the overall shape of the skull is the primary subject to selective pressure in lizard evolution whereas the osteodermal covering pattern and some character states of the brain case, mainly those connected with its proportions, are dependent on the type of skull. However, this dependence does not mean that the states of all these characters are unequivocally determined by the shape of skull or, specifically, by that of the maxillary segment, but they only tend to evolve in a certain direction instead.

The tooth replacement pattern is not directly correlated with any cranial characters. The transformation of the primitive, directly successional pattern of tooth replacement into the alternate one is presumed to be initiated by an increase of tooth spacing. This change having the advantage of the improvement of the sectorial efficiency of the dentition, is considered as an adaptation to predatory life. The shift of the successive teeth towards the interdental spaces is probably a simple consequence of this process.

HOMOLOGY VERSUS PARALLEL FORMATION OF CHARACTER STATES

The problem of homology or parallel formation of the above mentioned character states displayed by Scincomorpha and Anguimorpha is approached by contrasting the morphoclineal sequences and phylogentic hypotheses (comp., e.g., fig. 1 and 2). Examined will be the rate of development of the derived states and the problem of existence or absence of the common derived states. Independent of the case studied, two alternative hypotheses may be proposed (see e.g. fig. 2). The first one (fig. 2 *left*), assuming the early development of the derived state, consequently demands the evolutionary reversion ($3 \rightarrow 2$ or $3 \rightarrow 1$) to occur many times in the phylogeny owing to the diversity of states displayed by representatives of the taxa studied. Implying a simple correspondence between the morphocline and the chronocline, the second hypothesis (fig. 2 *right*) is more parsimonious.

The examination of character state distribution in the range of one of the infraorders is, thus, conclusive regarding the relationship between both of them, as the occurrence of primitive character states in any representative of the infraorder testifies against the early development of derived states.

Fossil data do not fully corroborate the second hypothesis (fig. 2 *right*) in the case of the osteodermal skull covering, but they do not falsify it either. The primitive type of the osteodermal covering occurs as early as the Late Jurassic in Scincomorpha (*Macellodus*, *Paramacellodus*, *Saurillus*, according to Hoffstetter 1967, figs. 1F, 2G, 4D, E) but it is associated

with the solid armour of the shield type in *Dorsetisaurus* (Anguimorpha, see Hoffstetter *l.c.*). According to the second hypothesis (fig. 2 *right*), *Dorsetisaurus* may be interpreted as already engaged in the diploglossan line (fig. 2*D*) or developed by early parallel evolution.

Similar reasoning holds when dealing with the brain case structure. The hypothesis (fig. 6 *left*) that the Anguimorpha and Scincomorpha had a common ancestral stage displaying a well developed alar process demands the evolutionary reversion to be assumed, since the primitive types occur in both infraorders although very scarce in Anguimorpha (see below). Such a reversion cannot be entirely ruled out though it seems improbable owing to the relative stability of the alar process observed within the range of infraorders, as already stated above (p. 34).

In Anguimorpha the primitive brain case wall occurs only in *Paravaranus*, a very small *Varanus*-like lizard (see Borsuk-Białynicka *in press*). All the remaining Anguimorpha, the Late Jurassic *Dorsetisaurus* included, display the derived type of brain case wall with a long anteriorly extended alar process. According to the hypothesis presented in fig. 6 (*right*), the primitive ancestral brain case has been inherited by both infraorders and have developed the derived states parallelly and in particular groups only. The case of *Paravaranus* supports this hypothesis until the anguimorphan nature of this genus is not questioned.

The sphenoccipital sutures are very similar in Scincomorpha and Anguimorpha but still display some differences which make them likely to be developed independently as a result of the process of shortening of the parasphenoid characteristic of all Sauria. The case of *Paravaranus*,

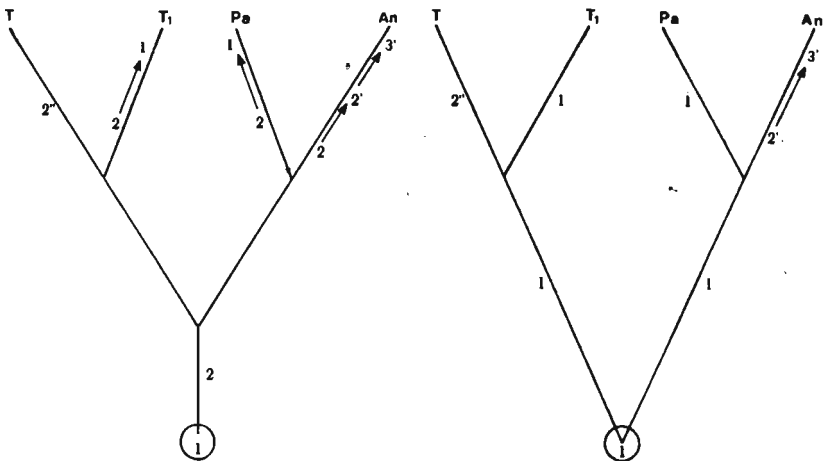


Fig. 6. Cladograms illustrating the rate of development of derived states of brain case wall in two infraorders of Squamata, Anguimorpha and Scincomorpha; *left* early appearance of the derived states; *right* late appearance of the derived states. *An* main anguimorphan stem, *Pa* *Paravaranus*, *T* main teiid stem *T*₁ Late Cretaceous teiid groups. Explanations to numbers as in fig. 3.

the only representative of Anguimorpha displaying the angular type of sphenoccipital suture (in addition to the primitive brain case wall) suggests that the process of shortening of the parasphenoid, resulting in the pure trapezoidal type of sphenoccipital suture, occurred only in the direct ancestor of the Diploglossa and the Platynota.

CONCLUSIONS

I would argue that the early divergence of Sauria included a formation of different adaptive types of skull connected with different life adaptations. The low and long skull with flat and broad frontals would be an adaptive type characteristic of both Anguimorpha and Scincomorpha in contrast to short types of Iguania and Gekkota. This would be the only craniological character states which may be considered as synapomorphic in both infraorders. However, it is not quite clear whether it is really derived and, if so, whether it has developed only once in the common ancestor of both infraorders or independently in the ancestors of each of them. This point demands some further elucidation and, thus, the problem of the relationship between Anguimorpha and Scincomorpha remains open. The large epidermal scale covering of the frontal region in both Anguimorpha and Scincomorpha was connected with the overall type of skull. The states of the osteodermal skull covering and brain case characters shared by both infraorders have clearly developed in parallel, owing to the correlations of characters (see p. 37) or are convergent.

The character state distribution in the Platynota and Diploglossa suggests that the common ancestor of these groups has already achieved the derived states of the brain case characters: the alar process, sphenoccipital suture and vena jugularis recess. The posterior end of the prootic crest is the only character state slightly retarded in its way upwards from the lower corner of the paroccipital process (see some Late Cretaceous platynotans, Borsuk-Białynicka in press). This ancestor was also characterized by a derived state of the dentition, namely — the intermediate pattern of the tooth replacement that qualified it as a predator. The primitive osteodermal covering of irregular bone thickenings probably persisted not only in anguimorphan ancestors but also in the early Platynota in which it turned into the small plate osteodermal covering or disappeared. Both processes were probably preceded by disintegration of large epidermal scaling over the skull roof. I would suggest that the development of the above complex of derived character states, characteristic of the common ancestor of the Platynota and the Diploglossa, has proceeded gradually in time. The most convincing hypothesis is the one,

according to which Anguimorpha appeared as a group of predators having changed their dentition from a closely spaced to a loosely spaced type. A certain adaptive radiation probably occurred at this early stage of anguimorphan phylogeny characterized by a derived pattern of tooth replacement, a primitive brain case structure and also by an unshortened splenial. The term Preanguimorphan grade introduced by Borsuk-Białynicka (in press) refers to the morphological level corresponding to this period of phylogeny. It seems that the early representatives of Anguimorpha displaying this morphological level may be difficult to discriminate from the early representatives of Scincomorpha on the basis of the skull and tooth characters. The derived pattern of the brain case appeared only in the direct ancestors of the Diploglossa and the Platynota.

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EXPLANATIONS OF PLATES 1—2

Plate 1

1. Brain case of *Physignathus lesueuri* ZPAL-R/1 (Agamidae), stereophotographs $\times 1.5$: *a* left side view, illustration to state 2'' of the brain case wall, as indicated in text-fig. 3; *b* ventral view, illustration to the modified "broad type" of the jugular recess. Note sphenoccipital suture of angular type (state 2''), text-fig. 5).
2. Brain case of *Ophisaurus apodus* HUB 42402 (Diploglossa), stereophotographs $\times 2$: *a* left side view, illustration to state 2' of the brain case wall, as indicated in text-fig. 3; *b* ventral view, illustration to the "narrow type" of the jugular recess. Note the distal end of the paroccipital process extending vertically rather than horizontally.
- 3, 4, 5. Different states of the osteodermal skull covering, all of the small element type corresponding to state 3' (text-fig. 1) illustrated by fragments of frontoparietal surface of: 3 *Ctenosaura* sp. ZPAL R-I/8 (Iguanidae); 4 *Xenosaurus grandis* MCZ 46785 (Diploglossa) and 5 a Late Cretaceous representative of the Platynota from the Gobi Desert, ZPAL MgR-III/64. Out of scale.

Plate 2

Different states of the osteodermal skull covering, as indicated in text-fig. 1, illustrated by fragments of frontoparietal surfaces of skulls. Out of scale.

1. Primitive state: 1 in *Tupinambis* sp. HUB 1050/35388 (Teiidae).
2. State 2 in *Ameiva amaeiva* ZPAL R-I/10 (Teiidae).
3. State 2 in juvenile specimen of *Gerrhonotus leiocephalus* ZPAL R-I/12 (Diploglossa).
4. State 2' in a Late Cretaceous representative of the Platynota from the Gobi Desert, ZPAL MgR-III/66.
5. State 3' in a Late Cretaceous representative of the Platynota from the Gobi Desert, ZPAL MgR-I/43.
6. State 2 in *Anguis fragilis* ZPAL R-I/5 (Diploglossa).
7. State 3 in *Ophisaurus apodus* ZIN unnumbered specimen (Diploglossa).
8. State 3 in *Gerrhonotus multicaarinatus* (?) ZPAL R-/13 (Diploglossa).

