AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3271, 19 pp., 9 figures August 10, 1999

Tooth Implantation and Replacement in Squamates, with Special Reference to Mosasaur Lizards and Snakes

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ABSTRACT

Different modes of tooth implantation in squamates are reviewed and defined. Three basic types of tooth implantation are recognized in reptiles: acrodonty, thecodonty, and pleurodonty. Only acrodonty and pleurodonty are present in squamates. Variations of the pleurodont condition include full pleurodonty, labial pleurodonty, and subpleurodonty.

Tooth implantation and replacement in mosasaur lizards and snakes are reviewed in order to evaluate previously proposed character definitions and hypotheses of primary homologies for three distinct characters associated with tooth replacement—the presence or absence of resorption pits, a recumbent or upright position of the replacement teeth, and the mode of tooth attachment to the bone. The first character is shown to be uninformative in respect to the controversy surrounding Mosasauroidea-snake affinities. Mosasaurs show replacement teeth in a normal upright position, and the occasional presence of recumbent teeth is the result of postmortem displacement. Finally, the mode of tooth attachment in snakes and mosasaurs is fundamentally different. The highly modified condition of tooth implantation described for the alethinophidian snakes is suggested to represent an additional synapomorphy of this taxon at the exclusion of the scolecophidians, which retain the plesiomorphic, fully pleurodont, lizard condition. The lower Middle Cretaceous fossil snake *Pachyrhachis* shows the alethinophidian type of tooth implantation.

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ISSN 0003-0082 / Price $2.60

INTRODUCTION

The long-standing debate on snake origins and interrelationships has recently gained new momentum (Caldwell and Lee, 1997; Fraser, 1997; Lee, 1997a, b; Zaher, 1998). Lee (1997b) analyzed the phylogenetic position of snakes within squamates and concluded that mosasauroids are the sister group of snakes, reviving a hypothesis first proposed by Cope (1869) and Nopcsa (1923). Subsequently, Caldwell and Lee (1997) reexamined the Cretaceous fossil *Pachyrhachis* (Haas, 1979, 1980) and claimed that this taxon represents the sister group of all other snakes: "the morphology of *Pachyrhachis* provides surprising and compelling new evidence for the hypothesis that, among lizards, the marine mosasauroids are the nearest relatives of snakes" (Caldwell and Lee, 1997: 709). However, a critical examination of the characters proposed by these authors to support a snake-mosasauroid sister-group relationship reveals some misconceptions and oversimplified interpretations of complex characters. A review of some of the characters used by Caldwell and Lee (1997) in their analysis is provided by Zaher (1998). Additionally, Lee (1997a) proposed two features of the mosasaur dentition that suggest affinities with snakes. These are the recumbent position of replacement teeth, and the fact that "In both groups, the teeth are associated with distinct sockets, and can therefore be described as 'thecodont'" (Lee, 1997a: 311). He acknowledged that there are what he considered to be "only slight differences between the two groups" (Lee, 1997a: 311) with respect to tooth morphology and implantation, but concluded that these slight differences do "not disprove the idea that the presence of distinct tooth sockets is potentially homologous (synapomorphic) in mosasauroids and snakes. However, the character "distinct tooth socket" (Lee, 1997a) does not appear in a cladistic analysis of snake affinities published barely a month earlier (Lee, 1997b). Instead, thecodonty is found to be autapomorphic for Mosasauridae, and "modified thecodont, teeth ankylosed to the margins of sockets" (Lee, 1997b: 71; character 86) becomes a synapomorphy of all snakes. Recumbent replacement teeth were found to be synapomorphic for Pythonomorpha (Lee, 1997b).

Given the current confusion surrounding the tooth implantation in squamates, and especially Lee's (1997a, b) assertions of homologies (de Pinna, 1992), we review both tooth implantation and tooth replacement in squamates in a critical evaluation of how this character complex bears on the affinities of snakes. The proposed terminology not only takes into account the type of tooth attachment, but also refers to the mode of tooth replacement associated with it. Such an approach is preferred to the traditional one, which considers tooth implantation only (e.g., Romer, 1956; Edmund, 1960, 1969; Motani, 1997), as this approach reflects more accurately important similarities and differences that may be found between taxa.

DEFINITION OF TERMS

We recognize three basic types of tooth implantation: thecodonty, acrodonty, and pleurodonty. Only the latter two types have been recorded for squamates (Owen, 1840; Romer, 1956; Edmund, 1969). The thecodont condition is restricted to the archosaurian and mammalian mode of tooth implantation, characterized by a syndesmotic attachment of teeth within discrete sockets (alveoli). This contrasts with the synostotic mode of tooth attachment in lepidosaurs, where the teeth are typically ankylosed to the supporting bone by the deposition of bone of attachment. The terms "subthecodont" and "ankylosed thecodont" have been proposed to account for a condition found in some extinct lepidosaurs, which is superficially similar to thecodonty (Romer, 1956; Edmund, 1960, 1969). However, the use of the term "thecodont" to define a synostotic mode of tooth attachment is misleading and must be avoided. This also applies to snakes and mosasaurs, which among squamates have been the only taxa erroneously considered as having a "thecodont" or "modified thecodont" mode of tooth implantation (Lee, 1997a, b; Bell, 1997).

Although only acrodonty and pleurodonty are present in squamates, a definition will be provided for all three types of tooth implantation and their subjacent modifications.

Thecodonty: In mature animals, each tooth is positioned in a discrete socket (Owen, 1840), and ankylosed syndesmotically (i.e., by ligaments). The interdental plate completely separates the tooth sockets in mature animals (which may remain confluent in juveniles: Edmund, 1962, 1969), with the result that the dental lamina (probably) becomes fragmented in the separate alveoli (i.e., sockets) (Edmund, 1962, 1969). The teeth are continually replaced throughout life; each replacement tooth develops from within the socket, at the base of the pulp cavity of the functional tooth (Poole, 1961). Thecodont tooth implantation is present in archosaurs and mammals.

Acrodonty: Well-developed labial and lingual flanges are present on the maxilla and dentary, which between themselves enclose (or form) an "alveolar" groove. The teeth are synostotically ankylosed to the margins of the alveolar groove both on their labial and lingual side. During early stages of ontogenesis, the anlagen of the teeth form a single row located dorsal to the alveolar groove. During later stages, the base of the teeth expands ventrally, invading the alveolar groove and ankylosing to its margins labially and lingually. Each tooth also contacts and fuses with its neighbors both anteriorly (i.e., mesially sensu Edmund, 1969) and posteriorly (i.e., distally sensu Edmund, 1969). This process was confirmed by personal inspection of embryos of *Sphenodon punctatus* (CNHM 65905) and *Chamaeleon hoehnelli* (FMNH 249166–71, 2288, 2292). The plane of tooth attachment to the supporting bone may be almost horizontally oriented, or inclined, i.e., the tooth ankyloses to the sloping labial and lingual margins of the alveolar groove ("totale Pleurodontie" of Lessman, 1952). Acrodont teeth are permanently ankylosed and are not replaced in mature individuals (Cooper et al, 1970; Cooper and Poole, 1973; Moody, 1980). Accordingly, the teeth have no alveolar foramen or resorption pit in the lingual side of their base. Acrodont teeth are the only teeth among squamates that lack an alveolar foramen or a resorption pit. Given the variability of the plane of tooth attachment, we suggest that the acrodont condition may be more precisely described by the lack of an alveolar foramen, a resorption pit, and of replacement of functional teeth, rather than solely by the mode of attachment of the tooth to the supporting bone.

Acrodont tooth implantation is present at least in the posterior regions of the maxilla and dentary of Rhynchocephalia and Acrodonta (agamids and chamaeleonids). Teeth on the premaxilla and on the anterior part of the dentary and maxilla may show pleurodont implantation in these taxa (Cooper et al., 1970; Cooper and Poole, 1973; Moody, 1980). Additionally, according to Etheridge (personal commun.), many acrodont species (and most Iguanians) ontogenetically increase the number of teeth on the maxilla and dentary by adding teeth at the posterior end of the tooth row. In these acrodont taxa, the new teeth are pleurodont until they reach full size, and then become permanently ankylosed (Etheridge, personal commun.). A pleurodont tooth at the posterior end of the otherwise acrodont tooth row has been found by Etheridge in subadults of various species of Leiolepidinae, Agaminae, and Chamaeleoninae.

Acrodont tooth implantation is also present within Amphisbaenia (Gans, 1960; Edmund, 1969).

Pleurodonty: The teeth are synostotically ankylosed to the obliquely sloping lingual surface of the pleura of the jaw element. The pleura corresponds to the labial ridge of the tooth-bearing element that receives the labial wall of the base of the teeth. Tooth replacement activity is permanent, and the dental lamina is continuous. The plane of attachment of the tooth to the supporting bone may be subject to considerable variation, as shown by Lessman (1952: figs. 10, 11) in transverse sections of the teeth of the pleurodont lizard *Phrynosoma*.

Pleurodonty is present in all squamates other than some members of Acrodonta and acrodont amphisbaenians, and may be present in the anterior and posterior rows of teeth of acrodontans and rhynchocephalians (Edmund, 1960, 1969; Cooper et al., 1970; Cooper and Poole, 1973; Robinson, 1976; Moody, 1980; Whiteside, 1986). However, most lizards show a special type of pleurodonty that has been characterized as labial pleurodonty by Lessman (1952). The description and definition of labial pleurodonty

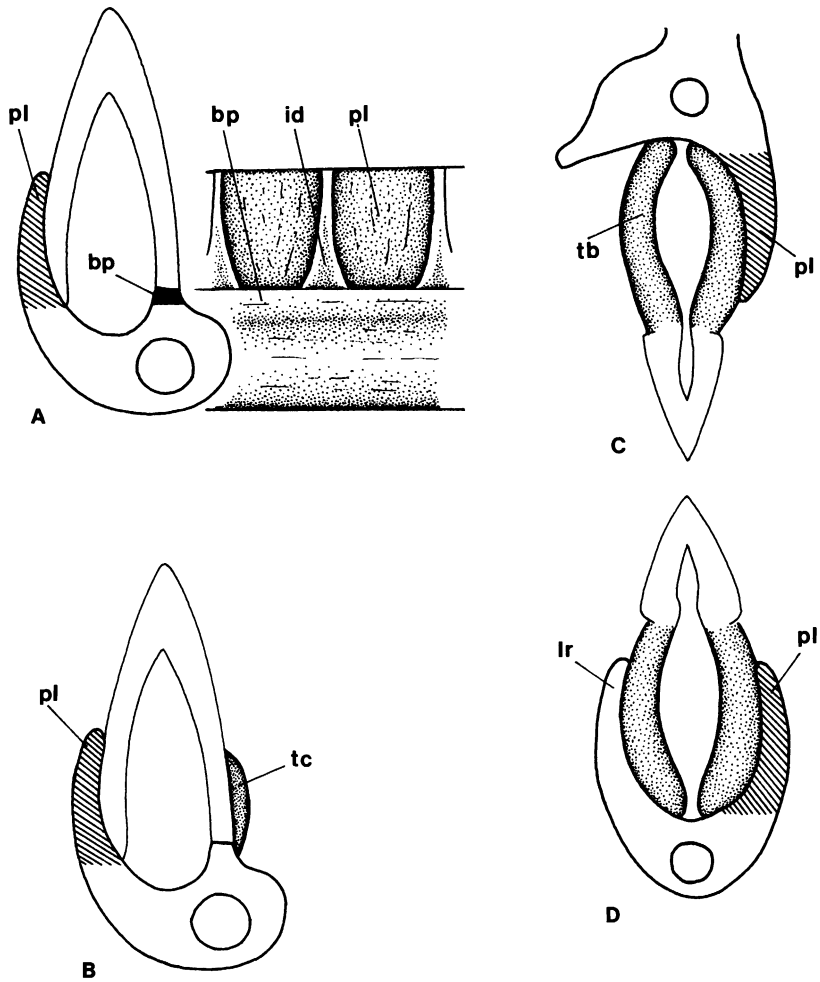

Fig. 1. Diagrammatic representation of tooth implantation in squamates. **A.** Labial pleurodonty: the labial wall of the base of the tooth is ankylosed to the pleura of the tooth-bearing element; the lingual wall of the base of the tooth is supported by the basal plate; the teeth are separated from one another by interdental ridges. **B.** A theca is formed if bone of attachment invades the lingual surface of the base of the tooth above the basal plate. **C.** Fully pleurodont maxillary tooth attachment in mosasaurs. **D.** Dentary teeth of mosasaurs are ankylosed to the labial and lingual surfaces of an alveolar groove that forms by the development of a lingual ridge on the dentary. Abbreviations: bp, basal plate; id, interdental ridge; lr, labial ridge of dentary; pl, pleura of the tooth-bearing element; tb, tooth base of mosasaurs made of bone of attachment; tc, theca.

require reference to a number of structures that may contribute to the tooth attachment in lizards, such as the *Bodenplatte* (basal plate), *Flankenwulst* (interdental ridge), and *Theca* (theca), terms that were introduced by Lessmann (1952) (see fig. 1).

Labial pleurodonty is characterized by the presence of the basal plate, which corresponds to a poorly to moderately developed lingual bony ridge on the jaw, receiving the lingual wall of the base of the tooth on a horizontal plane (Lessman, 1952) (fig. 1). The basal plate is not to be confused with the lingual margin of the jaw bone, from which a dorsal flange or ridge may develop in a position lingual to the tooth row, i.e., without supporting the base of the lingual wall of tooth (see fig. 1). In other words, a

tooth is labially pleurodont if the labial wall of the tooth base is ankylosed to the obliquely sloping surface of the pleura, while the lingual wall of the tooth base meets a horizontal bony shelf (Rieppel, 1978; and fig. 1). In addition, individual teeth may be separated from one another by a more or less prominent interdental ridge that develops from the pleura of the jaw. In cases where the interdental ridge is well developed and merges with the basal plate, the teeth appear to be sitting in very shallow and obliquely oriented "sockets." The replacement teeth develop in a lingual (most lizards) or posterolingual (anguimorphs) position relative to the functional tooth, within the increasing resorption pit of the latter. Formation of the resorption pits starts at the margins of an initially small alveolar foramen, located between the base of the tooth and its bony support. The term "resorption pit" should be used only in reference to those taxa that show extensive necrosis at the base of the functional teeth, thus creating a cavity that at least partially accommodates the developing replacement tooth, at least during later stages of the replacement cycle. This condition is characteristic for most lizards (Lessman, 1952), but it is absent in varanoids and in snakes.

In non-mosasauroid varanoid lizards, the mode of tooth attachment could be referred to as "full pleurodonty." A basal plate is lacking, and interdental ridges are poorly developed if at all. The teeth have a fluted base, and they are in basal contact with one another. Both the labial and the lingual wall of the base of the tooth, along with the dentine infoldings, meet the jaw along its gently sloping pleura. A basal plate is absent (Rieppel, 1979: fig. 9). As a consequence of the development of plicidentine, varanoid lizards do not develop a true resorption pit, i.e., there is no necrosis of the lingual or posterolingual base of the functional tooth to accommodate the replacement tooth. However, a small alveolar foramen may be located on the lingual side of the base of the tooth, between the latter and the supporting bone (Rieppel, 1978: fig. 2a). The replacement tooth develops in a posterolingual position relative to the functional tooth, and migrates into its position once the latter is shed.

"Subpleurodont" tooth attachment is characterized by the development of a theca, which corresponds to an invasion of the lingual side of the tooth base by bone of attachment (i.e., not by the interdental ridges—see comments on alethinophidian tooth implantation below). The theca thus connects one interdental ridge with the other above the basal plate, providing a reinforced attachment at the base of each tooth (Presch, 1974: fig. 1D) (figs. 1, 2). The fundamental difference between a theca and a basal plate is their developmental origin and their position. The basal plate is formed by permanent bone and supports the base of the lingual wall of the tooth, whereas the theca is composed of bone of attachment and covers the lingual side of the base of the tooth. A pleura with a variably reduced angle of inclination characterizes the subpleurodont condition observed in various macroteiids (Estes, 1961, 1964; Presch, 1974). Lessman (1952: figs. 5 and 6) figured sections of the subpleurodont teeth of *Trachydosaurus rugosus* (= *Tiliqua rugosa*), where a basal plate and interdental ridges are also clearly visible along with a well-developed theca (fig. 2).

TOOTH IMPLANTATION AND REPLACEMENT IN MOSASAUROID LIZARDS

In our review of mosasaur tooth implantation, we follow Bell (1997), whose taxonomic arrangement of this group supports a monophyletic Mosasauroidea (see also DeBraga and Carroll, 1993). According to Bell (1997), Natantia represents a monophyletic group including all mosasaurs to the exclusion of the "aigialosaurs" and *Halisaurus*. The monophyly of the Aigialosauridae (sensu DeBraga and Carroll, 1993) is still controversial and is not supported in his analysis. Among the known "aigialosaurs," *Opetiosaurus* appears as the sister group of all other Mosasauroidea (Bell, 1997). Relationships between the other "aigialosaurs," *Halisaurus*, and the Natantia are poorly resolved, with these groups forming a polytomy.

Tooth implantation of mosasaurs is commonly described as "thecodont" or "ankylosed thecodont." Our investigation of dentition in mosasaurs indicates that they do not share a thecodont tooth implantation, but

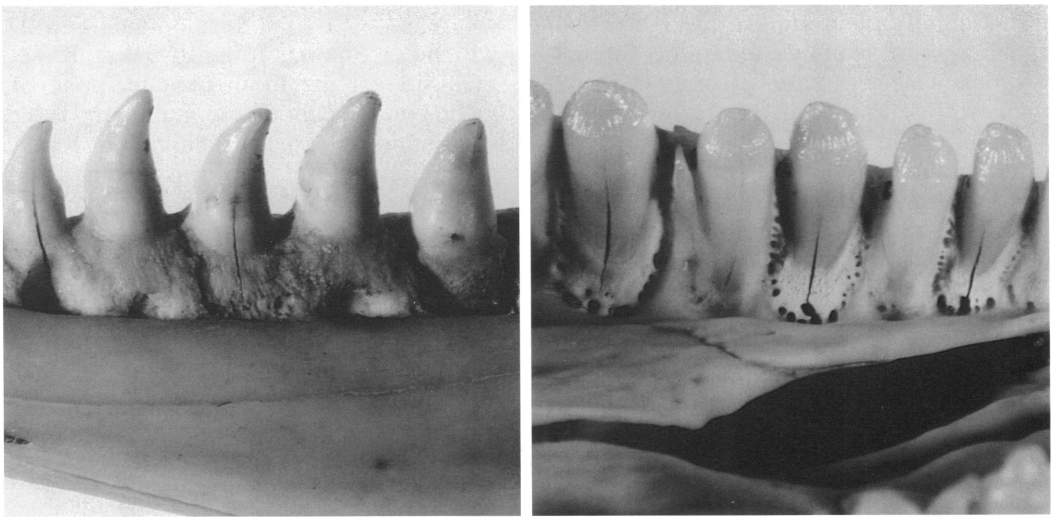

Fig. 2. Lingual views of the dentary of *Tupinambis teguixim* (FMNH 217382; left) and maxilla of *Tiliqua rugosa* (CNHM 195570; right).

rather a type of dentition secondarily derived from a fully pleurodont dentition as seen in varanoid lizards.

The teeth of mosasaurs have a unique (autapomorphic) morphology, in that the crown of the tooth sits on an extended bony base made entirely of bone of attachment (fig. 1). Unlike varanoid lizards, mosasaurs lack plicidentine. The maxilla of mosasaurs [as for example in an indeterminate mosasaur (FMNH PR674), fig. 3] shows the bony base of the teeth to be ankylosed to the pleura of the jaw in a way closely comparable to the fully pleurodont tooth attachment in *Varanus*. Similarly, a basal plate is absent. And again as in *Varanus*, the teeth are in basal contact with one another. But unlike the arrangement in *Varanus*, resorption pits develop in the bony base in a posterolingual position, into which migrate the replacement teeth at an early stage of their development. These replacement pits become larger as the replacement tooth increases in size within the pulp cavity of the functional tooth.

The appearance of a "thecodont" tooth implantation is created by a ridge that develops from the tooth-bearing element lingual to the tooth row (a ventral ridge on the maxilla, a dorsal ridge on the dentary). If present, this lingual ridge (the medial ridge of Carroll and DeBraga, 1992: 76) is generally much less developed on the premaxilla and maxilla than on the dentary, but even on the dentary the lingual ridge may be poorly (e.g., *Mosasaurus*) or greatly (e.g., *Leiodon*, *Platecarpus*) developed (compare figs. 3 and 4). This ridge lies fully medial to the teeth, and does not support the lingual base of the teeth as would the basal plate in a labially pleurodont dentition (fig. 1). The pleura of the jaw, together with the labial ridge, define an alveolar groove within which the teeth are located. The teeth remain in basal contact with each other, and ankylosis of the teeth is primarily to the pleura. But the space between the individual teeth is filled up with bone of attachment. If a tooth is shed or lost, it leaves a space that creates the impression of a distinct alveolus.

Tooth implantation on the pterygoid of mosasaurs basically corresponds to the pattern already described for the maxilla and dentary. A well-preserved left pterygoid of *Platecarpus* (FMNH UC 601) shows the medial wall of the bone produced into a ventrally projecting flange that represents the functional analog of the pleura of the jaw. The teeth are pleurodontally attached to this flange, and they retain their basal contact with each other. The interdental ridges are well developed, and bone of attachment invests the space between the tooth bases on their lateral (labial) side. A lateral ridge, covering the lateral (labial) aspect of the bases

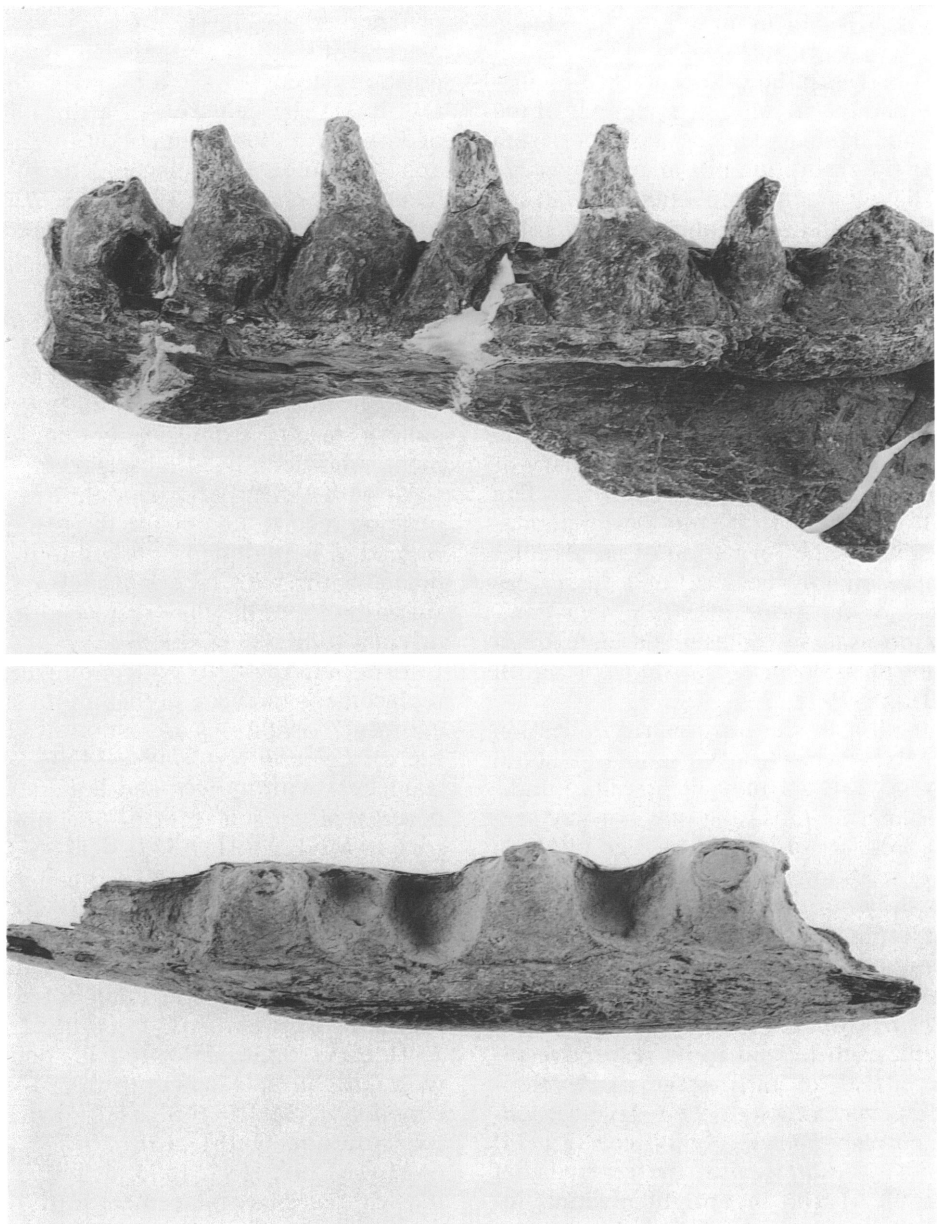

Fig. 3. Lingual views of the maxilla (FMNH PR 674; upper) and dentary (FMNH PR 483; lower) of two mosasaurids (indet.). The maxilla is shown with the dorsal border pointing downward so that tooth attachment can be compared to the other figures.

of the teeth, is not developed in this specimen. Other, larger specimens of different taxa of mosasaurs do show the development of a lateral ridge, which is analogous to the lingual ridge of the lower jaw. As a result, the teeth are located in an alveolar groove, which becomes filled by bone of attachment. If a tooth is shed or lost, the impression of a socket is created.

Replacement of teeth buried within an alveolar groove starts with the formation of a resorption pit in the bony base, located on its

posterolingual side (on the posterolabial side on the pterygoid) just below the enamel crown. This resorption pit is enlarged by distolabially and basally directed necrosis of the bone of attachment. The replacement teeth move into the resorption pits at an early stage of their development, and after appropriate enlargement of the resorption pit, they come to sit on the bottom of the alveolar groove inside the preceding functional tooth. They will develop and increase in size in an upright position inside the functional tooth until the latter is shed. At this point, the bony base of the tooth is almost completely resorbed.

Carroll and DeBraga (1992) reported the presence of a lingual ridge on the dentary of the aigialosaur genus *Opetiosaurus*. The teeth still display their pleurodont implantation, in spite of the formation of an alveolar groove, presumably because of a lesser development of the bone of attachment compared to mosasaurs. Replacement teeth are in an upright position in *Opetiosaurus* (Carroll and DeBraga, 1992: 76).

Examination of the mosasaurid collection in the AMNH (American Museum of Natural History), as well as relevant literature, indicates that marine mosasaurs do not have recumbent teeth as suggested by Lee (1997a). Several descriptions and figures of mosasaur material showing a normal anguimorph position of replacement teeth are available in the literature. Lingham-Soliar (1994: fig. 18B) figured the right maxilla and dentary of *Plioplatecarpus houzeaui* with three replacement teeth, each lodged in its respective resorption pit, in an early stage of development. However, although their developmental stage corresponds closely to Lee's (1997a) stages 3–4 of *Platecarpus*, the replacement teeth are clearly in an upright position instead of being recumbent. Lingham-Soliar (1995: fig. 11) also figured a fragment of a dentary of *Leiodon*, which shows a replacement tooth in an advanced stage of development, again positioned in an upright position within the resorption pit of its predecessor. Finally, Lingham-Soliar and Nolf (1989) figured the dentaries and maxillae of *Prognathodon solvayi* where the pattern of replacement teeth is clearly visible. One fragment of the maxilla shows a replacement tooth in upright position, whereas the dentary of another specimen presents various replacement teeth in a somewhat "recumbent" position (Lingham-Soliar and Nolf, 1989: pls. 2, 3). The dentaries of a third specimen of *P. solvayi* show both conditions of upright and "recumbent" replacement teeth (Lingham-Soliar and Nolf, 1989: figs. 20, 27).

In addition to specimens figured in the publications mentioned above, a significant number (see below) of specimens in the AMNH collection also display both conditions of "recumbent" and upright replacement teeth on the same jaw elements, strongly suggesting that the observed "recumbent" pattern results from postmortem displacement. Additionally, all observed replacement teeth with a clearly horizontal, "recumbent" position tend to lie outside the resorption pit instead of being fitted tightly into it, as in all other lizards with functional resorption pits, suggesting that they are displaced from their original (upright) position.

Taxa in the AMNH collection with upright replacement teeth or both upright and "recumbent" conditions are as follows (see also fig. 4): *Leiodon sertorius* (AMNH 1401; jaw fragments with upright and horizontally disposed replacement teeth), *Platecarpus ictericus* (AMNH 1821, 1532; dentary and premaxilla with upright replacement teeth), *P. coryphaeus* (AMNH 126, 127, 202, 1511; various fragments of dentary, pterygoid, premaxilla, and maxilla with replacement teeth in upright, "recumbent," and horizontal positions), *Mosasaurus maximus* (AMNH 1391, 2532, 2536, 2537; maxilla and dentary with upright replacement teeth), *Mosasaurus conodon* (AMNH 1408; left dentary with two upright teeth), *Clidastes propython* (AMNH 1507, 1541, 1593; dentary and maxilla with various replacement teeth of almost the same size in upright and horizontal positions), *Tylosaurus* sp. (AMNH 1534, 1767; jaw fragments with almost upright replacement teeth), *Tylosaurus proriger* (AMNH 1555, 1560, 1585, 2160, 4909, 1543; various jaw fragments with upright and horizontal replacement teeth), *Platecarpus* sp. (AMNH 14788; with both upright and horizontal replacement teeth in the maxilla).

A closer examination of AMNH 1820, described and figured by Lee (1997a), shows that all three replacement teeth are only

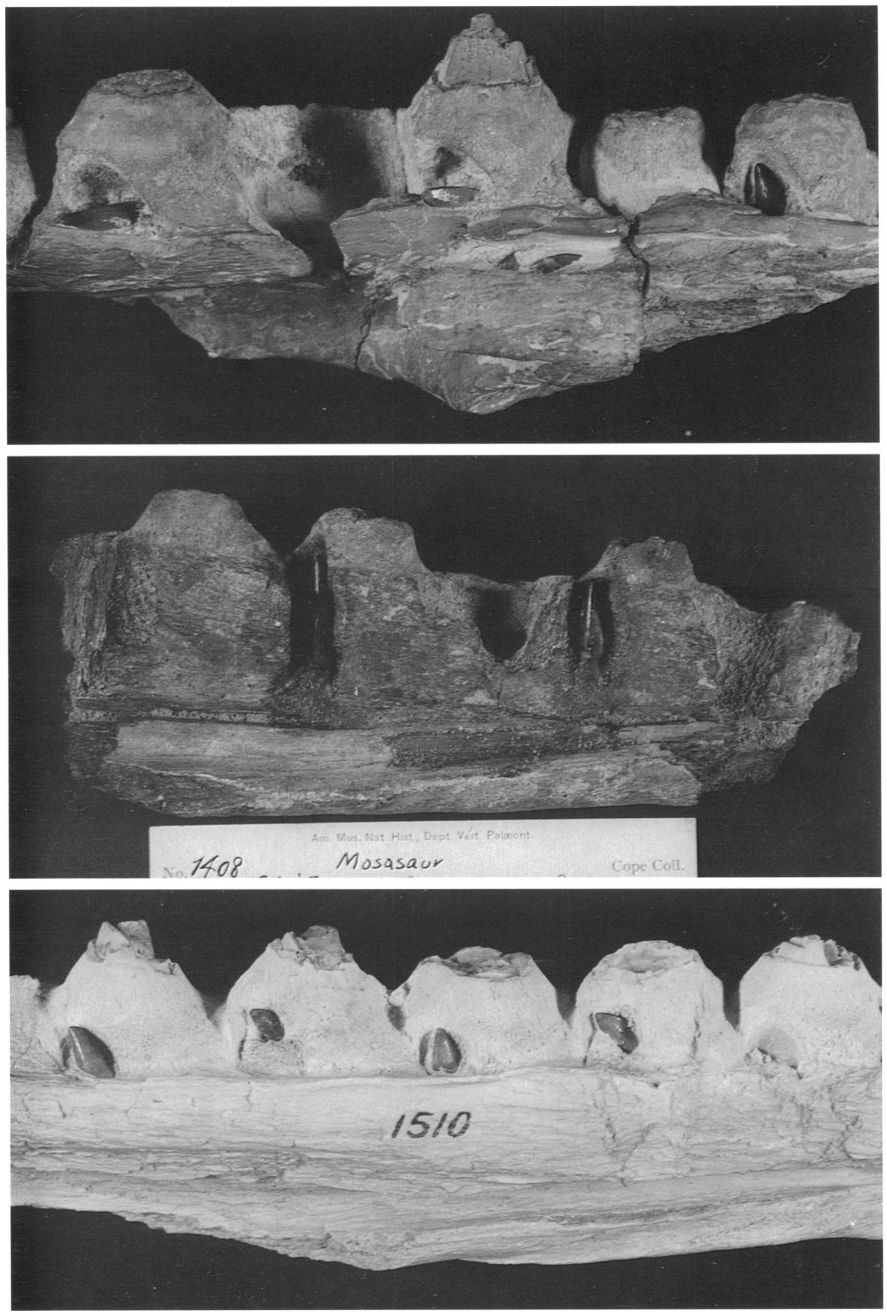

Fig. 4. Lingual views of the maxilla of *Platecarpus coryphaeus* (AMNH-VP 127; upper), and dentaries of *Mosasaurus conodon* (AMNH-VP 1408; middle) and *Platecarpus gracilis* (AMNH-VP 1510; lower). The maxilla is shown with the dorsal border pointing downward so that tooth attachment can be compared to the other figures.

slightly different in size and hardly could be in different stages of their cycle. However, the anteriormost replacement tooth is clearly in an upright position while the other two are in a "recumbent" position, contradicting Lee's ontogenetic tooth sequence illustrated in his figure 1. The anteriormost tooth is also transversely displaced since one of the carinae is clearly visible in a lingual position. This displacement is probably caused by crushing of the mediolingual wall of the maxilla at the level of the resorption pit. The position of the two other replacement teeth is also puzzling since they lie mostly outside their respective resorption pits, a condition not found in any other taxon showing resorption pits (Edmund, 1969), suggesting postmortem displacement. In this context, the pattern of tooth replacement shown by AMNH 1820 has to be interpreted with caution and seems inadequate to address the issue of replacement tooth position in mosasaurs. Similarly, the partial right pterygoid of *Platecarpus* (Lee, 1997a: fig. 4) also retains signs of postmortem displacement since none of the three replacement teeth are in normal positions (whether upright or recumbent): the first one is transversely displaced with one of its carinae facing lingually, the second lies inside the base of the socket of the functional tooth it was going to replace (it probably detached and fell from its upright position), and the third has clearly rotated posterolabially since the convex anterior facet of the crown points in that direction.

TOOTH IMPLANTATION AND REPLACEMENT IN SNAKES

Within Serpentes, we recognize a basal dichotomy between Scolecophidia and Alethinophidia. Within the Alethinophidia, we accept a nested hierarchy of monophyletic taxa, which comprises the Macrostomata (including all snakes at the exclusion of Scolecophidia and "anilioids"), and Caenophidia (including acrochordoids and colubroids) (Rieppel, 1988a,b; see also: Groombridge, 1979a, b, 1984; Kluge, 1991, 1993a, b; Cundall et al., 1993; Zaher, 1994a, b, 1998). The "anilioids" probably represent a paraphyletic group of basal alethinophidians (Rieppel, 1988a; Cundall et al., 1993). *Xenopeltis* and *Loxocemus* are regarded as basal macrostomatans (Kluge, 1991, 1993a, b; Cundall et al., 1993; Zaher, 1994a, b). Among the "anilioids," *Anilius*, *Cylindrophis*, and *Plecturus* were available for histological study.

We were able to identify three types of tooth implantation within the snakes examined. In *Leptotyphlops* (dentary) and *Liotyphlops* (an anomalepidid genus with teeth on the dentary and the maxilla), the teeth show pleurodont implantation (fig. 5). The jaws develop a distinct, highly developed pleura, to which is ankylosed the labial wall of the base of the tooth. The lingual wall of the base of the tooth remains unsupported by bone. Distinct interdental ridges fully separate the teeth from one another, but these do not expand to support the lingual side of the tooth base. There are no resorption pits and no development of an alveolar foramen. The tooth implantation of leptotyphlopids and anomalepidids resembles the full pleurodonty of varanoid lizards, but important differences are the lack of ankylosis of the lingual side of the tooth base, the lack of plicidentine, and the absence of an alveolar foramen (see also McDowell and Bogert, 1954: fig. 13E). The two specimens of *Liotyphlops* examined (IB 25344, 42519) confirmed the presence of recumbent replacement teeth in an anomalepidid, as predicted by Lee (1997a).

In *Typhlops*, as observed in the tooth-bearing elements of *Leptotyphlops* and *Liotyphlops*, the maxilla develops a distinct pleura to which the labial wall of the base of the teeth becomes ankylosed (fig. 6). The interdental ridges are much more prominently developed in *Typhlops* by comparison to *Leptotyphlops* and *Liotyphlops*, and they invest the distolingual and posterolingual side of the base of the tooth, providing increased bony support. On the lingual side of the tooth, a large opening persists between the base of the tooth and the proximal and distal interdental ridges. This opening can be called a (large) alveolar foramen, as it is located between the tooth and its bony support.

In alethinophidian snakes, the teeth appear to be set in distinct sockets, the condition referred to as acrodont by Romer (1956), and thecodont by Lee (1997a). However, alethinophidians again show a pleurodont tooth implantation, yet of a secondarily derived type

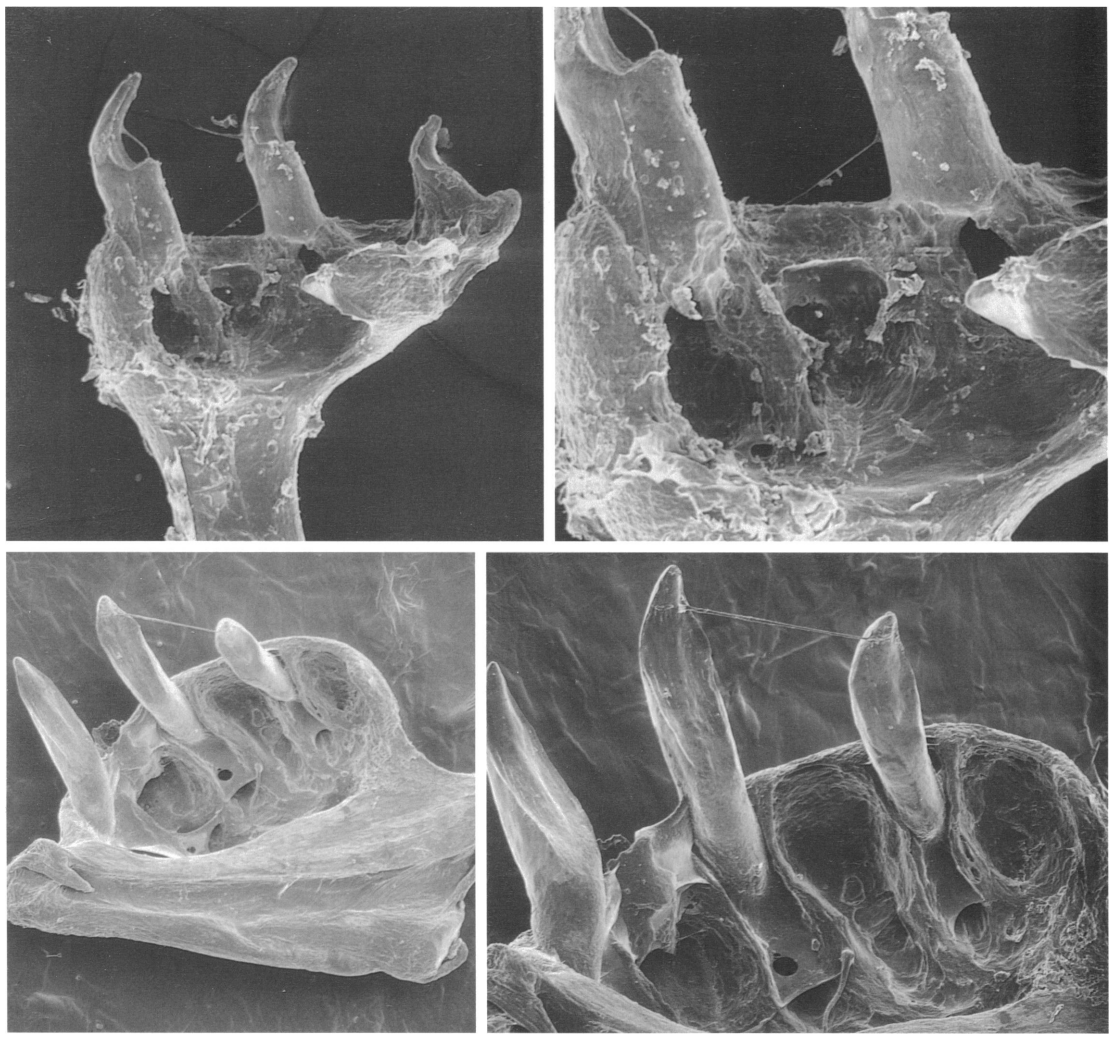

Fig. 5. SEM photographs of the lingual views of the maxilla of *Liotyphlops beui* (IB 42519; upper) and dentary of *Leptotyphlops humilis* (CNHM 77599; lower).

(see figs. 7, 8, 9). The labial wall of the socket of alethinophidian snakes is always distinctly higher than the medial wall. In fact, the labial wall of the socket corresponds to the pleura of the tooth-bearing element. The interdental ridges are prominently developed, and completely separate the teeth, and their sockets, from one another. Similar to those in *Typhlops*, yet to an even greater degree, the interdental ridges invest the lingual side of the tooth base, thus forming the lingual wall of the socket and providing bony support for the ankylosis of the lingual wall of the base of the tooth. Ankylosis is by means of bone of attachment, and a small alveolar foramen is preserved either in a lingual (anilioids), or in a proximodistal (macrostomatans) position (fig. 7). The alveolar foramen may be located either entirely within the bone of attachment, or between the latter and the lingual wall of the socket. Looking at a cross section of an alethinophidian tooth, the lingual wall of the socket appears as functional analog of the basal plate of lizards; given the dynamics of the ossification process, it is indeed difficult to clearly distinguish between these structures (compare the cross sections in figs. 8, 9). However, a basal

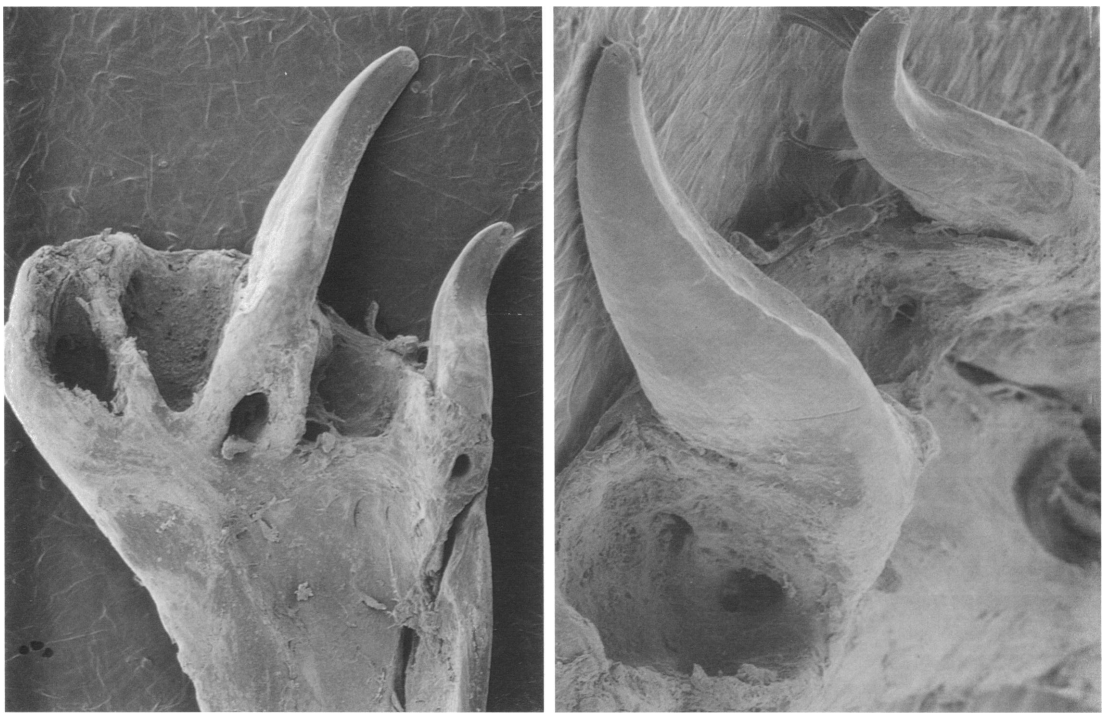

Fig. 6. SEM photographs of the lingual view of the maxilla of *Typhlops punctatus* (AMNH-R 11669).

plate in the sense of a more or less developed continuous ridge extending along the lingual surface of the jaw at the base of the pleura is always absent in snakes (fig. 7). In a preankylosis stage during the tooth replacement cycle, the alethinophidian tooth shows the perfect imitation of lingual pleurodonty: the labial wall of the base of the tooth meets the sloping lingual surface of the pleura, whereas the lingual wall of the base of the tooth meets the lingual wall of the socket in a horizontal plane (figs. 8, 9). During later stages of ankylosis, bone of attachment expands ankylosis to the pleura of the jaw, and invades the sloping labial surface of the lingual wall of the tooth socket (figs. 8, 9).

The palatine and pterygoid are dentigerous in alethinophidians, but edentulous in scolecophidians. Cross sections of the palatine of *Cylindrophis* show a mode of tooth attachment that is the mirror image of that of the maxilla and dentary: the socket shows a higher medial (lingual) wall compared to the lateral (labial) margin, and the tooth again imitates a labially pleurodont attachment in a preankylosis stage, prior to the invasion of the socket by bone of attachment during final stages of ankylosis (fig. 9).

Replacement teeth of snakes develop posterolingual (posterolabial on the palatine and pterygoid) to the functional tooth, in a recumbent position. They rotate rather than migrate into their functional position once the functional tooth is shed. Snakes never develop resorption pits.

CONCLUSIONS

Although mosasaurs and snakes show teeth that appear to be set in sockets, they both have a pleurodont mode of tooth implantation, yet specialized in different respects. In mosasaurs, the bases of the teeth are buried in an alveolar groove that results from the development of a medial longitudinal ridge, particularly on the dentary, that is located fully lingually to the base of the teeth and does not provide a support for the latter (figs. 1, 3, 4). The teeth of mosasaurs are not located in discrete sockets, but, as in *Varanus*, are in basal contact with one another. But because bone of attachment fills

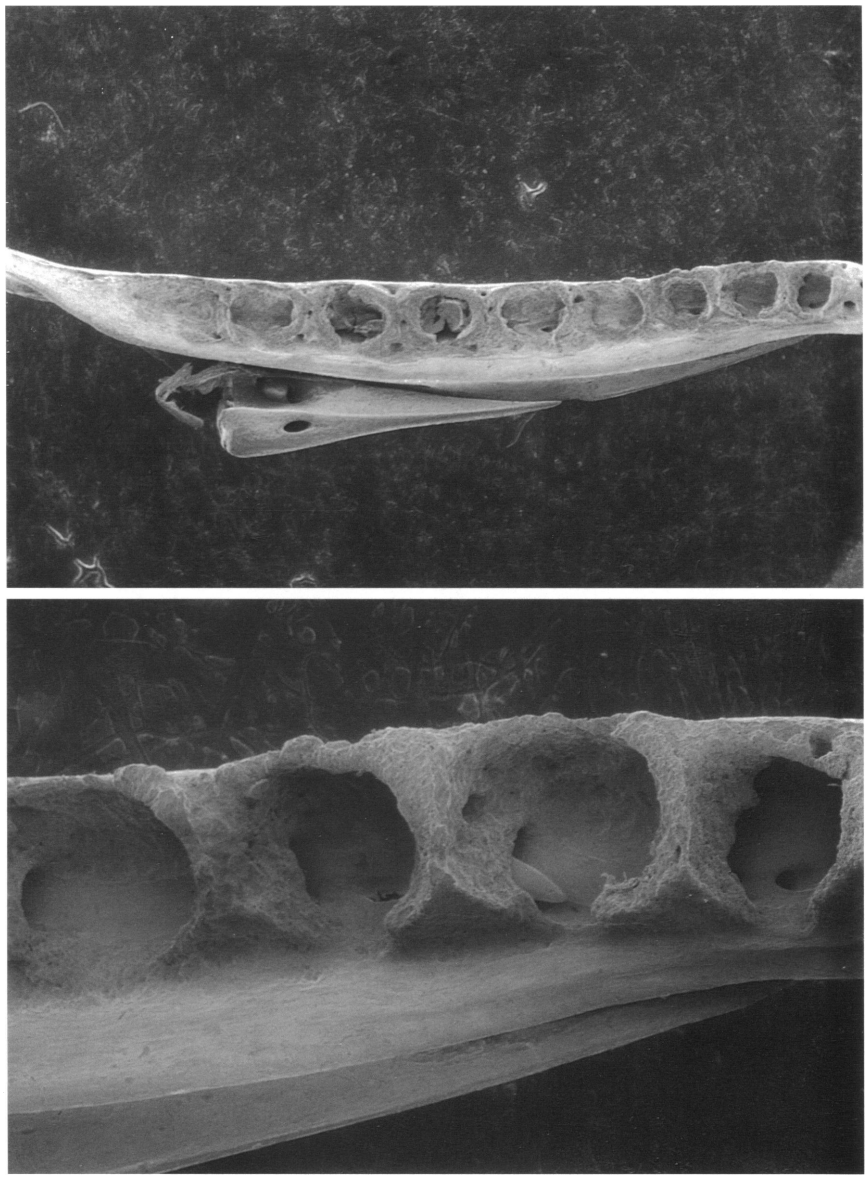

Fig. 7. SEM photographs of the lingual view of the dentary of *Pseudotyphlops philippinus* (BMNH 1978.1092).

the remaining space between the teeth within the alveolar groove, a lost or shed tooth creates the impression of a discrete socket. By contrast, the plesiomorphic condition of tooth implantation in snakes is pleurodont, albeit in a peculiar manner as exemplified by leptotyphlopids and anomalepidids, where the lingual wall of the base of the tooth is not ankylosed to supporting bone (fig. 5). Typhlopids show an extended proximal and distal ankylosis of the tooth base due to a greater development of the interdental ridge (fig. 6). In alethinophidians, discrete "sockets" develop on the maxilla and dentary due to further expansion of the original interdental ridges around the base of the tooth, a condition that during early stages of ankylosis imitates the labial pleurodonty of lizards

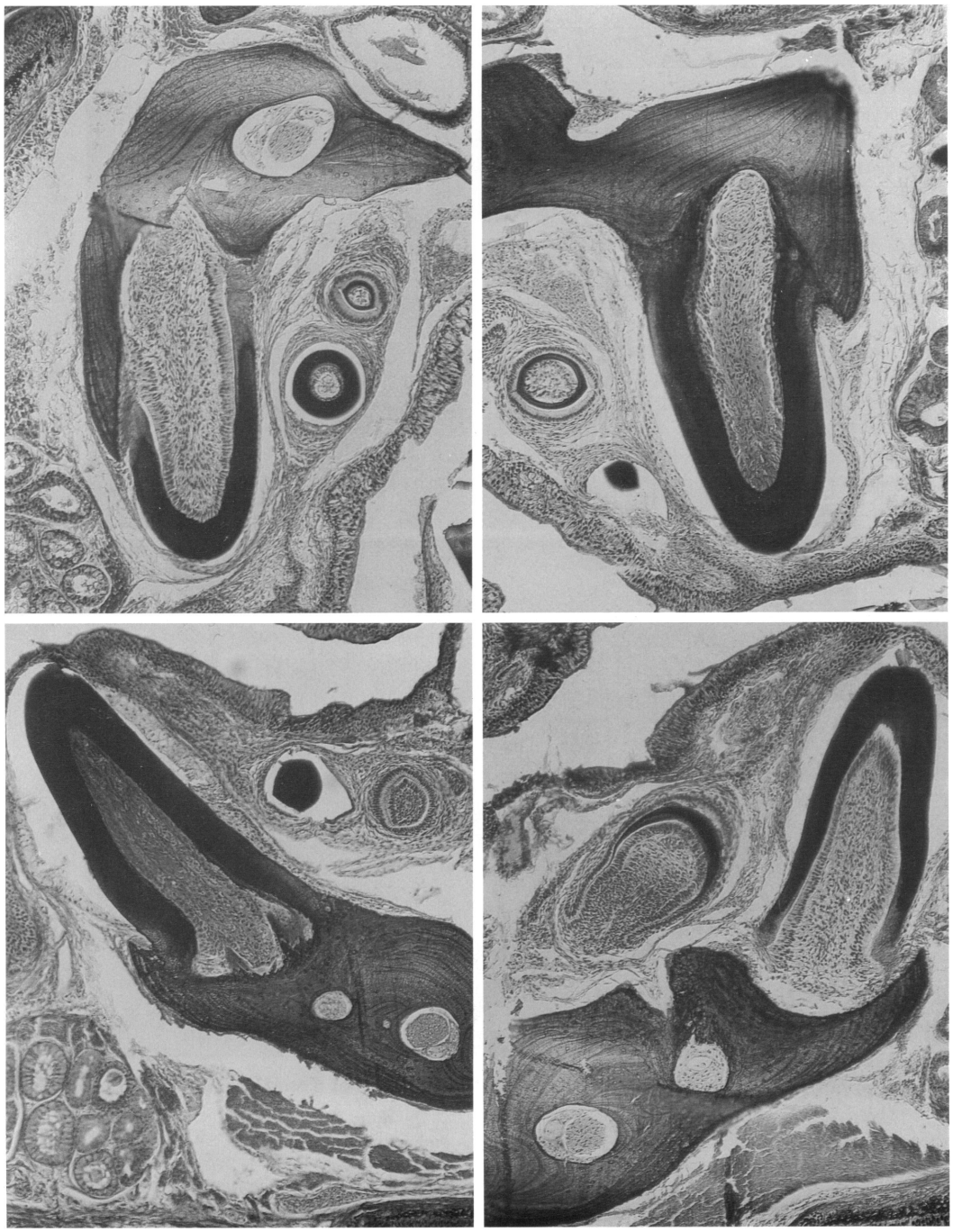

Fig. 8. Cross sections of the maxillae (upper) and dentaries (lower) of *Cylindrophis rufus*. Left maxillary tooth in preankylosis (upper left); right maxillary tooth in ankylosis (upper right); left dentary tooth in ankylosis (lower left); right dentary tooth in preankylosis (lower right).

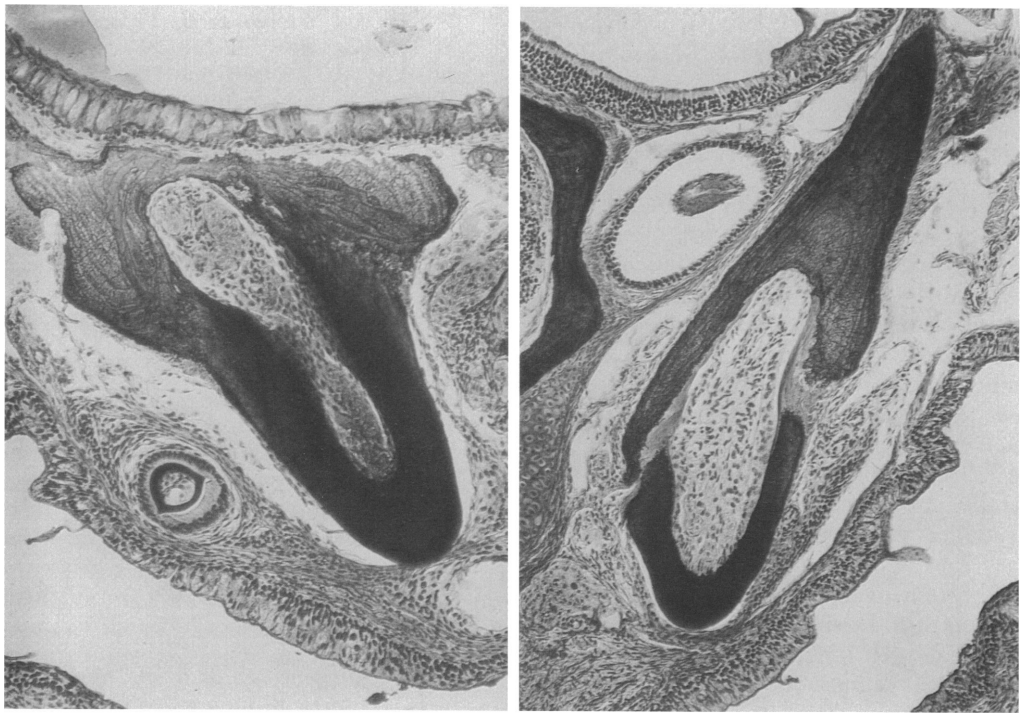

Fig. 9. Cross sections of the left pterygoid (left) and right palatine (right) of *Cylindrophis rufus*, showing teeth in ankylosed and preankylosed stages, respectively.

(figs. 7, 8, 9). Similarity in tooth implantation between higher snakes and mosasaurs is therefore derived independently from standard pleurodonty and is not evidence in support of a sister-group relationship of the two clades.

The replacement teeth on the pterygoids of mosasaurs, and on the palatines and pterygoids of alethinophidians, are positioned posterolabial to the functional ones, rather than posterolingual to the functional tooth as in the lateral jaw elements (Russell, 1967; Lee, 1997a). However, the attachment mode remains different between the two groups, yet fundamentally similar to the mode of attachment on the lateral jaw elements within each group. Additionally, one specimen of *Lanthanotus* examined also shows pterygoids with replacement teeth in a labial position (AMNH 113983; personal obs.), which shows that this character is not unique to snakes and mosasaurs. Furthermore, very shallow sockets are present on the pterygoid of *Lanthanotus* (FMNH 134771; personal obs.). In pleurodont animals, tooth-bearing palatines and pterygoids will always tend to form sockets, since the surface of the tooth-bearing element is horizontal. As far as palatal dentition is concerned, a superficially similar yet nonhomologous pattern of tooth attachment is found in *Lanthanotus*, mosasaurs, and alethinophidian snakes.

Finally, the alethinophidian condition of tooth implantation is strikingly different from that found in any other squamates, and is here suggested to be a synapomorphy of Alethinophidia + *Dinilysia* (which shows the same type of tooth implantation; Estes et al., 1970). Furthermore, Caldwell and Lee (1997, character B7) viewed "marginal teeth ankylosed to the rims of discrete sockets" as synapomorphous of *Pachyrhachis*, scolecophidians, and alethinophidians. Had the pleurodonty of scolecophidians been recognized, the presence of discrete sockets on the jaws could have been recognized as a potentially alethinophidian character of *Pachyrhachis* (Zaher, 1998). By contrast, the plesiomorph-

ic, pleurodont tooth implantation adds support to a basal position of Scolecophidia within snakes.

ACKNOWLEDGMENTS

The senior author wishes to thank Mark Norell for allowing him to use facilities in the Department of Vertebrate Paleontology and permitting access to the American Museum mosasaur collection. He is also grateful to Douglas A. Rossman (Museum of Natural Science, Louisiana State University), John E. Cadle (Museum of Comparative Zoology, University of Harvard), Harold Voris and Alan Resetar (The Field Museum), who made available specimens from the collections under their care. Photographs for the figures 7 to 9 were done by John Weinstein of the Department of Photography at The Field Museum. Darrel Frost, Charles W. Myers, Mark Norell, and Peter Makovicky provided helpful comments on a previous draft of the manuscript. This research is supported by grants from the Theodore Roosevelt Memorial Fund and the Field Museum Scholarship Program to the senior author.

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APPENDIX. Material Examined

Museum acronyms: American Museum of Natural History, Department of Herpetology, New York (AMNH-R); American Museum of Natural History, Department of Vertebrate Paleontology, New York (AMNH-VP); Field Museum of Natural History, Chicago (FMNH and CNHM); Instituto Butantan, São Paulo (IB); Museum of Comparative Zoology, University of Harvard, Cambridge (MCZ); Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ); The Natural History Museum, London (BMNH).

Rhynchocephalia—*Sphenodon punctatus* (CNHM 65905, an embryo).

Chamaeleonidae—*Chamaeleon hoehnelli* (FMNH 249166-71, 2288, 2292, a series of embryos).

Iguanidae—*Iguana iguana* (FMNH 51680), *Conolophus subcristatus* (FMNH 22406).

Teiidae—*Tiliqua rugosa* (FMNH 195570), *Tupinambis teguixin* (FMNH 217382).

Amphisbaenia—*Diplometopon* sp. (FMNH 206115), *Monopeltis capensis* (FMNH 75709), *Rhineura floridana* (FMNH 1937, 206117).

Helodermatidae—*Heloderma horridum* (AMNH-R 56439, 57863).

Lanthanotidae—*Lanthanotus borneensis* (AMNH-R 113983; FMNH 134711).

Varanidae—*Varanus bengalensis* (AMNH-R 71195, 118715), *Varanus exanthematicus* (AMNH-R 137237), *Varanus gouldi* (AMNH-R 82819), *Varanus indicus* (AMNH-R 58389), *Varanus komodoensis* (FMNH 22200), *Varanus niloticus* (AMNH-R 10522), *Varanus rudicollis* (AMNH-R 141071), *Varanus salvator* (AMNH-R 141155), *Varanus varius* (FMNH 218076), *Varanus* sp. (FMNH 235516).

Mosasauridae—*Clidastes propython* (AMNH-VP 1507, 1541, 1593), *Leiodon sertorius* (AMNH-VP 1401), *Mosasaurus conodon* (AMNH-VP 1408), *Mosasaurus maximus* (AMNH-VP 1391, 2532, 2536, 2537), *Mosasaurus* sp. (FMNH-PR 674, 483), *Platecarpus coryphaeus* (AMNH-VP 126, 127, 202, 1511), *Platecarpus gracilis* (AMNH-VP 1510), *Platecarpus ictericus* (AMNH-VP 1532, 1563, 1588, 1820, 1821, 5811), *Platecarpus planifrons* (AMNH-VP 1491), *Platecarpus* sp. (AMNH-VP 14788; FMNH-UC 600), *Tylosaurus nepaeolicus* (AMNH-VP 134, 1561, 1565), *Tylosaurus proriger* (AMNH-VP 1543, 1555, 1560, 1585, 2160, 4909), *Tylosaurus* sp. (AMNH-VP 1534, 1767, 2008).

Scolecophidia—*Leptotyphlops humilis* (FMNH 77599), *Liotyphlops beui* (IB 25344, 42519), *Typhlophis squamosus* (AMNH-R 25051), *Typhlops angolensis* (AMNH-R 11633), *Typhlops lumbricalis* (AMNH-R 73230), *Typhlops reticulatus* (AMNH-R 3001).

Anilioids—*Anilius scytale* (AMNH-R 85980, 85981, 85982), *Cylindrophis rufus* (AMNH-R 85647; FMNH 131780, 179033; LSUMZ 14075, 14221), *Cylindrophis lineatus* (AMNH-R 12872), *Cylindrophis maculatus* (BMNH 1930.5.8.48), *Melanophidium wynaudense* (BMNH 1930.5.8. 124-125), *Melanophidium punctatum* (BMNH 1930.5.8.119), *Platyplectrurus madurensis* (BMNH 1930.5.8.111), *Plectrurus perroteti* (BMNH 1930.5.8.105), *Pseudotyphlops philippinus* (BMNH 1978.1092), *Rhinophis sanguineus* (BMNH 1930.5.8.59), *Teretrurus rhodogaster* (BMNH 1930.5.8.98), *Uropeltis woodmasoni* (BMNH 1930.5.8.73-74).

Macrostomatans—*Aspidites melanocephala* (AMNH-R 69302), *Boa constrictor* (AMNH-R 74737), *Bothrochilus boa* (AMNH-R 44002), *Calabaria reinhardtii* (AMNH-R 10092; LSUMZ 34130), *Candoia bibroni* (AMNH-R 42164), *Candoia carinata* (AMNH-R 76701), *Casarea dussumieri* (MCZ 49135), *Charina bottae* (LSUMZ 15361, 36901), *Epicrates cenchria* (AMNH-R 75796), *Epicrates striatus* (AMNH-R 77633), *Eryx conicus* (LSUMZ 48005, 48050), *Eryx johnii* (LSUMZ 48221), *Eunectes murinus* (AMNH-R 62560; FMNH 212710), *Leiopython albertisii* (AMNH-R 104062), *Lichanura roseofusca* (LSUMZ 14088), *Lichanura trivirgata* (LSUMZ 15373), *Loxocemus bicolor* (AMNH-R 19393, 44902, 110151; LSUMZ 49634), *Morelia ameth-*

istina (AMNH-R 117804), *Morelia spilota* (AMNH-R 79043), *Python molurus* (AMNH-R 36573), *Python regius* (AMNH-R 75263), *Ungaliophis continentalis* LSUMZ 55454), *Xenopeltis unicolor* (AMNH-R 29969; LSUMZ 14074, 16821).

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