



The braincases of mosasaurs and *Varanus*, and the relationships of snakes

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The braincase structure of the mosasaur *Platecarpus* is described in detail and compared to that of *Varanus* and snakes. The braincase of mosasaurs and *Varanus* is found to be closely similar in most respects other than the consequences of obliteration of the metakinetic axis in mosasaurs. Neither *Varanus*, nor mosasaurs, approach snakes in braincase structure. The hypothesis of a sister-group relationship of snakes and mosasauroids is discussed in the light of how hypotheses of homology, or synapomorphy, can be established on an empirical, i.e. testable and potentially falsifiable basis. The establishment of homology *qua* synapomorphy is recognized as a procedure involving at least two levels of generalization. The most basic level is the conjecture of similarity of constituent elements of two or more organisms. Such conjectures of similarity maintain their testability, and falsifiability, only if established by reference to topographical equivalence, or equivalence of connectivity.

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ADDITIONAL KEYWORDS:—Squamata – Mosasauroida – Serpentes – phylogeny – evolution.

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INTRODUCTION

Establishing the affinities of snakes within squamate reptiles has long been one of the most fascinating problems in herpetology and palaeoherpetology (see Rieppel, 1988a, for a comprehensive review and references). In a number of recent publications, Lee (1997a, b) and Lee & Caldwell (1998), have suggested affinities of snakes with mosasauroids, resurrecting the Pythonomorpha of Cope (1869) to include these two clades, and providing cladistic evidence of its monophyly. Lee (1997b) did not test snake relationships throughout squamates, because Platynota (*Heloderma*, *Lanthanotus* and *Varanus*, and all taxa more closely related to these forms than to other anguimorphs: Lee, 1997b: 78) were specified as in-group, thus constraining possible snake relationships to within that clade. In this study, a large number of uniquely shared characters of the skull, lower jaw, and dentition was used to unite aigialosaurs, mosasaurs and snakes. This hypothesis of relationships was later supported by the redescription of a fossil snake from the lower Upper Cretaceous of Ein Jabrud, *Pachyrhachis* Haas, 1979, as an intermediate between mosasauroids and modern type snakes (Caldwell & Lee, 1997; Lee & Caldwell, 1998). Although reiterating a view expressed by Carroll (1988), this conclusion appeared problematical, because it had previously been recognized that those characters which *Pachyrhachis* does share with snakes are not characters of basal snakes, but rather those of advanced snakes (Haas, 1979, 1980; Rieppel, 1994). A re-analysis of the data base of Caldwell & Lee (1997) accordingly showed *Pachyrhachis* to be nested within snakes as the sister-group of Macrostromata, rather than being the sister-taxon of all Serpentes (Scolophidia and Alethinophidia), linking the latter to mosasauroids (Zaher, 1998). More recently, Lee (1998) tested snake relationships throughout squamates, and further corroborated the monophyly of Pythonomorpha. He also commented on Zaher's (1998) assessment of the relationships of *Pachyrhachis*, and defended its intermediate status between mosasauroids and all other snakes. However, the character evidence used by Lee (1998) in support of these hypotheses of relationships remained the same, although some character definitions were slightly reworded by comparison to earlier studies (Lee, 1997a, b). The contradictory results with respect to the relationships of *Pachyrhachis* prompted us to look in more detail into the character evidence used by Lee (1997a, b, 1998), and Lee & Caldwell (1998), in support of Pythonomorpha. In a previous study (Zaher & Rieppel, 1999) we documented that the dentitional characters found to be synapomorphous for mosasauroids and snakes by Lee (1997a, b, 1998) were either mistakes, or inaccurately assessed. In this study we address the characters of the braincase, and its relation

to the dermatocranium which were used in support of a monophyletic Pythonomorpha by Lee (1997b) and Lee & Caldwell (1998). At this time we defer the cladistic test of the monophyly of the Pythonomorpha to a later date, until our review of the anatomy of the intramandibular joint of mosasauroids and snakes is completed. Instead, we propose to discuss the concept of statements of primary homologies as testable, and potentially falsifiable, hypotheses of similarity. The character evidence of Lee (1997b) will in the following be referenced as L97, that of Lee (1998) will be referenced as L98, and the character evidence of Lee & Caldwell (1998) will be referenced as LC98.

MATERIAL

Platecarpus: AMNH 01487, partial braincase; AMNH 01488, braincase; AMNH 01563, braincase and parietal; AMNH 01566, braincase; AMNH 01645, braincase; AMNH 01820, braincase and parietal. FMNH UR600, quadrate; FMNH UR896 quadrate.

Tylosaurus: AMNH 04909, skull table.

Lanthanotus borneensis: FMNH 134711.

Varanus sp.: FMNH 195578.

Varanus exanthematicus: FMNH 17142, 228398, 212985.

Varanus komodoensis: FMNH 22199.

Varanus salvator: FMNH 31358, 31320.

Leptotyphlops humilis: FMNH 77599.

Liotyphlops beui: IB 25344, 42519.

Anilius scytale: FMNH 11175, 35688.

Cylindrophis ruffus: FMNH 131780; 179033.

Cylindrophis maculatus: BMNH 1930.5.8.48.

Melanophidium wynaudentense: BMNH 1930.5.8.124–125.

Melanophidium punctatum: BMNH 1930.5.8.119.

Platyplecturus madurensis: BMNH 1930.5.8.111.

Plecturus perroteti: BMNH 1930.5.8.105.

Pseudotyphlops philippinus: BMNH 1978.1092.

Python sebae: FMNH 22366.

Rhinophis sanguineus: BMNH 1930.5.8.59

Teretrurus rhodogaster: BMNH 1930.5.8.98.

Uropeltis woodmansoni: BMNH 1930.5.8.73–74.

Loxocemus bicolor: AMNH-R 19393, 44902, 110151.

Xenopeltis unicolor: AMNH-R 29969.

Institutional acronyms: AMNH, American Museum of Natural History, Department of Vertebrate Paleontology, New York; AMNH-R, American Museum of Natural History, Department of Herpetology, New York; FMNH, Field Museum of Natural History, Chicago; IB, Instituto Butantan, São Paulo.

COMPARISON OF THE BRAINCASE STRUCTURE OF *PLATECARPUS* AND *VARANUS*

Both Camp (1942) and Russell (1967) described the braincase of mosasaurs in general, and of *Platecarpus* in particular (Fig. 1), as closely resembling that of *Varanus*

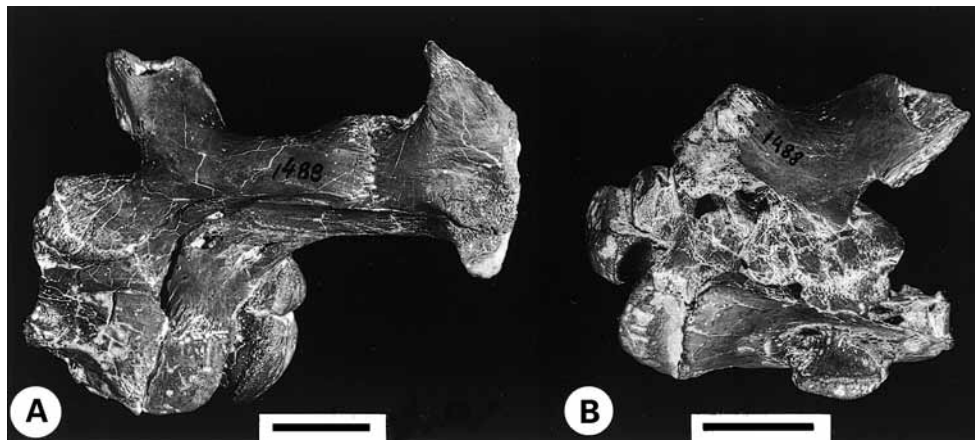


Figure 1. The braincase of the mosasaur *Platecarpus* (AMNH 01488). A, left lateral view. B, right lateral view. Scale bar = 20 mm.

with one important difference, which is the obliteration of the metakinetic axis (Versluys, 1912; Frazzetta, 1962). In squamates other than snakes, the metakinetic axis passes through the tips of the paroccipital processes and their suspension from the supratemporal and, in some taxa but not *Varanus*, the squamosal. In mosasaurs, the contact between the supratemporal and paroccipital process is sutural and hence immobile. To the extent that mesokinesis is believed to have been possible in mosasaurs, compensatory movements must have occurred at a gliding contact between supratemporal and squamosal (Russell, 1964, 1967). Cranial kinesis other than the streptostylic quadrate is lost in more derived mosasaurs (Russell, 1964, 1967).

Obliteration of the metakinetic axis in mosasaurs has several consequences for the suspension of the braincase within the dermatocranial frame. It affects the relation of the parietal to both the prootic and the supraoccipital, and the relation of the supratemporal to the paroccipital process.

The relation of the parietal to the prootic

In squamates other than snakes, the prootic carries an anterior extension of the cupola anterior of the otic capsule, made up of membrane bone (*Zuwachsknochen sensu* Starck, 1979: 15) and termed crista alaris by Oelrich (1956). The crista alaris is set off from the trigeminal notch at the anterior margin of the prootic by the supratrigeminal process (Oelrich, 1956). This crista extends in an anterodorsal direction and loosely overlaps the laterally descending flange of the parietal, and it also supports the dorsal head of the epipterygoid on its lateral side. *Varanus* is a perfect example of this condition (Fig. 2A). The crista alaris is extensively developed with a slightly expanded anterodorsal end which broadly overlaps the lateral surface of the descensus parietalis. The supratrigeminal process, located at its anterior base, is weakly developed in *Varanus*. The supratrigeminal process is generally reduced or absent in anguimorphs (Norell & Gao, 1997).

In mosasaurs (Fig. 2B, C), the prootic carries a broad and massive alar process

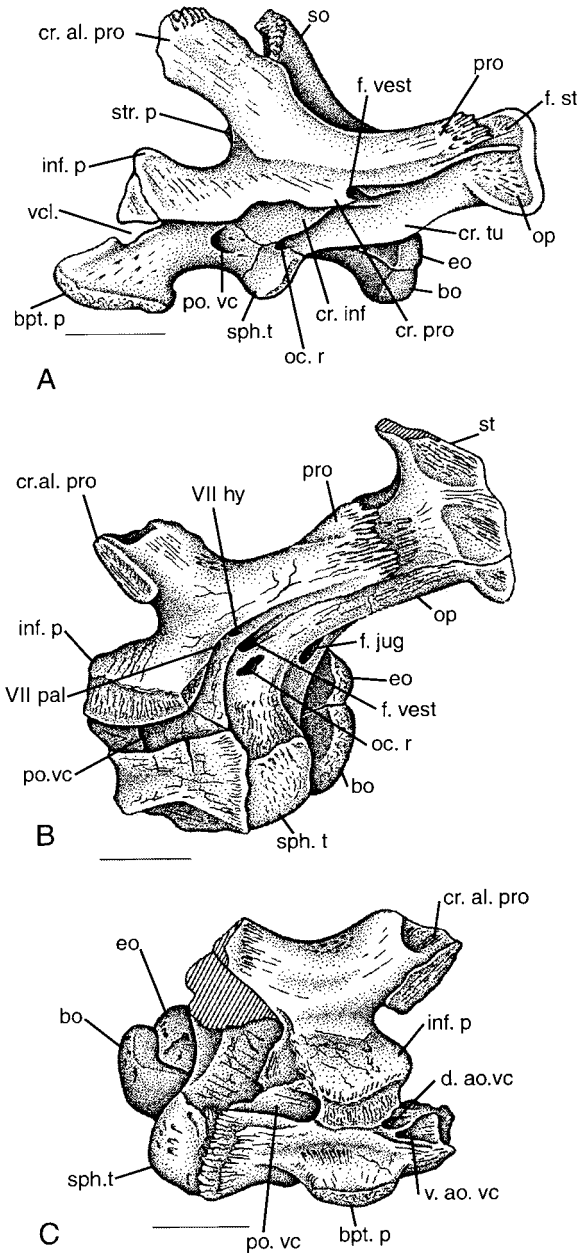


Figure 2. A, braincase of *Varanus* sp. (FMNH 195576), left lateral view. B, braincase of *Platecarpus* sp. (AMNH 01488), left lateral view. C, braincase of *Platecarpus* sp. (AMNH 01488), right lateral view. Scale bar = 20 mm. Abbreviations: bo, basioccipital; bpt.p, basipterygoid process; cr.al.pro, crista alaris of prootic; cr.inf, crista interfenestralis; cr.pro, crista prootica; cr. tu, crista tuberalis; f.st, facet for supratemporal; d.ao.vc, dorsal anterior opening of Vidian canal; eo, exoccipital; f.jug, jugular foramen; f.vest, fenestra vestibuli (ovale); inf.p, inferior process of prootic; oc.r, occipital recess; op, opisthotic; po.vc, posterior opening of Vidian canal; sph.t, spheno-occipital tubercle; pro; prootic; str.p, supra-trigeminal process; so, supraoccipital; sph.t, spheno-occipital tubercle; st, supratemporal; v.ao.vc, ventral anterior opening of Vidian canal; vcl, incisure for lateral head vein; VIIhy, hyomandibular branch of facial nerve foramen; VII pal, palatal branch of facial nerve foramen.

which extends anterodorsally from the otic capsule and establishes a closed sutural contact with the ventral margin of the lateral flange of the parietal (L97: char. 18; L98: chars. 58, 64, 65; LC98: char. B1). This is a consequence of elimination of metakinesis in mosasaurs, and by comparison to other squamates an autapomorphy of this group. The broad base of the alar process of the prootic constricts the trigeminal notch by comparison to *Varanus*. A supratrigeminal process is absent in *Platecarpus* (AMNH 01488).

Snakes, as well as amphisbaenians (Montero *et al.*, 1999) and *Dibamus* (Rieppel, 1984a), lack a crista alaris on the prootic, and the cupola anterior of their otic capsule is not sutured to, but rather loosely overlaps the descensus lateralis parietalis which extends ventrally medial to anteromedial margin of the otic capsule, adding to the problems of definition of the level of the primary lateral wall of the braincase in snakes that have rendered the identification of the topological relations of the laterosphenoid bone so difficult (Rieppel, 1976, 1993). Further back, the parietal does not form a descensus lateralis, but with a variably bifurcating lateral margin overlaps or clasps the dorsal surface of the otic capsule (prominentia canalis semicircularis anterior) in a syndesmotic contact with the prootic anteriorly, and with the supraoccipital posteriorly. In mosasaurs, as in all other non-ophidian squamates, the supraoccipital forms the dorsal part of the bony labyrinth, but it lies entirely behind the parietal.

The relation of the parietal to the supraoccipital

The degree of separation between supraoccipital and parietal in squamates (L97: char 49; L98: chars. 80, 81; LC98: char. B2) is generally related to the relative size of the brain, and therefore is subject to both ontogenetic and taxonomic variation. Old individuals of non-ophidian squamates such as *Varanus* may obliterate metakinetic movements by calcification of the contact of the supraoccipital with the parietal. Miniaturization in particular results in an increase of the relative size of the braincase, which may result in the closure of the posttemporal fossae and an extended and immobile contact of the supraoccipital with the parietal in a number of squamate lineages (Rieppel, 1984a), including *Dibamus*, amphisbaenians, and snakes.

The supraoccipital is narrow in mosasaurs, and positioned at an angle and ventral to the posterior margin of the parietal. This represents the plesiomorphic squamate condition which is also characterized by the presence of wide open posttemporal fossae. Where present, metakinetic motion between the supraoccipital and the parietal is generally supported by the cartilaginous processus ascendens of the tectum synoticum, which itself ossifies as supraoccipital. Among squamates, this processus ascendens is absent in Gekkota, *Dibamus*, and snakes (Rieppel, 1984b). In *Varanus*, a processus ascendens is present, and in the adult becomes embedded in a distinct notch on the posterior surface of the parietal, as is also the case in many other non-ophidian squamates. As described by Russell (1967), the parietal of many mosasaurs, including *Platecarpus* (AMNH 01820), carries a pair of knuckle-like projections located close to the midline on its posteroventral aspect (similar to comparable projections located lateral to the notch for the processus ascendens in *Varanus*), which form a sliding joint with the supraoccipital, and most probably embraced the cartilaginous

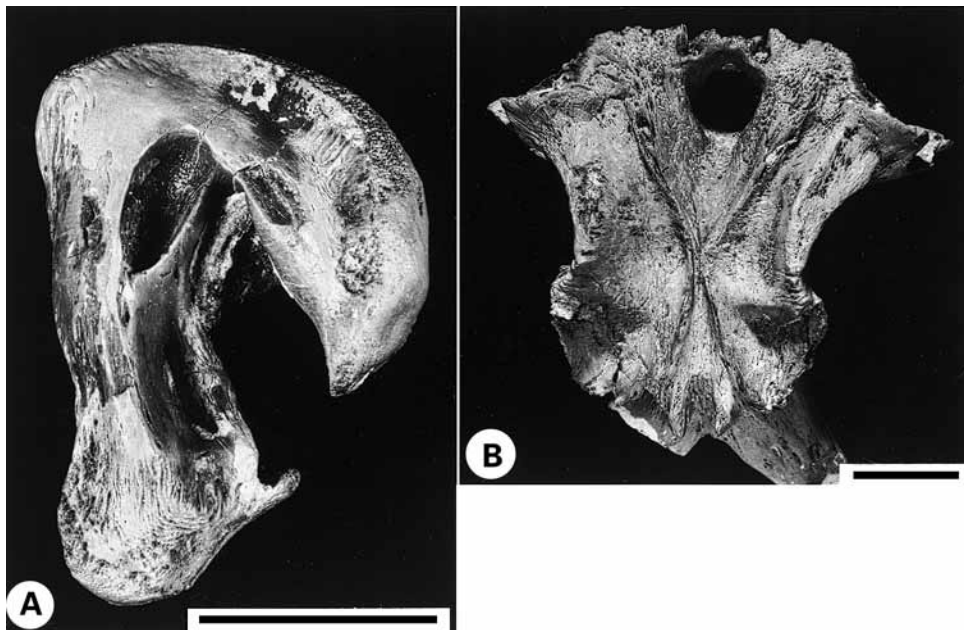


Figure 3. A, right quadrate of *Platecarpus* sp. (FMNH UR896), in medial view, showing the pit for the internal process of the columella auris. B, parietal of *Platecarpus* sp. (AMNH 01488), in ventral view, showing paired posteromedial processes enclosing a posteromedial groove for the ascending process of the supraoccipital.

processus ascendens of the tectum synoticum (supraoccipital) in life (Fig. 3B). *Mosasaurus* shows a longitudinal groove on the midline of the posteroventral part of the parietal which may again have accommodated the ascending process (Russell, 1967). The anterior margin of the supraoccipital of *Platecarpus* (AMNH 01488) shows a smooth surface which must have established a loose syndesmotomic contact with the parietal rather than an interdigitating suture. The contact between parietal and supraoccipital was not immobilized in mosasaurs, but whether metakinetic movement was indeed possible depends on the presence or absence of structural constraints at other critical areas of the skull (see Russell, 1964, 1967, and the discussion of the relation of the parietal to the prootic above).

A straight comparison of the degree of separation between supraoccipital and parietal in snakes and mosasaurs is misleading since the latter still retain a posttemporal fossae, a condition found in most squamates other than snakes. Snakes have lost the posttemporal fossae, as have other, burrowing, squamates such as amphisbaenians, *Dibamus*, and *Anniella*. Closure of the posttemporal fossae necessarily results in a broad contact of the supraoccipital with the parietal, since the latter is the only element adjacent and dorsal to the supraoccipital. Character coding therefore should account for the presence or absence of posttemporal fossae, rather than for the degree of contact between parietal and supraoccipital.

The relationship of the supratemporal to the paroccipital process

The streptostylic quadrate of squamates is generally suspended from the supratemporal, with occasional participation of the squamosal. From these same dermal

bones the paroccipital processes of the braincase are also suspended. In many squamates, the prootic and opisthotic, which together form the paroccipital process, fuse in the adult, making it difficult to establish the exact relations of the posterior end of the supratemporal to the distal tip of the paroccipital process (L97: char. 25; L98: chars. 46, 48; LC98, p. 1548, char. 25).

In *Varanus*, the prootic is seen to extend far posterolaterally on the lateral surface of the paroccipital process. However, the expanded distal tip of the latter is formed by the opisthotic only, which projects from behind the prootic. The disarticulated braincase of *Varanus* reveals a bipartite facet on the lateral surface of the expanded distal tip of the paroccipital process, of which only the upper division is bordered anteromedially by the prootic (Fig. 2A). The posterior tip of the supratemporal is received in this upper division of the facet on the distal end of the opisthotic, and establishes a loose syndesmotic connection with the distal tip of the prootic, allowing for metakinetic and mesokinetic (Frazzetta, 1962) mobility. The ventral division of the facet houses the intercalary cartilage (the tip of the dorsal process of the stapes, facilitating mobility of the streptostylic quadrate relative to the paroccipital process; for further details see below).

The mosasaur *Platecarpus* differs from *Varanus* only in an increased size of the facet on the lateral surface of the distal end of the opisthotic, which receives the broadened posterior end of the supratemporal, and in the formation of a closed, interdigitating suture between the posterior end of the supratemporal and the distal end of the prootic (Fig. 2B). Formation of that suture adds to the immobilization of the metakinetic axis, and by comparison to other squamates is an autapomorphy of mosasaurs. This arrangement is structurally very different from the relation the supratemporal has to the prootic in snakes.

As mentioned above, the parietal overlaps, or clasps, the dorsal margin of the prootic in snakes. The supratemporal in turn is syndesmotically attached to the dorsal and/or lateral surface of the prootic, capping the prominentia canalis semicircularis horizontalis. Its anterior part lies lateral to the parietal. Posteriorly the supratemporal lies lateral and superficial to the supraoccipital and exoccipitals. The rudimentary paroccipital process formed by a posterior projection of the opisthotic in some basal macrostomatan snakes (e.g. *Python*: Frazzetta, 1959) usually remains separate from the supratemporal, as it is located in a more ventral position in dried skulls (although mobility of the supratemporal may slightly alter these relations). However, this posterior projection of the opisthotic is never in contact with or even sutured to the supratemporal, as it is in *Varanus* and mosasaurs respectively. The lack of such a suture between the opisthotic and the supratemporal in snakes suggests that the condition found in this group is not comparable to the one present in mosasaurs, but rather is derived from a generalized squamate condition.

The question as to whether or not the supratemporal contributes to the braincase wall of squamates (L97: char. 27; L98: char. 46; LC98, p. 1548, char. 25) relates to the distinction of endoskeletal versus exoskeletal components of the skull. The braincase is usually considered to comprise the endocranium or neurocranium, with the dura defining the level of the primary wall of the braincase which itself is preformed in cartilage in the plesiomorphic condition. As such, the braincase is endoskeletal, in contrast to the dermatocranium which is exoskeletal. In several amniote lineages, the dermatocranium may contribute to the closure of the braincase by forming a secondary lateral wall, such as the epipterygoid and parietal in turtles,

the parietal in some squamate lineages including snakes, and the alisphenoid in mammals. In no squamate does the supratemporal participate in the formation of a secondary wall of the braincase, but always lies entirely superficial to braincase elements (ossified in the adult) as is characteristic for the dermatocranium in general. However, if the posttemporal fenestrae are reduced or closed (L98: char. 84), as in fossorial or burrowing squamate clades and snakes, the supratemporal approaches the braincase more closely, or becomes directly superimposed on it (Rieppel, 1984a, b).

The palatobasal articulation

The basiptyergoid processes of mosasaurs are different from those of *Varanus* (Fig. 2) and other non-ophidian squamates in that they are relatively short proximodistally, with an elongated distal articular surface (L97: chars. 33, 34; L98: chars. 74, 75; LC98: char. B5, and p. 1548, char. 34).

The basiptyergoid processes of squamates other than snakes develop by ossification of the polar cartilages which, during early cranial development, fuse to the posterior ends of the trabeculae cranii to form cartilaginous basitrabecular processes (deBeer, 1937). Meanwhile, the pterygoid ossifies around the ventral aspect of the palatoquadrate; the basal process separates from the main body of the palatoquadrate to form a pad of cartilage on the medial aspect of the pterygoid (in the pterygoid notch: Oelrich, 1956), engaging with the basiptyergoid process in the formation of a synovial palatobasal articulation between dermal palate and basicranium.

All non-macrostromatan snakes lack typical basiptyergoid processes. The pterygoid glides along the ventrolateral margin of the para-basisphenoid with which it is in a ligamentous, non-synovial connection (Rieppel, 1980a). In some macrostromatans, the anterolateral wings of the para-basisphenoid are drawn out into processes which articulate with the pterygoids. However, no snake has so far been recorded to show polar cartilages fused to the posterior ends of the trabeculae to form basitrabecular processes. Only in the booid genera *Eryx* (Kamal & Hammouda, 1965) and *Sanzimia* (Genest-Villard, 1966) have cartilaginous nodules been observed in an isolated position lateral to the posterior ends of the trabeculae and, in the case of *Eryx* (but not in *Sanzimia*), have been claimed to be precursors of basiptyergoid processes. The putative homology of these cartilaginous nodules with basitrabecular processes must remain questionable (Bellairs & Kamal, 1981). Finally, the palatoquadrate cartilage is atrophied in snakes except for the quadrate process. As a consequence, the palatobasal articulation is not synovial in snakes. As revealed by their ontogeny, the para-basisphenoidal processes found in some macrostromatans are not comparable to the basiptyergoid processes of non-ophidian squamates, as was also concluded by Kluge (1991).

The basicranium

The skull of *Varanus* has been described on various occasions (e.g. Bahl, 1937), with one paper addressing the basicranium in particular (Säve-Söderbergh, 1946). *Varanus* is fairly typical for the non-ophidian squamate morphology of the basicranium. The dorsum sellae is high, and distinctly overhangs the sella turcica, which accordingly

appears recessed below the dorsum sellae. The lateral edges of the dorsum sellae are drawn out into distinct clinoid processes (inferior process of basisphenoid *sensu* Oelrich, 1956), to which attach the pilae antoticae. The dorsal margin of the sella turcica is pierced on either side by a canal carrying the abducens nerve. Below and in front of the dorsum sellae expands the sella turcica housing the hypophysis. Anteriorly, the sella turcica narrows to form a basisphenoidal rostrum, which carries a crista trabecularis along its margin on either side. The cartilaginous trabeculae cranii continue the ossified cristae trabeculares of the basisphenoid anteriorly. Squamates other than snakes are characterized by a tropibasic skull, with the trabeculae fused to form a trabecula communis throughout the orbital region. The trabecula communis is supported by the narrow cultriform process of the parabasisphenoid, and itself supports the interorbital septum. A curved, dorsally concave cultriform process (L97: char. 36; L98: char. 62 [reworded]; LC98: char. B6) is simply an artifact in a dried skull which lost its cartilaginous components during preparation.

The basiptyergoid processes of *Varanus* are distinct and extend in an anterolateral direction. Their base is pierced by the Vidian canal. The posterior opening of the Vidian canal lies halfway between the posterior base of the basiptyergoid process and the basisphenoid-basioccipital suture, below the crista prootica. The internal carotid enters the posterior opening of the Vidian canal, and subdivides within this canal. The dorsal branch, the cerebral carotid, pierces the basisphenoid and exits through small foramina located on either side of the sella turcica. In *Varanus*, the location of these foramina is variable: they may lie close to the lateral margins of the posterior part of the sella turcica, or closely juxtaposed near the midline of the latter. The sagittal midline of the sella turcica and of the base of the dorsum sellae is developed into a low retractor crest (Säve-Söderbergh, 1946). The second, anterior branch of the internal carotid, the palatine artery, exits from the anterior opening of the Vidian canal, which is located at the anterior base of the basiptyergoid process. The vessel is accompanied by the palatine branch of the facial nerve, which also passes through the Vidian canal.

As indicated by Camp (1942) and Russell (1967), the basicranium of mosasaurs is again closely comparable to that of *Varanus*. In mosasaurs, such as *Platecarpus*, the dorsum sellae is less well developed than in *Varanus*, and it is bipartite with two halves separated by a deep medial cleft (Fig. 4). A sagittal retractor crest is therefore not developed at the base of the dorsum sellae. Lateral clinoid processes for the attachment of the pila antotica are distinct. As in other squamates, the abducens nerve pierces the dorsal margin of the dorsum sellae in a lateral position (Fig. 4). Unlike *Varanus*, the dorsum sellae does not overhang the sella turcica in *Platecarpus*, which is therefore more broadly exposed in dorsal view, whereas in *Varanus*, the sella turcica appears to narrow abruptly anteriorly (L97: char. 35; LC98: char. B4) as it emerges from below the overhanging dorsum sellae. The proportions of the sella turcica in itself are closely similar in *Varanus* and *Platecarpus*, and a narrow rostrum basisphenoidale lined by cristae trabeculares is also present in mosasaurs (Fig. 4). The difference between mosasaurs and *Varanus* is therefore not one of different proportions of the rostrum basisphenoidale, but relates to the differentiation of the dorsum sellae. The processus cultriformis is narrow in mosasaurs, suggesting a tropibasic skull.

In the specimens of *Platecarpus* at hand, the posterior opening of the Vidian canal is located well in front of the basisphenoid-basioccipital suture halfway between the

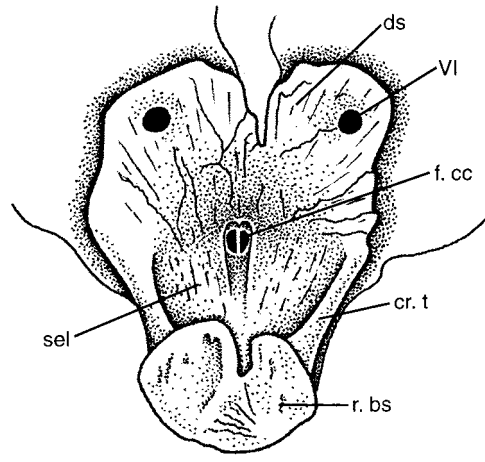


Figure 4. The rostrum basisphenoidale, sella turcica, and dorsum sellae of *Platecarpus* sp. (AMNH 01488) in cranial view. Scale bar = 20 mm. Abbreviations: cr.t, crista trabecularis; ds, dorsum sellae; f.cc, foramen for cerebral carotid; r.bs, rostrum basisphenoidale; sel, sella turcica; VI, abducent nerve foramen.

latter and the posterior base of the basiptyergoid process on the lateroventral aspect of the para-basisphenoid (L97, char. 38; L98: chars. 77, 78; LC98, p. 1548, char. 38). This is similar to that of *Varanus* (Fig. 2B, C). The position of the posterior opening of the Vidian canal is variable within the Varanoidea, and it is located far back close to the basisphenoid-basioccipital suture in *Heloderma* (Norell & Gao, 1997). *Platecarpus* (Camp, 1942; Russell, 1967) differs from *Varanus*, but also from other mosasaurs such as *Mosasaurus* and *Clidastes*, in that the anterior opening of the Vidian canal appears bipartite (Fig. 2C), a synapomorphy of platecarpines (G.L. Bell, pers. comm.).

The ventral opening of the Vidian canal of *Platecarpus* lies slightly anterior to the dorsal one, and must have carried the palatine nerve along with the palatine artery. In the absence of an extant model, the function of the dorsal opening is not entirely clear. Camp (1942) reconstructs a dorsal branch of the internal carotid that would have passed through this foramen, whereas Russell (1967) reconstructs this foramen as an exit for the basilar artery. However, as in other non-ophidian squamates, the cerebral carotid branches off the internal carotid within the Vidian canal and enters the sella turcica through a pair of closely juxtaposed foramina at the base of the sella turcica. A weakly developed, sagittal retractor crest separates the foramina for the cerebral carotids in *Platecarpus* (AMNH 01820).

Mosasaurs again differ from *Varanus* in that the anterior openings of the Vidian canal open into a shallow groove on the lateral aspect of the para-basisphenoid (Fig. 2C). This condition was compared to the differentiation of the Vidian canal in the Scolecophidia, and treated as a synapomorphy of the two clades (L97: char. 37 [retracted in Lee, 1998]; LC98, p. 1548, char. 37). The condition of the Vidian canal is variable in scolecophidians. In *Anomalepis*, the palatine nerve passes through the prootic into the prootic-basisphenoid suture from where it pierces the basisphenoid to emerge on its dorsal (intracranial) surface (Haas, 1968). In *Liotyphlops*, the palatine nerve exits from the prootic through the anterior of the two facialis foramina, and

together with the internal carotid pierces the basisphenoid close by the basisphenoid-prootic suture to gain an intracranial course on the dorsal surface of the basisphenoid (Haas, 1964). It re-emerges anteriorly through the basisphenoid-parietal suture. In *Typhlops*, the palatine nerve again exits from the prootic and becomes embedded in a groove on the lateral aspect of the prootic-basisphenoid fissure before slipping across the sutural margin of the basisphenoid to gain an intracranial course, which is a pattern closely similar to *Leptotyphlops*, except that in the latter genus the nerve pierces the basisphenoid narrowly below its sutural margin (Rieppel, 1979a). In all scolecophidians, as in alethinophidians (Rieppel, 1979b), the palatine nerve and artery gain an intracranial course on the dorsal surface of the basisphenoid, a condition which Lee (1997b) characterized as highly autapomorphic for Alethinophidia. The difference between scolecophidians and alethinophidians lies in the posterior part of the Vidian canal, which in the latter clade forms a true canal through the posterior part of the basisphenoid (Rieppel, 1979b) that is absent in scolecophidians. This difference might be explained by the absence of lateral wings of the parasphenoid in scolecophidians (Rieppel, 1979a). The basicranial relations of the palatine nerve and artery are different in all snakes from those of mosasaurs or most other non-ophidian squamates. The groove on the basisphenoid lies at the exit of the Vidian canal in mosasaurs, and well below and in front of its contact with the prootic; a groove carrying the palatine nerve leads to the entry of the Vidian canal in scolecophidians, and it lies on the basisphenoid-prootic fissure.

The basicranium of snakes differs from that of mosasaurs, *Varanus* and other non-ophidian squamates by a much lesser development of the dorsum sellae, a wide and shallow sella turcica, the absence of a sagittal retractor crest on dorsum sellae and sella turcica, a more posterior position of the posterior opening of the Vidian canal, and a platybasic skull characterized by paired trabeculae cranii throughout the orbital region. As a consequence, the basisphenoid rostrum and cultriform process often, but not always, are broader in snakes than in typical non-ophidian squamates. However, there are a number of squamate clades other than snakes which show a similar para-basisphenoid with a low dorsum sellae and a shallow and broad sella turcica, most notably miniaturized fossorial or burrowing clades such as *Anniella*, acontine skinks, *Dibamus*, and amphisbaenians. Similarity with basal snakes (non-scolecophidian) is particularly striking in *Anniella*, *Dibamus*, and *Typhlosaurus*, where the posterior opening of the Vidian canal is located in a posterior position. Anteriorly, the canal continues as a groove on the dorsal surface of the basisphenoid lateral to the low dorsum sellae and shallow sella turcica, before piercing the para-basisphenoid again in front of the basiptyergoid processes. A posterior position of the opening of the Vidian canal is also observed in amphisbaenians (Rieppel, 1978, 1984b).

The basioccipital

The basioccipital ossifies in the posterior part of the basal plate, and in the adult squamate forms the middle part of the occipital condyle. Posterioventrolateral projections of the basioccipital (Fig. 2), the spheno-occipital tubercles *sensu* Oelrich (1956), may carry separate apophyseal calcifications in non-ophidian squamates, and receive the insertion of the *longus capitis* muscles. In *Varanus*, the basioccipital is narrow posteriorly, forming the middle portion of the occipital condyle. Its lateral margins, contacting the exoccipital, are concave as the basioccipital widens anteriorly,

expanding into the sphenoccipital tubercles (L98: char. 76). The sphenoccipital tubercles are carried to the anterior margin of the basioccipital, to a level half-way between the occipital condyle and the basipterygoid processes. Between the basipterygoid processes, the basioccipital meets the basisphenoid in a relatively straight, slightly interdigitating transverse suture.

In mosasaurs (*Platecarpus* AMNH 01566), the basioccipital is relatively shorter than in *Varanus*. Again it forms the middle part of the occipital condyle, and expands anteriorly into the sphenoccipital tubercles. As in *Varanus*, the sphenoccipital tubercles are carried to the anterior margin of the basioccipital, to a level half-way between the occipital condyle and the basipterygoid processes. Between the basipterygoid processes, the basioccipital meets the basisphenoid in a V-shaped structure, the apex pointing forwards.

In basal snakes such as scolecophidians and non-macrostromatan alethinophidians, the sphenoccipital tubers are weakly developed. If present, they are located at the posteroventral corner of the crista circumfenestralis. Just as in non-ophidian squamates the sphenoccipital tubercles develop at the ventral end of the crista tuberalis. This topological relation confirms the hypothesis that the crista tuberalis forms the ventral part of the crista circumfenestralis in snakes. This relation also places the sphenoccipital tubercle of snakes ventral to the vestibular foramen. In contrast to mosasaurs and *Varanus*, the sphenoccipital tubers of snakes are located entirely behind the basioccipital-basisphenoid suture, which in basal snakes, possessing a flat basicranium forms a more or less straight, transverse line. In snakes with a keeled basicranium, such as some basal macrostromatans (e.g. *Python*: Frazzetta, 1959), the basioccipital-basisphenoid suture is V-shaped with the apex pointing backwards, the opposite of the situation observed in mosasaurs. In those basal macrostromatans which have basicranial processes ('basipterygoid' processes), these are positioned well in front of the basioccipital-basisphenoid suture, more so than is typical for mosasaurs or *Varanus*. This results from an elongation of the basisphenoid portion located behind the sella turcica by comparison to non-ophidian squamates.

The cranial nerves VII and VIII

The medial surface of the prootic of *Varanus* shows an acoustic recess with a single facialis foramen in its anteroventral corner, as is typical for other squamates (Oelrich, 1956; Rieppel, 1979b). Above and somewhat behind the facialis foramen, but still within the acoustic recess, are located two slightly smaller foramina for the entry of the acoustic nerve into the cavum vestibuli of the otic capsule, the anterior and posterior auditory foramen *sensu* Oelrich (1956). The posterior of these two foramina may be subdivided in *Varanus* (Camp, 1942; *Varanus komodoensis* FMNH 22199), in which the two posterior acoustic foramina are of unequal size, the anterior division being much smaller than the posterior division. By contrast, Oelrich (1956) distinguished two smaller anterior foramina from one large posterior acoustic foramen in the iguanid *Ctenosaura*. Potential systematic significance of this variation is discussed by Norell & Gao (1997).

Both Watkinson (1906) and Camp (1942) describe a single lateral opening in the prootic for the exit of the facial nerve in *Varanus* (L98: char. 68). A survey of the FMNH collections showed that the double facialis foramen is the more common condition found in the genus, with the possibility of variation even within the species

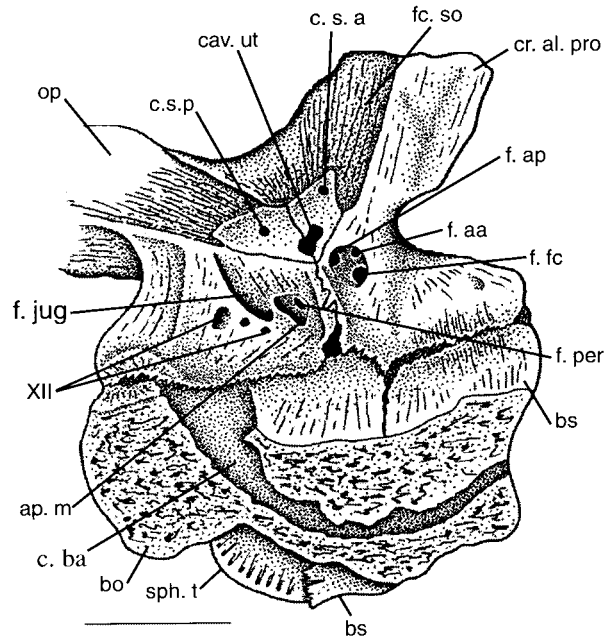


Figure 5. Braincase of *Platecarpus* sp. (AMNH 01488), medial view. Scale bar = 20 mm. Abbreviations: ap.m, apertura medialis of recessus scalae tympani; bo, basioccipital; bs, basisphenoid; cav. ut, cavum utriculi; c.ba, canal for basilar artery; cr.al.pro, crista alaris of prootic; c.s.a, canalis semicircularis anterior; c.s.p, canalis semicircularis posterior; f.aa, anterior acoustic foramen; f.ap, posterior acoustic foramen; fc.so, facet for supraoccipital; f.fc, facialis foramen; f.jug, jugular foramen; f.per, perilymphatic foramen; op, opisthotic; sph.t, spheno-occipital tubercle; XII, hypoglossal nerve foramina.

(*Varanus exanthematicus*: single in FMNH 17142, 228398, double in FMNH 212985; *Varanus salvator*: single in FMNH 31358, double in 31320). One skull in particular (*Varanus exanthematicus* FMNH 17142) shows the facialis foramen to be located in a deep groove below the crista prootica, and it is easy to visualize how this groove is closed superficially in other specimens by a ledge of bone growing across it, thereby creating an anterior and a posterior exit for the palatine and hyomandibular branches of the facial nerve. The geniculate ganglion of the facial nerve is generally located in an extracranial position in most squamates other than snakes, on the lateral surface of the prootic within the cranioquadrate passage, as is also the case in *Varanus* with a single facialis foramen (Watkinson, 1906). The ganglion is located within the prootic in those specimens with a double foramen, i.e. below the bony bridge developing across the groove carrying the posterior hyomandibular branch and the anterior palatine branch.

The medial wall of the otic capsule of mosasaurs (Fig. 5) again shows the acoustic recess located on the prootic, which is much more deeply recessed than in *Varanus*. A single facialis foramen, larger than either of the two acoustic foramina, is located in the anteroventral corner of the acoustic recess. The anterior acoustic foramen is located above the facialis foramen, and it is smaller than the posterior acoustic foramen located posterodorsal to the facialis foramen (Camp, 1942; Russell, 1967; *Platecarpus* AMNH 01488). The facial nerve pierces the prootic to exit from a foramen which is located slightly in front of, and above, the fenestra vestibuli and

which faces posteriorly. This foramen, identifiable in all braincase material of *Platecarpus* at hand, corresponds exactly to the exit of the hyomandibular branch in *Varanus* both in location and orientation. Camp (1942, for *Platecarpus*), but not Russell (1967, for *Clidastes*) shows a separate and more anteriorly located exit for the palatine branch. Situated below the crista prootica, this foramen is much closer to the exit of the hyomandibular branch than in *Varanus*. A separate foramen for the exit of the palatine branch of the facial nerve was not found in some *Platecarpus* specimens (AMNH 01487, 01566; 01820 is equivocal), but AMNH 01563 shows the exit of the facial nerve from within a deep groove which by close approximation of its dorsal and ventral margins in its central part is (perhaps incompletely) subdivided into an anterior and posterior slit-like opening for the palatine and hyomandibular branches respectively. Specimen AMNH 01488 (Fig. 2B) shows the complete separation of the exits of the two branches of the facial nerve as illustrated by Camp (1942). *Platecarpus* therefore appears to be subject to the same individual variation that is observed in *Varanus*, and separation of the exit of the two nerve branches from the prootic is superficial, i.e. by partial lateral closure of an otherwise open deep groove which carries the palatine branch forwards and the hyomandibular branch backwards from its passage through the prootic. Such similarity of morphology suggests that the geniculate ganglion of mosasaurs was in a position comparable to that in *Varanus*, i.e. located extracranially.

Snakes generally show a double facialis foramen (Rieppel, 1979b; although some variation exists) except in those cases where the palatine branch pursues an intracranial course into the Vidian canal (Rieppel, 1979a). However, the geniculate ganglion of snakes lies in an intracranial position. For alethinophidians, the validity of this statement may be viewed as dependent on the interpretation of the laterosphenoid as an element of the primary lateral braincase wall (Rieppel, 1976, 1989), but the geniculate ganglion is also in an intracranial position in scolecophidians (Haas, 1964, 1968; Rieppel, 1979a) which lack a laterosphenoid. Among squamates other than snakes, the geniculate ganglion is located in an intracranial position in *Dibamus* and amphisbaenians, two taxa which also show an intracranial passage of the palatine nerve into the Vidian canal.

The fenestra vestibuli (fenestra ovale)

In *Varanus*, the fenestra vestibuli (Fig. 2A) is a slit-like aperture which is located slightly below and behind the exit of the hyomandibular branch of the trigeminal nerve, above the occipital recess (see below), and slightly behind the level of the tip of the sphenoccipital tubercle (Oelrich, 1956). The crista prootica, a lamina of membrane bone projecting from the prominentia canalis semicircularis horizontalis in most squamates other than snakes (Oelrich, 1956), is prominently developed, and projects above the vestibular fenestra and the hyomandibular foramen, obscuring these openings in lateral view. In *Varanus* the crista prootica is always well developed, forming the roof of a well defined recess carrying the lateral head vein and the facialis branches, and in some specimens (e.g. FMNH 195576) the crista extends into a distinct, posterolateral projection (Fig. 2A). A distinct groove on the lower surface of the crista prootica runs from the hyomandibular foramen towards the vestibular fenestra, carrying the hyomandibular nerve to a level above the shaft of the stapes. The medial wall of this groove extends into a ventrally projecting prootic

flange which separates the vestibular fenestra from the posterior facial foramen. A stapedial groove runs from the vestibular fenestra along the lateroventral aspect of the paroccipital process, and in *Varanus* is located on the lower surface of the opisthotic running parallel to the prootic-opisthotic suture.

In mosasaurs, the vestibular fenestra is located above the lateral opening of the occipital recess (recessus scalae tympani), but somewhat more anteriorly than in *Varanus*, i.e. at the level of the tip of the spheno-occipital tubercle (Fig. 2B) which represents the plesiomorphic squamate condition (Norell & Gao, 1997). The fenestra also is wider than in *Varanus*, forming the internal auditory meatus and stapedial groove described by Camp (1942) and Russell (1967). The crista prootica is present in mosasaurs and overhangs the exit(s) of the facial nerve, but to a much lesser degree than in *Varanus* (Fig. 2B). The recess carrying the lateral head vein is consequently less clearly defined than in *Varanus*. A prootic bridge separates the facialis foramen from the vestibular fenestra, yet it is not thin and blade-like as in *Varanus*, but relatively broad with a convex ventral margin (Fig. 2B). A stapedial groove extends backwards from the vestibular fenestra, but it is broader in mosasaurs and located on the ventral surface of the prootic, running parallel to the prootic-opisthotic suture.

As described above, the vestibular fenestra is more deeply recessed in *Varanus* than in mosasaurs, but in both taxa remains separated from the occipital recess by the crista interfenestralis (Oelrich, 1956), a flange projecting from the anterior and ventral margin of the vestibular fenestra across the posterior and dorsal margin of the occipital recess. In basal snakes, the crista interfenestralis is not apparent in the lateral view of the braincase. Instead, the vestibular fenestra together with the perilymphatic foramen are located within a juxtastapedial recess surrounded by the so called crista circumfenestralis (Estes *et al.*, 1970). As the crista interfenestralis of *Varanus* and mosasaurs does not participate in the formation of the crista circumfenestralis in basal snakes (Fig. 6B, and discussion below), the bony flanges projecting around the vestibular fenestra (L97: 44; L98: char. 73; LC98, p. 1548, char. 44) in *Varanus* and mosasaurs are topologically not equivalent to those of snakes.

The fissura metotica

In reptiles in general, the embryonic fissura metotica forms as a space between the otic capsule and the occipital arch (deBeer, 1937). Dorsal closure of the metotic fissure occurs as the dorsal tip of the occipital arch contacts the posterior wall of the otic capsule. In squamates, the metotic fissure is subdivided during further development, into an anterior compartment, termed recessus scalae tympani, and a posterior compartment, the jugular or vagus foramen (Rieppel, 1985). The perilymphatic foramen, located in the posteroventral floor of the otic capsule, opens from above into the recessus scalae tympani, which in squamates other than snakes is also traversed by the glossopharyngeal nerve. In most non-ophidian squamates the recessus scalae tympani is typically represented by what Oelrich (1956) called the occipital recess, a wide open triangular cavity located behind the vestibular fenestra, separated from the latter by the crista interfenestralis, and separated from the posteriorly located vagus foramen by the crista tuberalis (Oelrich, 1956). This occipital recess is a tall yet narrow, almost slit-like structure in *Varanus*. Its medial

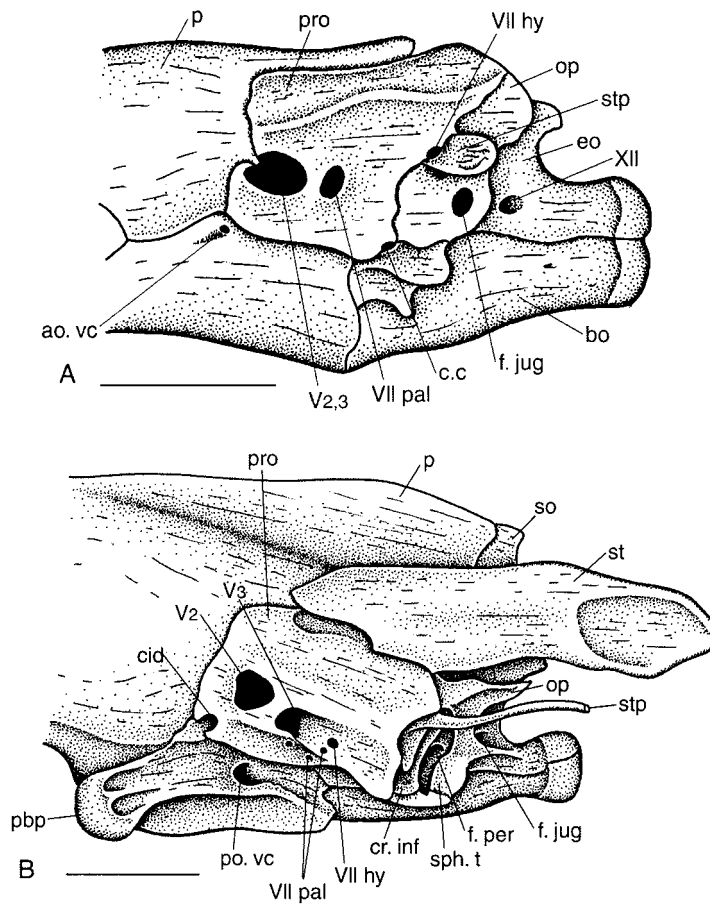


Figure 6. Brainscase of snakes in left lateral view. A, *Typhlops muelleri* (after Rieppel, 1979b). Scale bar = 2 mm; B, *Python sebae* (FMNH 22366). Scale bar = 5 mm. Abbreviations: ao.vc, anterior opening of Vidian canal; c.c., foramen for cerebral carotid; cr.inf, crista interfenestralis; eo, exoccipital; f.jug, jugular foramen; f.per, perilymphatic foramen; op, opisthotic; p, parietal; pbp, palatobasal process; po.vc, posterior opening of Vidian canal; pro, prootic; so, supraoccipital; sph.t, sphenoccipital tubercle; st, supraoccipital; stp, stapes; V_{2,3}, foramen for maxillary and mandibular branches of trigeminal nerve; VIIhy, foramen for hyomandibular branch of facial nerve; VIIpal, foramen for palatine branch of facial nerve; XII, foramen for hypoglossal nerve root(s).

aperture is located (in *Varanus komodoensis* FMNH 22199) between the otic capsule (prootic and opisthotic) and the basal plate (basioccipital). Its lateral aperture is recessed behind the prominently developed crista interfenestralis (Fig. 2A). The perilymphatic foramen is located deep in the dorsal part of the occipital recess, and is not exposed in medial, or lateral view of the brainscase. The crista tuberalis is broad and flaring, completely concealing the jugular foramen in lateral view (Fig. 2A).

The jugular foramen opens on the posterior surface of the occiput in *Varanus*. The internal view of the brainscase reveals the internal opening for the vagus nerve located between the opisthotic and the exoccipital. Behind this foramen, located within the exoccipital, are situated two or three smaller foramina for the passage of

the roots of the hypoglossal nerve. Watkinson (1906) described three roots of the hypoglossal nerve passing through two foramina in the exoccipital. The hypoglossal nerve roots anastomose with the trunk of the vagus nerve before emerging through the single opening on the posterior surface of the occiput.

In mosasaurs (Camp, 1942; Russell, 1967), the lateral opening of the occipital recess is well exposed in the lateral view of the braincase (Fig. 2B), but is reduced by comparison to *Varanus*. In specimen AMNH 01488 of *Platecarpus* it is a rounded aperture, while in the other specimens (AMNH 01563, 01645, 01820) it forms an obliquely oriented slit, closely similar to the illustrations given by Camp (1942) and Russell (1967). Separation of the lateral aperture of the occipital recess from the fenestra ovalis is not by means of a distinctly projecting, flange-like crista interfenestralis, as in *Varanus*, but rather by a weakly projecting and relatively broad bony bridge with a smoothly convex surface (Fig. 2B). The medial aperture of the occipital recess (recessus scalae tympani) is a relatively wide, cleft-like opening surrounded by the opisthotic without participation of the basicranium (basioccipital) in its ventral margin (Fig. 5), as is also shown for *Clidastes* by (Russell, 1967, text-fig. 13), but not as would be typical for other squamates, including snakes. In that respect, mosasaurs differ from other squamates, including snakes. Also in mosasaurs (*Platecarpus* AMNH 01488), the perilymphatic foramen opens into the occipital recess from in front rather than from above, and it is narrowly exposed in the medial view of the braincase (Fig. 5). The glossopharyngeal nerve is reconstructed to pass through the occipital recess in mosasaurs, as is the case in *Varanus* and other non-ophidian squamates.

Similar to the crista interfenestralis, the crista tuberalis is less well developed in mosasaurs, and instead of forming a flaring bony flange as in *Varanus*, it is represented by a relatively broad bony bridge which separates the occipital recess from the jugular foramen. As a consequence, the latter is exposed in the lateral view of the braincase, albeit recessed behind the crista tuberalis (Fig. 2B). The internal view of the braincase of *Platecarpus* (AMNH 01488) reveals three hypoglossal foramina located in the exoccipital behind the internal opening of the jugular foramen (Fig. 5). Of these, the dorsalmost is the largest. A similar arrangement of the hypoglossal foramina is shown by Russell (1967, text-fig. 13) for *Clidastes*.

In snakes, the otico-occipital complex is of a fundamentally different structure (Fig. 6). The crista tuberalis combines with the crista prootica to form the crista circumfenestralis (Estes *et al.*, 1970), which completely surrounds the stapedial footplate, and encloses the vestibular fenestra together with the lateral opening of the recessus scalae tympani (occipital recess of non-ophidian squamates) in a common space called the juxtastapedial recess. The perilymphatic duct enters the juxtastapedial recess through the lateral aperture of the recessus scalae tympani (located posteroventral to the vestibular foramen), and expands into a juxtastapedial sinus which covers the lateral surface of the stapedial foot plate as part of a reentrant fluid circuit (Wever, 1978). Other than in snakes, the perilymphatic system forms a re-entrant fluid circuit (yet in somewhat different ways) in some burrowing lizards and in amphisbaenians (Rieppel, 1988a). The glossopharyngeal nerve no longer exits from the recessus scalae tympani in snakes, but from the vagus foramen instead.

The sound-transmitting apparatus

In a typical squamate such as *Varanus*, the sound transmitting apparatus (columella auris) consists of an inner bony element, the stapes (otostapes), and an outer

cartilaginous element, the extracolumella. The cephalic condyle of the quadrate is extended into a suprastapedial process which projects posteriorly above the columella auris as it contributes to the formation of the posteriorly concave margin of the quadrate. The tympanic membrane is attached to the posterior margin of the quadrate anteriorly, and to the retroarticular process of the lower jaw ventrally. The extracolumella inserts into the tympanic membrane with its insertion piece (Versluys, 1898) composed of four processes (pars superior, pars inferior, anterior process and posterior process: Wever, 1978). The chorda tympani of the facial nerve passes dorsal to the extracolumella. The initial chondrification of the internal process proceeds from the otostapes, but after ossification of the stapes, the internal process appears as part of the cartilaginous extracolumella which inserts into a notch on the posteromedial aspect of the shaft of the quadrate (Oelrich, 1956). *Varanus* differs from the standard non-ophidian squamate, i.e. iguanian, type of middle ear in that the internal process is not anchored in a depression or groove on the quadrate, but loosely overlaps its surface, held in place by mucous membrane (Wever, 1978: 397).

Probably as a reflection of their marine habits, the quadrate of mosasaurs is derived in comparison to other lizards by a dramatically increased suprastapedial process, which curves around the stapedia shaft (Fig. 3A), and which may enclose the latter in a closed stapedia notch as it meets an infrastapedial process emerging from the posterior aspect of the quadrate below the stapes. The deep and well defined pit for the insertion of the internal process of the stapes lies in front of and slightly above the stapedia notch on the medial surface of the quadrate (Fig. 3A), i.e. on the posteromedial aspect of the dorsal part of the stapedia shaft as in other non-ophidian squamates where it is present (Russell, 1967, text-fig. 25c; *Platecarpus* FMNH UR 600, UR896). The distal end of the internal process does not contact the posteriorly sloping surface of the suprastapedial process, which corresponds to the posterior surface of the cephalic condyle of the quadrate (L97: char. 45).

The middle ear of snakes, by contrast, is much different from the condition observed in *Varanus*, *Lanthanotus*, and in mosasaurs. Again, the sound transmitting apparatus consists of a medial bony stapes and a lateral cartilaginous extension. However, the lateral cartilaginous extension is believed to correspond to the internal process of the otostapes, rather than to the extracolumella. Accordingly, the chorda tympani passes ventral to the cartilaginous distal part of the ophidian sound transmitting apparatus. A structure corresponding to the extracolumella of other squamates (including mosasaurs) is absent in snakes (as well as in amphisbaenians: Wever, 1978). Instead, the cartilaginous distal part of the stapes of snakes (internal process) makes contact with the stylohyal. The latter is an element that represents the tip of the dorsal process of the reptilian stapes which forms the intercalary cartilage with no function in sound transmission in non-ophidian squamates, but which fuses to the quadrate in snakes. In most advanced (macrostomatans) snakes which have lost a suprastapedial process, the stylohyal fuses to the quadrate shaft, but in anilioids and some basal macrostomatans, it fuses to the posteroventral margin of the suprastapedial process of the quadrate. It is in synovial contact with the internal process of the stapes (Rieppel, 1980b). The contact of the sound-transmitting apparatus to the quadrate is therefore of a different nature and in a different topological position in mosasaurs and snakes (L97: char. 45). In the relationships of stapes and quadrate, the only lizards approaching the ophidian condition are the fossorial genera *Feylinia* and *Dibamus* (Rieppel, 1984b), although details of topology and of the elements involved remain different.

DISCUSSION

The braincase in Platecarpus and Varanus

As previously noted by Camp (1942) and Russell (1967), the braincase structure and associated soft tissue in mosasaurs are closely similar to those of *Varanus*. If looked at in greater detail, some interesting differences can be recorded, however. Some of the major differences between the mosasaur *Platecarpus* and *Varanus* result from the obliteration of the metakinetic axis in mosasaurs, which results in the expansion of the posterior end of the supratemporal to establish a closed sutural contact with the prootic, and in the sutural contact of the alar process of the prootic with the laterally descending flange of the parietal. The contact of the supraoccipital with the parietal is comparable in the two groups, and indicates that the mosasaur skull is derived from a metakinetic squamate skull pattern.

Further differences in the braincase structure of *Platecarpus* and *Varanus* prevail in the basicranium. The dorsum sellae is less well developed in the mosasaur and bipartite, the sella turcica is not recessed below the dorsum sellae, the retractor crest is more weakly developed in mosasaurs, the basicranium (basioccipital) remains excluded from the medial aperture of the recessus scalae tympani (occipital recess) in mosasaurs, and the Vidian canal has a bipartite anterior opening in *Platecarpus*. Not all mosasaurs show the bipartite anterior opening of the Vidian canal, however (Camp, 1942; Russell, 1967), and in the absence of an extant model the interpretation of the nerves and blood vessels associated with these two anterior openings on the lateral surface of the basisphenoid remains somewhat equivocal.

In lateral view, the braincases of *Varanus* and *Platecarpus* differ primarily by a lesser development, in mosasaurs, of the bony flanges developed above the vestibular foramen (crista prootica), between the vestibular foramen and the occipital recess (crista interfenestralis), and between the occipital recess and the jugular foramen (crista tuberalis). As a result, the vestibular foramen, occipital recess and jugular foramen are more broadly exposed in lateral view in mosasaurs than in *Varanus*. Finally, the relations of the internal process of the stapes to the quadrate differ in the two groups.

The significance of these differences require further investigations at a larger, more encompassing scale. Few braincase characters have so far been brought to bear on the analysis of squamate (Estes *et al.*, 1988), or anguimorph (Norell & Gao, 1997; Gao & Norell, 1998) interrelationships. Analyzing braincase structure throughout the Squamata may have some bearing on the position of mosasaurs within the group, i.e. whether they are a subclade of platynotans (Lee, 1997b; Lee in Lee & Caldwell, 1998), or whether mosasaurs, and indeed pythonomorphs *sensu* Cope (1869), are the sister-group to Scleroglossa, i.e. all non-iguanian squamates (Caldwell, 1999).

The relationships of snakes: what is a character?

It is beyond doubt that snakes share a suite of characters with marine mosasauroid reptiles, as is reflected by traditional views on their relationships (Cope, 1869; Camp, 1923; McDowell & Bogert, 1954). The intramandibular joint of mosasaurs and snakes has frequently been referred to in this context, a topic to be dealt with in a

forthcoming paper. An ophidian character in the mosasauroid cranial anatomy is the smooth and rounded anterior end of the dentary, indicating the absence of a mandibular symphysis. Apart from osteological features, there are also soft anatomy features which relate snakes to varanoid lizards, such as tongue anatomy (McDowell & Bogert, 1954; McDowell, 1972; Schwenk, 1988). However, as the discussion above has made clear, snakes also share a number of characters with fossorial or burrowing clades of squamates (see also Hallermann, 1998), an observation which again holds true for many aspects of the sensory system (Walls, 1940; Senn & Northcutt, 1973; Northcutt, 1978). Such characters call for a comparison of snakes at a broader level (see also Evans & Barbadillo, 1998), as was eventually performed by Lee (1998). Lee (1997b) and Lee and Caldwell (1998) postulate a marine origin of snakes, and Lee (1998) accordingly found the snakes to be convergent upon the elongate fossorial ecomorph of non-ophidian squamates. This claim can only be justified by the assumption that fossorial or burrowing habits evolved within snakes after the latter diverged from mosasauroids and above the level of *Pachyrhachis*. This assumption rests on two premises, first that the character evidence on which the monophyly of the Pythonomorpha is built is robust, and second that *Pachyrhachis* is the most basal taxon of all snakes.

The classification of *Pachyrhachis* as the most basal of all snakes is controversial (Zaher, 1998), and is also the object of ongoing work by the authors. In this contribution, we address the validity of that part of the character evidence used in support of the monophyly of Pythonomorpha which relates to braincase structure, and we document not only important differences between *Varanus* and mosasaurs, but also profound differences in braincase organization in snakes as compared to non-ophidian squamates. This echoes our earlier findings with respect to those characters that relate to the dentition in mosasauroids, *Varanus*, and snakes. Such discrepancies of character description and definition raise problems of homology assessments which appear to underlie the comparison of braincase structure in mosasaurs and snakes, and the ramifications this has for cladistics as an empirical science, i.e. as a science rooted in observation which generates testable, and potentially falsifiable, hypotheses.

In the context of cladistic analysis, the establishment of similarity, and homology (or synapomorphy *sensu* Patterson, 1982) has been recognized to be at least a two step procedure. The first step is the recognition of similarity, or structural correspondence, i.e. the recognition of “the same but different” (Hawkins *et al.*, 1997), or, in general terms, the establishment of a “one-to-one” relation amongst units under comparison (Woodger, 1945). Patterson (1982) spoke of the “test of similarity” to establish a relation of similarity among constituent elements of the organic whole; Rieppel (1988b), talked about the search for topographical correspondence; dePinna (1991) considered this first step of the analysis to result in hypotheses of “primary homology”; for Brower & Schawaroch (1996), the initial step of analysis results in “conjectural homology”; and for Hawkins *et al.* (1997), it results in a “proposition of homology”. The second step of the cladistic analysis subjects these hypotheses of “primary homology”, of “proposed” or of “conjectural homology”, to the test of congruence. Congruence legitimates proposed homologies (Hawkins *et al.* 1997), it allows to discriminate between homoplasy and “secondary homology” (dePinna, 1991), “corroborated homology” (Brower & Schawaroch, 1996), or homology *qua* synapomorphy (Patterson, 1982; Rieppel, 1988b).

Brower & Schawaroch (1996) added another, intermediate, step to the search for

homology, i.e. they distinguished between topographical identity and character state identity. According to their epistemology, the first step of cladistic analysis is the recognition of topographical identity, reflected in the addition of another column (i.e. another character) to a data matrix. The second step is to code the cells of this column, which is equivalent to the identification of character state identity for the taxa under investigation. The third step is to subject the data matrix to the test of congruence, which discriminates between “conjectural homology” (which may turn out to be homoplastic), and “corroborated homology” (which is accepted as homology *qua* synapomorphy, i.e. as similarity due to common ancestry, on the basis of available character evidence). For Hawkins *et al.* (1997), the distinction of topographical identity and character state identity reflects Jardine’s (1969) view of characters as *nouns*, and character states as *adjectives*.

Certainly the most problematical step in all systematic studies represents the identification of primary homologies *sensu* dePinna (1991; see Patterson & Johnson, 1997, and the above discussion for examples). Although the test of congruence (Patterson, 1982) represents the ultimate arbiter on homology *qua* synapomorphy (i.e. similarity to be hypothetically explained as due to common ancestry) versus homoplasy (i.e. independently acquired similarity), it is in itself not rooted in anatomical investigation and comparison, but is merely designed to match the distribution of any one character with respect to all other known characters in order to maximize congruence and hence minimize homoplasy. In that sense, each character, while tested for congruence with respect to all other known characters, is at the same time contributing to the test of all other known characters, which prevents it from becoming an arbiter on the quality of anatomical comparison underlying statements of primary homology. Primary homologies are taken as statements of ‘sufficient similarity’ to be tested for potential homology in the sense of synapomorphy. However, a high degree of character congruence in itself says nothing about the quality of a phylogenetic hypothesis if it is based on a poorly developed character data base which includes questionable statements of primary homology.

The test of congruence, therefore, cannot be the only element in establishing relations of homology, but critically depends on the rigorous application of the test of similarity (Patterson, 1982) in the identification of primary homologies. ‘Sufficient similarity’ will never lend itself to an objective measurement or a stringent test, and it is for this reason that some element of subjectivity will necessarily remain part of comparative biology, the *bête noire* of systematic research (Pogue & Mickevich, 1990). As Smith (1994: 34) put it: “different workers will perceive and define characters in different ways.” While every observation corresponds to ‘something’ being observed, everything being observed is potentially observed in terms of a plethora of appearances by the same or different authors under different theoretical premises.

In comparative biology, the test of similarity historically is rooted in the establishment of topological equivalence (Rieppel, 1988b), or connectivity (Shubin & Alberch, 1986), of the constituent elements of the organisms that are being compared. As has long been recognized (Remane, 1952), topographic relations, compositional and ontogenetic similarity are essential attributes in the recognition of structural correspondence (Hawkins *et al.*, 1997). Without these tools of comparative anatomy, hypotheses of primary homology are no longer testable *qua* hypotheses of primary homology, and cladistic analysis is reduced to the exercise of testing for congruence among empirically empty character definitions. As Patterson & Johnson (1997: 361)

have cogently argued: in modern systematics, “the emphasis has shifted from observation, the source of the [data] matrix, to whatever message may be extracted from the matrix . . . This change of emphasis replaces our pernicious old black box, evolutionary systematics, with a new one, the matrix.”

The search for topographical correspondence or connectivity in the establishment of hypotheses of primary homologies remains a first principle of systematic research. A first principle is one that cannot, nor needs to, be further justified, as it justifies itself—by its success. The search for primary homology abstracts from the particular shape and function of constituent elements in the organic whole in the search for topographical equivalence or equivalent connectivity, as was laid out in detail by Etienne Geoffroy Saint-Hilaire and Etienne Serres (see discussion in Rieppel, 1988b). The “Haematherma affair” (Kirsch & Mayer, 1998) provided a perfect example of the consequences of violation of the principle of connectivity. One of the characters used in support of the monophyly of Haematherma that showed perfect congruence was the hypothesis of primary homology of the alisphenoid of mammals with the pleurophenoid of birds (Gardiner, 1982), while it was well established (e.g. Goodrich, 1930) that the pleurophenoid of birds is of neurocranial origin, whereas the alisphenoid is, at least in part, of splanchnocranial origin (Presley & Steel, 1976).

Similar problems of topographical inequality plague the comparison of braincase structure in mosasauroids and snakes as presented by Lee (1997b) and Lee & Caldwell (1998). The simple observation that proposed homologies do fall into a congruent pattern does not validate these as synapomorphies if the hypotheses of primary homology fail the test of similarity based on topographical correspondence and connectivity. If this were the case, phylogenetic analysis would become a matter of wording character definitions such as to match a preconceived result. If phylogeny reconstruction is to remain an empirical science, it must be based on testable, and at least potentially falsifiable hypotheses. A ‘primary’ or ‘conjectured’ homology can be tested by congruence, and refuted as historical signal by incongruence. In order to maintain a testability, and potential falsifiability of hypotheses of ‘primary’ homology *sensu* dePinna (1991), of conjectured homology *sensu* Brower & Schawaroch (1996), or of proposed homology *sensu* Hawkins *et al.* (1997), it is indispensable to maintain reference to topographical equivalence or connectivity rooted in anatomical comparison.

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