Did mosasaurs have forked tongues?

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Abstract

Ever since the first mosasaur restorations were published, these extinct marine reptiles have been pictured with either notched, forked or undivided tongues. Here, we present an overview of existing iconography, a review of the previous literature, and we discuss how best to reconstruct tongue form in mosasaurs. Despite disagreement about their precise phylogenetic position, most authors consider mosasaurs members of the Varanoidea, derived anguimorphans including Helodermatidae, Varanidae, *Lanthanotus* and probably snakes. All anguimorphans share a diploglossan (two-part) tongue, in which the foretongue is derived and modified into a highly protrusible chemosensor, while the hindtongue is plesiomorphic, retaining well-developed papillae, mucocytes and robust posterior lobes. We suggest that mosasaurs had a diploglossan tongue that remained in a relatively underived state. The form of the tongue would probably have been most like modern *Heloderma* or *Lanthanotus* with a protrusible chemosensory foretongue and a plesiomorphic, papillose hindtongue. Such a tongue is consistent with well-developed vomeronasal chemoreception through tongue-flicking, with the retention of the ancestral function of hyolingual food transport and swallowing following jaw-prehension of prey. The presence of paired fenestrae in the palate associated with the vomers, as well as the presence of pterygoid teeth are in accordance with such a tongue form in mosasaurs.

Keywords: feeding, mosasaurs, olfaction, restoration, tongue, vomeronasal organ

Introduction

With body lengths sometimes exceeding 15 metres, mosasaur skeletons make for impressive museum displays. Apart from mounted skeletal reconstructions, restorations of the possible appearance of extinct animals are (and have always been) an important tool in palaeontological communication, both 3-dimensionally as often seen in a museological context, as well as 2-dimensionally in printed or film-based media.

With the advent of new techniques, especially in the field of robotics and computer graphics, palaeontologists are more and more often faced with questions regarding the original external appearance of extinct plants and animals. The question of whether mosasaurs had a bifurcated tongue or not was recently brought to our attention. Here we present a review of the existing ideas, and a possible reconstruction of the mosasaur tongue.

Mosasaur discoveries and iconography

The first documented find of a mosasaur skull dates from 1766 and was recorded from the underground galleries of the St. Pietersberg near Maastricht. Between 1770 and 1774 another skull was discovered, also beneath the St. Pietersberg. This

second fossil, which was to be designated the type specimen of *Mosasaurus hoffmanni* Mantell, 1829, would become much more famous. In 1795 it was transported to the Muséum national d'Histoire naturelle in Paris, where it contributed to Georges Cuvier's thinking about the concept of extinction (Bardet & Jagt, 1996; Mulder, 2003).

During the late nineteenth and early twentieth centuries, European mosasaurs notably were described from Belgium by Louis Dollo (e.g. in 1889 and 1909). Simultaneously, numerous publications appeared in which mosasaur remains from North America were discussed. These works became steadily more extensive, particularly after 1880 when many excellent specimens were discovered, for example, in the Niobrara Chalk (Russell, 1967).

As early as 1800, the Dutch palaeontologist Adriaan G. Camper recognised the monitor (varanid) lizard affinities of these fossil vertebrates (Camper, 1800; Mulder, 2003), well before they were described as *Mosasaurus* (Conybeare, 1822).

Points of similarity between mosasaurs and snakes were recognised by Edward D. Cope. This inspired him to introduce the order Pythonomorpha (Cope, 1869a). In the further course of the nineteenth century, and later, the relationships between mosasaurs, varanids, helodermatids, other lizards and snakes, were thoroughly studied and debated.

The oldest restorations of mosasaurs we know of are found in Figuier (1863), and in Cope (1869b), where a mosasaur from New Jersey is illustrated (Fig. 1).

Many more 'realistic' restorations of mosasaurs are found in the works of Samuel W. Williston (1898a, b, 1900). The life restorations herein are by J. Carter Beard and Sidney Prentice, respectively. In both restorations, the mosasaurs are shown in a fully marine habitat, along with other animals known from the Upper Cretaceous of Kansas. The mosasaurs pictured show unmistakably snake-like (forked) tongues. Here we may see the influence of Cope. Sternberg (1898, p. 268), probably also following Cope, presents a very snake-like description: 'A long snake-like body follows, covered with scales about the size and shape of those of a Kansas bull snake. (...) His long forked tongue is stretched out of the mouth at full length, and the only sound we hear is a long dismal hiss. His lower jaws have a ball-and-socket joint back of the tooth bearing bone, which enables him to expand the cavity of the mouth by spreading the jaws, and lowering the skull between them, giving the ugly appearance of a rattlesnake when, as the boys say, he flattens his head ready to strike'.

A decade later, Dollo (1909, pl. 7) reconstructed the proportions and body shape of a representative of the genus *Mosasaurus* based on *M. lemonnieri* Dollo, 1889. As he stated, Dollo was clearly inspired by Williston's (1898b) illustration. Dollo however, deliberately eliminated the forked tongue, since he erroneously assumed that such a tongue 'does not exist in marine reptiles and is therefore not in accordance with the pelagic adaptation of the animal' (Dollo, 1909, pl. 7; see and compare also Lever, 1990, figs 13, 14). Interestingly, the surface texture of the scales covering the mosasaur in the restorations of Dollo (1909) appear much smoother and more snake-like than in most other restorations from that time.

While keeping in mind that famous illustrators such as Charles Knight and Zdenek Burian did not publish clear reconstructions of mosasaur tongues (at least none that we know of), we note that disagreement over mosasaur tongue reconstruction continues to the present time. Amongst restorations by modern palaeo-artists, both bifurcated and undivided tongues are seen. In the work of the Plainsboro, NJ (USA) palaeo-artist Dan Varner, the mosasaurs are routinely equipped with tongues that show a pronounced bifurcation, while Silver City, NM (USA) colleague Karen Carr recently depicted a mosasaur with a fleshy, almost 'ox-like' tongue. The mosasaur by Walters (published in Farlow & Brett-Surman, 1997) also shows an undivided tongue tip. L'histoire se répète! Hence, the question we ask ourselves now is: 'How probable was the presence of a bifurcated or forked tongue in mosasaurs, considering current views regarding the phylogenetic position of these extinct marine squamates and tongue function in their living relatives?'

## Reconstructing the tongue in mosasaurs

We can approach the reconstruction of mosasaur tongues, and soft tissues generally, using two sources of information: phylogenetic bracketing (the 'extant phylogenetic bracket' of Witmer, 1995) and by analogy to living organisms using functional inferences from their behaviour (Bryant & Russell, 1992; Witmer, 1995). These methods are not mutually exclusive.

Phylogenetic relationships of mosasaurs

Mosasaurs are universally regarded to be squamate reptiles, and most workers since Camper (1800) and Cuvier (1808) have considered them closely related to the living monitor lizards (Varanidae). Baur (1890) formerly classified them near the varanids within the Varanoidea. Most subsequent workers have continued to regard mosasaurs as varanoids (the group containing Varanidae, Helodermatidae and probably snakes), or at least, platynotans (Varanoidea plus the fossil taxa Aigialosauridae and Dolichosauridae) (e.g., Camp, 1923; McDowell & Bogert, 1954; Romer, 1966, Pregill et al., 1986; Carroll, 1988; Lee, 1997, 1998; Lee et al., 1999; Lee & Caldwell, 2000). Varanoids lie within a larger clade of lizards called the Anguimorpha (Fig. 2), which includes, in addition, the Anguidae, Xenosauridae, and *Shinisaurus* (e.g. Camp, 1923; Estes et al., 1988; Gao & Norell, 1998). Some palaeontologists have argued that mosasaurs are an earlier-branching clade of lizards sharing only superficial similarity to modern varanids (e.g., Osborn, 1899; Williston, 1925; Caldwell et al., 1995; Caldwell, 1999), other authors suggest that mosasaurs are varanoid lizards (Rieppel & Zaher, 2000b).
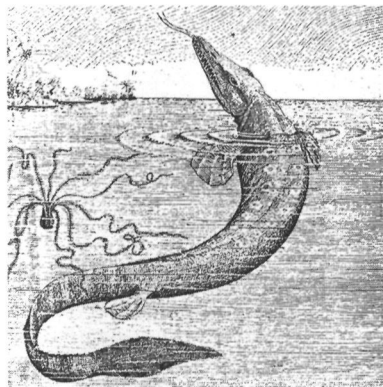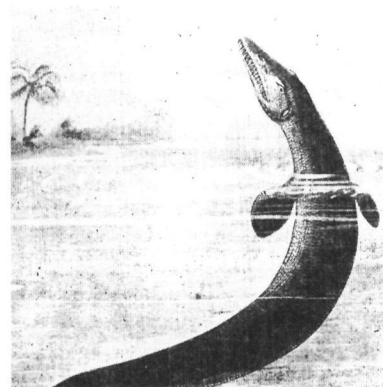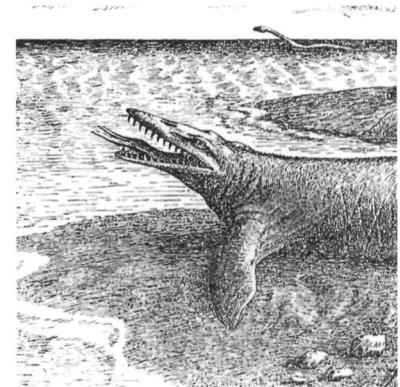
a. Figuier, 1863
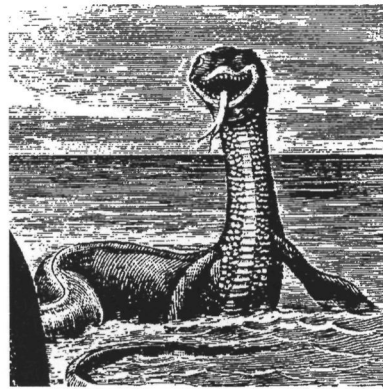
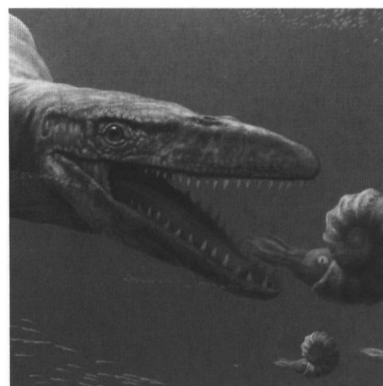b. Cope, 1869

c. Beard/Williston, 1898
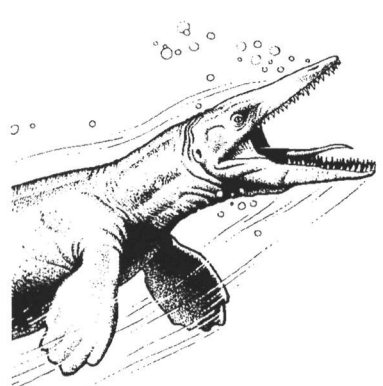
d. Prentice/Williston, 1898

e. Dollo, 1909

f. Prentice/Williston, 1900

g. Carr, 2000

h. Walters, 1997

i. Varner, 2002

Fig. 1. Selection of mosasaur restorations from 1863 to 2002, as discussed in text.

Figure 3 illustrates several hypotheses of mosasaur relationships within squamates. We show only the findings of morphological studies that include mosasaurs in their phylogenetic analyses (Camp, 1923; McDowell & Bogert, 1954; Lee, 1997; Lee & Caldwell, 1998; Caldwell, 1999; Rieppel & Zaher, 2000b). Several recent studies of squamate relationships are restricted to living taxa or otherwise did not consider directly the relationships of mosasaurs (e.g., Estes et al., 1988; Gao & Norell, 1998; Lee, 1998, 2000; Harris et al., 2001; Lee & Scanlon, 2002; Vidal & Hedges, 2004; Townsend et al., 2004). Recent molecular studies have controverted long-held hypotheses based on morphology, particularly with regard to the relationships of anguimorphans, generally, and the position of snakes, specifically (Harris et al., 2001; Vidal & Hedges, 2004; Townsend et al., 2004).

The morphological studies cited provide strong support for Anguimorpha as traditionally construed and for placement of mosasaurs within the derived anguimorphan group,
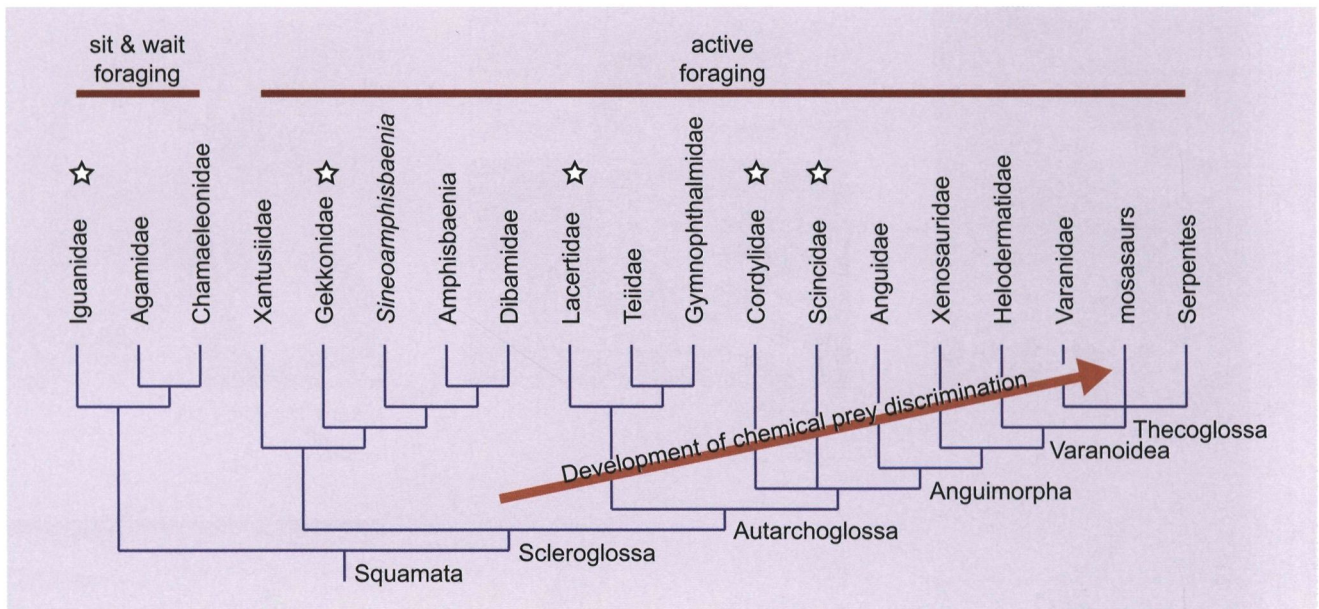
Fig. 2. Traditional, morphology-based phylogeny of squamate reptiles based on Lee (1998). Note that the position of Scincidae and Cordylidae in this phylogeny is controversial. Traditional phylogenies, such as Estes et al. (1988), would include these families within a clade along with the Lacertidae and Teiidae/Gymnopthalmidae to form the suprafamilial clade, Scincomorpha. Stars indicate reversal in foraging strategy.

Varanoidea (including Helodermatidae, Varanidae, *Lanthanotus* and snakes). However, there is significant disagreement over whether mosasaurs are the sister group of snakes (Cope's (1869a) Pythonomorpha: Lee, 1997; Caldwell, 1999; Lee et al., 1999), or whether varanoid (platynotan) lizards are not directly related to snakes (Camp, 1923; McDowell & Bogert, 1954; Zaher & Rieppel, 1999; Rieppel & Zaher, 2000a,b, 2001; O. Rieppel, pers. comm.), as traditionally thought. Since both snakes and varanid lizards share a long, slender and deeply forked tongue, whereas *Heloderma* and *Lanthanotus* have only a modestly forked tongue with a fleshy base, the precise position of mosasaurs within Varanoidea can affect our conclusions about tongue form in mosasaurs. We consider mosasaurs unlikely to be the sister group of snakes, but undoubted varanoid lizards of uncertain relationship relative to Varanidae, Helodermatidae and Lanthanotidae. Based on the data presented in the cited literature, a close relationship to the varanid-*Lanthanotus* lineage seems most likely (Fig. 4).

Tongue function in living squamates – feeding

The squamate tongue (Fig. 5) is exceptionally diverse in form (Schwenk, 1988, 2000). With the exception of dibamid lizards, the tongue tip of all squamates is bifurcated; however, the depth of the bifurcation ranges from a simple notch (e.g., Iguanidae) to a deep fork (e.g., Varanidae). The tongue has two principal functions in squamates – feeding and chemoreception. From a mechanical point of view, these functions impose conflicting demands on tongue structure that have been resolved historically in clade-specific patterns (Schwenk, 1988, 1993, 2000).

The tongue potentially serves several different functions during feeding in lizards (reviewed by Schwenk, 2000): (1) as a prehensile organ to capture food; (2) to manipulate food in the oral cavity after capture, either by positioning it between upper and lower tooth rows for gnawing, or to transport it towards the throat for swallowing; and/or (3) during swallowing, either to pack food into the pharynx or, along with the hyobranchial apparatus, to compress the pharynx in order to squeeze food into the oesophagus where peristalsis takes over transport of the bolus through the gut.

Lingual prehension of food is limited, for the most part, to iguanian lizards (Iguanidae, Agamidae, Chamaeleonidae) which have a blunt, muscular, highly papillose foretongue (Schwenk, 1988, 2000; Schwenk & Throckmorton, 1989). The tongue tip in these lizards is only slightly notched. The functional significance of this notch is unclear, although its presence is correlated with a direct connection between the vomeronasal chemosensory organs and the oral cavity through apertures in the anterior palate. Thus, the notch is assumed to be functionally related to chemoreception (Schwenk, 1993, 1994) (see below). Clearly, a deeply cleft or forked tongue would interfere with the prehensile function of the foretongue.

Food transport occurs on the fore- or midtongue. The bolus is progressively moved towards the pharynx by cyclical, posteroventral movements of the hyolingual apparatus (tongue plus hyobranchium). The bolus is held on the tongue by frictional contact with the lingual surface and by deformation of the muscular tongue, which either cups around the bolus or rises up in front of it to push it back towards the throat. In addition, the palate, and in some cases, palatal teeth, serve to hold the bolus in place each time the tongue protracts beneath
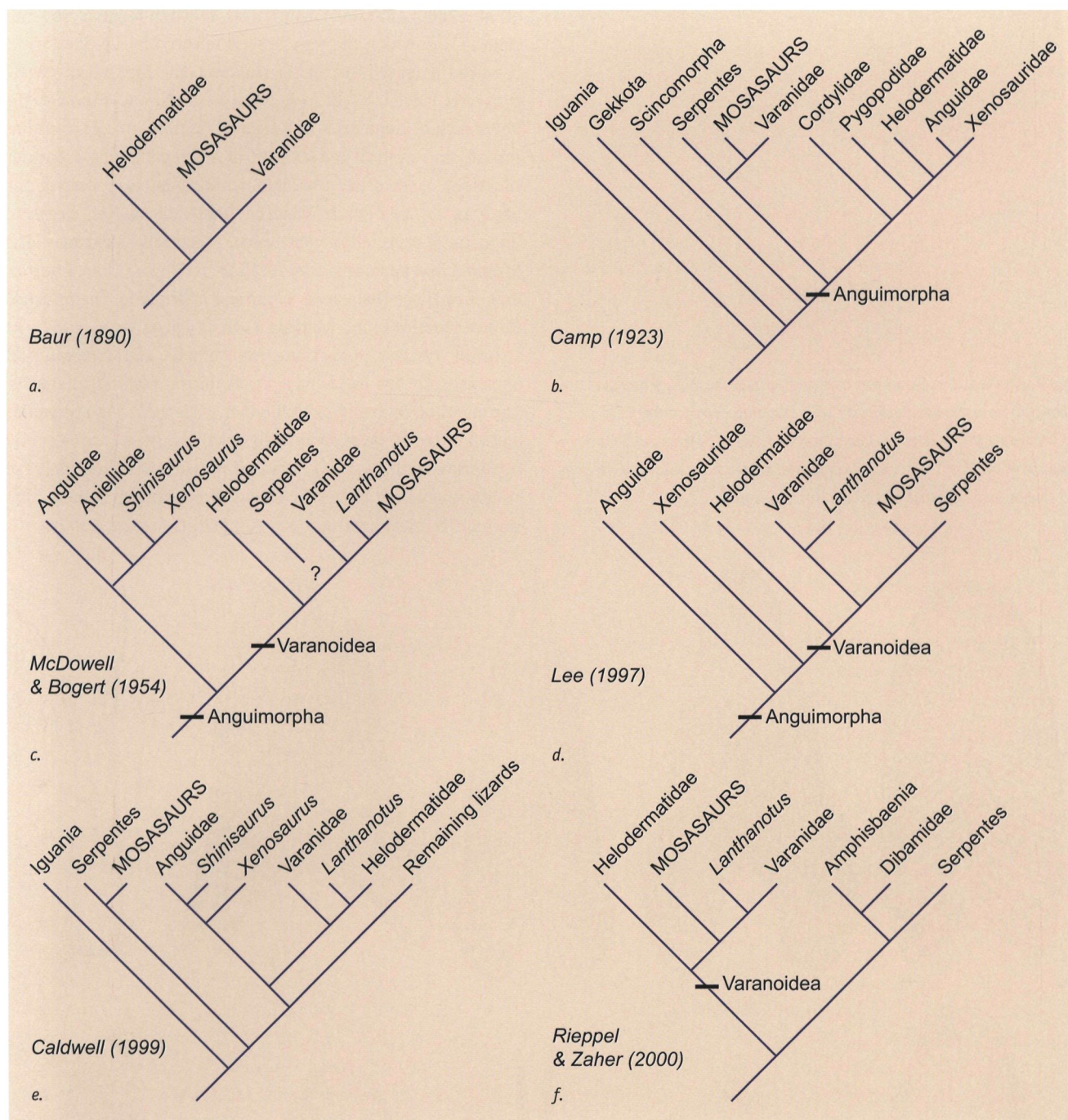
Fig. 3. Published phylogenetic hypotheses of mosasaurid relationships.

it during repeated transport cycles.

Finally, the hindtongue serves to pack the food into the pharynx or directly into the oesophagus for the final stage of feeding. Most squamates have well-developed 'posterior limbs' of the tongue (McDowell, 1972) that extend posteriorly on either side of the larynx to serve this function. Exceptions are snakes, varanids and some teiid lizards, all of which have deeply forked tongues and highly reduced hindtongues that are covered by a lingual sheath (McDowell, 1972). Modifications of the tongue in these taxa are related to chemosensory function (below). In these and other scleroglossans (non-

iguanian squamates), swallowing is accomplished primarily by means of pharyngeal compression, often associated with neck-bending. Having short necks, iguanians rarely employ pharyngeal compression during swallowing (Schwenk, 2000).

In varanid lizards, derived modifications of the tongue for chemoreception have reduced its role in feeding. As in other scleroglossan lizards, the jaws are the organs of prey prehension rather than the tongue. Loss of papillae and extreme narrowing of its entire length have also rendered the tongue virtually useless for hyolingual transport (although while feeding on unusually large prey, the tongue may become involved; Elias
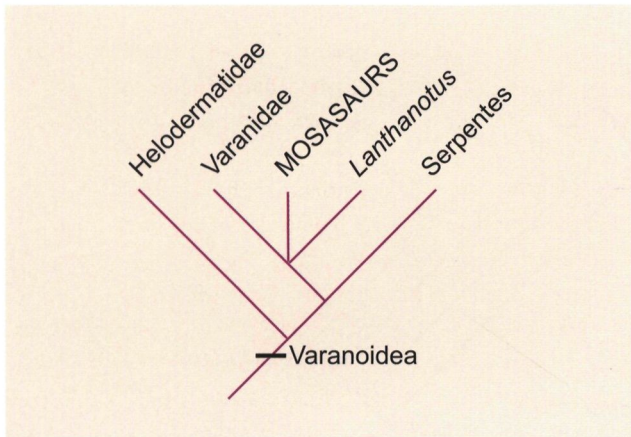
Fig. 4. *Our working hypothesis of mosasaur relationships. Mosasaurs are shown in an unresolved polytomy with Varanidae and* Lanthanotus. *It is also possible that mosasaurs branch more basally between Helodermatidae and the Varanidae/*Lanthanotus *clade, but we doubt its sister-relationship to snakes, as suggested by Lee and his colleagues.*

et al., 2000). Varanids substitute 'inertial feeding' for this function, in which the prey item is released by the jaws while the head is moved over it. In this way, the prey's own inertia is used to move it posteriorly towards the throat. However, the hyobranchial apparatus of varanids, unlike snakes, remains robust, and cyclical movements of the hyolingual apparatus function, as in other scleroglossan lizards, to compress the pharynx for swallowing (Smith, 1986). In snakes, however, lingual and especially hyobranchial reduction, is extreme. The hyobranchial apparatus is reduced to little more than a narrow fork of cartilage that serves as the site of origin for the principal tongue muscles (mm. hyoglossus) (e.g., Langebartel, 1968). As a result of this reduction, the tongue and hyobranchial apparatus do not participate at all during feeding in snakes. The marginal jaws and palatal bones (especially the pterygoids and their teeth) have completely taken over the tongue's roles in capture, transport and swallowing, with the final phase of swallowing accomplished by means of pharyngeal compression through cervical bending (e.g., Cundall & Greene, 2000).
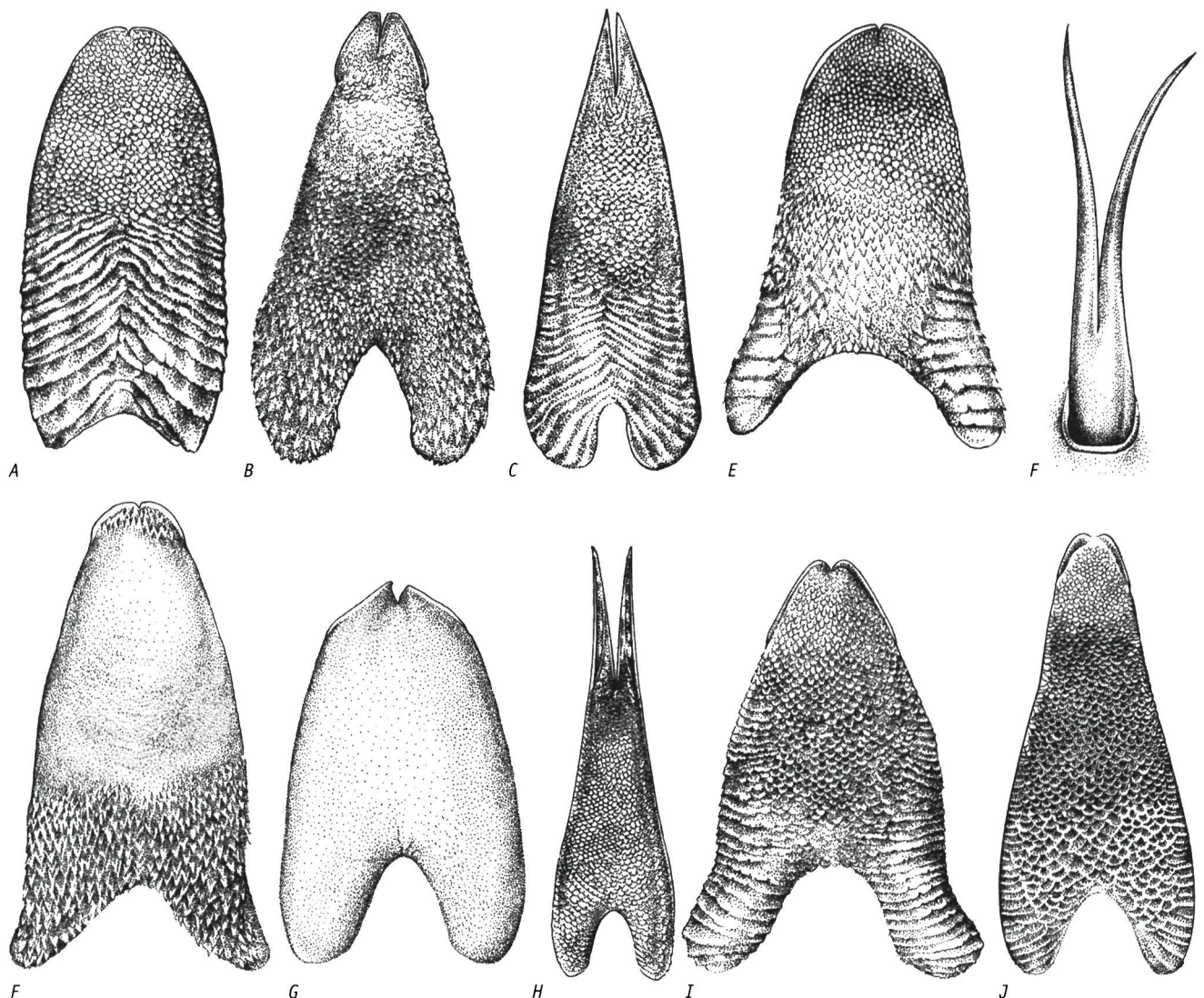

Fig. 5. *Diversity of superficial tongue form in squamate reptiles showing extreme variation in the extent of the bifurcated tongue tip (from Schwenk, 1995).*

Tongue function in living squamates – chemoreception

The squamate tongue participates in chemical reception in two ways: directly through gustation mediated by lingual taste buds (Schwenk, 1985) and indirectly as an organ of chemical retrieval and delivery for the vomeronasal (Jacobson's) organs (Halpern, 1992). We can disregard gustation here because the presence or absence of taste buds has no apparent affect on tongue form. In general, tongues more highly specialised for vomeronasal function have fewer taste buds, probably because of increasing keratinization of the tongue's epithelial surface (Schwenk, 1985).

The presence of well-developed vomeronasal organs (VNO) is a shared derived feature of all squamates, as is a direct connection between these and the oral cavity through the vomeronasal fenestrae, the absence of a connection between the VNO and the nasal cavities, the presence of a bifurcated tongue tip, and the behaviour of tongue-flicking (Schwenk, 1988, 1993). In varanoids, the vomeronasal fenestrae penetrate the palate anteriorly through paired openings in or adjacent to the vomers (Fig. 6).

'Vomerolfaction' is a nasal chemical sense evolutionarily and developmentally related to nasal olfaction, yet anatomically and functionally distinct (Halpern, 1992). The tongue serves vomerolfaction indirectly by retrieving chemicals from the environment on the tongue tips and delivering these into the mouth where they are transported to the vomeronasal fenestrae and drawn into the lumina of the VNO. The chemical retrieval process is mediated by 'tongue-flicking', a behaviour during which the tongue is extended from the mouth and oscillated from one to many times. The tongue tips usually contact the substrate, but often sample only the air, hence tongue-flicking serves to retrieve both non-volatile chemicals present on surfaces and volatiles present in the air. The chemicals sampled by the

vomeronasal system most often relate to sexual and reproductive behaviour, but prey and predator scents are also important for many species, as well as semiochemicals involved in kin recognition, territorial behaviour, dominance behaviour, etc. (e.g., Schwenk, 1995).

Tongue-flicking involves primarily the anterior part of the tongue. The mechanism of tongue protrusion during flicking is different from that used during lingual feeding and the design requirements for a tongue optimised for one function are in direct conflict with those for a tongue optimised for the other (Wagner & Schwenk, 2000; Schwenk & Wagner, 2001). For reasons discussed in the cited references, a tongue specialised for chemoreception should be long, narrow, smooth and deeply cleft, whereas a tongue specialised for feeding should be blunt, wide, papillose and no more than notched. Therefore, specialisation of the foretongue for chemoreception in the scleroglossan clade of lizards was only possible after lingual prehension of prey was no longer necessary owing to the acquisition of jaw prehension in scleroglossan ancestors (Schwenk, 1993, 2000; Wagner & Schwenk, 2000; Schwenk & Wagner, 2001).

Truly forked tongues (i.e., very deeply cleft with the tongue tips formed into long, narrow tines) evolved at least twice and probably three or four times independently within squamates (Schwenk, 1994). A forked tongue allows separation of the tips so that two *separate* points can be sampled for environmental chemicals simultaneously (Schwenk, 1994). As long as the chemical samples from the tips remain separate as they are delivered to ipsilateral VNOs, the central nervous system can assess the relative strength of the signal on each side and determine, with a single tongue-flick, the side on which the signal is strongest. Thus tongue-forking adds a spatial or directional component to odour detection analogous to stereoscopy with paired eyes or sound location with paired
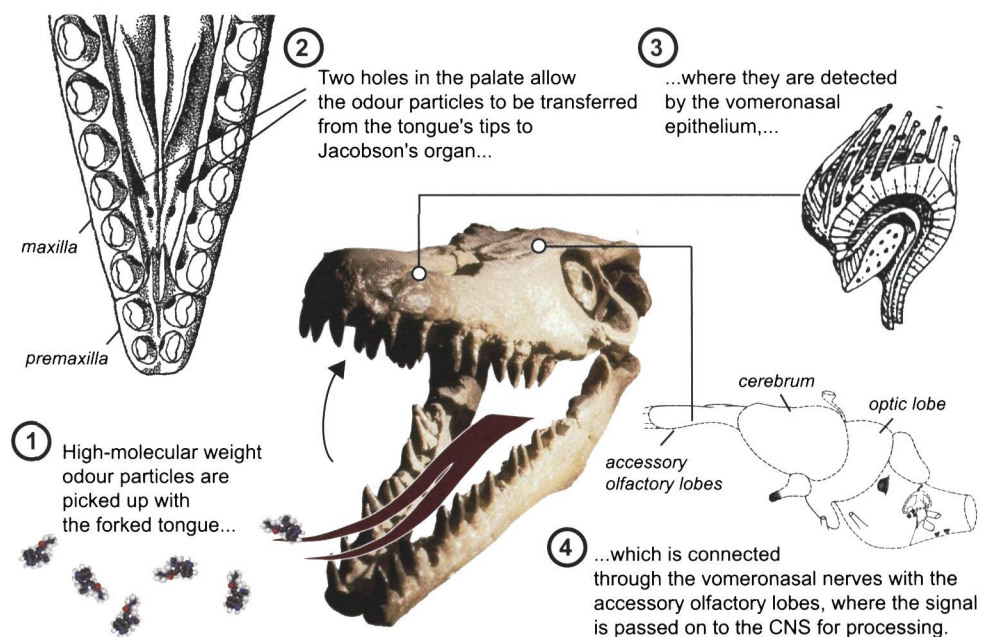
Fig. 6. Vomeronasal chemoreception in squamate reptiles as postulated for mosasaurs (2) from Russell (1967: p. 151); (4) modified after Camp (1942: p. 43).

2 Two holes in the palate allow the odour particles to be transferred from the tongue's tips to Jacobson's organ...

3 ...where they are detected by the vomeronasal epithelium,...

maxilla

premaxilla

1 High-molecular weight odour particles are picked up with the forked tongue...

cerebrum

optic lobe

accessory olfactory lobes

4 ...which is connected through the vomeronasal nerves with the accessory olfactory lobes, where the signal is passed on to the CNS for processing.

ears. The system is especially important for detecting the edges of chemical trails left by conspecifics and prey species, but it has been shown to work for air-borne (and one might assume, water-borne) chemical cues, as well. Although this mechanistic explanation for *forked* tongue function is strongly supported, the functional significance of notched or slightly cleft tongues remains poorly understood (Schwenk, 1994). As such, the origin of a notched tongue tip in ancestral squamates, as retained in living iguanians, cannot be explained by the directionality/edge detection hypothesis. Nevertheless, once the tongue tips reach a certain threshold length (probably as in most anguimorphan lizards, for example), it is likely that signal separation is sufficient to provide some directional information, leading to selection optimising this function and increasing fork length. The fork length at which this happens will depend on the nature of the environment, the nature of the chemical cue, and the steepness of the chemical gradient that is being sensed.

The extent to which the remainder of the tongue participates in food transport and swallowing is related to the extent to which it has been modified for chemoreception. In scincomorph squamates, for example, the entire tongue is modified to a greater or lesser extent for chemosensory protrusion. The papillae are smooth and flat along the entire length of the tongue, the entire tongue is often relatively narrow, the hindtongue and posterior limbs of the tongue are reduced and the tongue tip is, in most cases, deeply cleft or even forked. However, the mid- and hindtongue remain robust enough to support and manipulate food during transport and swallowing. Anguimorphans took a different approach to resolving the contest between chemosensory and feeding function. In this group the tongue has a unique 'diploglossan' (bipartite) form in which the foretongue is functionally and anatomically distinct from the hindtongue (McDowell & Bogert, 1954; McDowell, 1972; Schwenk, 1988, 2000) (Fig. 7). The foretongue is narrow, cleft or forked, devoid of glands and covered with smooth, flat papillae or none at all. The hindtongue, in contrast, retains the ancestral condition of being robust, with well-developed posterior limbs and long, glandular papillae. The foretongue is highly extensible and capable of movement independent of the hindtongue and hyobranchial apparatus, whereas movements of the hindtongue remain coupled to the hyobranchium (Schwenk, 2000). Thus, in anguimorphans the foretongue is specialised for chemosensory protrusion and tongue-flicking, whereas the hindtongue retains its plesiomorphic functions in food transport and swallowing.

Feeding and chemoreception in mosasaurs

Obviously we can only speculate about the role of the tongue during feeding and chemoreception in mosasaurs given that there are so few pieces of direct evidence revealed by fossils. However, some reasonable inferences can be made.
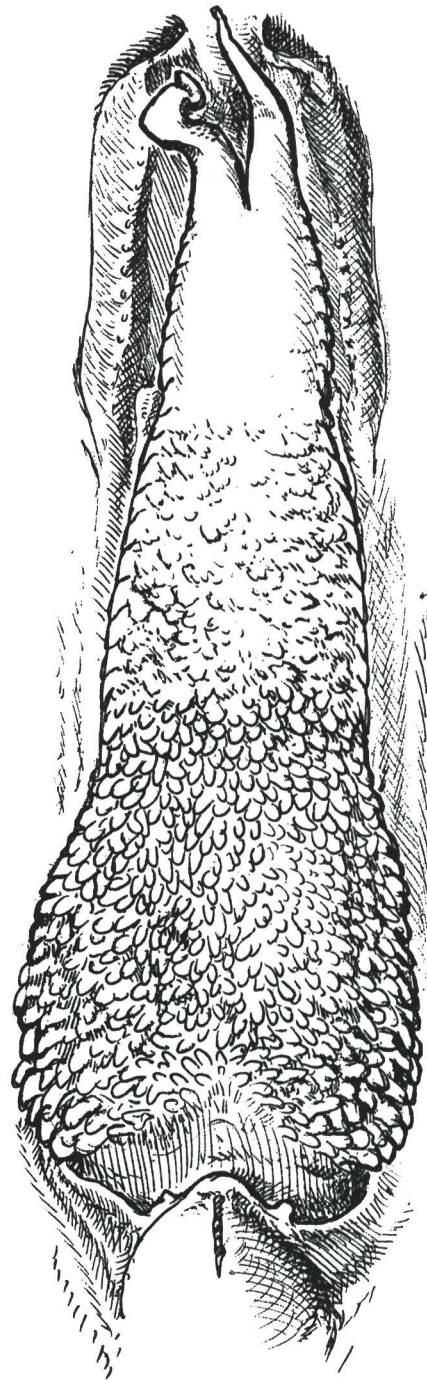

Fig. 7. Tongue form in Lanthanotus borneensis *(the Bornean earless monitor), our proposed structural model for the mosasaur tongue (from McDowell, 1972).*

First, there is little doubt that mosasaurs used the jaws and not the tongue for prehension of food. This is typical of all non-iguanian lizards. Further evidence for jaw prehension comes from the shape of the jaws, the teeth and the presence of an intramandibular joint (e.g., Rieppel & Zaher, 2000b), all of which are consistent with the kind of pincer-like jaw prehension of animal prey used by living monitor lizards (Schwenk, 2000).

All mosasaurs are likely to have had mobile quadrates (streptostyly), but only basal species had kinetic skulls (reviewed by Rieppel & Zaher, 2001). Mobility of the upper jaw is consistent with, but not an essential part of jaw prehension in scleroglossan lizards, including varanoids (Schwenk, 2000). The larger, more derived mosasaurs appear to have reduced or lost upper jaw mobility (Rieppel & Zaher, 2001), possibly because of their size. Loss of functional kinesis is typical of very large monitor lizards, as well, owing to hyperossification (KS, personal observation). Streptostyly is a universal squamate trait, hence its presence in a fossil is uninformative about feeding mode (*contra* Lingham-Soliar, 1995, who inferred the presence of 'ratchet feeding' based on this trait).

Related to the question of cranial kinesis in mosasaurs is the presence of an intramandibular joint and the absence of a mandibular symphysis (Lee et al., 1999; Rieppel & Zaher, 2000b, 2001). These traits suggest that each ramus of the lower jaw was capable of flexing outward and/or twisting along its axis. It is also possible that the mandibular rami actually separated to some extent, as in most snakes. These traits imply the ability to increase gape, permitting the passage of relatively large prey items, i.e., macrophagy (Lee et al., 1999; Rieppel & Zaher, 2001). Lee et al. (1999) also argued that the presence of large, recurved pterygoid teeth suggested macrophagy. However, Rieppel & Zaher (2001) considered that such teeth are only characteristic of large, derived mosasaurids, whereas those basal mosasaurs and related taxa that are known for this trait have relatively smaller pterygoid teeth.

A wealth of evidence is available on mosasaur dietary preferences (e.g. Kauffman & Kesling, 1960; Russell, 1967; Martin & Bjork, 1987; Massare, 1987; Martin et al., 1998; Stewart & Carpenter, 1990; Everhart, 2004; Martin & Fox, 2004; Kauffman, 2004; Schulp, 2005). However, the question of mosasaur macrophagy (or diet in general) may, in any case, be mostly irrelevant to our reconstruction of the tongue. With minor exceptions, tongue form in squamates is unrelated to diet (Schwenk, 1988; Wagner & Schwenk, 2000), although the more highly chemosensory scleroglossans are generally able to avoid noxious prey (Vitt et al., 2003). Tongue morphology is relatively uniform within families and even larger clades of squamates that display extreme variation in diet. It is worth noting, however, that the fork-tongued snakes and varanid lizards are entirely (snakes) or almost entirely (varanids) carnivorous, but within the limits of 'carnivory', both groups are exceptionally diverse in diet (e.g., Losos & Greene, 1988; Greene, 1997). The aspects of natural history that influence tongue form most fundamentally are not *what* is eaten (diet), but *how* (tongue-prehension vs. jaw-prehension vs. suction) and *where* it is eaten (water vs. land).

With regard to where mosasaurs ate, their full commitment to aquatic life raises an important question: did they use a jaw/hyolingual-based feeding system or did they secondarily evolve suction feeding, as suggested for at least one ancient marine reptile (Li et al., 2004)? The question is not trivial because many secondarily aquatic tetrapods have reverted to suction feeding and the tongues in these taxa are typically reduced, simplified, or even lost (Bramble & Wake, 1985; Schwenk & Rubega, 2005). In contrast, the hyobranchial apparatus in suction feeders is typically more robust and heavily ossified than in their terrestrial-feeding relatives owing to its role in generating rapid pharyngeal expansion. There is currently no evidence that mosasaurs had a robust hyobranchium or any other morphological feature associated with suction feeding (e.g., vaulted palate, small gape; Bramble & Wake, 1985), therefore it is unlikely that mosasaurs employed suction feeding.

All living aquatic reptiles, including squamates, use jaw-prehension of food followed by either inertial or hyolingual transport and swallowing. In these cases jaw-prehension may simply reflect retention of the ancestral feeding mode, but it is also true that lingual prehension under water is unlikely to be effective because it depends primarily on wet adhesion created by formation of a meniscus at the tongue-prey interface (which, additionally, only works well in relatively small animals). More relevant, perhaps, is the question of transport mechanics. Crocodilians snatch food within the water or at the surface, but then raise the head above the water to use inertial transport on relatively small prey items. Large prey items are dragged into the water and rent into smaller pieces which are then bolted inertially above the water (Cleuren & de Vree, 2000; Schwenk & Rubega, 2005). Semi-aquatic turtles also tend to capture food in or on the water, but then raise it above the surface for inertial or hyolingual transport. The same is true of lizards that capture food under water (with the possible exception of marine iguanas in which the mechanics of aquatic grazing on marine algae are unknown). In both crocodilians and highly aquatic turtles, the tongue is reduced and simplified, and not capable of participating in hyolingual transport. It is possible that transport and swallowing food under water, though mechanically feasible, might result in the involuntary consumption of excessive water that in marine environments, particularly, would have a deleterious effect on water and salt balance. Crocodilians circumvent this problem to some extent by forming a seal between the back of the tongue and the palate at the entrance to the pharynx. Although this permits them to capture and manipulate food under water, they must open the seal to swallow, hence they rise to the surface (some fishes have oesophageal valves, presumably for the same reason; Schwenk & Rubega, 2005). Fully aquatic turtles, however, feed entirely underwater, as do marine snakes. The former are suction feeders, like most fish, and tend to expel most of the captured water before swallowing prey, whereas the latter are unusual among advanced snakes in having relatively small mouths that restrict prey size. This might help to mitigate the problem of ingesting too much water.

With regard to vomeronasal chemoreception in mosasaurs, the presence of paired fenestrae in the palate associated with the vomers (e.g. Russell, 1967: p. 25, text-fig. 84), anterior to and separate from the choanae (internal nostrils providing passageways from the nose to the throat), is typical of varanoid lizards and snakes (Bellairs & Boyd, 1949), and positively indicative of VNOs and vomerolfaction. As noted, the presence of VNOs with openings to the mouth is a squamate synapomorphy and is correlated with tongue-flicking behaviour for chemical retrieval. In addition, the fairly detailed reconstruction of the mosasaur brain by Russell (1967, text-fig. 16) shows a well-developed accessory olfactory lobe (the part of the brain associated with afferents from the VNO). There is, therefore, strong evidence that mosasaurs used tongue-flicking and the VNO in life – probably in much the same way that living squamates do during foraging and courtship. Vomeronasal organs, tongue-flicking and a VNO-oral connection are also correlated in squamates with a bifurcated tongue tip. However, as noted previously, the degree of this bifurcation ranges from a simple notch (e.g., Iguania, Gekkota) to a deep fork (e.g., varanids, snakes, teiids and amphisbaenians). Nevertheless, the presence of vomeronasal fenestrae isolated from the choanae is associated in varanoids with a derived, highly sensitive tongue-vomeronasal system including a forked, or at least, deeply cleft tongue tip. Camp (1923, p. 325) also mentions the presence of 'lingual furrows in the prevomerine bones' of mosasaurs as part of his evidence that they are varanoids. Such furrows may not be general to all mosasaurs or even all varanoids, but their presence suggests a highly protrusible, narrow foretongue.

Finally, it is true that aquatic mammals have reduced or lost their VNO, as have crocodilians, and it is often assumed that life in water necessarily leads to a reduction in this chemical sense. However, aquatic squamates, notably snakes, do *not* tend to lose or reduce the VNO. Indeed, pelagic marine snakes (Hydrophiidae) have been described tongue-flicking while foraging and courting underwater (e.g., Heatwole, 1999; Shine et al., 2003, 2004; R. Shine, pers. comm.). Indeed, the forked tongue of some aquatic snakes (e.g., the freshwater species of *Achrochordus*) has unusually long tines (KS, pers. obs.), which might relate to the mechanics of chemical retrieval underwater. As such, there is no reason to suppose, as Dollo (1909) did, that mosasaurs' commitment to an aquatic habitat would have led to a reduction or loss of vomerolfaction and tongue-flicking. In fact, the available evidence suggests the opposite. A keen chemical sense might have been especially important to mosasaurs navigating the thick sea grass vegetation of the 'Maastricht Sea' (Mulder, 2003: pp. 99, 165).

A reconstruction of the mosasaur tongue

A first step in reconstructing the mosasaur tongue is to establish the 'extant phylogenetic bracket' (Witmer, 1995). The condition of the tongue in the closest, living relatives of mosasaurs can provide evidence for tongue form in mosasaurs under the assumption of parsimony. Parsimony is a reasonable assumption in this case because it has been shown that tongue form is not especially labile in squamate evolution, tending to remain stable at the family level and deeper (Schwenk, 1988). If, for example, mosasaurs were known to be nested between the extant clades of snakes and monitor lizards, parsimony would dictate that mosasaurs shared whatever traits these living taxa have in common, notably a slender, forked tongue retractile into a tongue sheath. However, only two studies that have included both living squamates and mosasaurs have suggested this relationship (Camp, 1923; Lee & Caldwell, 2000) (Fig. 3). Nonetheless, such a finding does not unambiguously support a snake or varanid-like tongue in mosasaurs because of the intervening position of *Lanthanotus*. Lee & Caldwell (2000) suggest that mosasaurs are the sister group of snakes and that together they comprise the sister group to a clade consisting of varanids and the Bornean earless monitor, *Lanthanotus*. Although both snakes and varanids have slender, forked tongues with a tongue sheath, in *Lanthanotus* the tongue tip is deeply cleft, but not nearly as forked as in snakes and varanids, and only the foretongue is slender and protrusible. The hindtongue remains robust with well-developed papillae and posterior limbs (McDowell, 1972; Schwenk, 1988 and unpublished data) (Fig. 7). Thus, under Lee & Caldwell's (2000) phylogenetic hypothesis, tongue form in the ancestor of varanids and *Lanthanotus* is equivocal and we cannot reconstruct the mosasaur tongue as snake/varanid-like with any confidence.

Other phylogenetic hypotheses (Fig. 3) are even more problematic. If mosasaurs are the sister group of either snakes or varanids, as suggested by various workers, in most phylogenies other groups with very different tongue types intervene between them, making the reconstruction of a slender, forked tongue once again problematic. Furthermore, virtually every study that has considered squamate relationships finds *Lanthanotus* to be more closely related to varanids than snakes are (indeed, *Lanthanotus* is often included within the family Varanidae), as described above. Thus, the phylogenetic evidence suggests that varanids and snakes evolved their forked tongues independently, an example of parallel evolution from a shared, diploglossan ancestor. Independent evolution of the forked tongue in snakes and monitor lizards is further supported by marked histological differences in the arrangement of the tongue musculature (Smith & MacKay, 1990; Schwenk, 1988), the ultrastructure of the tongue's epithelial surface (N. Filoramo and Schwenk, unpublished data) and the form of the hyobranchial apparatus (Langebartel, 1968; Rieppel, 1981).

To the extent that phylogenetic evidence supports anguimorphan affinities for mosasaurs, we can restrict the field of possible reconstructions to a diploglossan tongue form. Phylogenetic bracketing does not, however, support

reconstructing the mosasaur tongue as highly derived and snake-like. Rather, varanoid lizards are more likely to serve as appropriate models. Consideration of mosasaur feeding and chemoreception, based on fossil evidence and comparison to extant taxa, is also consistent with these hypotheses.

In conclusion, under the assumption that mosasaurs are varanoids, we suggest that they had a diploglossan tongue form, but one that was only modestly derived compared to monitor lizards and snakes. The form of the tongue would probably have been most like modern *Heloderma* or *Lanthanotus* (Figs. 7, 8) with a derived, chemosensory foretongue and a plesiomorphic, papillose hindtongue. Such a tongue is consistent with well-developed vomeronasal chemoreception through tongue-flicking while retaining the ancestral function of hyolingual food transport and swallowing following jaw-prehension of prey. Hyolingual transport in mosasaurs is further supported by the presence of pterygoid teeth, which would have functioned to hold prey in place while the tongue was protracted underneath it in preparation for the next transport cycle (particularly important for slippery prey such as fish). Hyolingual transport (or inertial transport) and swallowing would have been most effective above water, hence it is likely that mosasaurs carried whatever they captured up to the surface before swallowing. The degree of tongue-forking is difficult to reconstruct with confidence, however the tongue

tip is likely to have been at least as forked as modern *Heloderma* or *Lanthanotus*, to enhance the mechanics of chemical retrieval under water (as may be the case with some living, aquatic snakes). Thus the tongue would have been forked to a degree, but probably not to the extent seen in modern snakes and varanid lizards. During a tongue-flick, the protruded part of the tongue would have appeared relatively slender because of the independent, extensile nature of the foretongue, but the broad, fleshy base of the tongue would have remained within the mouth (as in modern varanoid lizards). Thus, tongue-flicking in *Lanthanotus* or *Heloderma* (Fig. 8) might provide the best living analogue for reconstruction of dynamic tongue form in mosasaurs.

Acknowledgements

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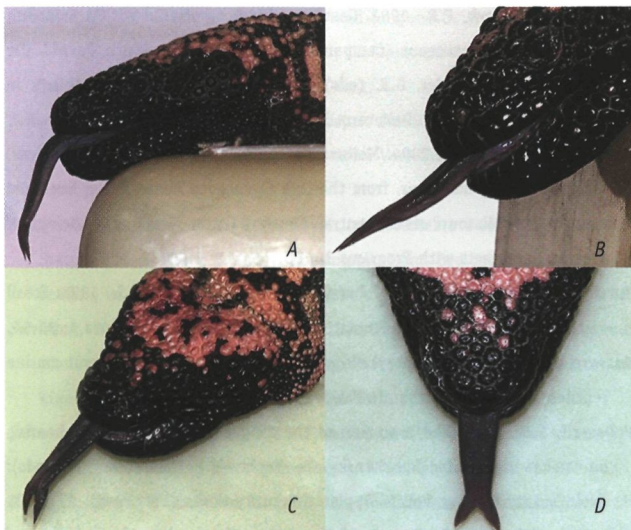
Fig. 8. Tongue-flicking in Gila monsters, Heloderma suspectum, *may provide a model for how the tongue would appear during similar behaviour in a mosasaur. Each panel captures the tongue in the midst of a tongue-flick. (C) and (D) show the extent of the forked tip and active separation of the tines during chemical sampling. Only the elongated front portion of the diploglossan tongue is visible during a tongue flick because only the foretongue is mechanically capable of extension and protrusion. Owing to the hydrostatic mechanism of protrusion, the foretongue becomes relatively long and narrow during tongue-flicking – very different from its resting form – but not so slender and deeply forked as in a snake or monitor lizard.*

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