Skin of the Cretaceous mosasaur *Plotosaurus*: implications for aquatic adaptations in giant marine reptiles

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The physical nature of water and the environment it presents to an organism have long been recognized as important constraints on aquatic adaptation and evolution. Little is known about the dermal cover of mosasauroids (a group of secondarily aquatic reptiles that occupied a wide array of predatory niches in the Cretaceous marine ecosystems 92–65 Myr ago), a lack of information that has hindered inferences about the nature and level of their aquatic adaptations. A newly discovered *Plotosaurus* skeleton with integument preserved in three dimensions represents not only the first documented squamation in a mosasaurine mosasaur but also the first record of skin in an advanced member of the Mosasauroidae. The dermal cover comprises keeled and possibly osteoderm-reinforced scales that presumably contributed to an anterior–posterior channelling of the water flow and a reduction of microturbulent burst activities along the surface of the skin. Thus, hydrodynamic requirements of life in the water might have influenced the evolution of multiple-keeled body scales in advanced mosasauroids.

Keywords: mosasaur; integument; collagen; keratin; aquatic adaptation; Cretaceous

1. INTRODUCTION

The extinct squamate superfamily Mosasauroidae comprises a hugely successful radiation of aquatic lizards, which originated, diversified and eventually vanished within the last 27 Myr of the Cretaceous (Russell 1967). The squamation of mosasauroids is seldom preserved in the fossil record. The result is that we have a limited understanding of how their skin transformed as they evolved from landlubbers to leviathans. The published record on mosasauroids with fossilized integument is restricted to a small number of basal forms with terrestrial-type limbs, informally referred to as aigialosaurs (e.g. Smith & Buchy 2008), and the moderately derived *Tylosaurus* (Snow 1878; Everhart 2005), where the skin is preserved either as shallow impressions or as

a mineralized film. The only other published reports detailing the squamation of an extinct marine squamate allied to mosasauroids are those of Caldwell & Dal Sasso (2004) and Caldwell (2006) who described the superbly preserved integument of the pontosaur *Pontosaurus kornhuberi*.

Thus, the new discovery of an advanced mosasaurine with patches of three-dimensionally preserved integument provides important insights into the skin architecture of advanced Mosasauroidae, as well as an opportunity to increase our understanding of the morphological adaptations that enabled mosasaurs to flourish during the latter part of the Cretaceous.

2. SYSTEMATIC PALAEONTOLOGY

Squamata Oppel 1811; Mosasauroidae Camp 1923; Mosasauridae Gervais 1853; Mosasaurinae Gervais 1853; *Plotosaurus* Camp 1951.

Plotosaurus bennisoni (Camp 1942).

3. DESCRIPTION

(a) Skeleton

The specimen we describe and illustrate (University of California Museum of Paleontology no. 152664) was collected in 1993 by one of us (A.R.F.) from the Tierra Loma Shale of the Moreno Formation in central California, and consists of an incomplete mosasaur skeleton with an estimated original length of approximately 6.4 m. The preservation of the bones is variable, and some elements are incomplete, plastically deformed and gypsum-impregnated, whereas others are in a reasonable condition and do not appear to have undergone significant diagenetic distortion. Even though no skull was located, the fossil can be confidently assigned to *P. bennisoni* on the basis of the stout proportions of the epipodial elements and distinctly hour-glass-shaped phalanges (see Lindgren *et al.* 2008).

(b) Squamation

Associated with the collection of bones are pieces of shale preserving articulated portions of integument originating from the body of the animal. The squamation comprises rhomboidal scales that are obliquely arrayed into an alternating pattern where neighbouring scales overlap one another (figure 1a–c). The scales are uniform in size, measuring approximately 2.2×2.2 mm. Some scales are preserved as multilayered organic films forming thin bedding-parallel surfaces, whereas others are represented by impressions with definite edges, or as a sulphurous coating that resolves itself into a regular network.

One portion of integument reveals details of the three-dimensional skin architecture (figure 1b). On this slab, the scales are cut tangentially some distance from the outer surface, exposing deeper structures of the skin. Moreover, as a consequence of uneven fracturing, the cross sections are located at multiple levels, providing an opportunity to reconstruct the three-dimensional shape of the scales. Accordingly, from comparisons of several scales, it is concluded that each scale was originally gently vaulted but with an acutely medially angled posterolateral margin. Sculpturing, in the form of a central keel, and, presumably also, a low ridge on either side of the

Figure 1. (a–c) Integument of the derived mosasaur *Plotosaurus* (UCMP 152664) preserved as multilayered organic films. Note the small size of scales (presumably an adaptation for improved hydrodynamic efficiency). (c,d) Comparison between (c) body scales of *Plotosaurus* and (d) abdominal scales of the extant Pygmy spiny-tailed skink *Egernia depressa* (Museum of Zoology, Lund University no. L897/3155). Note the presence of dark-coloured organic matter beneath the semi-translucent scales of *Plotosaurus* and extension of thin, plate-like osteoderms subjacent to the scales in the Pygmy spiny-tailed skink. Scale bars, (a) 1 cm, (b) 5 mm and (c,d) 2 mm.

Figure 2. Secondary electron images of body scales of *Plotosaurus* (UCMP 152664). (a) Isolated scale viewed from the inside to reveal microstructures on and beneath the inner scale surface. (b) Same photograph as in (a) with additional line drawings for clarity. Note the presence of longitudinal ridges and minute creases with a predominantly radial orientation along the scale margin (in modern squamates, raised structures on the inner scale surface do not always correspond to external surface features). (c) Marginal creases from another scale than the one depicted in (a,b) (see main text for interpretation). (d) Demarcated area in (b) showing presumed fibre layers (in tangential view) from the epidermis or superficial dermis running in opposite directions (arrows). Scale bars, (a) 1 mm and (c,d) 100 μ m.

central keel divide the external surface into parallel rows of raised structures separated by longitudinal grooves. The bright coloration in the region of the central keels in figure 1b originates from exposed underlying matrix. This suggests that the central keel had a higher relief than the other parts of the scale, rendering it more susceptible to abrasion.

Another slab preserves flattened scales that seemingly lack any type of surface ornamentations (figure 1a,c). This may be an artefact of preservation, or, alternatively, the scales may originate from the ventral face of the body (assuming that mosasaurs,

similar to many extant squamates, had smooth scales on their lower surface). The scales are semi-translucent, revealing underlying organic matter (figure 1c). A similar configuration is found in modern lizards possessing thin dermal ossifications (osteoderms) subjacent to the scales (figure 1d).

Under a scanning electron microscope, the scales appear to contain fibrous structures (figure 2d). The fibre-like entities run in opposing directions and may represent the carbonized remains of keratins from the epidermis or collagen bundles from the subjacent dermis (Videler 1993; Lingham-Soliar 2008).

Moreover, tiny creases with a predominantly radial orientation are seen near the antero–posterior apices of some fractured scales and also on a few imprints (figure 2a–c). The identity of these radial structures is unknown, although it is possible that they represent imbrication scars, sediment-filled capillaries from within the outer layers of the dermis or attachment sites for fibrous mucus located at the hinge region between succeeding scales.

Energy dispersive X-ray analysis showed that carbon and phosphorus predominate in the scales, although smaller amounts of iron and sulphur suggest a partial replacement of the organic content with pyrite.

4. SQUAMATION AND AQUATIC ADAPTATIONS IN MOSASAURS

Apparently, all mosasaurs, similar to other reptiles, had a skin covered in scales. Recently, Everhart (2005) suggested that certain advanced forms might have been smooth-skinned to better cope with the hydrodynamic constraints imposed by the surrounding water. However, judging from the preserved integument in UCMP 152664, and our observations of scalation in a number of other mosasaurs, including species of *Platycarpus*, *Ectenosaurus* and *Tylosaurus*, we consider it highly unlikely that there were any scale-less mosasaurs. On the contrary, small-sized, multiple-keeled and possibly osteoderm-reinforced scales might have served multiple functions, not only by means of protection from rivals, predators and ectoparasites, but also as an efficient cover to reduce frictional drag when swimming. By comparison to modern sharks (Raschi & Tabit 1992), a longitudinal ridge and valley topography might have reduced microturbulent burst activities within the boundary layer of the water thereby impeding an energetically expensive separation by this layer from the skin of the mosasaur (see Walker & Liem 1994 for drag reduction in extant animals). Moreover, because keeled scales reduce shininess (Klauber 1997), these rugosities may have provided a dull and non-reflective appearance, thus facilitating concealment during predation.

There are many elaborate features in the axial and appendicular skeleton of *Plotosaurus* that are readily recognizable as adaptations toward an obligate pelagic life (Lindgren et al. 2007, 2008). Based on gross anatomy, vertebral centrum morphometrics and process orientation, Lindgren et al. (2007) concluded that *Plotosaurus*, facing the same hydrodynamic constraints and probably similar selection pressures as both the earlier ichthyosaurs and later whales, had achieved a streamlined body form for optimized axial-undulatory locomotion. A high level of aquatic adaptation is further corroborated by the presence of longitudinally arranged rows of keels on, at least, the dorsal surface of the animal, resulting in an anterior–posterior channelling of the water flow and more energy-efficient forward motions. A similar concentration of keeled scales is present on the dorsal surface of *P. kornhuberi* (Caldwell & Dal Sasso 2004; Caldwell 2006), and in modern sea snakes and sea kraits. In a paper describing the pelvis and tail of a

basal mosasauroid, Smith & Buchy (2008) noted that whereas derived mosasaurs have keeled body scales, aigialosaur-grade forms do not (although keel-less scales, in fact scales of any kind, are only known from the belly region of one taxon, *Carsosaurus marchesetti*; Gorjanović-Kramberger's (1892) assertion of the presence of scales in *Aigialosaurus dalmaticus* was not confirmed by Dutchak & Caldwell (2006) and is refuted here).

If Smith & Buchy (2008) are correct, then the problem is an intriguing one because keeled body scales are supposedly ancestral for Anguimorpha (Gauthier 1982), including, by extension, mosasaurs (although admittedly, single-keeled scales appear and disappear across many groups of living squamates). However, as scales cannot be verified in *A. dalmaticus*, and only a small patch of abdominal or ventral scales are preserved in *C. marchesetti*, it is impossible to confirm Smith & Buchy's (2008) hypothesis. The presence of keeled scales in *P. kornhuberi* (preserved along the hypaxial margin of the tail, above the ventral 'belly' scale row) suggests that within the clade Pythonomorpha, as reconstructed by Lee & Caldwell (2000), single-keeled scales may be the plesiomorphic condition. Still, the possibility that such a feature might arise convergently within mosasauroids finds strong support from the presence of multiple parallel keels that are structurally similar to the longitudinal ridges on the crown surface of the dermal denticles in pelagic sharks (see Raschi & Tabit 1992). We therefore see no reason to reject the idea that the constraints imposed by the hydrodynamic requirements of life in the water might have influenced the evolution of multiple-keeled body scales in advanced mosasauroids, such as *Plotosaurus*.

Access to UCMP 152664 was graciously provided by Patricia A. Holroyd and Mark B. Goodwin. Thanks to Lars Lundqvist (MZLU) for allowing examination of modern squamates in his custody. The comments of three anonymous reviewers greatly improved the final manuscript. This research was funded by the Swedish Research Council (award no. 623-2005-3611).

- Caldwell, M. W. 2006 A new species of *Pontosaurus* (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a phylogenetic analysis of Pythonomorpha. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **34**, 1–42.
- Caldwell, M. W. & Dal Sasso, C. 2004 Soft-tissue preservation in a 95 million year old marine lizard: form, function, and aquatic adaptation. *J. Vertebr. Paleontol.* **24**, 980–985. (doi:10.1671/0272-4634(2004)024[0980:SPIAMY]2.0.CO;2)
- Camp, C. L. 1923 Classification of the lizards. *Bull. Am. Mus. Nat. Hist.* **48**, 289–481.
- Camp, C. L. 1942 California mosasaurs. *Mem. Univ. Calif.* **13**, 1–68.
- Camp, C. L. 1951 *Plotosaurus*, a new generic name for *Kolposaurus* Camp, preoccupied. *J. Paleontol.* **25**, 822.
- Dutchak, A. R. & Caldwell, M. W. 2006 Redescription of *Aigialosaurus dalmaticus* Kramberger, 1892, a Cenomanian mosasauroid lizard from Hvar Island, Croatia. *Can. J. Earth Sci.* **43**, 1821–1834. (doi:10.1139/E06-086)

- Everhart, M. J. 2005 *Oceans of Kansas: a natural history of the Western Interior Sea*. Bloomington, IN: Indiana University Press.
- Gauthier, J. A. 1982 Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contr. Geol. Univ. Wyoming* **21**, 7–54.
- Gervais, P. 1853 Observations relatives aux reptiles fossiles de France. *Acad. Sci. Paris Compt. Rendus* **36**, 374–377, pp. 470–474.
- Gorjanović-Kramberger, C. 1892 *Aigialosaurus*, eine neue Eidechse aus den Kreideschiefern der Insel Lesina, mit Rücksicht auf die bereits beschriebenen Lacertiden von Comen und Lesina. *Glasnik hrvatskoga naravoslovnoga društva (Societas historico-naturalis croatica) u Zagrebu* **7**, 74–106.
- Klauber, L. M. 1997 *Rattlesnakes: their habits, life histories, and influence on mankind*, 2nd edn. Berkeley, CA: University of California Press.
- Lee, M. S. Y. & Caldwell, M. W. 2000 *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. *ŷ. Paleontol.* **74**, 915–937. (doi:10.1666/0022-3360(2000)074<0915:AATAOM>2.0.CO;2)
- Lindgren, J., Jagt, J. W. M. & Caldwell, M. W. 2007 A fishy mosasaur: the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. *Lethaia* **40**, 153–160.
- Lindgren, J., Caldwell, M. W. & Jagt, J. W. M. 2008 New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). *ŷ. Vertebr. Paleontol.* **28**, 1043–1054. (doi:10.1671/0272-4634-28.4.1043)
- Lingham-Soliar, T. 2008 A unique cross section through the skin of the dinosaur *Psittacosaurus* from China showing a complex fibre architecture. *Proc. R. Soc. B* **275**, 775–780. (doi:10.1098/rspb.2007.1342)
- Oppel, M. 1811 *Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. Munich, Germany: Joseph Lindauer Verlag.
- Raschi, W. & Tabit, C. 1992 Functional aspects of placoid scales: a review and update. *Aust. ŷ. Mar. Freshw. Res.* **43**, 123–147. (doi:10.1071/MF9920123)
- Russell, D. A. 1967 Systematics and morphology of American mosasaurs (Reptilia, Sauria). *Bull. Peabody Mus. Nat. Hist.* **23**, 1–241.
- Smith, K. T. & Buchy, M.-C. 2008 A new aigialosaur (Squamata: Anguimorpha) with soft tissue remains from the Upper Cretaceous of Nuevo León, Mexico. *ŷ. Vertebr. Paleontol.* **28**, 85–94. (doi:10.1671/0272-4634(2008)28[85:ANASAW]2.0.CO;2)
- Snow, F. H. 1878 On the dermal covering of a mosasauroid reptile (*Liodon dyspelor* cope). *Trans. Kansas Acad. Sci.* **6**, 54–58.
- Videler, J. J. 1993 *Fish swimming*. London, UK: Chapman & Hall.
- Walker Jr, W. F. & Liem, K. F. 1994 *Functional anatomy of the vertebrates: an evolutionary perspective*, 2nd edn. Fort Worth, TX: Saunders College Publishing.