

Complex rostral neurovascular system in a giant pliosaur

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Abstract Pliosaurus were a long-lived, ubiquitous group of Mesozoic marine predators attaining large body sizes (up to 12 m). Despite much being known about their ecology and behaviour, the mechanisms they adopted for prey detection have been poorly investigated and represent a mystery to date. Complex neurovascular systems in many vertebrate rostra have evolved for prey detection. However, information on the occurrence of such systems in fossil taxa is extremely limited because of poor preservation potential. The neurovascular complex from the snout of an exceptionally well-preserved pliosaur from the Kimmeridgian (Late Jurassic, c. 170 Myr ago) of Weymouth Bay (Dorset, UK) is described here for the first time. Using computed tomography (CT) scans, the extensive bifurcating neurovascular channels could be traced through the rostrum to both the teeth and the foramina on the dorsal and lateral surface of the snout. The structures on the surface of the skull and the high concentrations of peripheral rami suggest that this could be a sensory system, perhaps similar to crocodile pressure receptors or shark electroreceptors.

Keywords *Pliosaurus* · Neurovascular system · Prey detection · Digital model · CT scans

Introduction

Pliosauridae (Plesiosauria, Sauropterygia) is an ecologically important group of Mesozoic marine predators, with a

large-headed, short-necked body plan and an extensive range of body sizes. This group had a stratigraphic range extending from the Early Jurassic to the early Late Cretaceous (Ketchum and Benson 2010). Many biological and taxonomic aspects of pliosaurs have been investigated (Massare 1987; Halstead 1989; Motani 2002; O’Keefe and Chiappe 2011), but little is known about the internal anatomy of soft tissues because of difficulties in accessing these structures and poor preservation.

To date, no reconstructions of the sauropterygian neurovascular system have been published, and the available literature mainly reports the presence of foramina and sometimes grooves on the external surface of pliosaurian rostra (Sassoon et al. 2012; Taylor and Cruickshank 1993; Benson et al. 2013). The corresponding internal structures have never been deeply investigated.

Material and methods

The specimen, DORCMG 13,675 (Dorset County Museum), is a large pliosaur skull belonging to *Pliosaurus kevani* (Benson et al. 2013) from the Upper Jurassic, Kimmeridge Clay Formation of Osmington Bay (Dorset, UK). After preparation, the cranium and rostrum were subjected to computed tomography (CT) scanning using a custom built Nikon 450 kV micro-focus X-CT system at the ‘ μ -VIS’ Centre for Computed Tomography University of Southampton. Most of this work is based on data from the premaxillae because this section of the fossil gave the highest resolution (0.5256 mm/pixel, spacing 1.5 mm, 237 slices). The digital modelling, processing, and measurements of the scans were made with the 3D Analysis Software, Avizo[®] version 6.3 in the University of Bristol.

Previous attempts to study the soft structures of extinct taxa have been hindered by the lack of well-preserved material and adequate investigative techniques. Some data exists for

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Spinosaurus (Dal Sasso et al. 2005, 2009), and it is sometimes possible to infer the distribution of soft tissues by making comparisons with extant taxa. However, for pliosaurids, there are no directly analogous living taxa for comparison. We compared cranial structures in extinct and extant species and used the fact that nerves and blood vessels are highly similar between taxa and easily identifiable according to their position and supposed function (Romer 1956).

Results

Both premaxillae show the neurovascular system, which was highlighted simply by labelling the internal cast of the channels during image segmentation in Avizo. The channels are filled with sediment and pyrite (matching the superficial foramina), and these make it possible to distinguish the digital endocasts from the bone enclosing it.

The canals range in dimensions (Figs. 1 and 2) from 23 mm (larger, deeper canals before bifurcation) to less than 2 mm where they taper significantly rostrally and peripherally. In each premaxilla, a complicated web of ramifications develops; at the level of the sixth premaxillary alveolus, there is evidence of major branching from which a second channel originates, as observed in *Spinosaurus* (Dal Sasso et al. 2005, 2009) and *Baryonyx* (personal observation). In rostro-caudal view, the major canals run from a middle internal position to a more superficial and dorsal location, approaching the anterior end of the snout. All the main canals bend dorso-laterally, passing externally to the functional third–fifth tooth sockets

(Fig. 2). Many peripheral vessels originate mainly, but not exclusively, from the ventral and lateral sides of each main cavity. Some of them reach tooth alveoli, both primary and secondary (as in Buchy et al. 2006), while others pass through a high number of foramina located on the lateral and dorsal surfaces of the snout. The premaxillae and maxillae are rostrally pitted by more than 200 sub-circular foramina that represent outlets for the internal channel network. On the premaxillae and maxillae, clear furrows develop from each pit, creating clear superficial grooves.

Discussion

The extreme retraction of the external nares in pliosaurs and their distance from the orbits suggests that the channels are not related to olfaction or vision. Thus, we can confidently state that the network of cavities is neurovascular, most likely a rostral extension of the trigeminal nerve (cranial nerve V) and the most distal maxillary blood vessels (Buchy et al. 2006).

The trigeminal nerve divides into three branches, namely *ramus mandibularis*, *ramus ophthalmicus* and *ramus maxillaris* (Romer 1956). Each vessel in the network terminates in tooth sockets or in foramina on the dorso-lateral surface of the premaxillae. The network is most likely a combination of branches from the *ramus ophthalmicus* and the *ramus maxillaris*. The *ramus maxillaris* sends sensory information from the upper jaw, including the teeth, to the brain, whilst the *ramus ophthalmicus* sends sensory information from the skin. In extant members of *Varanus*, a similar

Fig. 1 *Pliosaurus kevani*, DORCM G 13,675, premaxillaries, ventral view. Comparison of the fossil (right) and the digital model reproduced from CT scans showing the neurovascular web of peripheral rami of cranial nerve V and blood vessels. Scale bar is equal to 10 cm



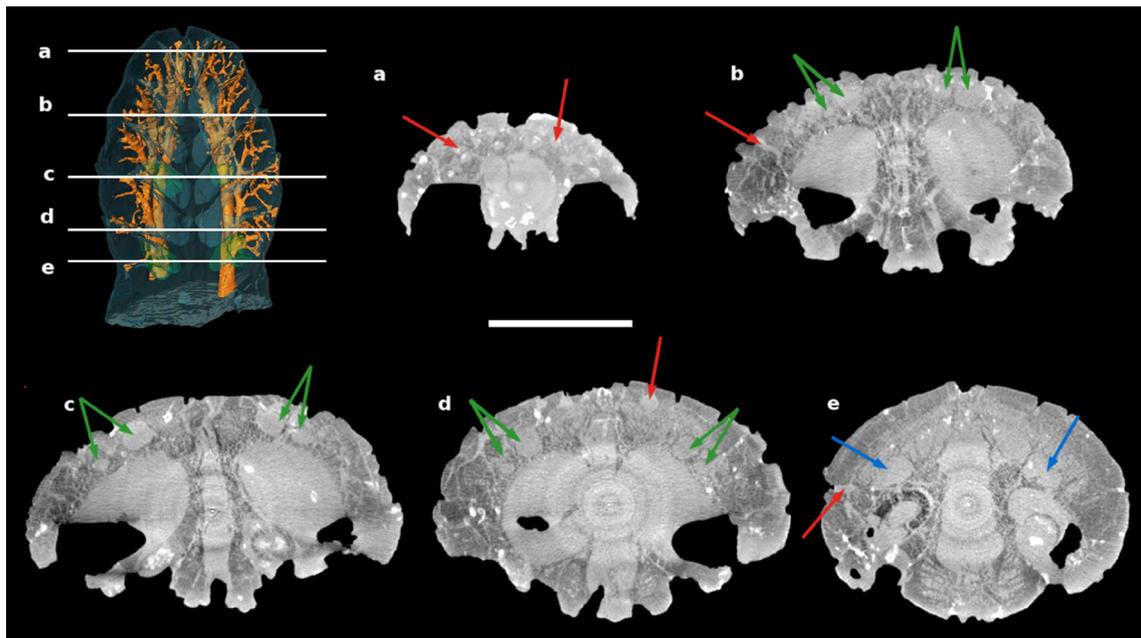


Fig. 2 *Pliosaurus kevani* digital model of the neurovascular cavity and sections along the premaxillaries with corresponding CT scan slices. **a** Anterior peripheral minor rami (red arrows), **b**, **c**, **d** paired large canals (green arrows) and peripheral rami (red arrows) between the second and

sixth premaxillary alveoli, **e** the major channels caudal to the bifurcation (blue arrows) and peripheral rami (red arrows). Scale bar is equal to 10 cm for **a–e**

situation occurs (Bellairs 1949); the two rami of the cranial nerve extensively communicate with each other and form a combined network of nerves and blood vessels, perhaps similar to the structures we see in *P. kevani*. In Amniota, the peripheral blood vessels often run parallel to the nerves (Romer 1956), and it is common for the vascular system to be extensively innervated (Burnstock 1969). We conclude that the observed network comprises the terminal ramification of the maxillary artery running together with the two terminal branches of the trigeminal nerve.

Such a large number of pits and foramina and sometimes longitudinally oriented furrows have been reported in various extant amniotes and in Mesozoic marine reptiles such as Mosasauroida, Placodontia, Pachypleurosauria and Ichthyopterygia (Goldfuss 1845; Baur 1892; Lingham-Soliar 1995; Rieppel 1995; Kear 2005; Klein 2009). These features can be detected in the maxillae, premaxillae and dentaries of many plesiosaurs and pliosaurs (Buchy et al. 2006; Ketchum and Smith 2010; Smith and Vincent 2010; Ketchum and Benson 2011a, b; O’Gorman and Gasparini 2013) and in many cases are associated with longitudinally directed grooves. Similar skull ‘ornamentations’ also occur in numerous other extant and extinct taxa. Certain crocodiles, for example, show a network of pits, ridges and interlacing grooves that develop with age (Iordansky 1973).

Occasionally, similar structures have different functions in different groups, so inferences are not always possible. However, in predators, many neurophysiological structures are

commonly associated with prey detection and apprehension, and it is possible that the extensive rostral pitting in pliosaurs had a sensory function. Cranial branches of the trigeminal nerve innervate these sensory organs in both Archosauromorpha (e.g. dome pressure receptors in crocodylians and possibly *Spinosaurus*) and Lepidosauromorpha (e.g. thermoreceptors in snakes and lizards) (Dal Sasso et al. 2005, 2009; Soares 2002; Seebacher and Franklin 2005). The premaxillae in numerous ichthyosaurs also show evidence of similar innervating structures (Romer 1956; McGowan 1973; Godefroit 1993; Maisch 1998; Kear 2005). In the ichthyosaur *Platypterygius australis* and in the polycotyloid plesiosaur *Sulcusuchus erraini*, foramina connected with superficial and/or intra-osseous channels have been suggested to be evidence of special dermal sensory systems (Kear 2005; O’Gorman and Gasparini 2013). Similar structures allow for electroreception in monotremes and certain cetaceans, whilst amphibians and sharks independently and convergently evolved them as modifications of the lateral line system (Seebacher and Franklin 2005; Czech-Damal et al. 2011). It has previously been suggested that pliosaurs were mainly visual predators (Taylor 1992). However, it seems unlikely that a predatory marine vertebrate would rely only on visual stimuli. The nature of the neurovascular network described here cannot address whether it had a specific function such as thermal, chemical, electrical or mechanical reception. However, the unusually high number of innervated rostral pits on the pliosaur skull suggests some kind of sensory function may

be linked to the detection of movement. Such a system would be of paramount importance for orientation and prey detection in conditions of poor visibility.

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