

The internal cranial anatomy of the Plesiosauria (Reptilia, Sauropterygia): evidence for a functional secondary palate

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LETHAIA



Buchy, M.-C., Frey, E. & Salisbury, S.W. 2006 12 01: The internal cranial anatomy of the Plesiosauria (Reptilia, Sauropterygia): evidence for a functional secondary palate. *Lethaia*, Vol. 39, pp. 289–303. Oslo. ISSN 0024-1164.

In the late 19th Century, the choanae (or internal nares) of the Plesiosauria were identified as a pair of palatal openings located rostral to the external nares, implying a rostrally directed respiratory duct and air path inside the rostrum. Despite obvious functional shortcomings, this idea was firmly established in the scientific literature by the first decade of the 20th Century. The functional consequences of this morphology were only re-examined by the end of the 20th Century, leading to the conclusion that the choanae were not involved in respiration but instead in underwater olfaction, the animals supposedly breathing with the mouth agape. Re-evaluation of the palatal and internal cranial anatomy of the Plesiosauria reveals that the traditional identification of the choanae as a pair of fenestrae situated rostral to the external nares appears erroneous. These openings more likely represent the bony apertures of ducts that lead to internal salt glands situated inside the maxillary rostrum. The 'real' functional choanae (or caudal interpterygoid vacuities), are situated at the caudal end of the bony palate between the sub-temporal fossae, as was suggested in the mid-19th Century. The existence of a functional secondary palate in the Plesiosauria is therefore strongly supported, and the anatomical, physiological, and evolutionary implications of such a structure are discussed. □ *Choanae, Plesiosauria, respiration, salt glands, secondary palate.*

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The Order Plesiosauria is traditionally divided into two superfamilies, the Plesiosauroidea and the Pliosauroidae, mainly on the basis of the ratio of neck length/size of the head (Welles 1943; Tarlo 1960; Brown 1981, 1993). Within the Plesiosauroidea are placed the long-necked forms of the families Plesiosauridae, Elasmosauridae and Cryptoclididae (e.g. Brown 1993). Taxa with a large head and a short neck relative to the Plesiosauroidea are placed within the Pliosauroidae, comprising a variable number of families depending on the features studied, usually the Pliosauridae and the Polycotyliidae (e.g. White 1940; Persson 1963; Tarlo 1959; Brown 1981; see also Bardet 1995, for the most recent comprehensive compilation of pre-1995 literature).

This traditional view is currently challenged by the inclusion of the Polycotyliidae (with a short neck and a large head: thus classically considered as Pliosauroidae) within the Plesiosauroidea. This was proposed by Carpenter (1996, 1997), who observed anatomical similarities in the pterygoid of a polycotyliid (*Dolichorhynchops osborni*) and an elasmosaur (*Libonectes morgani*). Storrs (1999) suggests that this hypothesis should

be supported by further anatomical evidence, while other authors such as O'Keefe (2001, 2004) support Carpenter's (1996, 1997) views; the systematics of the Plesiosauria is therefore in much need of clarification.

The origin of the Plesiosauria has long been searched for within the Nothosauria, now recognized as polyphyletic (Rieppel 1997a, and literature therein). The Pachypleurosauroidea are currently considered the sister-group of the Eusauropterygia, which comprises *Simosaurus*, the other former 'nothosaurs', Pistosauridae and Plesiosauria (see Rieppel 1997a for a discussion). The monophyly of the Plesiosauria themselves has not been questioned since the group was first established (Blainville 1835, see also Sues 1987), despite the most recent diagnoses (Tarlo 1960; Brown 1981; Noè 2001; O'Keefe 2001) appear to be based mainly on overall similarities in body construction, though this is sometimes contradicted by other aspects of the anatomy of the taxa included in the group (e.g. the absence of a nasal is diagnostic of the order according to Brown (1981), while a nasal undoubtedly exists in the pliosaurians *Liopleurodon ferox* and *Silmolestes vorax*; Noè 2001).

Clarification, both of the relationships within the group, and of its origins, can only emerge as the result of detailed anatomical redescription of historical but poorly known taxa (Noè 2001; Noè et al. 2004), and a better understanding of the palaeobiology of these fossil reptiles. As a contribution to this, we here examine the palatal and internal cranial anatomy of the Plesiosauria in a functional context, with the aim to identify the position and nature of the choanae, focusing on the implications for the air-intake method of these animals. Our aim is to determine common features of the group, and interpret the internal and external palatal anatomy (Figs 1, 2), and how this relates to the internal cranial anatomy (excluding the brain case) as determined by examination of cross-sections (Figs 3, 4), and published descriptions (Table 1).

Nomenclatural note. – As a result of the systematical confusion within the group, and of the long use of vernacular or abbreviated names in the literature (Noè 2001), we feel it necessary to explicitly define the terms used in this paper:

The term Plesiosauria refers to members of the Order as defined by Brown (1981). We follow Noè (2001) in applying the term plesiosaurs to the valid taxa of the Superfamily Plesiosauroidea Seeley, 1874 *sensu* Brown

(1981), but exclude the genera *Trinacromerum*, *Dolichorhynchops* and *Polycotylus*, and all other members of the Family Polycotylidae as defined by Carpenter (1996) including those described subsequently (e.g. *Edgarosaurus* Druckenmiller 2002; *Thililua* Bardet et al. 2003; *Manemergus* Buchy et al. 2005). *Trinacromerum*, *Dolichorhynchops*, *Polycotylus*, *Edgarosaurus*, *Thililua* and *Manemergus* will be designated as the Polycotylidae or polycotylids. Considering the uncertainties about their inclusion within the Plesiosauroidea, they are also excluded from what is here named plesiosaur, pending clarification of the relationships of these animals within the Plesiosauria. The term plesiosaur here refers to the Superfamily Plesiosauroidea (including the Families Plesiosauridae, Elasmosauridae and Cryptoclididae, following Brown 1981, 1993; Cruickshank & Fordyce 2002), but excluding the Polycotylidae as defined above. The term plesiosaur does not apply to the Order Plesiosauria as a whole.

The palatal anatomy of the Plesiosauria in historical perspective. – In ventral aspect, the preorbital part of the cranium of the Plesiosauria forms a triangle, whilst the postorbital region has a square to rectangular outline (Fig. 1; Table 1). The premaxillae form the rostral-most corner of the triangle. The elongation of the rostrum, as

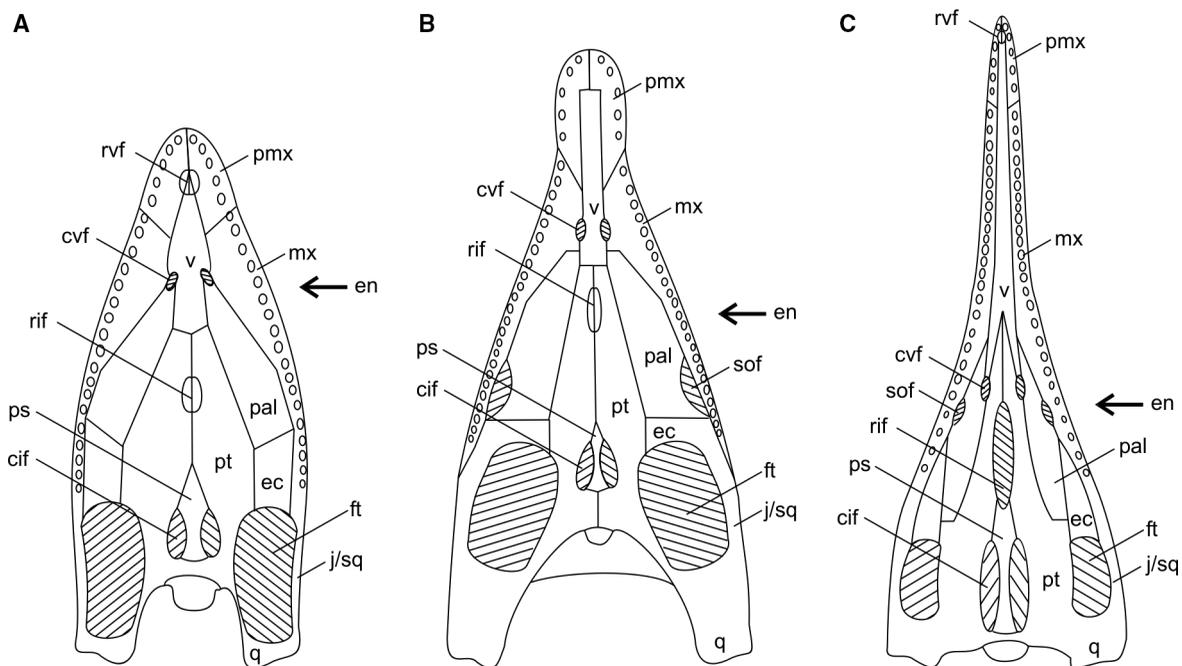


Fig. 1. Reconstruction of the palatal anatomy of the cranium in the Plesiosauria, based on the compilation of the references given in Table 1. Schematic drawings of the cranium in ventral view of □ A. Elasmosauridae, Plesiosauridae and Cryptoclididae. □ B. Plesiosauridae. □ C. Polycotylidae. The level of the external nares on the dorsal surface of the cranium is marked by an arrow. Abbreviations: cif: caudal interpterygoid fenestra; cm: cranium midline; cvf: caudal vomerian fenestra; ec: ectopterygoid; en: external naris; f/pf: frontal and prefrontal; ft: subtemporal fossa; ioc: interorbital cavity; j/sq: jugal and squamosal; mc: medial canal; md: mandible; mx: maxilla; nuc: nutritive canal; oc: olfactory canal; opfc: orbitoprefrontal canal; orb: orbit; pal: palatine; par: parietal; pff: prefrontal fenestra; pmx: premaxilla; pob: postorbital bar; ps: parasphenoid; pt: pterygoid; ptd: dorsal process of the pterygoid; q: quadrate; R: right side of the specimen; rc: rostral cavity; rif: rostral interpterygoid fenestra; rvf: rostral vomerian fenestra; sof: suborbital fenestra; v: vomer; vc: vomerian cavity; vs: sulcus rostrally preceding the caudal vomerian fenestra.

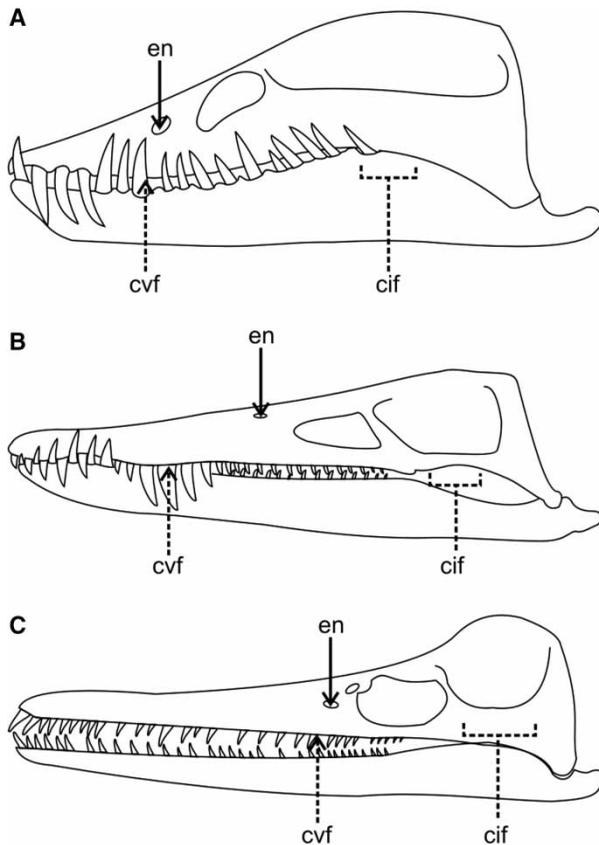


Fig. 2. Cranium and mandible outline in left lateral view. □ A. The elasmosaur *Callawayasaurus colombiensis* (redrawn from Welles 1962). □ B. The pliosaur *Liopleurodon ferox* (redrawn from Noè 2001). □ C. The polycotyloid *Dolichorhynchops osborni* (redrawn from Carpenter 1997); showing the position of the external naris, the caudal vomerian fenestra and the length of the caudal interpterygoid fenestra. The latter two crania are also used in Figs 3 and 4 as stereotypes of their family. Abbreviations as for Fig. 1.

seen in Polycotyliidae, and less markedly in Pliosauridae, is due to the rostral extension of the maxilla. The jugal forms the major portion of the lateral margin of the postorbital area. In the Plesiosauroidea and the Pliosauroidae, the occipital margin of the cranium is notched in ventral aspect, and the quadrate is situated further caudally than the medial margin of the cranium, which is formed by the basioccipital (forming the occipital condyle) and the pterygoid. Only in the Polycotyliidae are the quadrate and occipital condyle situated approximately at the same level.

In ventral aspect, the lateral-most portion of the palatal surface is formed by the premaxilla and the maxilla rostrally, and the jugal caudally. The palatine is bordered laterally by the maxilla, and caudally by the ectopterygoid, which forms the rostral margin of the subtemporal fenestra. Medially, the vomer separates the premaxillae and the maxillae. In the Plesiosauroidea and the Polycotyliidae, as well as in most pliosaurs, the vomer contacts the pterygoid caudally. In the pliosaurs

Liopleurodon and *Brachauchenius*, a medial extension of the palatine separates the vomer from the pterygoid. The pterygoid forms almost all of the mediocaudal part of the palate, extending from a point rostral to the orbits to the basioccipital caudally, and bordering the subtemporal fenestrae medially. The interpterygoid suture is interrupted between the subtemporal fenestrae by a medial bar formed by the parasphenoid.

Apart from the subtemporal fossae, the palatal surface bears numerous foramina and fenestrae, but only those that appear to be constant in the group are dealt with here.

At the rostral-most medial contact between premaxilla and vomer, a rostral vomerian fenestra has been described in several taxa, including *Dolichorhynchops osborni* (Polycotyliidae; Carpenter 1996, 1997), *Libonectes morgani* (Elasmosauridae; Carpenter 1997), *Plesiosaurus guilelmiimperatoris* and *Plesiosaurus brachypterygius* (Pliosauroidae; Fraas 1910; Maisch & Rücklin 2000), and *Simolestes vorax* (Pliosauroidae; Noè 2001). The preservation of many specimens – several of them forming monotypical taxa, with the mandible obscuring the lateral portions of the cranium in ventral view – makes a definitive statement about the general presence of this fenestra virtually impossible. When described it is usually interpreted as the opening of Jacobson's organ (Carpenter 1997). The lack of such an organ, or its aperture at a completely different place on some well-known taxa having no such rostral vomerian fenestra, should be considered as important in the framework of an evolutionary analysis of the group.

Further caudally, a pair of fenestrae is situated at the junction of the vomer, the maxilla and the palatine in plesiosaurs, the vomer and the maxilla in pliosaurs, and the vomer, the palatine and pterygoid in polycotyliids. These openings are traditionally described as being the internal nares or choanae. They are more or less elongate, sometimes hourglass-shaped in outline, having a proportionately small diameter, often smaller than that of the external nares (e.g. Williston 1903; Cruickshank *et al.* 1991; Taylor & Cruickshank 1993). They are also situated several tens of millimetres (in pliosaurs) to some millimetres (in plesiosaurs and polycotyliids) rostral to the external nares. Here they are designated as caudal vomerian fenestrae, using a functionally neutral terminology in order to avoid confusion when discussing the function of these fenestrae.

The caudal vomerian fenestrae are preceded in some taxa (e.g. the pliosaur *Rhomaleosaurus thorntoni*) by a shallow rostrocaudally aligned sulcus that extends either rostrally or rostromedially (Cruickshank *et al.* 1991; Cruickshank 1994).

Along the median line, at least all adequately preserved polycotyliids (Williston 1908; Carpenter 1996, 1997; Druckenmiller 2002), the pliosaurs *Leptocleidus*

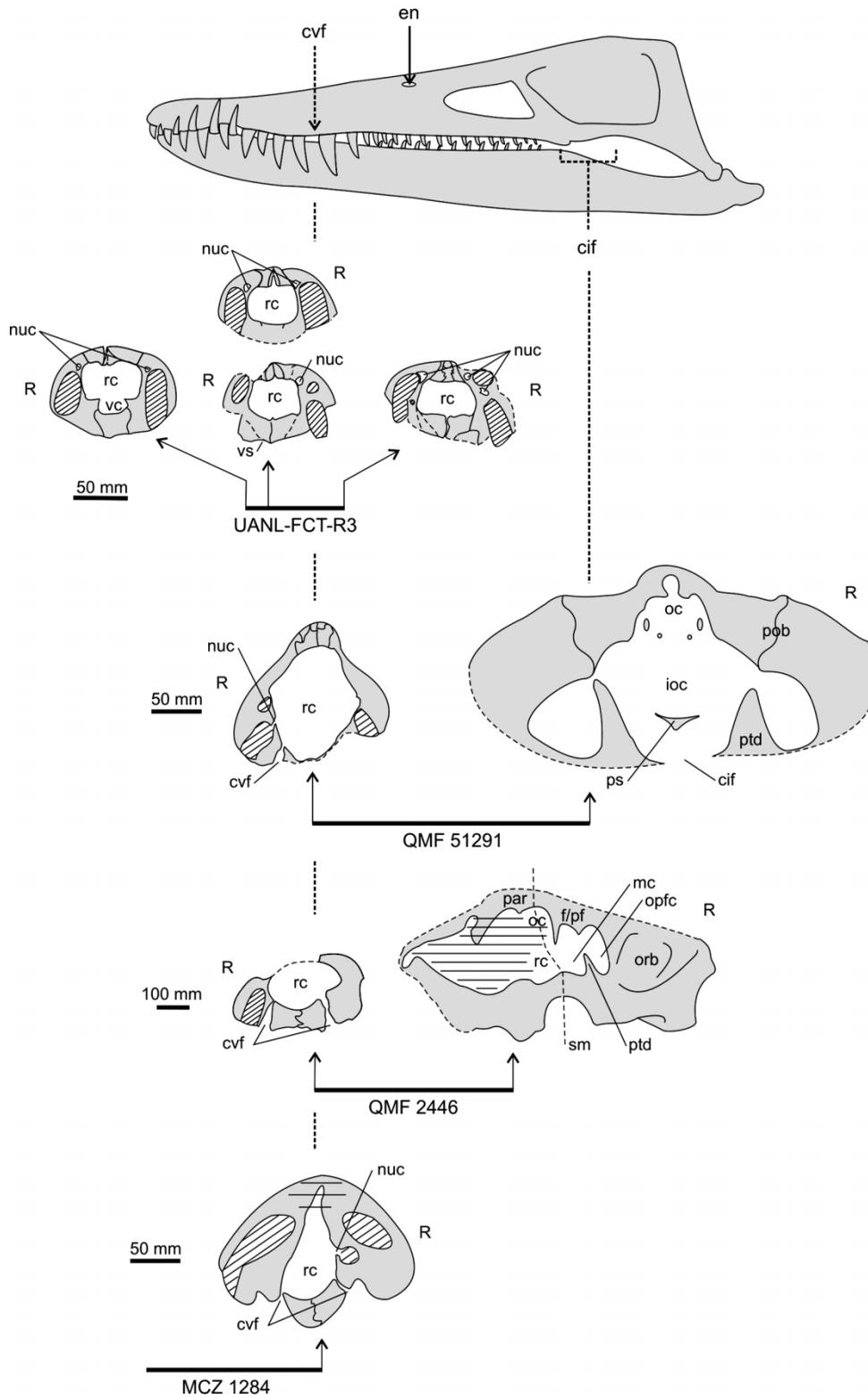


Fig. 3. Cross-sections through the cranium of the pliosaurs. The continuous line above the specimen number indicates the location of the preserved fragment in relation to the outline of the *Liopleurodon* cranium on top (see Fig. 2), and the upward arrows indicate the location of the cross-sections. Abbreviations as for Fig. 1. Drawing conventions: bone: grey; tooth material: oblique hatching; damaged or obscure areas: horizontal hatching; unclear sutures or damaged margin: dotted lines.

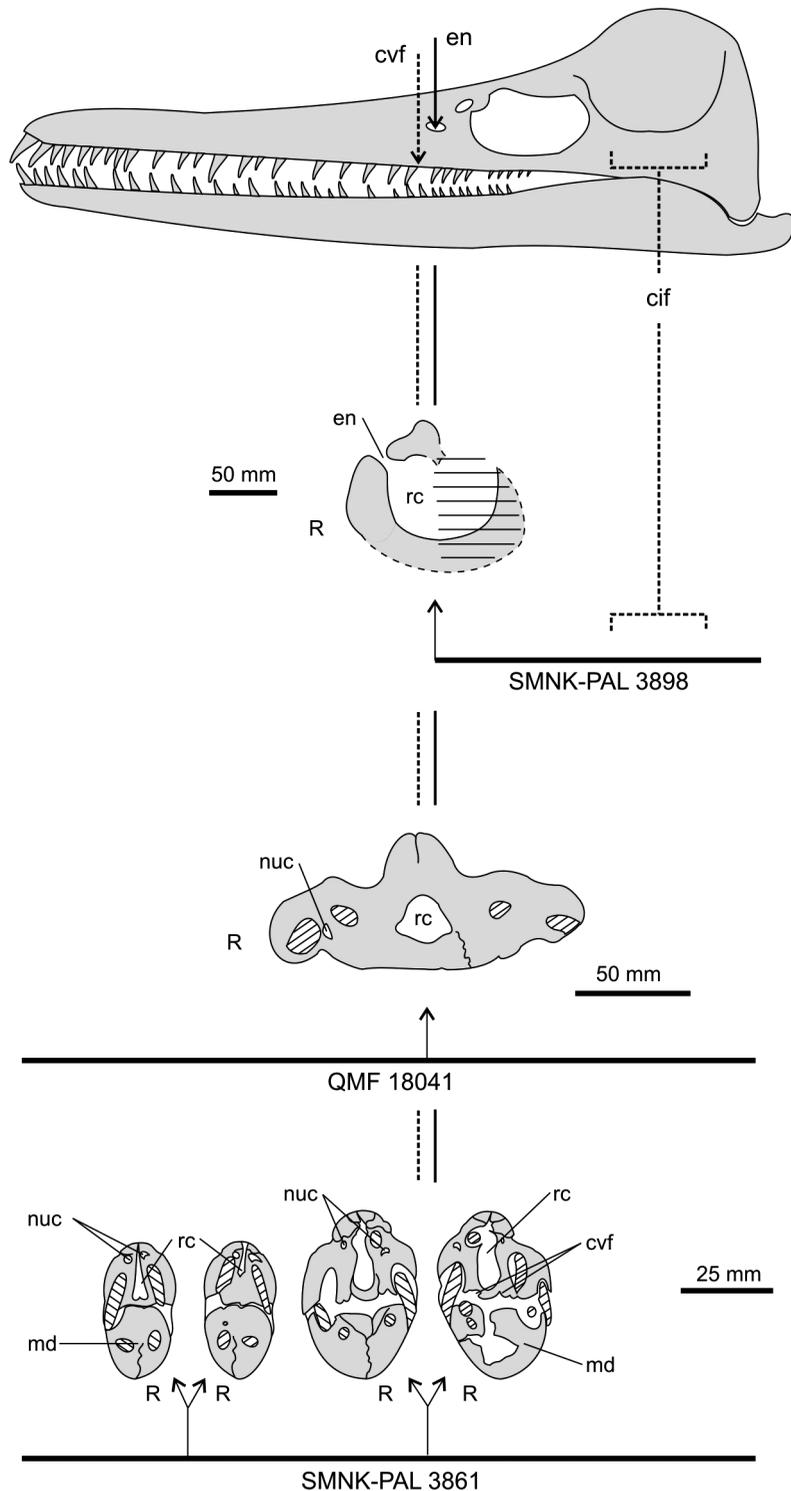


Fig. 4. Cross-sections through the cranium of the polycotyliids. The continuous line above the specimen number indicates the location of the preserved fragment in relation to the outline of the *Dolichorhynchops* cranium on top (see Fig. 2), and the upward arrows indicate the location of the cross-sections. Abbreviations as for Fig. 1. Drawing conventions as for Fig. 3.

capensis (Cruikshank 1997) as well as the three species of *Rhomaleosaurus* (Fraas 1910; Cruikshank 1994, 1996) and the plesiosaur *Plesiosaurus dolichodeirus* (Storrs 1997) exhibit a rostral ('anterior') interpterygoid

fenestra or vacuity. This fenestra has a rostrocaudally elongate oval outline, reaching several tens of millimetres in maximum length. It is clearly present in some taxa, but in those represented only by juvenile animals

Table 1. List of references describing the palatal anatomy of the Plesiosauria, upon which the reconstructions in Figure 1 are based.

Family	Taxon	Reference	Illustration of the palatal anatomy
Pliosauridae	<i>Brachauchenius lucasi</i>	Williston 1903	pl. XXIV
	<i>Brachauchenius lucasi</i>	O'Keefe 2001	fig. 13
	<i>Hauffiosaurus zanoni</i>	O'Keefe 2001	fig. 2
	<i>Kronosaurus queenslandicus</i>	White 1935	fig. 2
	<i>Leptocleidus capensis</i>	Cruickshank 1997	fig. 3
	<i>Leptocleidus superstes</i>	Andrews 1922	pl. XIV, fig. 2
	<i>Liopleurodon ferox</i>	Noè 2001	fig. 6
	<i>Macroplata longirostris</i>	O'Keefe 2001	fig. 9
	<i>Maresaurus coccai</i>	Gasparini 1997	fig. 2c
	<i>Pachycostasaurus dawni</i>	Noè 2001	fig. 20
	<i>Peloneustes philarchus</i>	Andrews 1913	pl. IV, fig. 1
	<i>Peloneustes philarchus</i>	O'Keefe 2001	fig. 11
	<i>Rhomaleosaurus megacephalus</i>	Cruickshank 1994	fig. 4
	<i>Rhomaleosaurus megacephalus</i>	O'Keefe 2001	fig. 8
	<i>Rhomaleosaurus thorntoni</i>	Cruickshank 1996	fig. 2
	<i>Rhomaleosaurus victor</i>	Fraas 1910	fig. 7
	<i>Rhomaleosaurus victor</i>	Bakker 1993	fig. 11G
	<i>Rhomaleosaurus victor</i>	O'Keefe 2001	fig. 7
	<i>Simolestes vorax</i>	Noè 2001	fig. 14
	Polycotyliidae	<i>Dolichorhynchops osborni</i>	Williston 1903
<i>Dolichorhynchops osborni</i>		Carpenter 1996	fig. 7C
<i>Dolichorhynchops osborni</i>		Carpenter 1997	fig. 6C
<i>Edgarosaurus muddi</i>		Druckenmiller 2002	fig. 10
<i>Trinacromerum bentonensis</i>		Williston 1908	fig. 1
<i>Manemergus anguistrostris</i>		Buchy et al. 2005	figs 2, 4
Elasmosauridae	<i>Alzadasaurus pembinensis</i>	Welles & Bump 1949	fig. 3
	<i>Callawayasaurus colombiensis</i>	Welles 1962	fig. 4a, c
	<i>Libonectes morgani</i>	Carpenter 1997	fig. 2
	<i>Microcleidus brachypterygius</i>	Bakker 1993	fig. 9
	<i>Morturneria seymourensis</i>	Chatterjee & Small 1989	fig. 4
	<i>Occitanosaurus tournemirensis</i>	Bardet et al. 1999	fig. 3b
Plesiosauridae	<i>Plesiosaurus brachypterygius</i>	F. von Huene 1923	Pl. 1, fig. 3
	<i>Plesiosaurus brachypterygius</i>	Maisch & Rücklin 2000	fig. 4
	<i>Plesiosaurus dolichodeirus</i>	Storrs 1997	figs 4, 7
	<i>Plesiosaurus dolichodeirus</i>	O'Keefe 2001	fig. 6
	<i>Thalassiodracon hawkinsi</i>	Storrs & Taylor 1996	fig. 11
	<i>Tricleidus seeleyi</i>	O'Keefe 2001	fig. 16

(sensu Brown 1981) the fenestra could also be the result of the distortion of the unfused pterygoids. Partly as a result of the uncertainties about its actual occurrence within the group, the function of this fenestra is unknown.

Laterally, a suborbital fenestra, opening in the maxillopalatine suture ventral to the orbit, is present in most pliosaurs, in the polycotyloid *Trinacromerum* (Williston 1908) and in the plesiosaur *Microcleidus* (Bakker 1993). The preservation of many specimens makes the general presence or absence of this fenestra within the group difficult to determine.

Between the subtemporal fenestrae, all the Plesiosauria exhibit a pair of fenestrae, bordered by the pterygoid laterally and the parasphenoid medially, here designated caudal ('posterior') interpterygoid fenestrae. Owen (1865, p. 29 and explanations to pl. XVI) named these paired fenestrae palatonares, and implied that a

soft tissue duct linked these fenestrae with the external nares, and therefore the existence of a functional secondary palate in the Plesiosauria. Huxley (1858; Williston 1903, p. 60), and later Sollas (1881) discussed and refuted this interpretation, and suggested the fenestrae bordered by the vomer and maxilla, or the vomer, maxilla and palatine, or the vomer, palatine and pterygoid, were in fact the choanae. Sollas (1881, p. 474), in a somewhat circular argument (as diplomatically expressed by Seeley in the discussion following Sollas' paper), writes: 'the oval foramina [the now called choanae] appear to represent the internal nares, since they are similarly situated with respect to the surrounding bones as the posterior nares of many Lacertilia; and it is with this order that *Plesiosaurus* stands in the closest connexion [sic]'. The fact that the choanae would be situated rostral to the external nares puzzled Sollas, but

did not make him modify his interpretation. Andrews (1896) accepted Sollas' (1881) interpretation, and it was not until 1903, that the matter was discussed again, this time by Williston, who considered it in the context of growing knowledge of Plesiosauria, as well as of the anatomy and biology of more fossil and recent reptiles. Williston (1903), when describing the new pliosaur *Brachauchenius lucasi*, saw the incoherence implied by Sollas' (1881) interpretation: the caudal retreat of the external nares in the Plesiosauria, not being accompanied by a similar retreat of the choanae; the osteologically variable position of the suggested choanae in the different families; the small size of the choanae compared to the external nares; and, all this unknown in any other reptile. Williston (1903, pp. 59–61) also suspected the caudal interpterygoid fenestrae were the actual choanae, because of their constant caudal situation in the Plesiosauria, being separated by a constantly well-ossified parasphenoid, an unusual feature among the Reptilia, and because whether the choanae are situated rostral to the external nares or caudal to them, a soft tissue duct had to be invoked anyway. Despite his doubts, Williston accepted Sollas' (1881) nomenclature in his description, and to our knowledge only briefly mentioned the matter in one subsequent article (Williston 1908, p. 719).

Fraas (1910, pp. 126–127), shortly recapitulating this history, did not accept Owen's palatonares, and followed Andrews' (1896) interpretation. He also agrees with Williston (1903), citing the description of the palatal anatomy of *Dolichorhynchops osborni*. Fraas (1910) refers to p. 22 of Williston (1903), which contains no reference to the function of the fenestrae: more likely Fraas (1910) was referring to p. 23, where Williston (1903), calling 'nares' the fenestrae situated at the junction of the vomer, palatine and pterygoid, refers to the above-mentioned discussion with an asterisk. Fraas (1910) apparently ignored this asterisk. To our knowledge, no subsequent author has discussed the identification of the choanae in the Plesiosauria in print, and Sollas' (1881) interpretation found its way into text books (e.g. Saint-Seine in Piveteau 1955, p. 425, fig. 4; Romer 1956, p. 172), although C. McHenry did briefly revive the idea of a secondary palate in the Plesiosauria in oral contributions at the 46th Symposium of Vertebrate Palaeontology and Comparative Anatomy at Bournemouth in 1998, and the 7th Conference on Australian Vertebrate Evolution, Palaeontology and Systematics at Sydney in 1999.

Cruickshank *et al.* (1991) were the first authors to examine the functional consequences of Sollas' (1881) interpretation. It is noteworthy that these authors do not question the identification of the choanae, only their functionality. With the choanae (the caudal vomerian fenestrae, as suggested by Sollas in 1881) being situated

in the rostral half of the palatal surface, any air that is inspired would have to reach the trachea via the whole postchoanal portion of the mouth (Figs 1, 2). As the tooth row extends further caudally, at least to the level of the middle of the orbit, the existence of soft cheeks sealing the jaws laterally cannot be convincingly suggested. Additionally, in some pliosaurs, the caudal vomerian fenestrae are situated several tens of millimetres rostral to the external nares. Therefore, from the external nares, air would have to pass first rostrally to the choanae, and then caudally to the tracheal opening at the back of the mouth. Facing such an illogical air path, Cruickshank *et al.* (1991) suggested that the nares were secondarily involved in underwater olfaction, and no longer played a role in respiration (see also Taylor & Cruickshank 1993). The animal, under this hypothesis, would have to have breathed with the mouth agape and above the surface of the water, a muscular tongue and glottal valve sealing the trachea during swimming.

Examination of new specimens, as well as reinterpretation of specimens already described in the literature, suggests that this rather problematic method of air intake is erroneous and the result of a misinterpretation of the palatal anatomy of the Plesiosauria, corroborating the supposition made by Williston (1903).

Materials and methods

Institutional abbreviations. – QM: Queensland Museum, Brisbane, Australia; MCZ: Museum of Comparative Zoology, Harvard, USA (the specimens belonging to the MCZ described herein are on long-term loan to the QM); SMNK: Staatliches Museum für Naturkunde Karlsruhe, Germany; UANL-FCT: Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexico.

This study is partly based upon a compilation of literature describing the palatal anatomy of the Plesiosauria (Table 1).

The internal anatomy of the skull is usually poorly preserved and/or not prepared, and therefore rarely described. It is best accessible either by X-ray and/or computed axial tomography (CAT) scanning, or along breaks in a specimen, provided they were not glued together during preparation. The first method was applied to the pliosaur *Rhomaleosaurus megacephalus* by Cruickshank *et al.* (1991) and to the elasmosaur *Libonectes morgani* by Carpenter (1997). The accuracy of the results, which depends primarily on the density contrast between the matrix and fossilized bone, will be discussed in comparison with other specimens studied herein.

Breaks provide the most reliable data on the internal anatomy of the skull, but these are restricted to the level

of the break, and rely on 3-dimensionally preserved specimens being broken; complete, 3-dimensionally preserved crania of the Plesiosauria appear too rare to be subject to thin-sectioning as for other groups such as the Ichthyosauria (Sollas 1916). Such breaks were described by Cruickshank *et al.* (1991) and Cruickshank (1994) in the skull of the pliosaur *Rhomaleosaurus megalcephalus*. Additional specimens exhibiting breaks, kept in the collections of the SMNK, UANL-FCT and QM are examined for the first time. We use reconstructions of the skulls of *Liopleurodon ferox* (Noè 2001) and *Dolichorhynchops osborni* (Carpenter 1997), which are taken as stereotypes for their families.

Evolutionary presumption

The objective of this paper being to identify the position and nature of the choanae, comparisons are made between taxa of different superfamilies (the Plesiosaurioidea and the Pliosauroida), assuming that breathing is an essential biological function, therefore strongly subject to evolutionary pressure. The first members of the group whose cranial anatomy is sufficiently known (Storrs & Taylor 1996) already possess external nares situated close to the orbits (which is also the case in the sister group of the Plesiosauria, the Pistosauridae, see Sues 1987 and Rieppel *et al.* 2002, but not in the next closest sister group, the 'Nothosauria', see e.g. Rieppel 1997b), and no sequence of fossils following this caudalward retreat has been recognized. In addition to this conservative dorsal anatomy of the cranium, the anatomy of the palatal area is also conservative throughout the stratigraphical extension of the group (Fig. 1, Table 1). The structures linked with the respiratory function as observed in the Plesiosauria must therefore have been acquired prior to our first recognition of the Plesiosauria as a coherent, anatomically defined group. It is here assumed that all the Plesiosauria possessed the same respiratory system, inherited from a common ancestor, which allows us to compare the constructional features of the respiratory system within the Order.

Internal cranial anatomy of the Plesiosauria

Maxillary rostrum. – All specimens examined (Figs 3, 4), as well as those described in the literature (Sollas 1881, fig. 11; Carpenter 1997, fig. 5; Cruickshank 1994, fig. 2) show that the maxillary rostrum is essentially a hollow tube, containing a continuous cavity, the internal surfaces of which are smooth. Most of the volume of the lateral (bony) encasement is occupied by tooth roots. In

the polycotyliids SMNK-PAL 3861 (Buchy *et al.* 2005) and QM F18041, along with the Late Jurassic pliosaur UANL-FCT-R3 (Buchy *et al.* in press a, b), a system of branching nutritive canals runs dorsomedial to the tooth roots, leading into the pulp canal of the teeth. In the Early Cretaceous pliosaurs QM F51291 and MCZ 1284 the alveoli are directly linked to the rostral cavity via a medially directed canal. Except for this nutritive system and tooth alveoli, no other accessory canal or potential respiratory duct, even partially enclosed, is visible at any level of the rostral cavity, including between the caudal vomerian fenestrae and the external nares.

Carpenter (1997, fig. 5D) reconstructed the rostral vomerian fenestrae as opening into the rostral cavity. In none of the specimens that we examined is this fenestra visible. UANL-FCT-R3, however, presents on its rostral-most cross-section a vomerian cavity ventrally adjacent to the rostral cavity, possibly aligned with a rostral vomerian fenestra. In the polycotyliid SMNK-PAL 3861, the floor of the rostral cavity curves ventrally and appears paired in its rostral-most portion, which supports Carpenter's (1997) reconstruction. It would also be coherent with the usual location of the rostral vomerian fenestrae in other polycotyliids (Fig. 1).

As is visible on QM F2446, QM F51291 and MCZ 1284, the caudal vomerian fenestra opens into the rostral cavity via a subvertical canal, the diameter of which is similar to that of the fenestra (Fig. 3). Carpenter (1997, fig. 5A) also illustrates these fenestrae as directly opening into the rostral cavity of the elasmosaur *Libonectes morgani*, the palatal area in this taxon being thinner than in the pliosaurs studied here, with no real canal being present.

The external nares also open directly into the rostral cavity, as is visible on SMNK-PAL 3898 (Fig. 4) and specimens depicted by Sollas (1881, fig. 11) and Carpenter (1997, fig. 5A, C). In external view, and in addition to what can be deduced from the sections through SMNK-PAL 3861 and QM F18041 (Fig. 4), the lumen of the external nares is ventrocaudally directed, as was noted by Cruickshank *et al.* (1991) in the pliosaur *Rhomaleosaurus megalcephalus*.

These observations partly contradict those of Sollas (1881, pp. 473–474 and fig. 11), who described a vertical transverse break through the skull of *Plesiosaurus megalcephalus* (now *Rhomaleosaurus megalcephalus*; Sollas [1881] gives no accession number, but the specimen described was the holotype skull numbered Cb 2335, destroyed in Bristol during World War II; Swinton 1948). According to Sollas (1881, p. 473), the break runs from the external naris on one side of the specimen, to the caudal vomerian fenestra on the other side; however, it seems more likely to us that the break actually passed rostral to the caudal vomerian fenestra, directly through

the groove rostrally preceding the fenestra – described by Cruickshank *et al.* (1991) and Cruickshank (1994) – since the fenestra itself is only marked by the concave ventral margin of the palatal area and does not open into the rostral cavity. In this section, the palatine and vomer send a medial process dorsally, partly separating the rostral cavity from a lateral canal which Sollas interpreted as the respiratory canal. This section probably led Sollas (1881) to interpret the caudal vomerian fenestrae as choanae.

No such vomeropalatine process is seen on any of the sections described herein, nor other specimens described in the literature (including in the neotype of *Rhomaleosaurus megacephalus* designated by Cruickshank in 1994, see below). Moreover, if the break actually passed rostral to the caudal vomerian fenestra, then the supposed respiratory canal would have extended rostral to the choanae, bordered medially by a process having the same height at the level of the external nares as it has rostral to the choanae. Because the specimen has been destroyed, it is impossible to judge its preservation, but the figure given by Sollas (1881, fig. 11) appears rather imprecise if compared with another cross-section he gives in the same article (Sollas 1881, fig. 14; through the rostrum of *Plesiosaurus brachycephalus*, situated rostral to the caudal vomerian fenestrae but without further precision, therefore not discussed herein). In his figure 11, Sollas (1881) for example could not distinguish the tooth material in the maxilla, nor the porous aspect of the bones, which are illustrated in his figure 14. Together with the cross-sections described by Cruickshank (1994; see below) of the neotype skull of this taxon that show no hint of such a respiratory canal, we can only assume that the canal described by Sollas (1881, pp. 473–474; fig. 11) results from a misinterpretation of a poorly preserved cross-section, oriented by his conviction that the Plesiosauria are closely related to the Lacertilia (see also the discussion following Sollas' [1881] communication by Seeley, p. 480).

Our observations also differ from those presented by Cruickshank *et al.* (1991, fig. 5). These authors performed CAT scanning of the nasal region of the pliosaur later described by Cruickshank (1994) as the neotype of *Rhomaleosaurus megacephalus*. Interpreting the results of the scanning, they describe a duct that is circular in cross-section, running dorsocaudally from the caudal vomerian fenestra to the external naris. The portion they examined covers the area from the rostral margin of the caudal vomerian fenestrae to the caudal margin of the external nares. It is therefore equivalent to some of the sections presented here (Figs 3, 4), none of which reveal the presence of such a duct. However, the image obtained by CAT scanning (Cruickshank *et al.* 1991, fig. 5a) is extremely difficult to interpret. The interpretation of it given by

Cruickshank *et al.* (1991, fig. 5b) shows the rostrum as having a very thin dorsomedial wall, compared to the volume of the rostral cavity, while the specimens described herein all possess a thick median bar (Figs 3, 4). Immediately caudal to the caudal vomerian fenestrae, the image shows a ventrally directed crest, which does not exist in the specimen when viewed ventrally (Cruickshank 1994, fig. 4). It also shows a circular cross-section through what appears to be a transverse bar inside the cavity of the maxillary rostrum, dorsal to the caudal vomerian fenestra, which none of the specimens described here reveal. Noé (personal communication 2005) suggests this structure might represent a tooth. Additionally, the duct running from the caudal vomerian fenestrae appears geometrically illogical. The rostral and caudal margins are visible in vertical section ventrally, after which they disappear at mid-height. The canal is then suggested to run dorsally, but is visible from outside, and not in section. The ventral horizontal section that should mark the transition between the two views is not visible. In addition, the external naris does not appear to be closed caudally on the image they obtained (Cruickshank *et al.* 1991, fig. 5a); whether the canal linking the external naris and the caudal vomerian fenestra described by Cruickshank *et al.* (1991) is actually present in the specimen they studied cannot be confirmed, and no evidence is presented by these authors that the external nares were connected exclusively to the caudal vomerian fenestrae. The existence of such a canal as a feature shared by all the Plesiosauria is not supported by the data presented here.

Interorbital and postorbital areas. – The ventral surface of the skull roof in the interorbital area and caudal to it is grooved medially for the passage of the olfactory (I) nerve, as described by Carpenter (1997, fig. 5) and Maisch (1998), and visible in cross-sections through QM F2446 and QM F51291 (Fig. 3).

QM F2446 additionally reveals a medial high oval space in the interorbital area, the width of which approaches the diameter of the external naris. It is situated in line rostrocaudally with the external naris; QM F51291 also shows this space to be in line with the caudal interpterygoid fenestrae, which is situated further caudally. Cruickshank (1994, fig. 2) describes a transverse break through the neotype skull of *Rhomaleosaurus megacephalus* level with the caudal margin of the postorbital bar, and rostral to the rostral margin of the caudal interpterygoid fenestra. It shows that the basisphenoid covers the parasphenoid dorsally, and formed the ventral margin of the brain cavity. In QM F2446, there is an oval space lateral to the basisphenoid, and medial to the dorsal process of the pterygoid adjacent to

the epipterygoid that may represent the caudal continuation of the medial canal. The cross-sections from CAT scans of the skull of the elasmosaur *Libonectes morgani* described by Carpenter (1997, fig. 5A) show that a dorsal process of the pterygoid is present in the interorbital area, though it is not as well expressed as it is in QM F2446.

In all the relevant specimens and cross-sections (Figs 3–5) that we examined, the caudal interpterygoid fenestrae open into the interorbital cavity as rostrocaudally directed, rostrocaudally elongate slits. Their lateral margin is formed by a caudal prolongation of the dorsal process of the pterygoid, which separates them from the subtemporal fossae. The dorsomedial margin of the caudal interpterygoid fenestrae is formed by the parasphenoid medial bar. Carpenter (1997, fig. 5) additionally confirms that the caudal interpterygoid fenestrae are closed caudodorsally as is observed on SMNK-PAL 3898 (Fig. 5).

Discussion and conclusions

Review of the literature and observations of new specimens demonstrate that the following points concerning the internal cranial anatomy of the Plesiosauria can be deduced:

1. Even if it exists in the specimen studied by Cruickshank *et al.* (1991), a bony duct linking the caudal vomerian fenestrae and the external nares is not a general feature in the Plesiosauria. Furthermore, even if this duct does exist in the specimen studied by Cruickshank *et al.* (1991), in

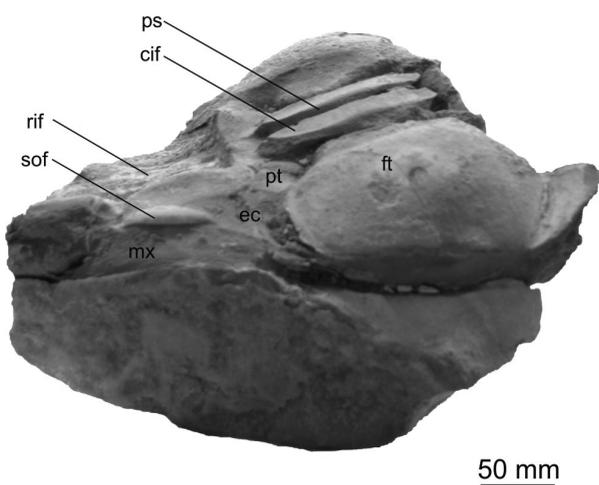


Fig. 5. SMNK-PAL 3898, portion of the cranium as preserved, in ventrolateral view (ventral side up). Note the dorsostral orientation of the openings of the caudal interpterygoid fenestrae preserved as internal moulds. Abbreviations as for Fig. 1.

our opinion and in the light of the present study these authors failed to prove that the external nares were exclusively linked to the caudal vomerian fenestrae. The consequences of the interpretation of these authors for the inhalation method of the animals, weighed against the problematic interpretation of CAT scans, are difficult to accept. Obligatorily inhalation and exhalation with the mouth agape requires that the whole head is lifted above the surface of the water. While conceivable, this type of inhalation and exhalation would have been highly unsuited for a group that survived world wide throughout the Jurassic and Cretaceous without modification of their palatal anatomy, and included animals reaching 15 meters in length, with an estimated head length of 3 meters (Buchy *et al.* 2003; Noè *et al.* 2004).

2. The caudal interpterygoid fenestrae are the only fenestrae in the palatal area that are osteologically and topographically constant within the Plesiosauria. O'Keefe & Wahl (2003) mention two specimens lacking caudal interpterygoid fenestrae. The first comprises cranial fragments, including the caudal portion of the palatal area and occipital condyle in articulation, and articulated vertebrae; it was referred to the cimoliasaurid plesiosaur *Tatenectes* (O'Keefe & Wahl 2003, figs 2–4). This specimen is poorly preserved, the cranial fragments are very fragmentary and the absence of caudal interpterygoid fenestrae could easily be the result of breakage. A second cranium more obviously lacking caudal interpterygoid fenestrae, from the Oxfordian of Cuba, is illustrated by O'Keefe & Wahl (2003, fig. 6). In our opinion, this specimen probably represents a thalattosuchian crocodile (compare e.g. with Vignaud 1995, fig. 42).
3. The external nares, the caudal vomerian fenestrae, and probably also the rostral vomerian fenestrae open directly into the rostral cavity. The caudal interpterygoid fenestra opens into the interorbital cavity and its caudal prolongation between the subtemporal fossae.
4. The external nares open internally in a caudal direction, while the caudal interpterygoid fenestrae open internally in a rostradorsal direction. The direction of the internal opening of the external naris and the caudal interpterygoid fenestra are in line rostrocaudally in all views. Between these openings, in the interorbital area, a longitudinal groove is present on the floor of the palate, therefore leaving the space for a duct linking the external naris and caudal interpterygoid fenestra. The groove is delimited by

- processes from the parietal, the frontal and/or prefrontal dorsally and the pterygoid ventrally. This system of processes strongly hints at the anchoring of fascias, which would then form a completely enclosed canal. The canal would therefore be protected against the bulging of the ocular muscles, and keep its internal volume independent from the movements of the eye.
5. Caudal to the orbit, a longitudinal dorsal process of the pterygoid separates the caudal interpterygoid fenestra from the subtemporal fossa. These processes would protect the integrity and the volume of a canal originating from the caudal interpterygoid fenestra against the bulging of the mandibular musculature. Similar to the independence of the medial canal from the eye, the latter process would also keep a canal originating from this fenestra independent from the mandibular movements.
 6. Such a duct linking the external naris and the caudal interpterygoid fenestra via the medial canal would have had a constant diameter along

its path, similar to the diameter of the external naris, and would fulfil all other requirements to be interpreted as a respiratory duct, being osteologically constant within the Order and independent of adjacent muscular activity inside the head.

The conclusion drawn here from the anatomy, as well as from Owen's (1865) and Williston's (1903) early demonstrations, is that the choanae in Plesiosauria are the caudal interpterygoid fenestrae. The respiratory duct was probably cartilaginous, housed in the rostral cavity, and the medial canal further caudally (Fig. 6). Plesiosauria therefore possessed a secondary palate, functionally if not osteologically, comparable to the secondary palate of crocodylians (Buffetaut *in* Ross 1989). The relatively small diameter of the external nares, compared to the size of the animal, is among the arguments against their involvement in respiration (Cruickshank *et al.* 1991; Taylor & Cruickshank 1993). However, proportionately they are no smaller than the nostrils of living crocodylians, which, in these reptiles, are considerably

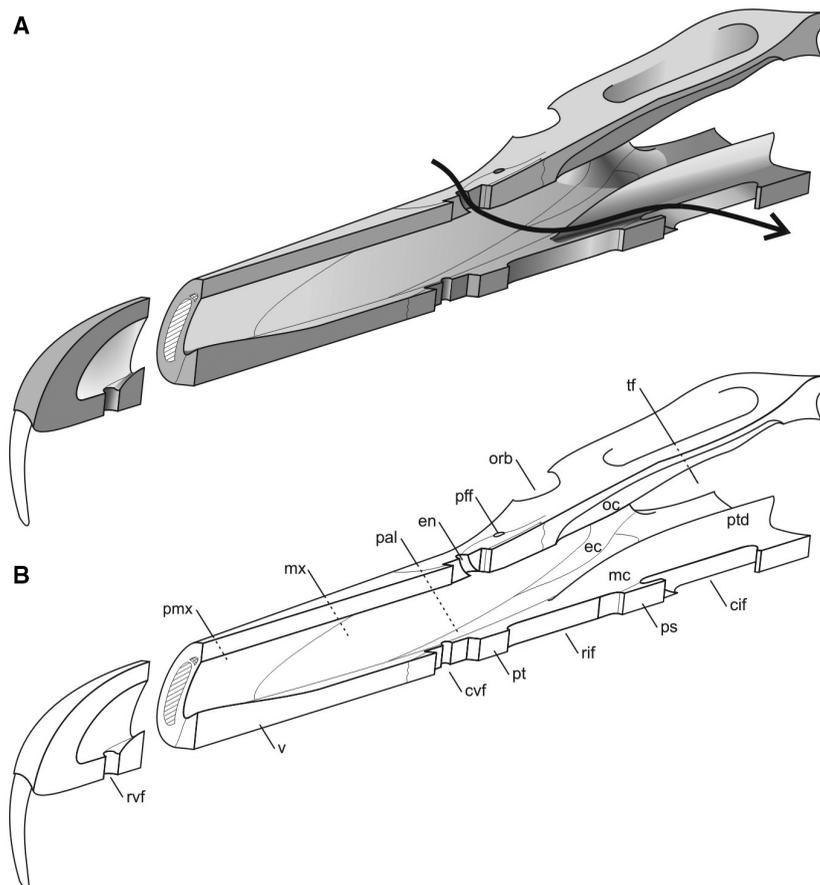


Fig. 6. 3D reconstitution of the internal cranial anatomy of the specimen SMNK-PAL 3861 as deduced from the cross-sections described herein. The braincase, the occipital area and the teeth (except the rostral-most one) are not shown for clarity. □ A. The probable air path from the external nares to the caudal interpterygoid fenestra. □ B. Line drawing. Abbreviations as for Fig. 1. Drawing conventions as for Fig. 3.

smaller openings than both the bony external nares and the primary and secondary choanae. Moreover, the oxygen requirements of the Plesiosauria are unknown to us, as are their physiology and behaviour in relation to respiration. Taylor (1992) describes sculpturing on the margins of the external nares of the pliosaur *Rhomaleosaurus zetlandicus*, indicating the existence of a muscle operating a narial valve, such that the narial passage could be closed during swimming. The relatively small size of the external nares could also be a compromise between oxygen requirements and the necessity to seal the openings during diving.

Additionally, by comparison with recent crocodylians (Mazzotti *in* Ross 1989), it is likely that a glottal valve sealed the opening of the trachea while swallowing (Cruickshank *et al.* 1991; Taylor & Cruickshank 1993).

What still has to be investigated is the mechanism of lung ventilation itself. Plesiosauria possessed girdles, both pectoral and pelvic, in shape of large ventral plates (see e.g. Brown 1981). A tight basket of gastralia was situated between these plates, which were additionally almost in contact with the ribs dorsolaterally. The venter was therefore enclosed, and respiratory movements of the thoracic region had a restricted amplitude. In principle, three options for respiration known from recent tetrapods are available for the Plesiosauria (Wood & Lenfant *in* Gans 1976; Perry 1983 and references therein):

1. A muscularized diaphragm similar to mammals.
2. A hepatic piston similar to crocodylians.
3. A gular pump combined with girdle movements as in turtles.

Which of these options were operational for the plesiosaur construction will be subject of further studies in order to solve the question on how inhalation and exhalation were performed.

Plesiosauria were marine animals (see e.g. Bardet 1995), therefore they must have had salt glands to excrete the excess salt, as is the case in all Recent marine reptiles and birds (Fänge *et al.* 1958; Schmidt-Nielsen 1979; Taplin & Grigg 1981; Pough *et al.* 1989; Hua & Buffetaut 1997; Noè 1999, 2001; Fernández & Gasparini 2000). The rostral cavity of Plesiosauria could have housed such a gland (or most likely a pair of glands), as its smooth internal margins suggests; the caudal vomerian fenestrae, formerly considered as the choanae, appear to be a likely candidate for its palatal apertures. The amount of excess salt obtained when feeding depends on the type of prey consumed: invertebrates are isoosmotic to sea water, therefore as prey they bring large amount of salt, while vertebrates usually maintain a low internal salt concentration (Schmidt-Nielsen 1979). A predator feeding on invertebrates therefore needs large salt glands, while a predator preying upon

vertebrates mainly has to eliminate the salt obtained by swallowing sea water together with the prey, and therefore its salt glands are smaller (see Schmidt-Nielsen & Kim 1964 about the artificial increase of the volume of the salt glands in birds in response to a hypersaline diet). The volume of the salt gland, as deduced from the volume of the rostral cavity relative to the size of the rostrum, could then be representative to some extent of dietary preferences.

Finally, the existence of a functional secondary palate in the Plesiosauria must be seen in an evolutionary perspective. The Pistosauridae is considered the sister-group of the Plesiosauria (Rieppel 1997a; Sander *et al.* 1997; Rieppel *et al.* 2002). Among the Pistosauridae, the cranial anatomy of *Pistosaurus* is poorly known, based mainly on casts of lost original material, while the skull of *Augustasaurus* is known by an excellent complete holotype specimen (Rieppel *et al.* 2002). Both taxa possessed a palatal anatomy similar to the Plesiosauria in the presence of well-developed caudal interpterygoid fenestrae, as well as retracted external nares (Edinger 1935; Sues 1987; Rieppel *et al.* 2002). The presence of a functional secondary palate similar to that hypothesised for the Plesiosauria can therefore be suggested, supporting the proposed relationships of the Pistosauridae with the Plesiosauria (Sander *et al.* 1997; Rieppel *et al.* 2002). A further argument in favour of the independence of the external nares and caudal vomerian fenestrae in the Eusauropterygia is that the caudal vomerian fenestrae in both *Pistosaurus* and *Augustasaurus* are located at a level caudal to the external nares (Rieppel *et al.* 2002). In the Nothosauria (Rieppel 1994; 1997b), being the proposed sister-group of the combined Pistosauridae and Plesiosauria (the Pistosauria of Rieppel *et al.* 2002), there is no caudal retreat of the external nares, and no interpterygoid fenestrae. Therefore they could not possess a functional secondary palate as described here, and their choanae were most likely the fenestrae located in a situation topographically and osteologically similar to the caudal vomerian fenestrae of the Plesiosauria (e.g. Rieppel 1997b). Provided the most recent cladograms dealing with sauropterygian relationships are correct (Sander *et al.* 1997; Rieppel 1997a; O'Keefe 2001; Rieppel *et al.* 2002), if the caudal vomerian fenestrae of all Eusauropterygia would be the choanae, these would have migrated caudally in the Pistosauria then rostrally in the Plesiosauria. In regard of an essential biological function like respiration this appears unlikely, but less in the case of the opening of a glandular system. The first embryological opening of Jacobson's organ is confluent with the primary choanae in Recent reptiles, and a caudal retreat of the choanae takes place later in ontogeny (Voeltzkow 1899a, b; Pasteels *in* Grassé 1970). The embryology of Recent reptiles would therefore explain the topographical and osteological similarities

between the choanae of the Nothosauria being also the opening of Jacobson's organ, and the opening of Jacobson's organ and/or salt glands in the Pistosauria under our functional analysis of the rostrum in this group.

The evolution of the secondary palate in the Plesiosauria and potentially the Pistosauridae must therefore have taken place after the dichotomy between them and the Nothosauria. The re-study of the internal cranial anatomy of the Nothosauria and other Triassic sauropterygian taxa in a functional context would help explain how the secondary palate, the soft structures associated with it, and the other palatal fenestrae of the Plesiosauria and soft structures aligned with them (e.g. salt glands) could evolve. This could reveal a more complicated early history for the Sauropterygia. As discussed by Sander *et al.* (1997), the actual diversity of Triassic sauropterygians is probably greatly underestimated due to their shallow marine to coastal habitat. We suggest that, in addition to searching for new material, the re-examination of known taxa in a functional perspective, in order to determine biomechanical options for locomotion, feeding, breathing, and other biological requirements, as defined e.g. by Hekner (1999) and Salisbury (2001), would be essential to clarify their relationships.

Acknowledgements. – It is our great pleasure to acknowledge Alex Cook (QM), and José Guadalupe López-Oliva (UANL-FCT) for access to the collections in their charge. This study benefited from fruitful discussions with Nathalie Bardet (Paris), Arthur Cruickshank (Leicester), Jeff Liston (Glasgow), Colin McHenry (Newcastle, Australia), David Martill (Portsmouth), Franck Métayer (Karlsruhe), Leslie Noè (Cambridge) and Michael Taylor (Edinburgh). Leslie Noè as well as an anonymous reviewer greatly improved our work thanks to their thoughtful comments.

This research was partly financed by the Deutsche Forschungsgemeinschaft (grants numbers FR 1314/4-1, FR 1314/6-1, FR 1314/8-1 and FR 1314/9-1), the von Kettner Foundation and the late Raymonde Rivoallan. Current financial support for SWS at The University of Queensland is provided by the Australian Research Council Linkage-Project Scheme (LP0347332), in association with the Queensland Museum, Land Rover Australia, Winton Shire Council and Isisford Shire Council.

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