

Paleoneurological evidence against a proboscis in the sauropod dinosaur *Diplodocus*

Preuve paléoneurologique contre la présence d'une proboscide chez le dinosaure sauropode *Diplodocus*

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Received 29 April 2004; accepted 3 November 2004

Available online 20 January 2006

Abstract

The dinosaur *Diplodocus* has a single, relatively large external bony narial orifice that is positioned far back between the orbits. In some mammals, such as elephants and tapirs, the caudal position of the narial opening is associated with a proboscis, so it has been suggested that *Diplodocus* possibly also had a trunk. In elephants, the facial nerve is large as it emerges from the brain. A branch of this nerve and a branch of the trigeminal nerve unite to form the proboscis nerve that supplies the muscles of the powerful and complex motor system of the trunk. In contrast to the situation in modern elephants, the absolute as well as the relatively small size of the facial nerve in *Diplodocus* (deduced from an endocranial cast) indicates that there is no paleoneuroanatomical evidence for the presence of an elephant-like proboscis in this genus.

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Résumé

Le dinosaure sauropode *Diplodocus* possède un orifice nasal osseux unique, relativement grand et situé loin en arrière, entre les orbites. Chez certains mammifères, tels que les éléphants et les tapirs, la position caudale de l'ouverture nasale est associée à la présence d'une trompe. Il a ainsi été suggéré que *Diplodocus* avait peut-être une trompe. Chez les éléphants, le nerf facial est remarquablement gros à sa base. Une branche de ce nerf s'unit à une du trijumeau pour former le nerf proboscisidial auquel le puissant et complexe appareil moteur de la trompe est dévolu. En comparaison avec l'éléphant actuel, la petite taille (relative aussi bien qu'absolue) du nerf facial chez *Diplodocus*, telle que l'on peut la déduire d'un moulage endocrânien, met en avant l'absence d'élément paléoneuroanatomique soutenant la présence d'une trompe éléphantine chez ce genre.

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Keywords: Dinosauria; Saurischia; Sauropoda; *Diplodocus*; Palaeobiology; Palaeoneuroanatomy

Mots clés : Dinosauria ; Saurischia ; Sauropoda ; *Diplodocus* ; Paléobiologie ; Paléoneuroanatomie

Abbreviations: AMNH, American Museum of Natural History New York; MB HMN, Humboldt Museum für Naturkunde, Berlin; YPM, Yale Peabody Museum, New Haven.

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1. Introduction

The famous sauropod dinosaur *Diplodocus* (Late Jurassic, western USA) has a single, relatively large bony narial orifice (Fig. 1B) that is positioned far back above the orbits (see Wilson and Sereno, 1998: Fig. 6). Bakker (1971) remarked that in some mammals, such as elephants and tapirs, the caudal position of the osseous narial opening is associated with a proboscis or trunk. Based on the resemblance between the foreheads of the elephant and *Diplodocus*, Bakker (1986) noted that *Diplodocus* possibly had a muscular trunk that attached at the

level of the bony narial orifice, descended along the snout, and hung in front of the muzzle (Fig. 1B). Although the hypothesis of trunk-bearing sauropods has not gained wide acceptance amongst paleontologists, they have been portrayed as such in popular books or exhibitions (e.g. Dixon, 1991).

The musculature of the face is non-existent amongst non-mammalian vertebrates. It has progressively differentiated in mammals to give, in particular, the sophisticated device of the human mimic (Dastugue, 1972). Accordingly, no bird and no crocodylian (at least amongst extant representatives) have anything comparable to an elephantine or tapiroid nose (and

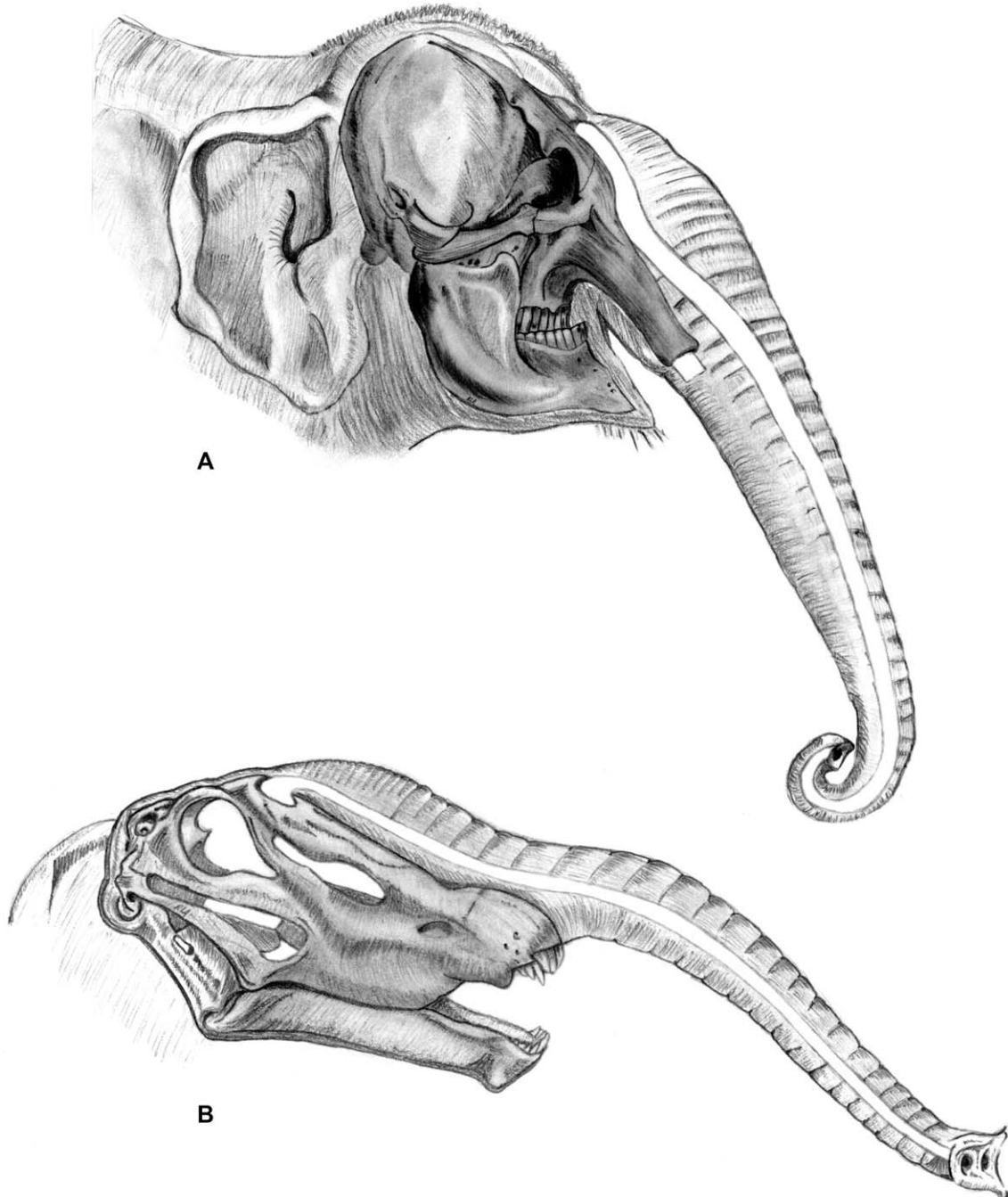


Fig. 1. Trajectory of the nasal conduit in right lateral view. **A.** In *Elephas* (Asian elephant). **B.** In a hypothetical proboscis-bearing *Diplodocus*.

Fig. 1. Trajectoire suivie par le conduit nasal en vue latérale droite. **A.** Chez *Elephas* (éléphant d'Asie). **B.** Chez un hypothétique *Diplodocus* muni d'une proboscide.

neither have any other living sauropsids). Therefore, the presence of a proboscis in sauropods is a level III inference in the context of the Extant Phylogenetic Bracket approach (Witmer, 1995, 1998) for reconstructing unpreserved attributes. This suggests that it is a priori a doubtful conjecture. However, the inference of a proboscis in *Diplodocus* may be justified if the causally associated osteological correlates of this novel soft-tissue structure are compelling. Hence, the question is whether any of the latter can be observed in *Diplodocus*.

2. The proboscis in extant and extinct mammals

The proboscis is a device in which the nose, while keeping its ventilation and sensory functions, is modified for seeking food or for prehension. Amongst mammals, a proboscis is not the exclusive appendage of elephants (Proboscidea: Elephantidae) because various other clades have independently evolved such a specialized narial structure (Boas and Paulli, 1908: pp. 47–50; Negus, 1958: pp. 217–218; Clifford and Witmer, 2002a; Clifford, 2003): the desmans (Insectivora: Talpidae), the elephant-shrews (Macroscelida: Macroscelididae), the solenodons (Deltatheridia: Solenodontidae), the tapirs (Perissodactyla: Tapiridae), the saiga antelope (Artiodactyla: Bovidae), and the elephant seals (Carnivora: Phocidae), to cite but a few examples of mammals with various diets.

In most cases, the proboscis is formed by the fusion of tissues of the upper lip with those of the nostrils into a fleshy appendage that extends in front of the incisors. The proboscis does not enclose bone (and therefore is unlikely to fossilize). Nonetheless, it generally contains cartilage all along its length, which has partially calcified in some taxa (talpids and macroscelidids). However, the nasal cartilage does not extend into the proboscis in elephants and tapirs (Boas and Paulli, 1908: p. 49).

The proboscis can be qualified as a prehensile organ only in elephants and tapirs (Boas and Paulli, 1908: p. 50). Due mainly to its shortness, the proboscis of tapirs cannot perform feats comparable to those of elephants. The mobility and flexibility of the proboscis of elephants allows it to be orientated in all directions so it can be used like a snorkel (ventilation) or to capture molecules traveling in the air that inform the animal about its environment (olfaction). Garnished by vibrissae and sensory cells disseminated in the skin, it is also a very sensitive tactile organ that can pick up small objects, as well as lift heavy loads. It is definitely a multi-purpose device that can dig, grasp plants or break boughs and carry them into the mouth, spray water, dust or mud on to various parts of the body, or be employed for communication, defense or offense.

The development of the proboscis correlates generally with osseous modifications that provide space for the proboscis and allow for its free movement. These include the widening of the bones of the face, but the most important of these key cranial characters remains the shortening of the nasals (Wall, 1980). The later transformation results in the retraction (and/or enlargement) of the bony narial opening(s). Therefore, the acquisition of a trunk (or another voluminous, muscular labionasal organ) is a strong factor in determining the general shape of

the skull. However, retracted nasals by themselves are not sufficient to warrant reconstruction of a trunk-like proboscis nor are their absence a proof to the lack of it (Clifford and Witmer, 2002b, 2004).

Maybe the first published suggestion of the presence of a proboscis in an extinct species is found in the historical study of the “Madrid *Megatherium*” (Xenarthra: Megatheriidae) by Cuvier (1796: p. 309). Subsequently, the existence of a proboscis has been suspected (more often than not rightly) in a variety of unrelated, non-proboscidean, extinct mammals that have various cranial configurations, but a comparable narial structure. These include *Palorchestes* (Marsupialia: Palorchestidae), *Dimyloides* (Insectivora: Dimylidae), *Brachycrus* (Artiodactyla: Merycoidodontidae), *Cadurcodon* (Perissodactyla: Amynodontidae), *Palaeotherium* (Perissodactyla: Palaeotheriidae), *Astrapotherium* (Astrapotheria: Astrapotheriidae), *Macrauchenia* (Litopterna: Macraucheniidae), *Pyrotherium* (Pyrotheria: Pyrotheriidae), and *Glyptotherium* (Xenarthra: Glyptodontidae).

3. The proboscis in dinosaurs

The theory of probosciferous dinosaurs, especially hadrosaurs (Ornithopoda: Hadrosauridae), was developed in a series of papers by Wilfarth (1938, 1939, 1940, 1948, 1949). He postulated that the beak and “hood” of the duck-billed dinosaurs were for the attachment of powerful muscles that controlled an air-breathing trunk. This was convincingly refuted by Sternberg (1939) who emphasized, in particular, the redundancy of the development of both elongated narial passages (actually the “hood”) and a proboscis.

Coombs (1975) stated that the presence of a proboscis for display (i.e. not highly maneuverable and not used for food gathering), like that of the male elephant seal, is quite possible in some sauropods, though there was no way to prove it on the basis of only the skull. Incidentally, Colbert (1993) noted that the sauropod jaws, gathering plant food at the end of a long, supple neck, would have functioned in a manner parallel to the terminal portion of the trunk of elephants. The long neck of sauropods would have enabled them to reach far and wide from a single standing position to gather their food, although in a much less supple fashion than the trunk of an elephant (Colbert, 1993; Martin et al., 1998).

Under these conditions, the development of a proboscis in a sauropod, such as *Diplodocus*, appears even more superfluous than it was for hadrosaurid dinosaurs. Indeed, the voluminous and energetically mobile trunk of elephants “compensates” for the shortness of their necks. It allows elephants, especially the Asian species, to feed from the ground without limiting them to the lower foliage (or forcing them to kneel). Thanks only to their trunk, elephants have a wide foraging area, from side to side and up and down.

On the basis of the backward movement and enlargement of the osseous narial openings, the existence of a trunk is commonly acknowledged in a number of quadrupeds in which the neck was not too short for the head to reach the ground. Ex-

amples include *Astrapotheria*, like *Astrapotherium* (Astrapotheridae), and *Litopterna*, like *Theosodon* (Macrocheniidae). Definitely, inferring the possession of a trunk for a fossil taxon is not a straightforward procedure and the possibility of the presence of a proboscis in sauropods, long-necked animals par excellence, must not be rejected a priori.

Recently, Witmer (2000, 2001a, 2001b) convincingly argued that the fleshy nostrils of dinosaurs were located far forward of where they are usually portrayed. On the cover of the issue in which the comprehensive study was published (Witmer, 2001a), a new flesh restoration of the head of *Diplodocus* was given. In some ways, this represents a middle outlook between the traditional reconstruction of the face of this animal and the trunk-bearing one, albeit the presence of a trunk in *Diplodocus* in particular, and in sauropods in general, was not specifically addressed.

4. Neurological data

4.1. Neuroanatomy of elephants

As the branchial apparatus atrophied throughout vertebrate evolution, the hyoid arch musculature progressively invaded

the face, taking its motor nerves along with it. In mammals this process formed the important facial musculature innervated by the facial nerve (Cordier, 1954). The elaboration of the facial muscles is concomitant with an increase in the numbers of fibres that are associated with the facial nerve (VII). In principle, this nerve innervates the totality of the muscles of the face, including those of the specialized devices such as the trunk. As extant proboscis-bearing mammals have highly developed intrinsic nasal muscles (Clifford and Witmer, 2002b), their facial nerve is correlatively enlarged.

The anatomy of the elephants has been the subject of numerous studies over a long period of time. The great size of the facial nerve, as well as the relation of this with the trunk, was remarked on as early as the first real scientific studies on elephants (see e.g. Blair, 1710). In both genera of extant elephants, the facial nerve is very large (Fig. 2B). It emerges from the cranium by a large stylomastoid foramen. According to the unrivaled study of Boas and Paulli (1925) on the Indian elephant, the facial nerve is one centimeter broad a little ventral to the jaw joint, where it comes into view after having passed under the parotid gland. The root of the facial nerve is similarly large in the baby Indian Elephant specimen studied by Dexler (1907: Figs. 10, 12 and 20; Pl. 1).

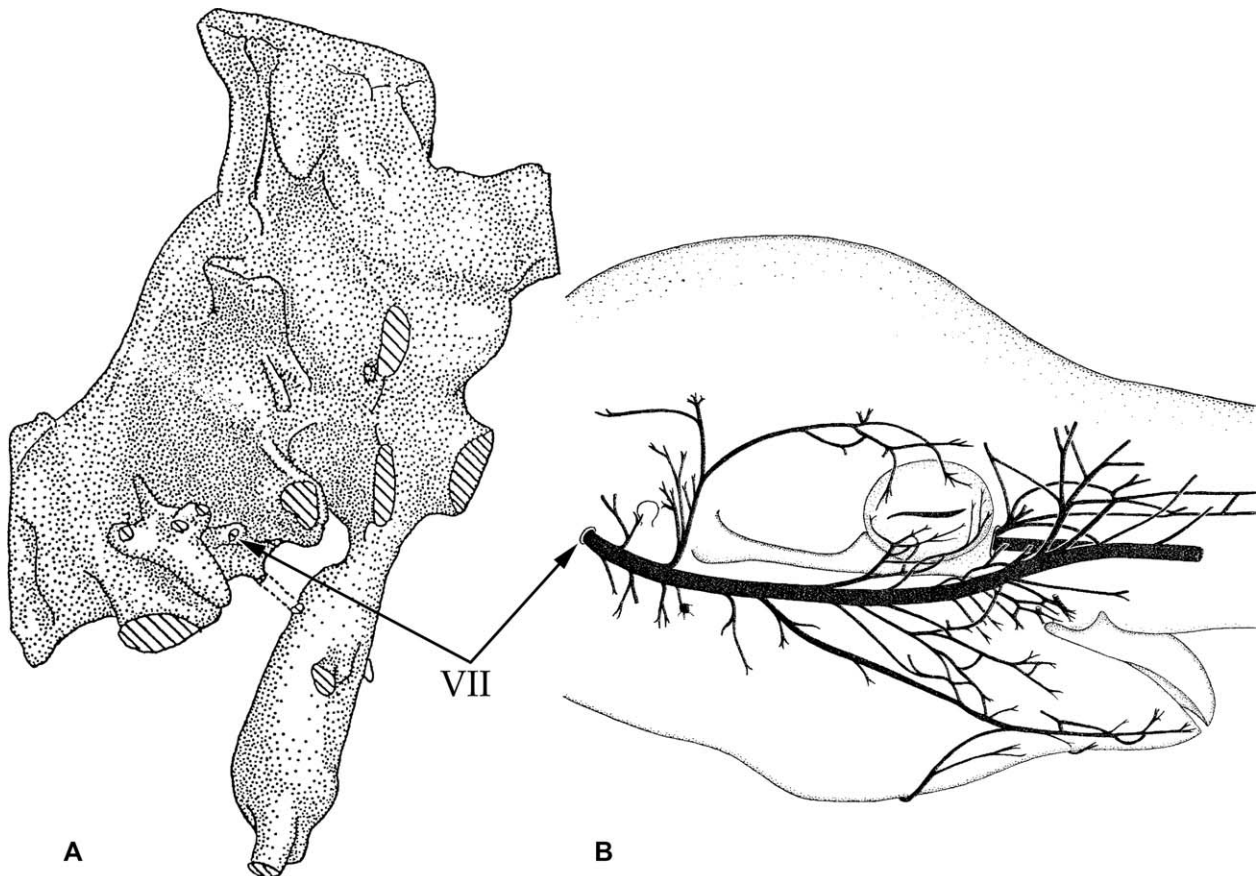


Fig. 2. Palaeoneuroanatomical comparisons in right lateral view. **A.** Endocranium of *Diplodocus* (AMNH 694) showing the diminutive size of the facial nerve (VII). **B.** Head of a fetal *Loxodonta* (African elephant) displaying the distribution of the facial nerve (VII) (after Eales, 1926).

Fig. 2. Comparaisons paléoneuroanatomiques en vue latérale droite. **A.** Moulage endocrânien de *Diplodocus* (AMNH 694) montrant la petite taille du nerf facial (VII). **B.** Tête d'un fœtus de *Loxodonta* (éléphant d'Afrique) présentant la distribution du nerf facial (VII) (d'après Eales, 1926).

A branch of the facial nerve, the ramus maxillaris, unites with the infra-orbital (maxillary) division of the trigeminal nerve (V_2) to form the proboscoidal nerve that extends along the lateral face of the proboscis deep in the maxillolabialis muscle. Its facial component supplies the numerous muscular bundles of the powerful and complex motor system of the proboscis whereas its trigeminal fraction mainly innervates the follicles of sensory hairs distributed at the tip of the trunk (Sprintz, 1952; Mariappa, 1986). In elephants, the ramus maxillaris is so considerably developed that it appears to be a direct continuation of the root of the facial nerve.

Due to the importance of the innervation of the proboscis, the area covered by the facial nerve is immensely much larger in elephants than in mammals not possessing a proboscis, which is clearly indicated by the expansion of its nucleus with large neurons and its huge root (Verhaart, 1962: p. 512; Cozzi et al., 2001). Thus, tapirs, which have developed a mobile proboscis akin to that of elephants, but shorter and not nearly as useful, also have a remarkably large facial nerve (Boas and Paulli, 1908: Pl. 7; Witmer et al., 1999: Fig. 2A, 4).

4.2. Paleoneuroanatomy of *Diplodocus*

In living reptiles the head musculature is essentially represented by the muscles of the masticatory apparatus, which can be divided into two groups on the basis of their innervation: the facial group and the trigeminal group (Guibé, 1970). It should be remarked that, in crocodiles, the narial muscles are not innervated by the facial nerve, but instead by the autonomic nervous system (Bellairs and Shute, 1953). However, an elephant-

like proboscis cannot naturally function in an involuntary manner and it cannot, therefore, depend on the autonomic system.

AMNH 694 includes a partial skull of a young individual of *Diplodocus*, the artificial endocast (Fig. 2A) of which was described by Osborn (1912: Fig. 16), Hopson (1979: Fig. 16), and Galton (1985: Fig. 7U). The optic nerve (II) lies far below the level of the olfactory peduncle (I). Above the optic nerve, on the side of the forebrain swelling is a large “process” that was probably for the trochlear nerve (IV) and the anterior cerebral vein. The oculomotor nerve (III) exited through the more ventral, slit-like, fenestra metoptica, between the optic and trigeminal nerves (V), dorsal to the pituitary fossa. A dorsoventrally elongate process represents the trigeminal nerve. Foramina for the abducens nerve (VI) are seen caudoventral to the trigeminal nerve and, continuing through the dorsum sellae, into the pituitary fossa (a third foramen on the rostral side of the pituitary fossa may also have been for the abducens). Caudal to the trigeminal nerve is the small root of the facial nerve (VII) that is linked to the vestibular region (Fig. 2A). Assuming that the facial nerve filled the facial foramen, which is an option that at worst gives an overestimation, then its diameter was about 1.5 mm in AMNH 694. This specimen is genuinely representative of *Diplodocus* with respect to the smallness (both absolutely and relatively speaking) of the facial nerve foramen. In fact, this observation is not biased by ontogenetic variability or individual variation because it has proved to be fairly consistent in various braincases pertaining to this genus (L.M. Witmer, personal communication).

The presence of a proboscis has also been suspected for other sauropods (Macronaria) with a relatively short face and large narial openings in the upper part of the skull, such as

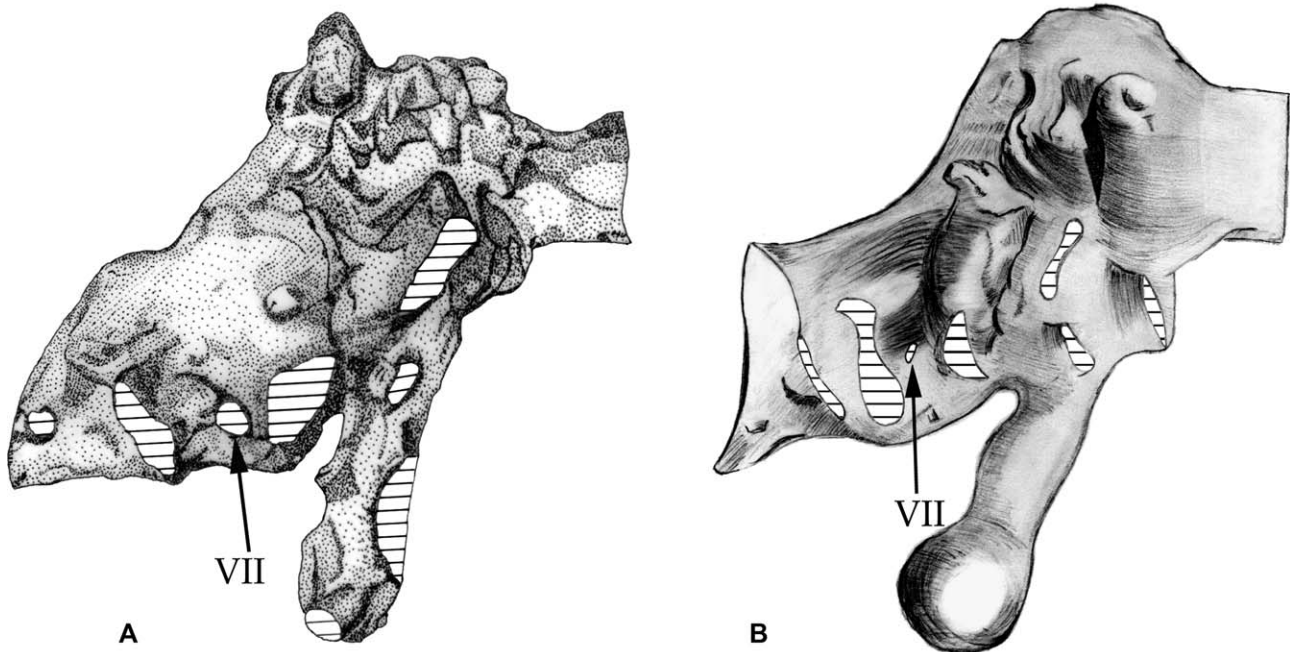


Fig. 3. Endocranial casts of other sauropod taxa for which the presence of a proboscis has been assumed. **A.** *Brachiosaurus* (MB HMN S. 66). **B.** *Camarasaurus* (YPM 1905). VII indicates the cast of the foramen for the pathway of the facial nerve.

Fig. 3. Moulages endocrâniens d'autres taxons de sauropodes pour lesquels la présence d'une proboscide a été suggérée. **A.** *Brachiosaurus* (MB HMN S. 66). **B.** *Camarasaurus* (YPM 1905). VII indique le moulage du foramen pour le passage du nerf facial.

Brachiosaurus and *Camarasaurus*. The foramen that accommodated the root of the facial nerve is much larger in *Brachiosaurus* than in *Diplodocus*: more than 6 mm in diameter (Fig. 3A). In *Camarasaurus*, on the contrary, the facial nerve, close to the acoustic region, was relatively small in diameter: less than 3 mm (Fig. 3B).

5. Discussion and conclusion

Ashton and Oxnard (1958) demonstrated that, in mammals, the size of the division of the infraorbital nerve (which accommodates sensory fibres connected with the integument, the vibrissae of the upper lip, and the side of the nose) is related to the development of specialized facial features such as the mystacial vibrissae and the disc-like ending of the pig snout. Similarly, Adam and Berta (2002) stated that a large infraorbital foramen (that allows for the passage of the infraorbital vessels and the infraorbital nerve) in pinnipedimorphs reflect an enlargement of the maxillary branch of the trigeminal nerve in relation to increased vibrissal innervation. Wall (1980: p. 971) remarked on the large diameter of the infraorbital canal of *Cadurcodon* (Perissodactyla: Amynodontidae) and concluded that the increased complexity of a proboscis, and its function as a sensitive tactile organ, probably resulted in an increase in the size of the infraorbital vessels and nerve, and therefore of the canal itself. In fact, the infraorbital vessels irrigate the nose and upper lip and are the major blood supply of the proboscis in the tapir (Witmer et al., 1999).

In much the same way, the small diameter of the canal that accommodated the facial nerve root in *Diplodocus* indicates that there is no paleoneuroanatomical evidence for the presence of musculature associated with an elongated, elephant-like proboscis in this genus. In fact, this absolute small size evidently constrains the number of axons that the facial nerve can contain (especially if each nervous fibre has a large individual diameter) and therefore the ability of the facial nerve to transmit information.

The data cited above is consistent with other anatomical characteristics such as the absence of any marks of muscular attachment in the narial area (Bakker, 1986). On the whole, the evidence is for a moderately developed, basically reptilian, skull musculature in sauropodomorphs in general (Christiansen, 2000) and in *Diplodocus* in particular (Haas, 1963; Barrett and Upchurch, 1994). In fact, the absence of observable muscle scars on the skull bones surrounding the narial opening in sauropods is a clear-cut argument against the existence of a heavily muscled trunk.

We conclude that the anatomy of the head and of the endocranial cavity unambiguously indicates that a proboscis (at least a large muscular one) was not present in *Diplodocus*. This also holds true for *Camarasaurus*, which had necessarily a small facial nerve, but not for *Brachiosaurus* (although the presence of a proboscis in the latter genus has not been convincingly argued, this hypothesis remains).

Acknowledgements

We thank M.J. Benton (University of Bristol, Bristol), K.L. Martin (Pepperdine University, Pepperdine) and P. Tassy (Muséum national d'Histoire naturelle, Paris) for their comments on this paper. PMG thanks W.D. Heinrich (Humboldt Museum für Naturkunde, Berlin), D. Brinkman and L.K. Murry (Yale Peabody Museum, New Haven), and M. Norell (American Museum of Natural History, New York) for assistance while studying endocasts from Tendaguru sauropods, *Camarasaurus*, and *Diplodocus*, respectively. L.M. Witmer (Ohio University, Athens) kindly shared information based on his own observations on the consistency of the small size of the facial nerve foramen in *Diplodocus*. M. Moser (Staatliches Museum für Naturkunde, Stuttgart) provided us with a copy of Dexler's paper.

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