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Neurovascular system and dental renewal in the rostrum of Spinosauridae: new descriptions and implications on non-olfactive snout sensitivity of dinosaurs

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Reconstitution de deux spécimens adultes de *Cristatusaurus lapparenti* Taquet & Russell, 1998, pêchant depuis la rive et utilisant les récepteurs sensoriels de leur museau pour chasser de petits cœlanques. Illustration originale d'Alain Bénéteau/*Life restoration of two adult individuals of* Cristatusaurus lapparenti *Taquet & Russell, 1998, fishing from the bank and using their snout sensitive receptors to hunt small coelancanths. Original illustration by Alain Bénéteau*.

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Neurovascular system and dental renewal in the rostrum of Spinosauridae: new descriptions and implications on non-olfactive snout sensitivity of dinosaurs

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*A tribute to **Alain Bénéteau**, whose collaboration was rich and sincere, reflecting his wonderful work in paleoillustration throughout these years. He was able to show that art and science could be combined admirably, and that this alchemy is the best key to representing "lost worlds".*

*In memory of Professor **Philippe Taquet**, for the discovery and the first descriptions of these dinosaurs, for his support and his precious encouragement throughout my research.*
Thank you for your trust and our passionate discussions about Cuvier, old books and the most beautiful creatures the Earth has ever borne. Your broad legacy to science will continue to inspire generations of researchers, and you will forever remain my mentor in Palaeontology.

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ABSTRACT

The morphological analogy between the Spinosauridae and crocodilians rostrum has been widely documented. More recently, the supposed existence in Spinosauridae of specialized sensory organs such as those encountered in crocodilians (called ISOs for *Integumentary Sensorial Organs*) has been advanced by some authors. However, no complete representation of the neurovascular network in Spinosauridae rosette had yet been described and the association between dense neurovascular branching and skin sensitivity remained only a hypothesis. The amazing internal preservation of the premaxillae of *Cristatusaurus lapparenti* Taquet & Russell, 1998 and *Spinosaurus maroccanus* Russell, 1996 from the MNHN of Paris finally gives us now a precise idea of the situation. We show by our tomographic results one of the best-preserved neurovascular complex discovered in a dinosaur and the very first complete in a Spinosauridae with the mature specimen of *Cristatusaurus lapparenti*. We found that the volume of the neurovascular system, the size of the foramina that coincides admirably with that of the underlying branches, and the complexity of the observed ramifications represent additional evidence supporting the hypothesis of a hypersensitivity of the rosette of these animals. Comparisons with other extinct and modern creatures that have developed efficient sensory structures on the front of their snouts were also made. In addition, our results tend to show a particularly high rate of tooth replacement in Spinosauridae from a very young age.

KEY WORDS
Spinosauridae,
Dinosauria,
Cristatusaurus,
Spinosaurus,
neurovascular,
sensitivity,
premaxillae,
sensorial organs,
foramen,
teeth.

RÉSUMÉ

Système neurovasculaire et renouvellement dentaire du rostre des Spinosauridae : nouvelles descriptions et implications sur la sensibilité non-olfactive du museau des dinosaures.

L'analogie morphologique entre le rostre des Spinosauridae et des crocodiliens a été largement documentée. Plus récemment, l'existence supposée chez les Spinosauridae d'organes sensoriels spécialisés tels que ceux rencontrés chez les crocodiliens (appelés ISO pour *Integumentary Sensorial Organs*) a été avancée par certains auteurs. Cependant, aucune représentation complète du réseau neurovasculaire chez la rosette des Spinosauridae n'avait encore été décrite et l'association entre une ramification neurovasculaire dense et la sensibilité cutanée ne restait qu'une hypothèse. L'étonnante conservation interne des prémaxillaires de *Cristatusaurus lapparenti* Taquet & Russell, 1998 et *Spinosaurus maroccanus* Russell, 1996 du MNHN de Paris nous donne enfin une idée précise de la situation. Nous montrons par nos résultats tomographiques l'un des complexes neurovasculaires les mieux conservés découverts chez un dinosaure et le tout premier complet chez un Spinosauridae avec le spécimen mature de *Cristatusaurus lapparenti*. Nous avons constaté que le volume du système neurovasculaire, la taille des foramens qui coïncide admirablement avec celle des branches sous-jacentes et la complexité des ramifications observées représentent autant d'indices supplémentaires soutenant l'hypothèse d'une hypersensibilité de la rosette de ces animaux. La comparaison avec d'autres créatures disparues et modernes ayant développé des structures sensorielles performantes sur le devant de leur museau a également été faite. De plus, nos résultats tendent à montrer un taux de remplacement dentaire particulièrement élevé chez les Spinosauridae dès le plus jeune âge.

MOTS CLÉS
Spinosauridae,
Dinosauria,
Cristatusaurus,
Spinosaurus,
neurovasculaire,
sensibilité,
prémaxillaires,
organes sensoriels,
foramen,
dents.

INTRODUCTION

Previous research has shown that the largest representative of Spinosauridae, *Spinosaurus aegyptiacus* Stromer, 1915, had a highly developed neurovascular network in its muzzle (Dal Sasso *et al.* 2009; Ibrahim *et al.* 2014). The morphological analogy between the Spinosauridae and crocodilians rostrum has been widely documented (Taquet 1984; Rayfield *et al.* 2007; Brazaitis & Watanabe 2011; Cuff & Rayfield 2013; Ibrahim *et al.* 2014). The lateral flattering and the antero-posterior elongation of the snout resemble the arrangement encountered in crocodilians, pushed to the extreme in the gharial, *Gavialis gangeticus* (Gmelin, 1789). The teeth of the Spinosauridae are also very similar to those of the crocodilians, to such an extent that it is sometimes difficult to differentiate them. The evolutionary convergences between Spinosauridae and crocodilians probably do not stop there; more recently, the supposed existence in Spinosauridae of specialized sensory organs such as those encountered in crocodilians has been advanced by Dal Sasso *et al.* (2009). The complex neurovascular network revealed by the CT scans of our three specimens of Spinosauridae was therefore the seat of blood vessels, but also and above all probably of the maxillary branch of the trigeminal nerve (*V2*). This branch being essentially sensitive (and non-olfactive), the fact that the muzzle of these animals (and the rosette in particular) was extremely sensitive is beyond doubt. A comparable network has been described in crocodylomorphs (Leitch & Catania 2012; Di-Poï & Milinkovitch 2013; George & Holliday 2013; Bowman *et al.* 2022) and even in pliosaurs (DeGusta *et al.* 1999; Foffa *et al.* 2014).

We assess and discuss the degree of cutaneous sensitivity in Spinosauridae compared to other extinct or modern vertebrates that have developed efficient sensory structures on the front of their snout. We hypothesize that the density of foramina on the front part of the snout and the degree of branching of the sensory channels are directly related to the non-olfactive snout sensitivity (Langner & Scheich 2009; Cunningham *et al.* 2010; Amendano *et al.* 2021; Lessner *et al.* 2023; Miyamae *et al.* 2024).

We subject our hypothesis to empiricism by quantitative observations that can not only show that Spinosauridae effectively have ultrasensitive snout, but also that the latter reflects the compensation of another sense otherwise diminished for environmental or morphological reason rather than to an aquatic or semi-aquatic lifestyle/diet, as commonly suggested. Indeed, many clearly terrestrial and/or not necessarily piscivorous taxa have performed in the development of snouts covered with sensory receptors (especially mechanoreceptive). For example, the oviparous mammals Monotremata Bonaparte, 1837 like *Tachyglossus aculeatus* Shaw, 1792 with their long snout (Gregory *et al.* 1989; Manger & Pettigrew 1995; Langner & Scheich 2009; Doneley & Sprohnle-Barrera 2021), the moles (Crumpton & Thompson 2013) or even many birds such as the kiwis or the ibises are concerned (Cunningham *et al.* 2007, 2010, 2013).

THE VERTEBRATE NEUROVASCULAR SYSTEM

Amniota Haeckel,1866 have developed a large number of cutaneous sensory structures, glands and organs over the course of evolution. Examples include the lateral line of bony fishes (Bleckmann 2006; Bleckmann & Zelick 2009; Coombs *et al.* 2014; Webb 2023) or the ampullae of Lorenzini of sharks for electroreception (Murray 1960; Kalmijn 1972; Josberger *et al.* 2016; Wueringer *et al.* 2021), the vomeronasal organs of snakes for olfaction and chemoreception (Halpern & Frumin 1979; Takami 2002; Erudaitius *et al.* 2024), and the clusters of specialized cells of mammals and Sauropsida Huxley, 1864 with highly varied functions (Romer 1956; Butler & Hodos 2005; Crowe-Riddell & Lillywhite 2023; Lessner *et al.* 2023; Miyamae *et al.* 2024).

The shape, arrangement, size and location of these structures vary from one group to another, but they all have one thing in common: they are connected to afferent nerve fibers that send electrical signals back to the animal's central nervous system. The environmental stimuli to which they are sensitive depend of their function: mechanoreception (for the most part), electroreception, chemoreception, magnetoreception, photoreception, etc. Sometimes, the same organ can send several of these informations simultaneously, like for the ISOs (Integumentary Sensorial Organs), specific to crocodilians and which we will develop further (Soares 2002; Brazaitis & Watanabe 2011; Leitch & Catania 2012; Di-Poï & Milinkovitch 2013). We will focus here on the receptors located on the front of the skull of the animals, since the object of the present research focuses on the neurovascular network of the premaxillae of Spinosauridae. More precisely, we will deal with those which are connected to the nerve fibers of the trigeminal nerve.

Interestingly, for current species, we can easily make the link between superficial sensory organs and the bony foramina on the snout in birds, crocodilians, etc. (Berkhoudt 1976; Soares 2002; Cunningham *et al.* 2007, 2010, 2013; Di-Poï & Milinkovitch 2013; Moore *et al.* 2017; Amendano *et al.* 2021). However, the absence of foramina on the bone does not necessarily mean an absence of sensitivity since it can also be found on a horny structure of the snout as in the platypus (Scheich *et al.* 1986; Gregory *et al.* 1988; Manger & Pettigrew 1995; Langner & Scheich 2009) or even specialized soft structures as in the elephant's trunk (Rasmussen & Munger 1996; Dagenais *et al.* 2021; Deiringer *et al.* 2023), the star-nosed mole (Grand *et al.* 1998; Sawyer & Catania 2016), the snout of the sirenians (Reep *et al.* 2001; Moore *et al.* 2022) or the naked mole rat (Crish *et al.* 2016). Luckily, most of the dinosaurs and the Spinosauridae in particular show a density of well-identifiable foramina on their snout (Berkhoudt 1976; Charig & Milner 1997; Taquet & Russell 1998; Sereno *et al.* 1998; Dal Sasso *et al.* 2005; Ibrahim *et al.* 2014; Barker *et al.* 2017; Bouabdellah *et al.* 2022).

The afferent nerve fibers transmitting sensory information from the jaws (including teeth and tongue) are part of branches of the same nerve, namely the trigeminal nerve (cranial nerve V). It is a character homologous to all *Vertebrata* Lamarck, 1801 (Murakami & Kuratani 2008), from *Agnatha* Cope, 1889 such as lampreys to *Osteichthyes* Huxley, 1880 and *Tetrapodomorpha* Ahlberg, 1991. This nerve has mostly sensory but also motor fibers. The sensory (or afferent) fibers transmit environmental information to the brain following surface stimuli (dental pain, tactile pressure, temperature differences, etc.) while the motor (or efferent) fibers transmit electrical impulses to the jaw muscles to contract the muscles to cause voluntary movement (chewing). We are interested here in the sensory aspect of this nerve V to discuss the non-olfactory sensitivity of the muzzle of Spinosauridae.

Several kinds of sensory organs located in the snout have developed during the evolution of tetrapods. They may contain chemoreceptors (olfaction), mechanoreceptors, thermoreceptors and electroreceptors. Mechanoreceptors are by far the most common on the snout of animals and they are innervated by the trigeminal nerve, which evolved in parallel in several clades of tetrapods. From the brain, the trigeminal nerve originates from the trigeminal ganglion and divides into three major branches or rami (Romer 1956): 1) the ophthalmic branch or *ramus ophtalmicus* (*V1*) passes over or in the orbit. It has a sensitive role and supplies the anterior skin of the snout; 2) the maxillary branch or *ramus maxillaris* (*V2*) has a sensitive role as well and sends to the brain the sensitive information from the skin of the pre- and maxillary region of the snout, the upper lips and teeth. It runs along the alveolar margin, passing under the orbit; and 3) the mandibular branch or *ramus mandibularis* (*V3*) extends along the mandible in the Meckel's canal and then goes through the Meckel's foramen to the tip of the lower jaw. It provides information about sensitive stimuli (lower lips and teeth, but also the external auditory canal, tongue and oral cavity) and has a mechanical function as well. The anterior portion of the upper jaw is innervated by ophthalmic and/or maxillary branches of the trigeminal nerve (Butler & Hodos 2005). These branches correspond to the neurovascular complex observed in the snout of Spinosauridae and other theropods.

The integumentary sense organs (ISOs) system has been particularly studied in last years in living crocodilians. The first in depth work on these specific sensory structures was from Soares (2002) in living alligators. Considered initially solely as mechanoreceptors adapted to feel vibrations in the water-air interface, these organs were then called DPRs (Dome Pressure Receptors). It was shown that the dark domes found on the scales of the alligators (ISOs) were therefore a vital utility for identifying aquatic prey, especially at night, when the eyes cannot be used (Soares 2002). Recent studies showed that the ISOs in crocodiles evolved in mechanosensory but also thermo-, chemo-, and electrosensory functions, even exceeding the ultra-mechanoreceptor sensitivity of the highly innervated fingertips of primates, including humans (Di-Poï & Milinkovitch 2013).

MATERIAL AND METHODS

Superficially, the fossils retained for this study present foramina and other structures described below. Tomography allowed us to identify the underlying neurovascular network. The material consists in fossils from two taxa: *Cristatusaurus lapparenti* Taquet & Russell, 1998 (MNHN.F.GDF365, MNHN.F.GDF366) and *Spinosaurus maroccanus* Russell, 1996 (MNHN.F.SAM124; Taquet & Russell 1998), both housed in the paleontology collections of the Muséum national d'Histoire naturelle, in Paris. The *Cristatusaurus lapparenti* fossils belong to two different individuals from the

Tegama Formation (Aptian, Early Cretaceous) of Gadoufaoua (Niger): two unfused premaxillae and a fragment of the right maxilla from a smaller animal (MNHN.F.GDF366), and two other more massive premaxillae from an adult (MNHN.F.GDF365), allowing some ontogenetic considerations for this genus. The *Spinosaurus maroccanus* material consists of the two premaxillae and two incomplete maxillae from the Albian of Gara Samani, on the northwestern edge of the Tademaït in the Algerian Sahara (Taquet & Russell 1998).

CT scanning of fossil specimens MNHN.F.GDF365, MNHN.F.GDF366 and MNHN.F.SAM124 were performed at the X-ray Tomography Imagery Platform AST-RX (Accès Scientifique à la Tomographie par Rayons X) of the MNHN, using a GE Sensing and Inspection Technologies phoenix|x-ray v|tome|x L240-180 CT scanner. All the data were optimized (rotation, crop and contrast correction) with ImageJ v.1.51 (Schneider *et al.* 2012), resulting in 16 bits TIFF images.

MNHN.F.GDF365 (premaxillae): The scan was acquired with an isotropic voxel size of 0.10599047 mm under a voltage of 185 kV and a current of 450 µA (stack of 1068 slices).

MNHN.F.GDF366 (right maxillary): The scan was acquired with an isotropic voxel size of 0.05957385 mm under a voltage of 150 kV and a current of 300 µA (stack of 1860 slices).

MNHN.F.GDF366 (premaxillae): The scan was acquired with an isotropic voxel size of 0.06263297 mm under a voltage of 155 kV and a current of 350 µA (stack of 965 slices).

MNHN.F.SAM124 (maxillae): Due to the size of the specimen, two scans were acquired with an isotropic voxel size of 0.13000978 mm under a voltage of 178 kV and a current of 425 µA (stacks of 1699 and 1781 slices).

MNHN.F.SAM124 (premaxillae): The scan was acquired with an isotropic voxel size of 0.13423581 mm under a voltage of 185 kV and a current of 460 µA (stack of 1843 slices).

Furthermore, two extant crocodilians were employed for the purpose of comparison:

A skull and mandible of a *Gavialis gangeticus* (Gmelin, 1789) from the Natural History Museum of Geneva (MHNG S14.25). CT data of this specimen was performed at the Hôpitaux Universitaires de Genève (HUG), using a Siemens Biograph 128 Edge CT scanner with an isotropic voxel size of 0.222656 mm under a voltage of 125 kV and a current of 140 µA (stack of 3361 slices).

A CT dataset of a skull with mandibles from *Crocodylus moreletii* (Duméril & Bibron, 1851) was obtained from DIGIMORPH. This specimen, a female adult crocodile, came from the Gladys Porter Zoo in Brownsville, Texas. It was made available to The University of Texas High-Resolution X-ray CT Facility for scanning courtesy of the Texas Memorial Museum Vertebrate Paleontology Laboratory (specimen number TMM M-4980). Funding for scanning was provided by a National Science Foundation Digital Libraries Initiative grant to Dr. Timothy Rowe of The University of Texas at Austin (USA). This specimen was scanned by Matthew Colbert on 21 August 2003 along the coronal axis for a total of 663 slices. Each slice is 0.5 mm thick, with an interslice spacing of 0.5 mm.

Segmentations of these datasets were completed at the 3D Imaging Facilities Lab of UMR 7207 CR2P (MNHN-CNRS-SU), using the Mimics Innovation Suite (v.20, Materialise).

ABBREVIATIONS

Institutional abbreviations

BHI	Black Hills Institute, Hill City, South Dakota;
BMNH	British Museum of Natural History, London;
FMNH	Field Museum of Natural History, Chicago;
HUG	Hôpitaux universitaires de Genève;
MHNG	Muséum d'Histoire naturelle de Genève;
MNHN	Muséum national d'Histoire naturelle, Paris;
MNN	National Museum of Niger, Niamey;
MSNM	Museo di Storia Naturale di Milano;
TMM	Texas Memorial Museum, Austin;
CR2P	Centre de recherche en Paléontologie de Paris, MNHN;
SU	Sorbonne Université, Paris;
CNRS	Centre national de la recherche scientifique, Paris.

Other abbreviations

CT	computed tomography;
DPRs	dome pressure receptors;
ISOs	integumentary sensory organs.

DESCRIPTIONS AND RESULTS

Originally, Taquet (1984) described unknown Spinosauridae remains from two different individuals, apparently belonging to a same taxon from the Aptian of Gadoufaoua locality in Niger: supposedly dentaries, which were eventually identified as premaxillae some years later by Kellner & Campos (Kellner & Campos 1996). They made a description of both specimens with a discussion on teeth morphology and serrations. Taquet & Russell (1998) named this new taxon *Cristatusaurus lapparenti* and attempted to differentiate all then known Spinosauridae taxa based on teeth serrations and on the morphology of the snout. The authors differentiated *Cristatusaurus* Taquet & Russell, 1998 from *Spinosaurus* Stromer, 1915 and *Irritator* Martill, Cruickshank, Frey, Small and Clarke, 1996 by the fact that the teeth are serrated in the former genus. It thus approaches more early branching forms such as *Baryonyx* Charig & Milner, 1986. *Cristatusaurus* would belong to the subfamily of Baryonychinae Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998. A few months after the description of *Cristatusaurus*, Sereno *et al.* (1998) described other Gadoufaoua spinosaur material under the name *Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varrichio, Wilson & Wilson, 1998, arguing that *Cristatusaurus* lacked any distinctive features or proportions and therefore considered it as a *nomen dubium*. In a supplementary information file, Hendrickx *et al.* (2016) gave the latest description of the spinosaurid material kept in the MNHN, Paris (*Cristatusaurus lapparenti* and *Spinosaurus maroccanus*). The description provided no details about premaxillary foramina or sensorial structures and the lack of apomorphic characters for a pertinent diagnosis on the premaxilla only cause the authors to consider

Cristatusaurus lapparenti as a *nomen dubium* rather than a synonym of *Suchomimus tenerensis* or *Baryonyx* (Charig & Milner 1997). Here, we provide a new description of the MNHN material of *Cristatusaurus lapparenti* and *Spinosaurus maroccanus*, with a focus on the presence and density of foramina on the surface of the premaxillae and maxillae, as well as on their internal analysis by CT scan. That now gives us new information on the precise number, position and organization of the teeth of each specimen as well as a new vision of the neurovascular network of these animals. We will describe the superficial foramen distribution with respect to the underlying neurovascular complex for each specimen. The presence of certain furrows on the external or internal surface of the bone also informs us about the aspect and the arrangement of this neurovascular network.

Dental asymmetry has already been described in a same *Baryonyx* individual (Charig & Milner 1997) with a different number of alveoli between the left and the right dental rows. This feature is probably irrelevant for any diagnosis. Thus, the passage taken by the neurovascular network in the muzzle of these animals will depend on the dental distribution and the available interdental spaces, which will explain, in our opinion, certain variations between the left and the right, in particular on the length of the branches or the complexity of their subdivisions.

Interestingly, absolutely all foramina visible on the surface relate to preserved internal neurovascular branches. So, we can assume the hypothesis it is the same case on other fossils that would not have been tomographed and presenting such foramina. However, some foramina are difficult to detect on the surface depending on the preservation and/or preparation of the fossil. Some other very thin branches were detected by tomography.

SYSTEMATIC PALAEONTOLOGY

Superorder DINOSAURIA Owen, 1842
Order SAURISCHIA Seeley, 1888
Suborder THEROPODA Marsh, 1881
Clade TETANURAE Gauthier, 1986
Superfamily MEGALOSAUROIDEA Fitzinger, 1843
Family SPINOSAURIDAE Stromer, 1915
Subfamily BARYONYCHINAE Sereno, 1998

Genus *Cristatusaurus* Taquet & Russell, 1998

TYPE SPECIES. — *Cristatusaurus lapparenti* Taquet & Russell, 1998 by monotypy.

Cristatusaurus lapparenti Taquet & Russell, 1998
(Figs 1-11; 20A; 21; Appendices 1-3)

Cristatusaurus lapparenti Taquet & Russell, 1998: 347-353.

TYPE MATERIAL. — **Holotype**. **Niger** • 1 specimen (premaxillae and right maxilla portion); Gadoufaoua, Niger; GAD 5, Tegama Formation; Aptian, Early Cretaceous; MNHN.F.GDF366.

OTHER SPECIMEN EXAMINED. — **Niger** • 1 specimen (premaxillae of mature specimen); Gadoufaoua, Niger; GAD 5, Tegama Formation; Aptian, Early Cretaceous; MNHN.F.GDF365.

ETYMOLOGY. — From *cristatus*, “crested” in Latin and *sauros*, “lizard” in Greek. *Cristatusaurus lapparenti* was described in recognition of Albert F. de Lapparent.

ORIGINAL DIAGNOSIS. — premaxillae and right maxilla portion of the holotype specimen MNHN.F.GDF366; premaxilla short, strongly ‘hooked’ in lateral profile, increases in height posteriorly. Dorsal surface narrows into crest posteriorly. Anteriormost premaxillary alveolus relatively large, lateral alveoli uniformly closely spaced. Maxillary and dentary teeth laterally compressed in cross-section, maxillary teeth vertically oriented posteriorly. Dentary slightly constricted vertically in mid-section, alveoli closely spaced. Maxillary and dentary teeth with, finely serrated carinae. *Cristatusaurus* may be separated from *Angaturma* Kellner & Campos, 1996 and *Irritator* Martill, Cruickshank, Frey, Small and Clarke, 1996 by presence of dental serrations, from *Baryonyx* by brevirostrine condition of premaxilla.

DESCRIPTION OF MNHN.F.GDF365 (PREMAXILLAE)

Surface description

The specimen consists of two strongly fused5 premaxillae. The bony surface is relatively well preserved with the original ornamentation for a total length of 19.2 cm and an 8.2 cm maximum height. The suture between them is visible on the dorsal surface (Appendix 1). Compared with the spinosaurins *Spinosaurus* and *Irritator* (Sereno *et al.* 1998), premaxillae are relatively short and robust. The maximal width of the rosette in ventral view is 8.8 cm at the 3rd alveolus (Fig. 2) and becomes thinner and thinner posteriorly (5.4 cm at the 7th alveolus). There is a crest on the dorsal margin of premaxillae increasingly large posteriorly (Figs 1; 4A). On more complete premaxillae of spinosaurids such as *Baryonyx* (Charig & Milner 1986, 1997), *Suchomimus* (Sereno *et al.* 1998) and *Spinosaurus* (Sasso *et al.* 2005), a complex posterior margin of premaxillae can be observed in lateral view, consisting of a bifurcation of the bone in two distinct rami: a short one below and a longer one above, forming an elongated process articulating with nasal dorsoposteriorly. It lacks this posterior portion, however, on both *Cristatusaurus* specimens (MNHN.F.GDF365 and MNHN.F.GDF366). But on the right bone in lateral view, we can clearly notice a concavity on the posteroventral portion marking the articulation with the maxilla (Figs 1B; 7A), just after the 7th alveolus and below the short ramus (visible on the left maxilla of MNHN.F.GDF366, too). This structure is found in *Baryonyx* (Charig & Milner 1997) and *Suchomimus* (Sereno *et al.* 1998) and we know that the external naris are located close to this junction in these taxa, unlike Spinosaurinae (Fig. 20B, C). It must have been the same for *Cristatusaurus*. The distance between the tip of the muzzle and the 7th alveolus is proportionally short (13.7 cm) compared with “Spinosaurinae” taxa such as *Spinosaurus maroccanus* (Fig. 13A).

As noted by Kellner & Campos (1996), there are two bony ridges in the ventral side, which in this specimen are apparently well connected with the premaxillae. Because of the incomplete preparation of the specimens, the authors made the hypothesis these ridges are the rostral region of vomers. By examining this structure in other spinosaurids, it is clear

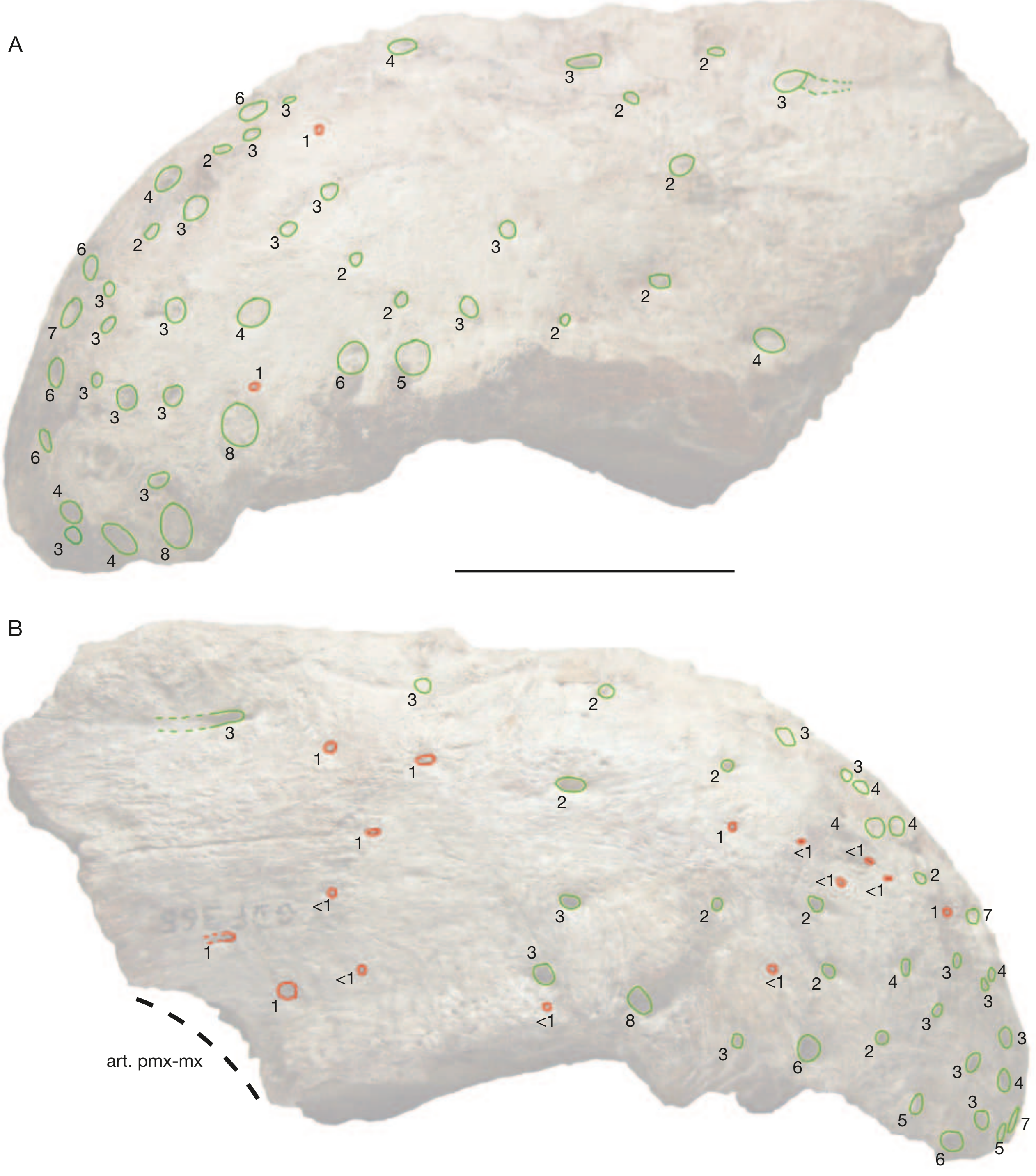


FIG. 1. — MNHN.F.GDF365, *Cristatusaurus lapparenti* Taquet & Russell, 1998, precise distribution of neurovascular foramina on left (**A**) and right (**B**) premaxilla. Small foramina are represented by red circles (1 mm or less) and others by green circles (more than 1 mm). Scale bar: 5 cm. Units in mm. Models by Frédéric Pittet.

that it is not the anterior segment of the vomers, but a part of the premaxillae themselves. For example, in *Cristatusaurus lapparenti* (MNHN.F.GDF366), there is no bony suture between premaxillae and these processes, nor in *Spinosaurus maroccanus* (Figs 2; 13A). Taquet & Russell (1998) assumed that these ventral bony processes did belong to premaxillae (by addition of a contact with the vomers further back, below the anterior part of maxillae as in *Spinosaurus* MNHN.F.SAM124).

The foramina identified by combining the external observations and the tomographic results amount to 49 on the right premaxilla and 42 on the left. Their diameter varies from 1 to 8 mm (for an average of 3 mm). Their density increases particularly on the first anterior third of the bone, from the maximum concavity of the alveolar margin to the tip of the snout, which corresponds to the rosette. Finally, we note the good preservation of which we can call a "pre-

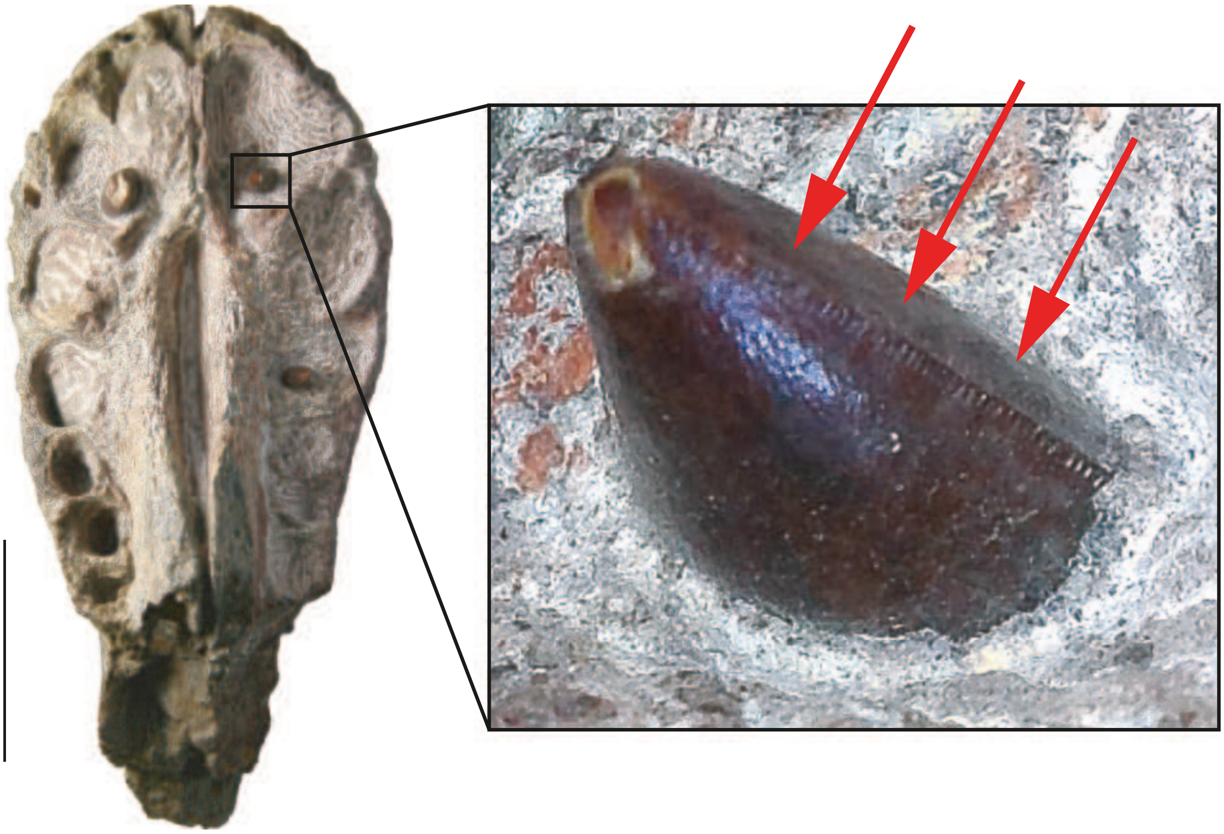


FIG. 2. — MNHN.F.GDF365, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **red arrows** point the serrated carina of a visible tooth. Scale bar: 5 cm. Photographs by Frédéric Pittet; figure by Florent Goussard.

narial foramen” of 3 mm in diameter on both premaxillary surfaces and which extends its furrow posteriorly towards the maxillae (Fig. 1).

Seven alveoli are present on each side, with a relative symmetry between the two bones. Replacement teeth with serrated carinae are visible in several alveoli (Fig. 2): on the 2nd right, the 2nd left, and the 4th left alveolus. We observed generally 5 serrations each millimeter (Fig. 2) and the profile of teeth is laterally compressed, as typical for Baryonychinae (Sereno *et al.* 1998).

Internal description

Tomographic results indicate a neurovascular network among the best-preserved discovered in a dinosaur and the very first complete described in a spinosaurid (Fig. 4B; Appendix 1B, D, F, H). In addition, the presence of the two fused premaxillae makes it possible to compare the structure of this network on the bones of the same individual and to study eventual symmetry in the arrangement of the branches connected to the superficial foramina (Fig. 4; Appendix 1B, D).

The neurovascular network is described here from the posterior to the anterior part of the specimen.

Two large and parallel branches run along the suture of the premaxillary bones on their entire length. In the most posterior part, they occupy a ventral position, just above the alveolar cavities, and fill almost the entire width of the muzzle at this level, each branch having a diameter of 1.4 cm for a bone width of 2.1 cm (Figs 3; 4B).

Then, they go up anteriorly at an angle of about 30° to the level of the fourth alveolus and then form a rounding along the upper margin of the bones, just below its surface to the apex. This anterior region, which in fact represents the rosette, is clearly the most supplied in ramifications (generally pointing forward), all leading to the few large superficial foramina (Figs 1; 4A, B).

At the level of the 7th alveolus, a first important secondary branch runs dorsally (Fig. 4B; Appendix 1 B,D). It almost divides in two, at the base of the main branch. A first branch with an angle of 60° relative to the main branch goes back to the surface of the bone to lead to a prenarial foramen (Fig. 4A, B, red squares). The location of this foramen is special, because it leads to bone depression reflecting the close presence of the (not preserved) external naris at the back (Figs 4; 8; 20). A groove is also visible on the surface of the bone in continuation of this prenarial foramen (see description below). A second branch, this time, points forwards at an angle of 40° with the main branch and ends up at a substantially identical size foramen, about 3 mm in diameter. The alliance of these two branches connected at their base forms in lateral view what we will call the “neurovascular bowl-shaped structure” (Fig. 4D). Several other much smaller, more or less preserved, secondary ramifications were revealed by the scan. They also join surface foramina. Interestingly, this is where the only two rearward-pointing rami are visible in the entire scanned neurovascular network

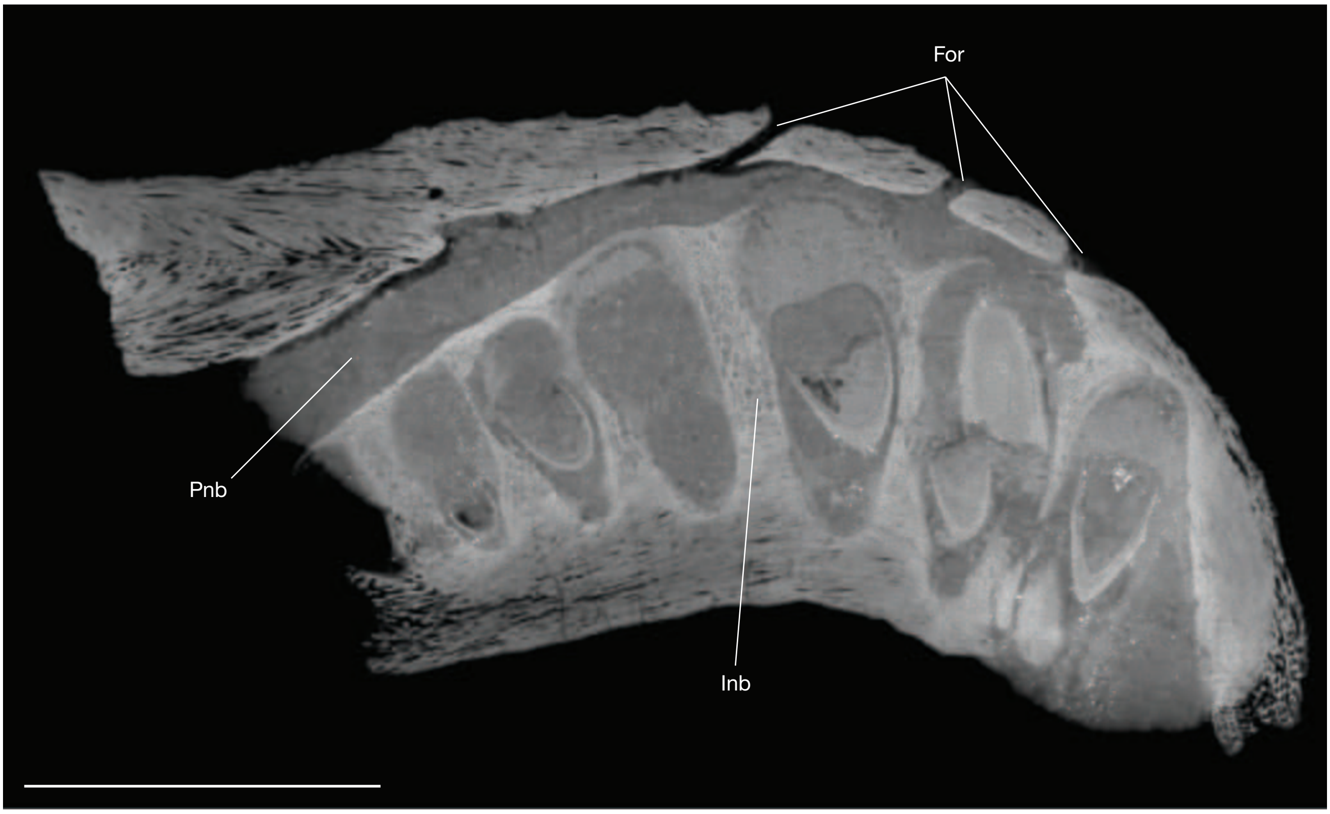


Fig. 3. — MNHN.F.GDF365, *Cristatusaurus lapparenti* Taquet & Russell, 1998, sagittal section of the right premaxilla highlighting the volume occupied by the main neurovascular branch; **Pnb**, principal neurovascular branch; **For**, foramen; **Inb**, interalveolar bone. Scale bar: 5 cm. Scan by Frédéric Pittet; figure by Florent Goussard.

(also seen in the younger *Cristatusaurus* specimen). They open at the level of the prenarial foramen and are only present on this junction zone between premaxillae and maxillae. In front of the 7th alveolus, all other branches are projected forward, or for some perpendicularly, on the lateral or dorsal surfaces of the bones. Between the 7th alveolus and the base of the rosette, an increase in the number and size of the surface foramina – which is reflected in the fossil by a complexification of the underlying neurovascular network – can be observed (Figs 1; 4A, B). A branch detaches from the main right neurovascular trunk, from the back of the 7th alveolus, while on the left it does so at the level of the 5th alveolus. There is therefore a certain asymmetry here. The left and right branches both extend to the margin of the third alveolus in a foramen, rounded off. The left one is opening slightly more anteriorly. Besides the location of the start of these two branches, a second difference can be noticed: the left branch is approximately twice as thick than the right one (Appendix 1B, D). Again, a significant number of secondary rami break off from the thicker branches and emerge on the outside of the bone by foramina. We sometimes detect interconnections or anastomoses between them (Fig. 4B). The rosette extends from the point of maximum concavity of the lower premaxillary margin (from the 3rd alveolus) to the tip of the snout where this one is the widest (8.2 cm). It is here that the complexity of the network becomes the highest. The thickest and most connected branches are found on the rosette with the largest foramina visible in anterior view. A minority of these branches directly innervates the roots of the teeth, while most follow longitudinally the alveolar cavities and lead to a foramen on the lateral surface of the bone.

Specific observations

Though a relative symmetry between the network of the premaxillae, some notable differences should be noticed. The changes between the left and the right premaxillae are here mainly due to the great variability in the location and size of the teeth alveoli (Figs 5; 6). However, some structures present a recurrence in MNHN.F.GDF365 for example, between each dental root, a ramus is detached from each of the two main neurovascular branches to rise dorsally to large foramen. Several pairs are easily recognizable (Fig. 4A, B, red circles).

The most posterior pair is directly connected on the surface by prenarial foramina, which open into a well-preserved superficial groove on the two premaxillae and which runs along the bone dorsally. From the prenarial foramen, the pattern of these superficial furrows displays an astonishing symmetry between the two faces, with a clearly visible “cross” shape, which excludes an artefact (Fig. 4C).

It is very important to note at this point that this prenarial foramen is also visible and preserved on the other specimens

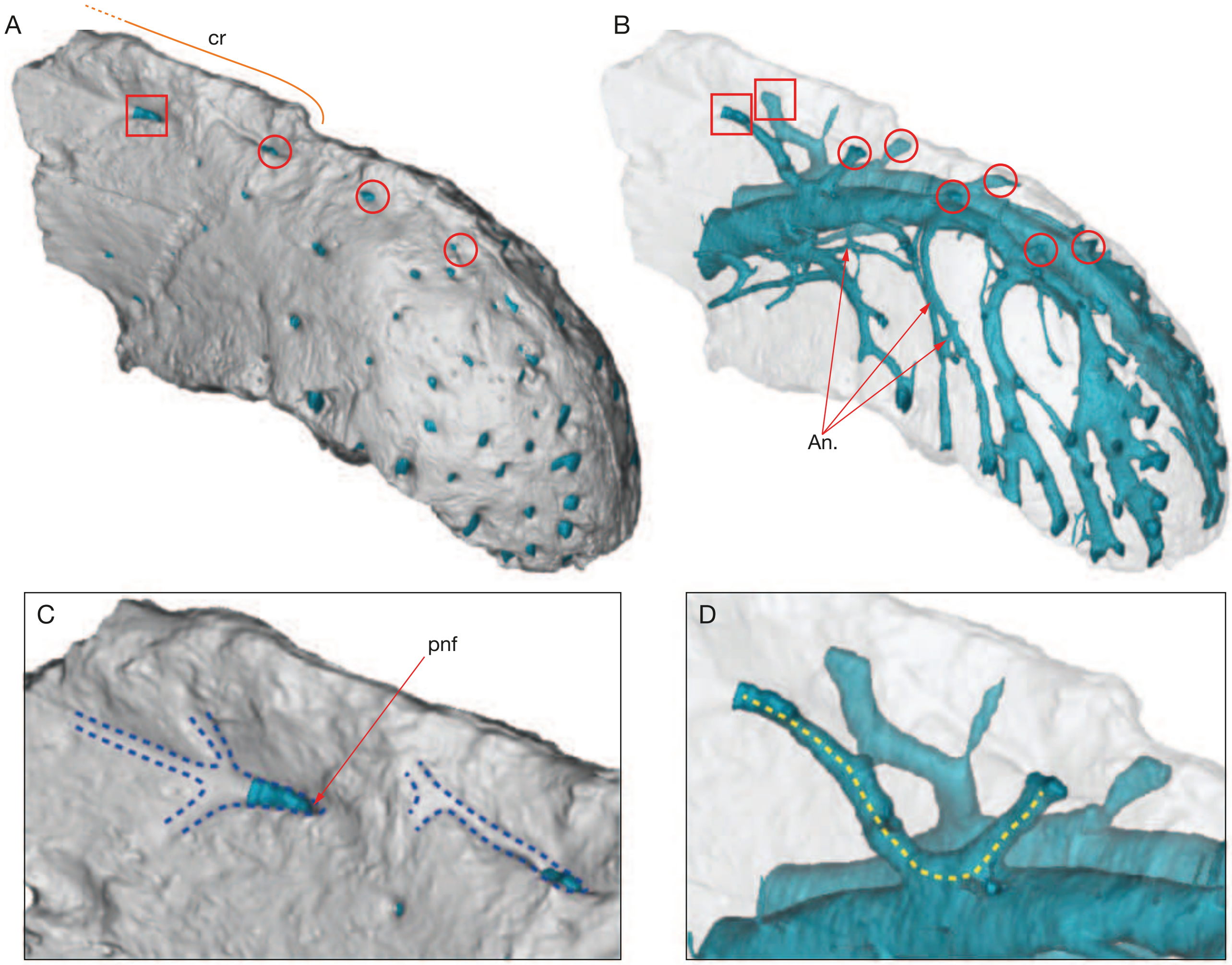


FIG. 4. — MNHN.F.GDF365, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **A**, right surface anterolateral view; opening of the right prenarial foramen (**red square**); openings of the first three right neurovascular rami pointing in an anterodorsal position (**red circles**); **B**, right surface anterolateral view in transparency with neurovascular network; openings of the prenarial foramina (**red squares**); openings of the first three neurovascular rami pairs pointing in an anterodorsal position (**red circles**); evidence of a few anastomoses (**red arrows**); **C**, close-ups of the superficial grooves extending the posterior (prenarial foramen) and anterior openings of the neurovascular bowl-shaped structure (**blue dots**); **D**, details on the right neurovascular bowl- shaped structure (**yellow dashed dots**) with antero and posterodorsal rami (corresponding to the prenarial foramen). Abbreviations: **An**, anastomoses; **Cr**, crest; **Pnf**, prenarial foramen. Models by Frédéric Pittet and Florent Goussard. Not to scale.

of Baryonychinae (Fig. 20), namely on the premaxilla of the European *Baryonyx walkeri* (Charig & Milner 1986, 1997) and that of *Suchomimus tenerensis* from Niger (Sereno *et al.* 1998). We now know that this important foramen marks the exit of the posterior branch of the "bowl structure" described above and recurrent in the two specimens of *Cristatusaurus lapparenti*, MNHN.F.GDF365 and MNHN.F.GDF366. It indicates in a way the separation between the branches pointing forwards (in the direction of the rosette) and those pointing backwards (in the direction of the external nostrils). This new character will be examined in the discussion section, as will the interpretation of the prenarial grooves (Figs 1B; 4C). The right premaxilla shows another well-preserved nerve branching imprint just anterior to that described above (Fig. 4C). Grooves and channels of a similar nature have been described on maxillae of *Tyrannosaurus rex* Osborn, 1905 and interpreted by the authors as natural molds for the rami of the maxillary nerve (Brochu 2003).

Teeth

All teeth have typical apical curve found in most theropods. The first pair of alveoli has proportionally rather small teeth compared to those usually found there in Spinosauridae: 1.75 cm long on the left and 2.25 cm on the right. They had not yet protruded while the animal was alive, either because they were not sufficiently developed (possible ontogenic reasons), or because they are replacement teeth in formation, the main ones having been lost during decomposition or the fossilization process itself (Fig. 5B). We can also note the presence of an orphan fragment of about 1 cm long at the tip of the right tooth, forming an angle of 90° with the axis of the tooth. Small replacement teeth are sometimes partially or even completely returned in the alveolar cavity they occupy, probably due to movements and compression of the sediment over time (Fig. 6). The second pair of alveoli reveals a tooth of 5.3 cm long on the left side and 6.4 cm on the right. The latter appears to be the most complete in the specimen, from

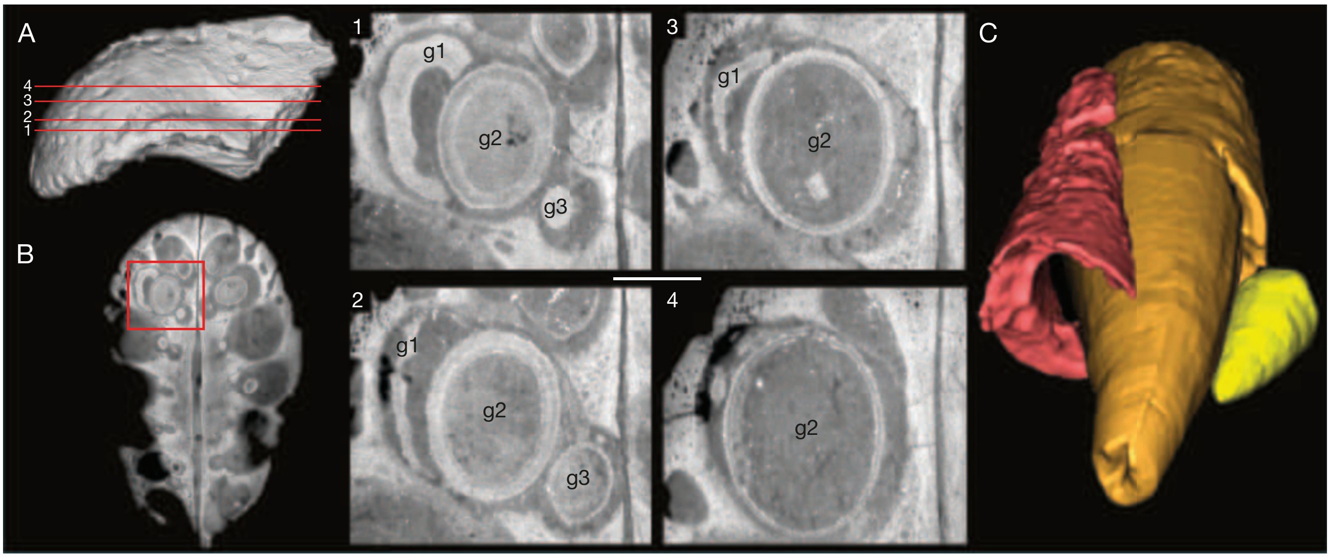


FIG. 5. — MNHN.F.GDF365, *Cristatusaurus lapparenti* Taquet & Russell, 1998, CT scans views of premaxillae: **A**, left labial view showing location of each slice; **B**, axial view with highlighting on the 2nd right alveolus showing three generations of teeth simultaneously (**red square**); **1**-**4**, axial slices through premaxillae, with number 1 occupying the most ventral position and number 4 the most dorsal (close to the tooth root); **C**, 3D rendering of the three generations of teeth of the 2nd right alveolus: tooth almost completely demineralized (**red**), main tooth (**orange**) and replacement tooth (**yellow**). Abbreviations: **g1**, demineralized tooth; **g2**, main tooth; **g3**, replacement tooth in its crypt fused with alveolar cavity. Scale bar: 1 cm. Models by Frédéric Pittet and Florent Goussard.

the root (indeed very close to the bone margin) to the apex. A small replacement tooth of about 1 cm is present medially to the left main tooth. The scan shows us a very intriguing structure: a sort of half-moon sheath around this tooth in labial position (Fig. 5C). We initially thought of an artifact, but an in-depth study of the density of this lunula shows us that it is indeed a vestige of the previous main tooth, which occupied this alveolus. This second right alveolus therefore offers us both the vision of three dental generations in the same cavity but also a very good example of the last stage of the demineralization process of a tooth. Multiple levels of bone sections in axial view were highlighted by CT scans (Fig. 5). The third pair contains replacement teeth of 3.2 cm on the right and 2.3 cm on the left. The principal tooth is lacking on the right side and the left one is incomplete. Each third alveolus has a second small replacement tooth, like the one seen on the first pair (the right one is completely turned with an angle of 180°). The fourth pair preserved a relatively complete 4.8 cm tooth only in the left alveolus. Here a fragment of the apex of a tooth is identifiable. It could be a small replacement tooth. Its angle and position could also match with the apex location of a mandibular tooth when the animal had its jaws almost closed. The fifth pair reveals a tooth 1.5 cm on the left (probably a replacement tooth) and 1.9 cm on the right with again a small "characteristic" second replacement tooth, this time pointing up. The sixth pair retained only a small tooth of about 1 cm on the right. The seventh and final pair of alveoli is free of preserved teeth (Fig. 6).

While the apex of only three teeth is visible superficially (one, incomplete, on the 2nd right alveolus, two on the 2nd and the 4th left alveoli), the CT-scans reveal a total of 12 clearly identified fossilized teeth inside the bones (Fig. 6). From a general point of view, the replacement teeth were formed medially, along the premaxillary groove, to gradually occupy a more labial position as they grew, corresponding to the alveolar openings visible on the surface. These replacement teeth developed in resorption crypts, lingually to the principal tooth, as described in crocodilians (Edmund 1960; Peyer & Zangerl 1968) and several theropods such as *Tarbosaurus* Maleev, 1955a (Hanai & Tsuihiji 2019), *Allosaurus* Marsh, 1877 (LeBlanc *et al.* 2017a), *Gorgosaurus* Lambe, 1914 (LeBlanc *et al.* 2017a) or *Coelophysis* Cope, 1889 (Fong *et al.* 2016). The new tooth recovered minerals from the old one for its own construction during this gradual demineralization. This process had never been observed or described in Spinosauridae. We therefore observe a similar tooth ontogeny in the two specimens of *Cristatusaurus lapparenti* and also in *Spinosaurus maroccanus* (Figs 5; 6; 13; 17A).

DESCRIPTION OF MNHN.F.GDF366 (PREMAXILLAE)

Surface description

This specimen has two separate premaxillae, with a smooth surface. This indicates that the bones are more eroded than on the mature specimen (MNHN.F.GDF365). Small parts are lacking on the very anterior portion. Some foramina are there strongly denatured, sometimes even fused with their neighbors. Furthermore, dark streaks on this area indicate the typically tubular structure of the internal bone with lamellae and osteons canaliculi (Müller 2009).

The right premaxilla is 11.8 cm long and 6.6 cm high. The left one is 11.4 cm long and 6.5 cm high. The ventral view shows a total of 7 alveoli containing the principal teeth on both premaxillae (Fig. 9C). Secondary alveoli are visible on the 3rd alveolus for the right premaxilla and on the 3rd and the 7th alveoli on the left one (where replacement teeth apexes are visible). All principal teeth are crushed or lack-

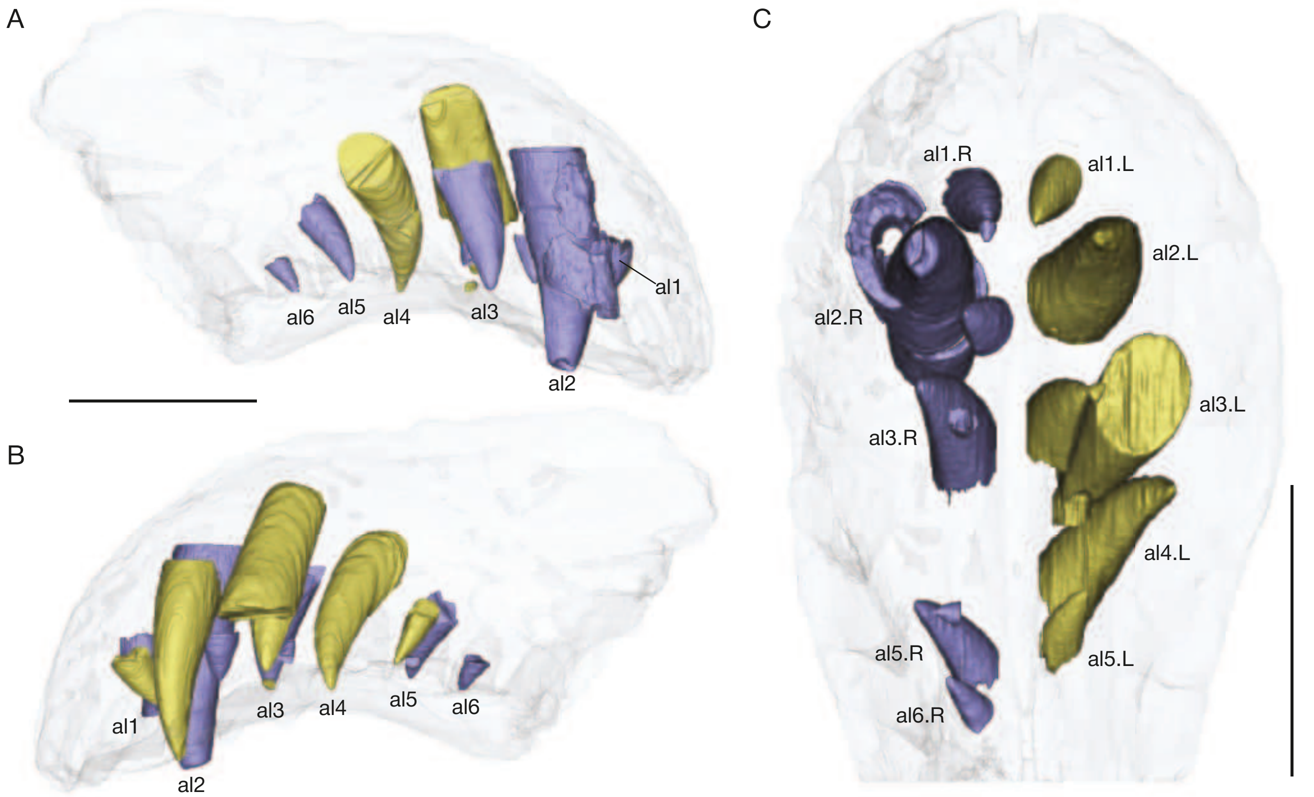


Fig. 6. — MNHN.F.GDF365, *Cristatusaurus lapparenti* Taquet & Russell, 1998, internal arrangement of the preserved teeth with premaxillae in transparency (right premaxilla teeth in **purple**, left premaxilla teeth in **yellow**): **A**, right labial view; **B**, left labial view; **C**, ventral view. Abbreviations: **al1-6.R**, right alveolus 1-6 ; **al1-6.L**, left alveolus 1-6. Scale bars: 5 cm. Models by Frédéric Pittet and Florent Goussard.

ing (Fig. 9). The structure of laterally compressed teeth of the Baryonychinae type (Sereno *et al.* 1998) can, however, be demonstrated by the observation of the tooth in the second alveolus of the left premaxilla; the denticulate carina is clearly recognizable there. Once again, the analysis of the CT scans made it possible to refine the number, size and exact distribution of the foramina spotted on the surface of the specimen. Some of them, questionable, could be retained in this description because their direct link with underlying neurovascular preserved branches. We counted 50 foramina on the right premaxilla and 54 on the left one (Fig. 7). Their diameter varies from less than 1 mm to 4 mm (for an average of 1 mm). It also made it possible not to consider certain depressions that could have been mistaken for foramina without internal analysis of the fossil. The density of foramina is greater on the front of the muzzle, at the level of the rosette (Fig. 7; Appendix 2).

A subcircular depression of about 1 cm in diameter was noted on the posterior portion of the right premaxilla, 1.5 cm above the alveolar margin. This is difficult to interpret but it seems to be the result of any trauma during the animal's lifetime, like an abscess, shock or bone callus that has left a scar (Fig. 7B).

Internal description

The difference in density between the bone and the sediment was lower than with MNHN.F.GDF365, probably for taphonomic reasons. The result of the scans nevertheless allows revealing a complex strongly branched network. We note again the presence of the two main parallel branches in each bone that run along the premaxillary suture, with a diameter corresponding again to almost the entire bone in its posteroventral part (Appendix 2B, D). These branches then rise rapidly to reach the dorsal edge of the premaxillae at the level of the 3rd alveolus (Appendix 2F, H). They then branch very strongly in the rosette into numerous smaller secondary branches and open out via the foramina. These general observations coincide well with the arrangement described in MNHN.F.GDF365; no striking difference was noted. The notable differences between the two specimens relate to the length of each branch rather than their general arranging and could therefore be related to ontogeny.

Although the dorsoposterior part of the premaxillae is lacking, the neurovascular complex is not affected. As in MNHN.F.GDF365, the peculiarity of this area is the presence of the "bowl-shaped structure" with vascular ramifications pointing for the first time backwards (prenarial foramen). It marks the anterior beginning of the bony depression leading to the nasal cavity (Fig. 8). On the right main branch, behind the 7th alveolus, two secondary branches with the same base stand out, one pointing towards the back and the other laterally towards the edge of the bone, perpendicularly. On the left main branch, the structure is more confused but is nevertheless present (Fig. 8B, C).

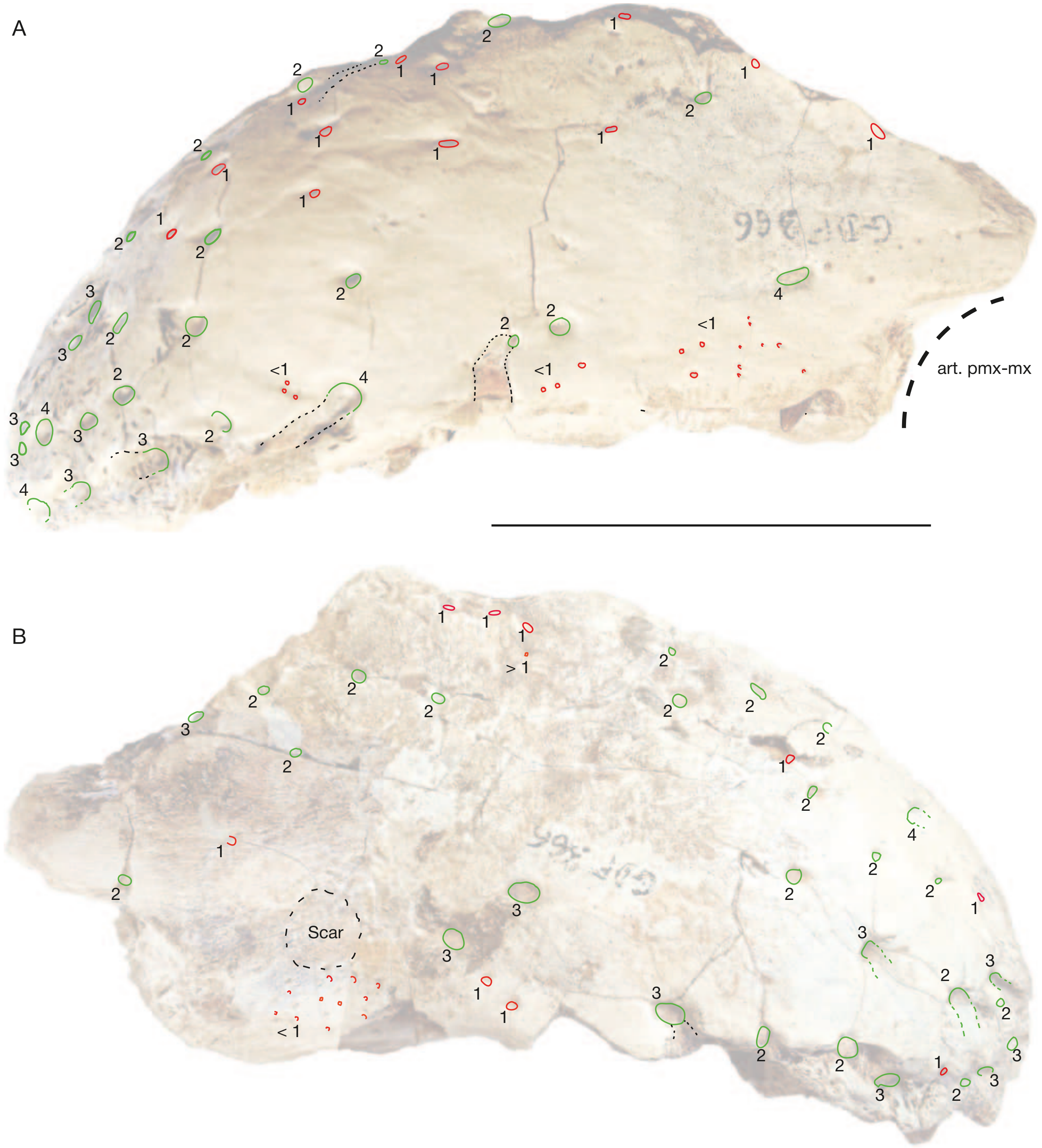
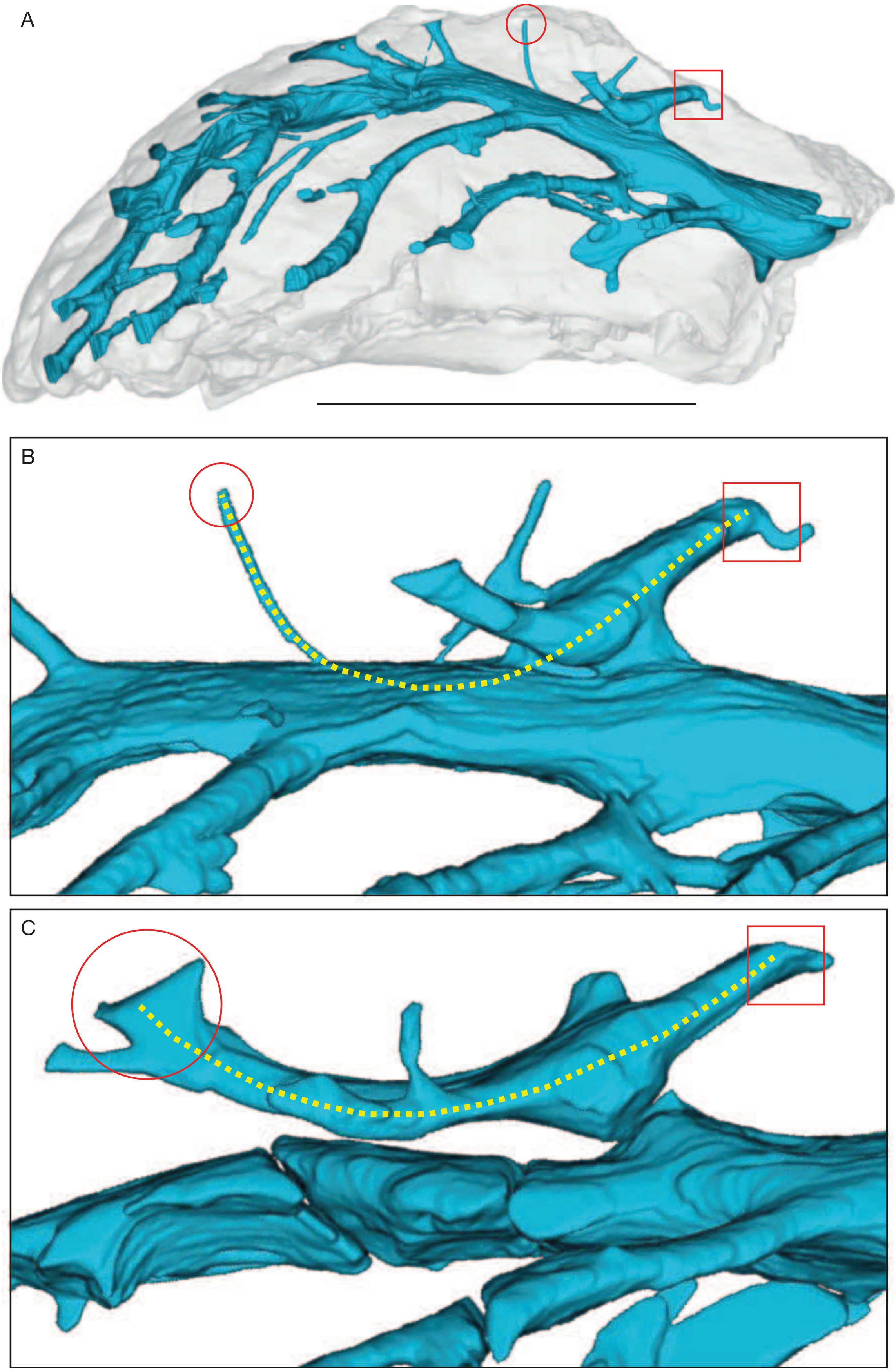


Fig. 7. — MNHN.F.GDF366, *Cristatusaurus lapparenti* Taquet & Russell, 1998, precise distribution of neurovascular foramina on left (**A**) and right (**B**) premaxillae; small foramina are represented by **red circles** (1 mm or less) and others by **green circles** (more than 1 mm); **slashed lines** represent grooves extending the foramina and a subcircular depression in the posteroventral position that resemble old hurts or a scar on the bone. Scale bar: 5 cm. Units in mm. Models by Frédéric Pittet.

Just behind the 6th alveolus of the two premaxillae, another secondary branch is detached with an opening angle of approximately 20° with respect to the main branch, then which further subdivides into two smaller rami opening out to the surface of the bone at the 5th and 4th alveoli. In the part starting at the front of the 7th alveolus up to the maximum concavity point of the lower margin of the bone (base of the rosette), the preservation of the network is very choppy and incomplete in

Fig. 8. — MNHN.F.GDF366, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **red square** indicates the opening of the most posterior portion of the ramus leading to the prenarial foramen in the left (**A** and **B**) and right (**C**) premaxillae; **red circle** indicates the opening of the first neurovascular ramus pointing in an anterodorsal position in the left (**A** and **B**) and right (**C**) premaxillae; **A**, left premaxilla, labial view in transparency with its almost complete neurovascular network; **B**, details of



the left atrophied neurovascular bowl-shaped structure (**yellow dashed dots**); **C**, details of the right neurovascular bowl-shaped structure (**yellow dashed dots**) in mirror effect for better comparison of their asymmetry. Scale bar: 5 cm. Models by Frédéric Pittet and Florent Goussard.

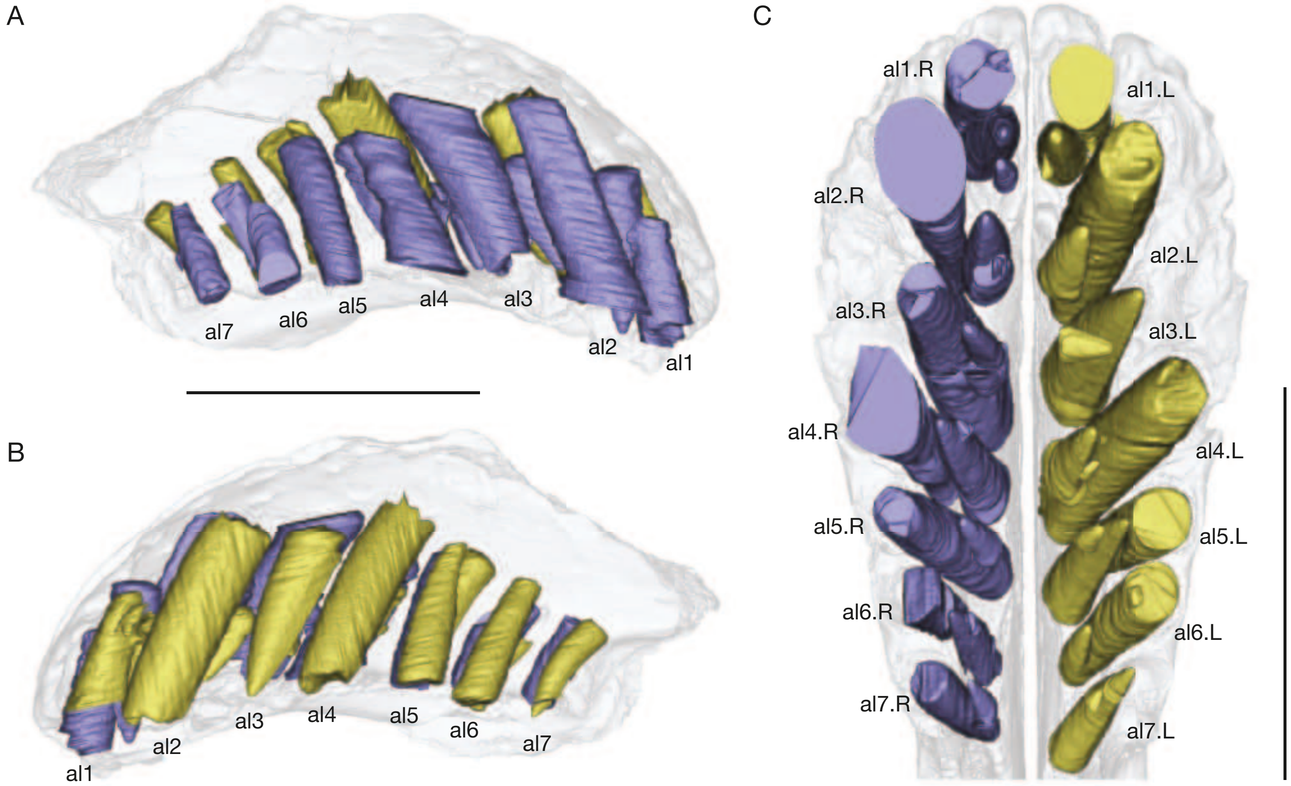


FIG. 9. — MNHN.F.GDF366, *Cristatusaurus lapparenti* Taquet & Russell, 1998, internal arrangement of the preserved teeth with premaxillae in transparency (right premaxilla teeth in **purple**, left premaxilla teeth in **yellow**): **A**, right labial view; **B**, left labial view; **C**, ventral view. Abbreviations: **al1-7.R**, right alveolus 1-7; **al1-7.L**, left alveolus 1-7. Scale bars: 5 cm. Models by Frédéric Pittet and Florent Goussard.

the right premaxilla but much better preserved in the left one (Appendix 2B, D). There is the birth of a secondary branch which detaches from the main branch at the same angle as those back (approximatively 20°). It begins between the 4th and 5th teeth to move towards the surface of the bone leading to large foramina, mostly in the rosette (Fig. 8A).

From the base of the rosette (the middle of the 4th alveolus) to the apex of the bone, the internal conservation of the left premaxilla is more complete. As in MNHN.F.GDF365, the network here is much more branched, with most secondary branches (5 of the 6 in all raised on the left) leading to large foramina in this zone. Most of the branches in turn subdivide before reaching the surface of the bone. Finally, the diameter of the foramina is on average larger on the front of the rosette: 3 or even 4 mm compared to 2 or 1 mm further behind (Fig. 7).

Specific observations

The secondary branches opening dorsally in pairs described in MNHN.F.GDF365 are found in this specimen, too (Fig. 8A). They are relatively symmetrical, except for the most posterior pair. This area corresponds to the anterior foramina of the "bowl-shaped" structure. The ramus is atrophied and/or badly preserved on the left side. There seems to be fewer interconnections between the secondary branches than in the more mature specimen (Figs 4B; 8A). However, the quality of preservation of the neurovascular network being of lower quality here, it is possible that these connections are not visible. The grooves described on the surface in MNHN.F.GDF365 running along the internal roof surface of the bone and connecting different foramen is partly found in MNHN.F.GDF366 but is much less preserved. The superficial breaks and the absence of the posterodorsal portion of the bones make its follow-up difficult, but we were able to highlight a trace of a groove over 2 cm from one of the foramina of the "bowl" structure, as in the more mature specimen (Figs 4; 8).

Teeth

Surprisingly, we were able to count a total of 35 main and replacement teeth on both premaxillae: 18 on the right and 17 on the left (Fig. 9). Apart from the seventh left alveolus, all others have principal teeth preserved but broken above the alveolar margin. Each alveolus contains a replacement tooth in addition to the main tooth. We sometimes even notice a second replacement tooth, always small and placed on the lingual side of the first ones. Each of the alveoli of the first pair contains a main tooth and two replacement teeth. The second pair has a main tooth in each alveolus as well as a replacement tooth. A second replacement tooth is visible on the right side. The third pair of alveoli shows two main teeth and two replacement teeth. The main tooth on the left, however, is reduced and not sufficiently developed to come out of the gum line. It was growing back following the loss of a mature tooth in this location (indeed, each main tooth was quickly replaced when it broke or fell out). The fourth pair has a main

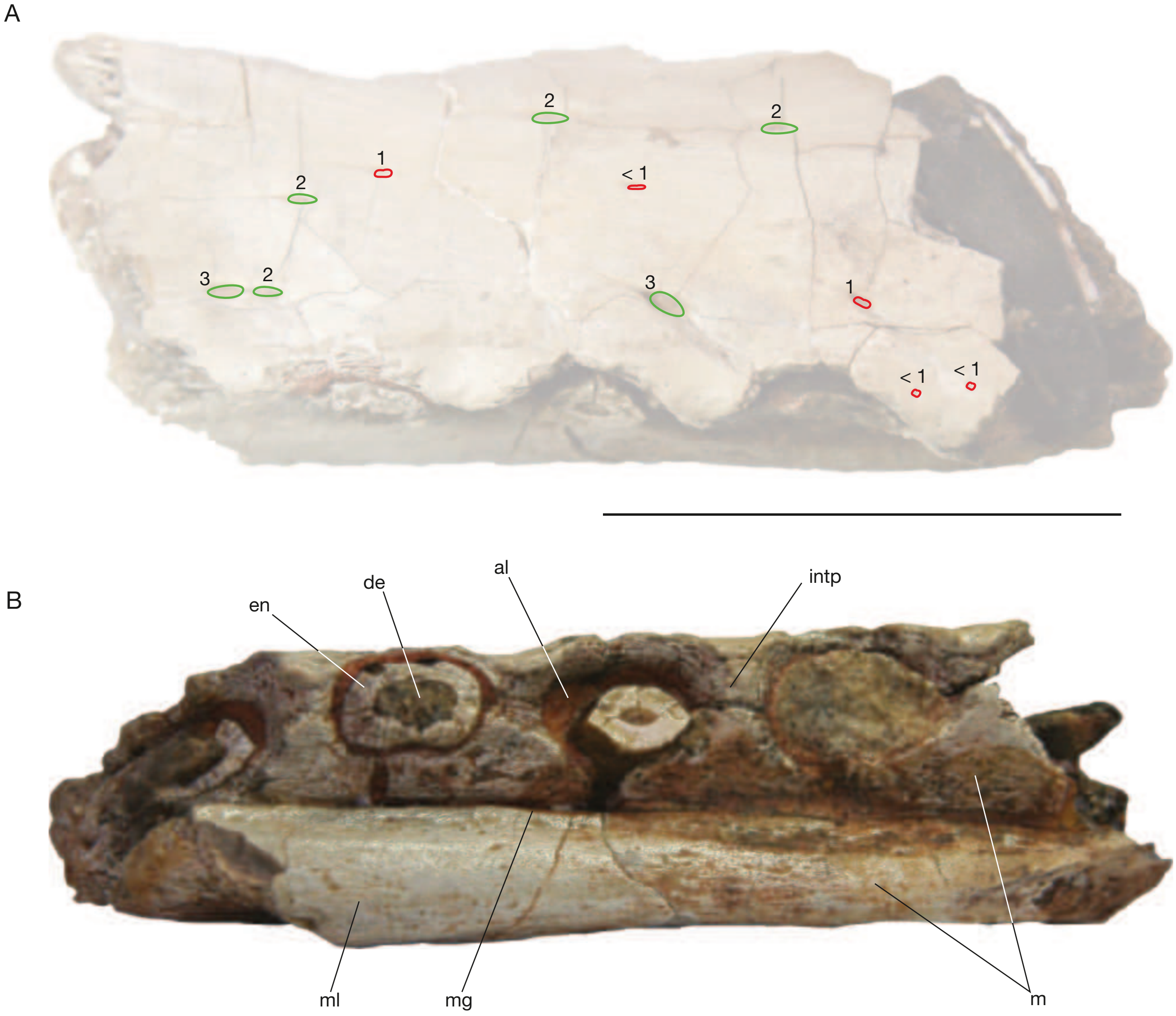


Fig. 10. — MNHN.F.GDF366, *Cristatusaurus lapparenti* Taquet & Russell, 1998, right maxilla portion: **A**, labial view of the maxilla with foramina; the diameters are shown in the Figure; **red lines** show the furrows in the bone that prolong the opening of some foramina; **B**, ventral view. Abbreviations: **al**, alveolus; **de**, dentin; **en**, enamel; **intp**, interdental plate; **m**, maxilla; **mg**, maxillary groove. Scale bar: 5 cm. Units in mm. Models by Frédéric Pittet.

tooth as well as two replacement teeth in each alveolus. The fifth pair illustrates a good example of a tooth replacement stage. The replacement tooth here present indeed begins its lateral demineralization action, with a second replacement tooth in the making. The sixth and seventh pairs both have main teeth accompanied by developing replacement teeth (a second replacement tooth is visible in the sixth right alveolus).

Description of MNHN.F.GDF366 (maxilla)

Surface description

The sample is a portion of a right maxilla with the anterior and posterior parts missing. It is 10.6 cm long and approximately 3.5 cm high. There are five alveoli on the specimen. The first coincides with the anterior fracture of the bone and highlights what seems the pulp cavity of a main tooth 3.8 cm long (probably 0.5 cm more with the dentin and enamel layers). The three more posterior alveoli have the same diameter as the first (1.4 cm) but the teeth are broken there. They nevertheless have well-preserved enamel around their dentin. The fifth is on the posterior fracture of the bone and is not complete. The tooth there is broken longitudinally. The thickness of the dentin layer covering the pulp cavity is approximately 2 mm on each tooth. The lateral surface of the maxilla has 11 clearly identifiable foramina (Fig. 10A). Two of them open forward at a 45° angle and are associated with furrows in the bone, as observed in *Baryonyx walkeri* (Charig & Milner 1997), a sign that they were probably innervating the lips below the alveolar margin (Reisz & Larson 2016). The lingual surface is difficult to describe due to the bad preservation of the fossil.

In ventral view, we identify lingually a bony lamina running along the maxilla, separated with alveoli by the maxillary groove. As can be seen in other Spinosauridae, this lamina gradually grows in width anteroposteriorly (Sereno *et al.* 1998; Dal Sasso *et al.* 2005) with 1 cm wide at the front of the sam-

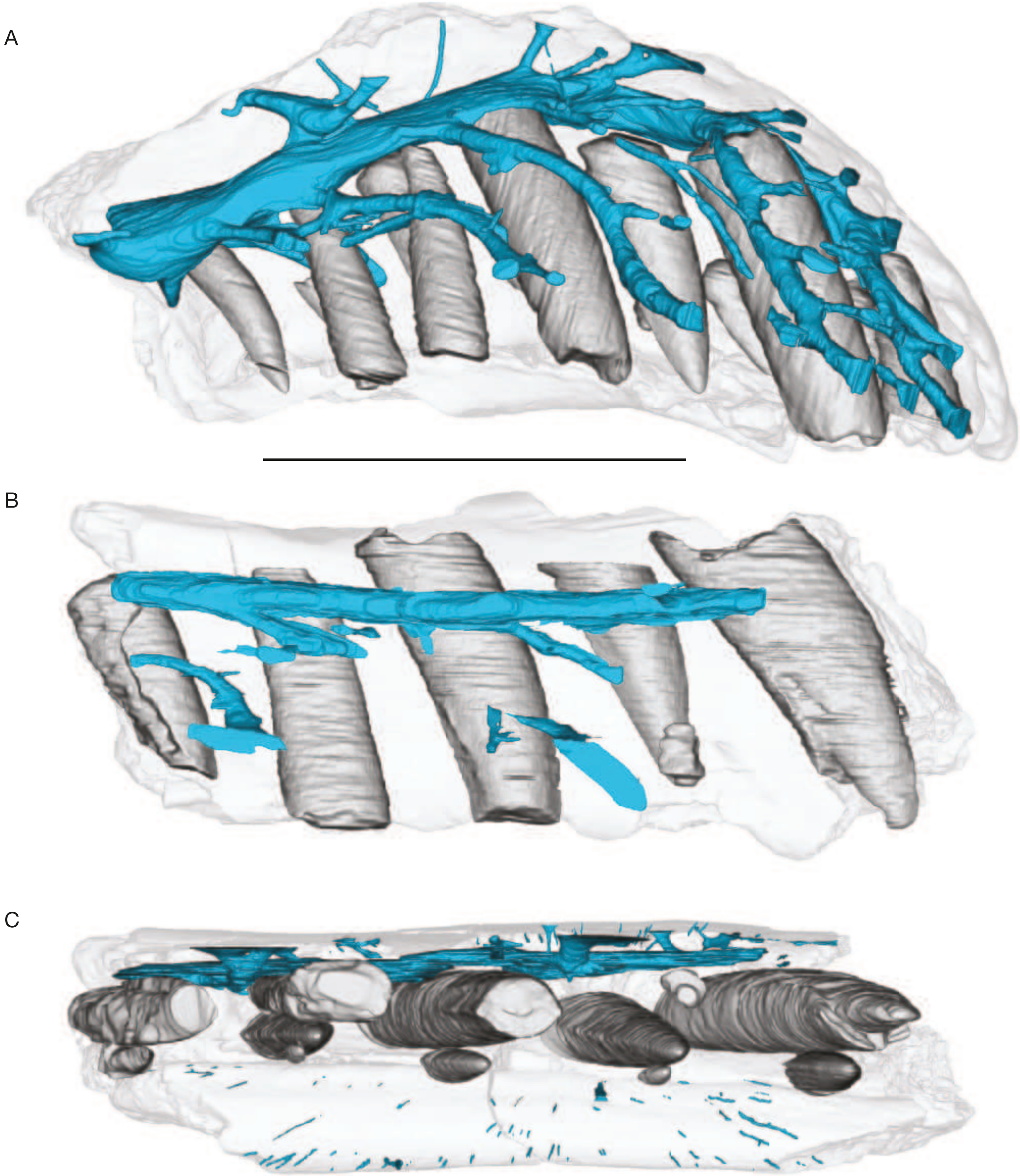


Fig. 11. — MNHN.F.GDF366, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **A**, mirrored left premaxilla (with best-preserved neurovascular network), labial view in transparency with teeth; main branch above the tooth roots; **B**, right maxilla portion, labial view in transparency with teeth; main branch extending labially along the tooth alveoli for the upper third of their length; **C**, right maxilla portion, ventral view in transparency with teeth and many neurovascular rami radiating outwards, much more developed on the labial surface, indicating a greater sensory need in this area. Scale bar: 5 cm. Models by Frédéric Pittet and Florent Goussard.

ple to reach 1.3 cm at the rear (Fig. 10B). Conversely, the alveolar zone decreases (1.8 cm wide at the front and 1.4 cm at the rear). Thanks to the breaking of the bone coupled with the information of the CT scans, it can be confirmed that the maxillary groove does not mark the separation of two bones and is only an invagination of the surface of the maxilla, containing pits of resorption of the teeth. It shows that the maxillary lamina does not belong to the vomer but to the maxilla itself (Dal Sasso *et al.* 2005). The interdental plates are also clearly visible between each alveolus (Fig. 10B).

Internal description and teeth

The tomography shows us that the configuration of the neurovascular complex in the maxillae differs from that encountered in the premaxillae (Appendix 3B, D, F, H). The main branch no longer overhangs the alveolar roots, but labially runs along the alveolar cavities on their first upper third by projecting secondary branches under an angle of about 45° between each tooth and leading to surface foramina (Fig. 11A, B). The teeth show a very good quality of preservation and two to three generations of teeth are present in each of the five alveoli (Fig. 11C). Only the first two main teeth do not have their apex broken. The first alveolus (the most anterior) contains this famous tooth of 3.8 cm partially visible externally due to the breakage of the bone with a replacement tooth in formation of 1.5 cm; the second alveolus contains a main tooth of 2.8 cm, a replacement tooth of 0.4 cm and a very reduced vestige of the old main tooth almost completely demineralized on the labial margin of the alveolar cavity. The third alveolus shows an incomplete tooth of 3.2 cm and a replacement tooth of 1.2 cm. The fourth one has three generations of teeth with the main (incomplete) 3.1 cm tooth already hollowed out laterally by a robust 2.2 cm replacement tooth accompanied by a second tiny 0.5 cm replacement tooth. The fifth alveolus contains a broken main tooth of 2.6 cm and still a replacement tooth of 1 cm. It should be noted that the replacement teeth always begin their formation at mid-depth of the alveolar cavity, on the lingual surface and occupying more and more space in the basal direction before growing distally to finally “come out” of the alveolus, as if the tooth takes the time to ensure good root strength before exposing itself outside the bone.

Subfamily SPINOSAURINAE Sereno, 1998

Genus *Spinosaurus* Stromer, 1915

TYPE SPECIES. — *Spinosaurus aegyptiacus* Stromer, 1915, by monotypy.

Spinosaurus maroccanus Russell, 1996
(Figs 12-17; Appendix 4)

Spinosaurus maroccanus Russell, 1996: 355-360. — Taquet & Russell 1998: 347-353.

TYPE MATERIAL. — **Holotype**. **Morocco** • 1 specimen (mid-cervical vertebra); Kem Kem Beds, Morocco; Albian, Early Cretaceous; Canadian Museum of Nature; NMC50791.

OTHER MATERIAL EXAMINED. — **Algeria** • 1 specimen (partial premaxillae and partial maxillae); Gara Samani, Algeria; Albian, Early Cretaceous; MNHN.F.SAM124.

TYPE LOCALITY. — Kem Kem Beds, Morocco.

TYPE AGE. — Early Cretaceous (Albian).

ETYMOLOGY. — From *spina*, “spine” in Latin and *sauros*, “lizard” in Greek. The name *Spinosaurus maroccanus* was attributed in reference to the red infracenomanian sandstones of southern Morocco (Kem Kem Beds), where the specimen was discovered.

ORIGINAL DIAGNOSIS. — Ratio between length of centrum (excluding anterior articular condyle) and height of posterior articular facet of centrum approximately 1.5 in mid-cervical vertebrae.

DESCRIPTION OF MNHN.F.SAM124 (PREMAXILLAE)

Surface description

The premaxillae are incomplete, particularly on the left side of which the dorsal part of the rosette is missing (Fig. 12A). We are in the presence of a mature animal considering the “strongly fused” aspect of the two bones (Taquet & Russell 1998). The length of the right premaxilla, the most complete, reaches 24.5 cm.

Overall, there is no notable difference between these premaxillae and those belonging to the species *Spinosaurus aegyptiacus*, except for the number of alveoli: seven in *S. maroccanus* and six in *S. aegyptiacus* (Fig. 13A). However, intraspecific or ontogenic variations in the number of alveoli appear to occur in dinosaurs and even on the same specimen, as on the *Baryonyx* holotype (six alveoli on the left and seven on the right (Charig & Milner 1997). The number of dental alveoli is therefore generally not considered a relevant feature in the diagnoses. For some authors, significant differences between the two species were found by comparison of cervical vertebrae (Taquet & Russell 1998) and some others consider *Spinosaurus maroccanus* as a nomen dubium (Dal Sasso *et al.* 2005; Ibrahim *et al.* 2014). In lateral view, the anterodorsal margin of the rosette forms a typical curve for Spinosaurinae. The curve of the alveolar margin is proportionally more ovoid than in the genera of the Baryonychinae types (as in *Cristatusaurus*). The posterior branches of the premaxillae are not preserved. Total length of existing bones are approximatively 24.5 cm and a maximum height in frontal view of 10.4 cm. There are 28 foramina on the left premaxilla and 36 on the right one with a diameter of less than 1 to 9 mm, but most have a diameter between 4 and 6 mm (Fig. 12). The scan showed the location of several additional foramina, either inconspicuous on the surface or questionable to the naked eye. The numerical difference between the left and the right is due to the incompleteness of the left premaxilla, with a missing area of approximately 25 cm^2 on the top of the rosette (Fig. 12A).

The maximum concavity of the rosette on the alveolar margin is 8 cm from the apex of the snout (at the level of the 3rd alveolus). This is also where the rosette is the widest in ventral view at 13.5 cm (Fig. 14A, B). The diameter of the alveoli varies from 1.4 cm for the smallest to 4.4 cm for the largest. It should be noted that the first pair of alveoli subsequently has additional sub-cavities separated by a bony part with “autonomous” replacement teeth (Fig. 13B1). We could think of interdental plates, as has already been observed in many dinosaurs such as some hadrosaurs (LeBlanc *et al.* 2016), heterodontosaurs (Butler *et al.* 2012) and theropods like juvenile dromaeosaurids (Norell *et al.* 1994), *Coelophysis* Cope, 1889 (LeBlanc *et al.* 2017a), tyrannosaurs (Hurum &

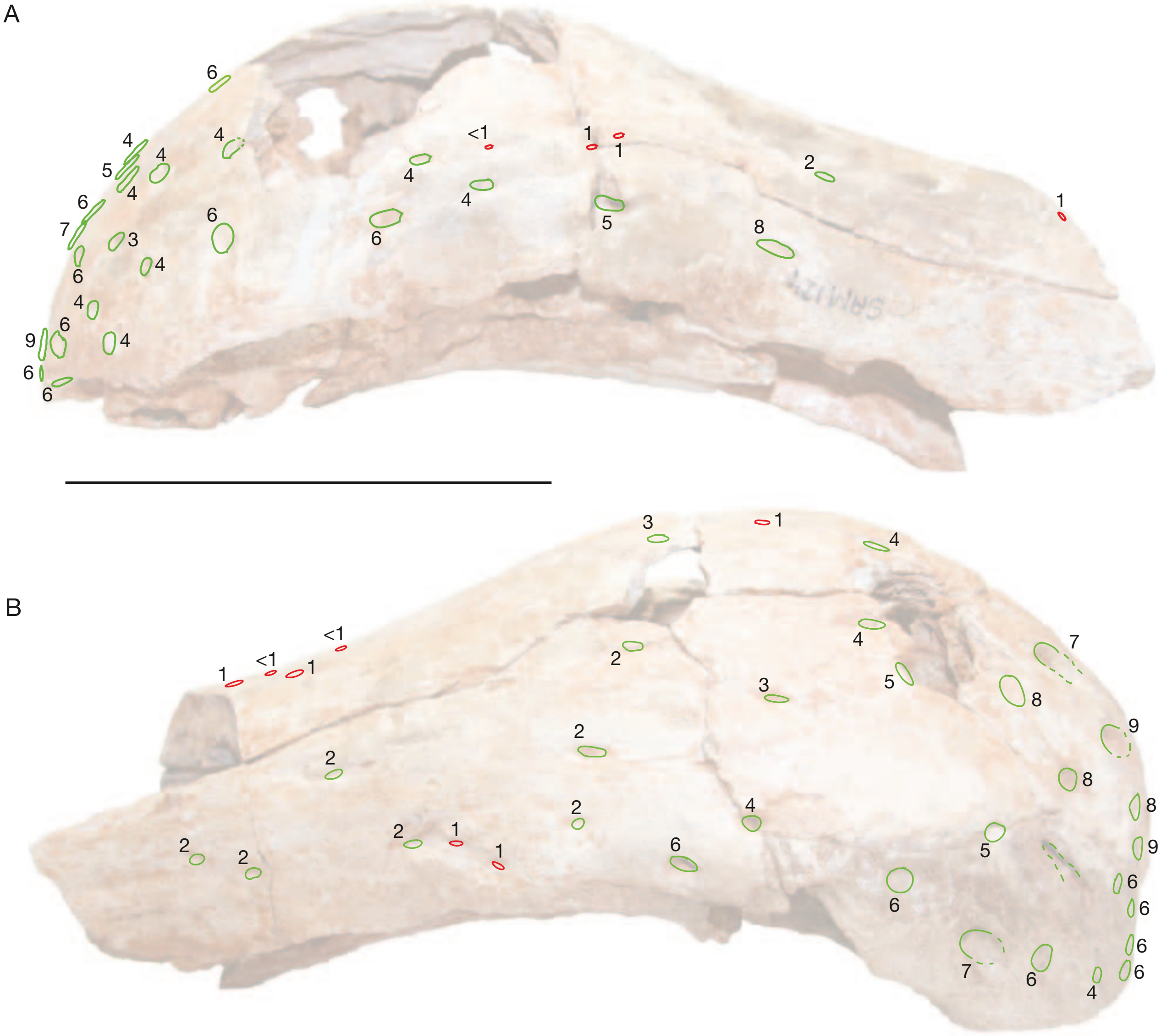


Fig. 12. — MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996, precise distribution of neurovascular foramina on right (**A**) and left (**B**) premaxillae; small foramina are represented by **red circles** (1 mm or less) and others by **green circles** (more than 1 mm). Units in mm. Scale bar: 10 cm. Models by Frédéric Pittet.

Sabath 2003; Funston *et al.* 2021; Sattler & Schwarz 2021) or *Archaeopteryx* von Meyer, 1861 (Wellnhofer 1994). It seems to be a primitive character in archosaurians for some authors (Elzanowski & Wellnhofer 1993). Such interdental plates have also been described in other taxa such as mosasaurs (Caldwell *et al.* 2003; Rieppel & Kearney 2005; LeBlanc *et al.* 2017b) or even snakes (Budney *et al.* 2006; LeBlanc *et al.* 2017b). Our CT scans have not detected any notable difference in densities between the premaxillary bone and this potential interdental plate (Fig. 13B1-B3). Given all of these indications, we believe that this bone separation could well be an interdental plate, insofar as the two teeth takes root in the same place (Fig. 13B3). More pushed comparisons with other Spinosauridae are necessary to support this hypothesis.

This potential interdental plate separating a replacement tooth from the main tooth in the first alveolus is not found both in either small (MNHN.F.GDF366) or more mature (MNHN.F.GDF365) *Cristatusaurus* individuals (Fig. 13C1-C3). The tomographic results indicate in ventral view that the replacement teeth at this location, mostly invisible on the surface, developing very clearly in the same base alveolus as the main tooth, without any bony separation (not observed on the surface for MNHN.F.GDF365 because of the sediment but visible on CT scans).

Internal description

The internal configuration in Spinosaurinae is necessarily partly different from that of Baryonychinae, such as *Cristatusaurus*. Indeed, the posterior bone processes of the premaxillae are more developed in Spinosaurinae and their external nostrils occupy a much more posterior position compared to Baryonychinae. We can clearly observe that the neurovascular branches take an increasingly ventral position posteriorly, eventually to emerge below the exter-

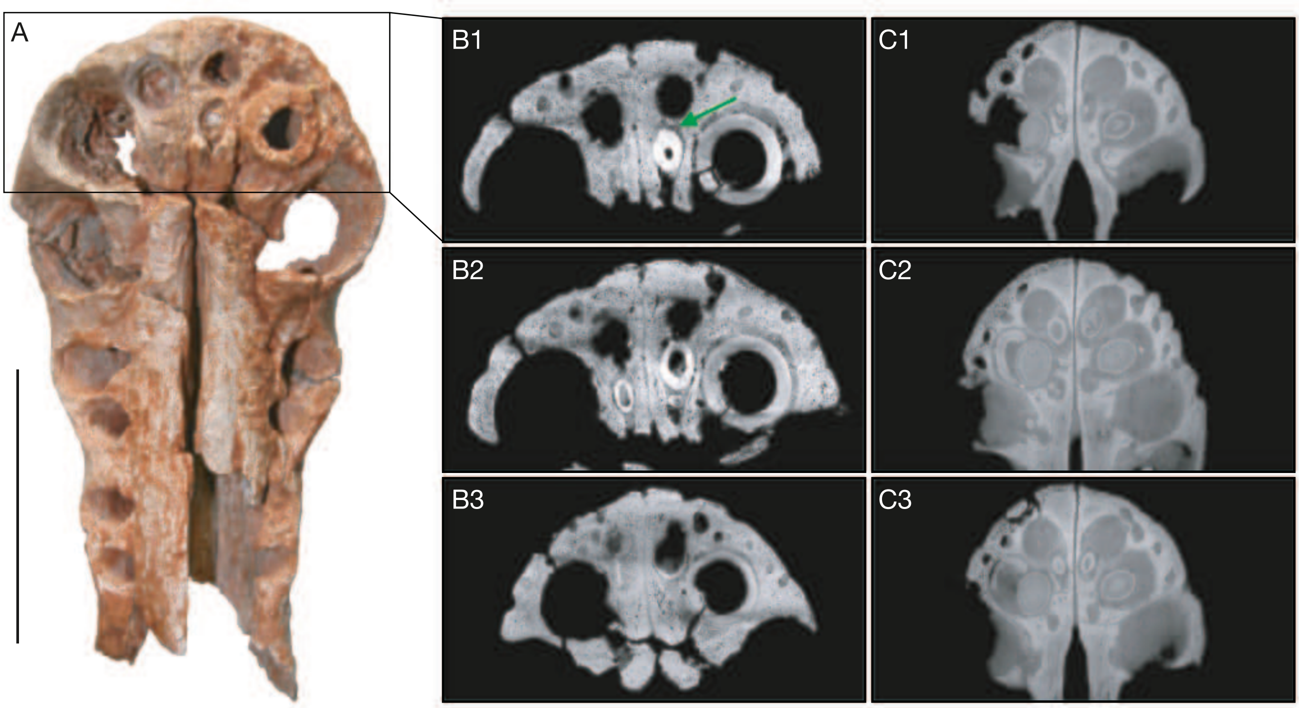


Fig. 13. — **A**, **B**, MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996: **A**, ventral view of premaxillae showing the independent "double pairs of apical alveoli"; **B1**-**B3**, CT scans, transverse views from bottom to top, with visible bony separation (**green arrow** on **B1**) more and more reduced as we go back along the teeth to finally reveal a single root cavity (**B3**); **C**, *Cristatusaurus lapparenti* Taquet & Russell, 1998, MNHN.F.GDF365: **C1**-**C3**, CT scans, transverse views from bottom (**C1**) to top (**C3**), without bony separation for the first alveolus; the same disposition is true for the junevile *Cristatusaurus lapparenti* specimen (MNHN.F.GDF366). Scale bar: 10 cm. Photograph and CT scans treatment by Frédéric Pittet.

nal nostrils in *Cristatusaurus* (see internal descriptions of MNHN.F.GDF366 and MNHN.F.GDF365). This is not the case in *Spinosaurus* where the two main neurovascular branches remain in a dorsal position all along the premaxillae to operate a descent very probably just before the opening of the external nostrils, at the level of the posterior suture between premaxillae and nasals (Fig. 14).

The left premaxilla being very incomplete, the underlying network is impossible to reconstruct, except at the apex of the rosette. The backward pointing secondary branches and the bowl structure described in *Cristatusaurus* specimens are not observed here perhaps due to lack of preservation here. However, it is very likely that such a structure was also present in *Spinosaurus* but further back, to invade the upper area of the outer nostrils while the main branches were to dip below them, as in *Cristatusaurus*.

On the posterior half of the specimen, the secondary branches extending from the two main branches are generally thin (in the order of 1 mm) and emerge more or less perpendicular to the surface. From the 3rd alveolus and up to the apex of the muzzle, the teeth widen considerably (Fig. 14A, B). The secondary branches also widen in this area, to reach a diameter of several millimeters (up to 6 mm for the widest); Furthermore, the orientation of the branches change, and they all point towards the front of the muzzle (Fig. 14B). Even though teeth are missing, the neurovascular network is once again found to follow their shape from the root to the alveolar bone margin. Globally, we find the same neurovascular arrangement as in *Cristatusaurus*. The widest branches directly give rise to a series of six foramina, which run along both sides of the bony symphysis between the premaxillae on the front of the rosette, in a relatively symmetrical way (Fig. 14A; Appendix 4B).

Teeth

Internal scans reveal seven teeth still preserved out of the total 14 premaxillary alveoli (Fig. 14B). On the left premaxilla, there is a first tooth 2.2 cm long in the first alveolus, pointing backwards at an angle of approximately 45° with respect to the alveolar margin and probably in a transitional situation between replacement tooth and main tooth. A residue is also visible on the scan in the apical position of the tooth (probably the broken tip). Still on the left premaxilla, the largest preserved tooth of the specimen is housed in the second alveolus. Although broken on the surface, it measures 6 cm in length (probably more than 10 during the animal's lifetime) and 2.6 cm in diameter at the root. Since the dentin has dissolved, the enamel thickness can easily be measured here: 5.1 mm.

On the right premaxilla, the first alveolus also contains a 1.3 cm tooth, which this time can reasonably be described as a replacement tooth (the main tooth not being preserved). The second right alveolus contains the remains of an extremely fragmentary tooth but suggests a size comparable to that which occupies the second left position. The third, fourth and fifth alveoli only contain replacement teeth with the respective sizes of 2 cm, 1.9 cm and 1.2 cm (not visible on the surface).

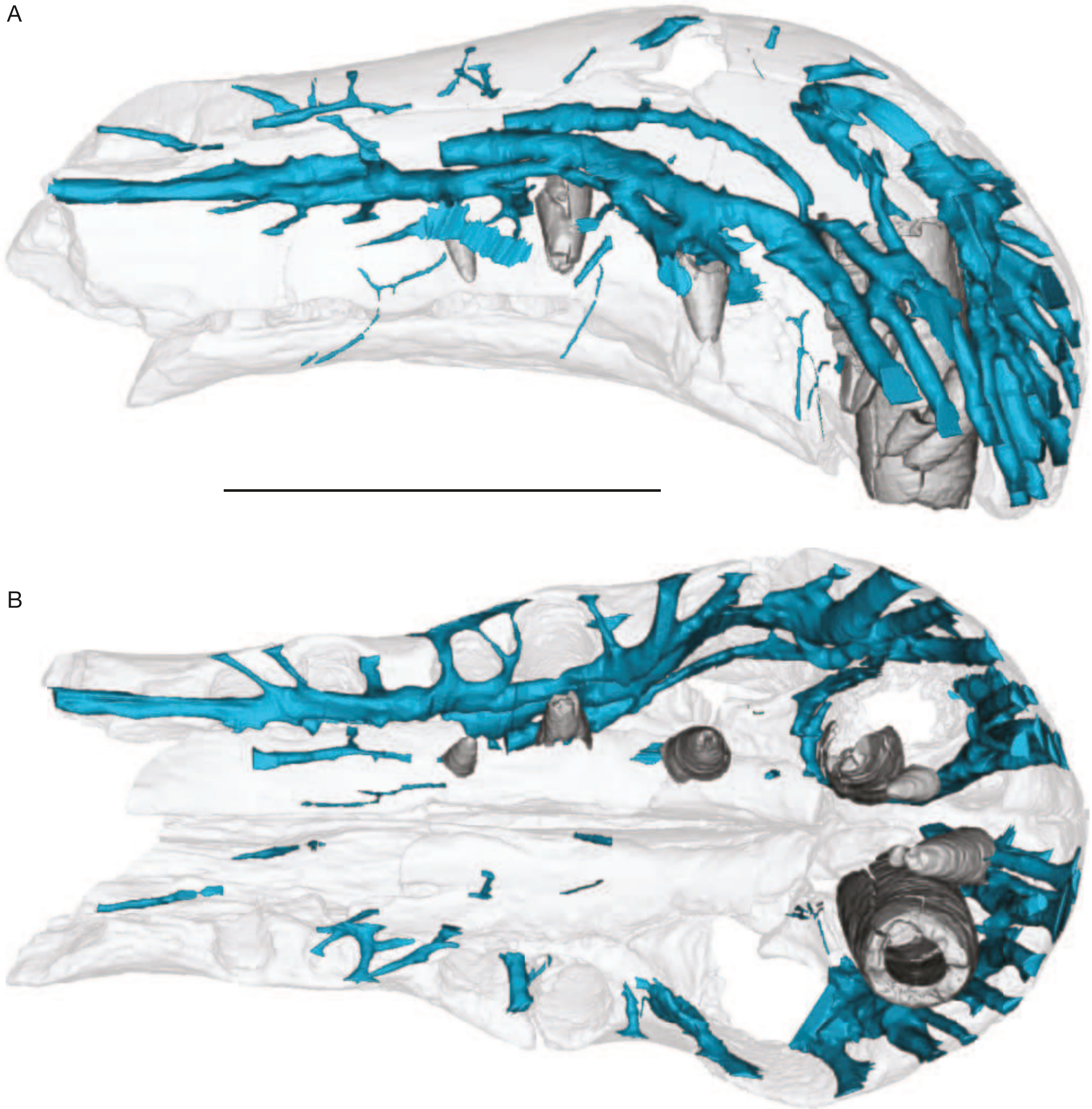


FIG. 14. — MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996: **A**, right premaxilla, labial view in transparency with teeth; main branch above the tooth roots; **B**, premaxillae, ventral view in transparency with teeth. Scale bar: 10 cm. Models by Frédéric Pittet and Florent Goussard.

DESCRIPTION OF MNHN.F.SAM124 (MAXILLAE)

Surface and internal description

The maxillae are incomplete, especially on the dorsal part, but allow a global and direct view of the inner cavity of the bones (Fig. 16A; Appendix 4A). This is why we decide here to describe the exterior and the interior of the fossil in the same section.

The right maxilla is preserved on a length of 32.5 cm and the left one on 28 cm. The two bones are well fused together and the distribution between the left and right alveoli is relatively symmetrical, both in position and in size (Fig. 15). The left bone is caudally broken at the level of the eighth maxillary alveolus while the right extends a little bit more to the ninth one. The first two pairs of alveoli are relatively small in diameter (1.4 cm for the 1st pair and 1.8 cm for the 2nd one) compared to those further back: 3.5 cm for the 3rd pair, 4.1 cm for the 4th pair (the widest), then they gradually decrease in diameter for the following ones (3.7, 3.4, 3.2, 3 and 2.9 cm for the 9th pair). This configuration is identical to that observed on the specimen of *Spinosaurus* MSNM V4047 from the Kem Kem beds, southern Morocco (Dal Sasso *et al.* 2005). Ven-

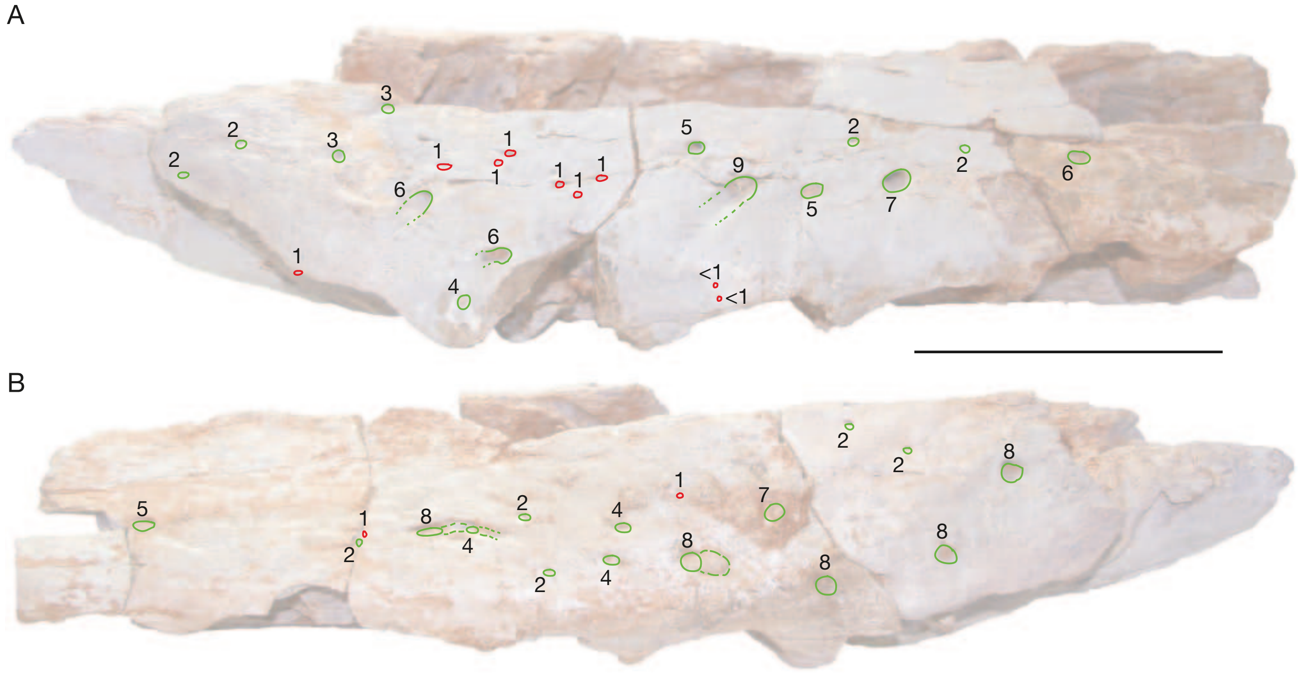


Fig. 15. — MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996, precise distribution of neurovascular foramina on right (**above**) and left (**below**) maxillae; small foramina are represented by **red circles** (1 mm or less) and others by **green circles** (more than 1 mm). Units in mm. Scale bar: 10 cm. Models by Frédéric Pittet.

trally, proximal processes of the premaxillae are visible and strongly sutured with rostromedial processes of the maxillae at the level of the 3rd maxillary alveolus on the first anterior 12 cm (Appendix 4C).

There are 17 neurovascular foramina superficially, on the right side, and 23 on the left side. Some are very thin (less than 1 mm in diameter) and others much thicker (up to 9 mm in diameter). Of course, some could not have been detected without the tomographic data, but the roof of the bones is here missing and, consequently, many other foramina must have been present, as evidenced by the numerous grooves preserved on the inner face of the bone (Fig. 15).

Indeed, several furrows of respectable diameters (from 1 to 4 mm) and showing a certain anatomical regularity are visible on the labial internal walls of the bones, distal to the dental alveoli (Fig. 16B-D). The conjunction of the trajectories of these furrows with those of the scanned neurovascular rami allows us to assume that the main branch must have labially followed the alveolar cavities. The proximity between dental cavity, bone and neurovascular network described in the premaxillae is found in the maxillae as well. The branches are interconnected, cross the bone, then follow the dental wall in a groove (partially in the alveolar lumen) to “plunge” back into the interdental bone, and then join the next alveolus and/or the surface of the maxilla by one or more foramina (Fig. 16D).

The branches revealed by the tomography are the largest of the scanned specimens (between 0.4 and 0.8 cm in diameter) and lead outwards at an angle of approximately 45° with respect to the surface of the bone for those located between the 1st and 6th pairs of alveoli, the most posterior branches tend to pierce the bone perpendicularly or even to point backwards, like a “neurovascular fan”. Moreover, they systematically occupy the interalveolar bone zones and are the extension of a very complex and interconnected network whose arrangement can be sketched by observing the grooves on the internal walls of the bones, labially and along the alveolar cavities (Figs 16; 17B). All these elements show, again, that these rami were probably connected to two main neurovascular branches that should run along the maxillae labially to alveolar cavities on their first upper third, like what was described in the right maxilla fragment of *Cristatusaurus lapparenti*.

Teeth

The left maxilla still contains four alveoli with broken and/or fragmented teeth. In the 2nd alveolus is the best-preserved tooth with its 3.2 cm and such visible characteristics of Spinosaurinae such as a rather circular section with a slight carina without serrations and typical longitudinal striations (Fig. 17Aa1). A first-generation replacement tooth of 2.1 cm is in the 4th alveolus. The 5th alveolus houses a main tooth 3.4 cm long. The 6th alveolus contains a main tooth 4.1 cm long and in the process of lateral demineralization by a well-preserved replacement tooth of 3 cm with a second-generation replacement tooth of 0.5 cm (Fig. 17Aa2).

The right maxilla reveals a main tooth broken in two longitudinally in the 3rd alveolus as well as a replacement tooth fragment of barely 0.5 cm in the 6th alveolus.

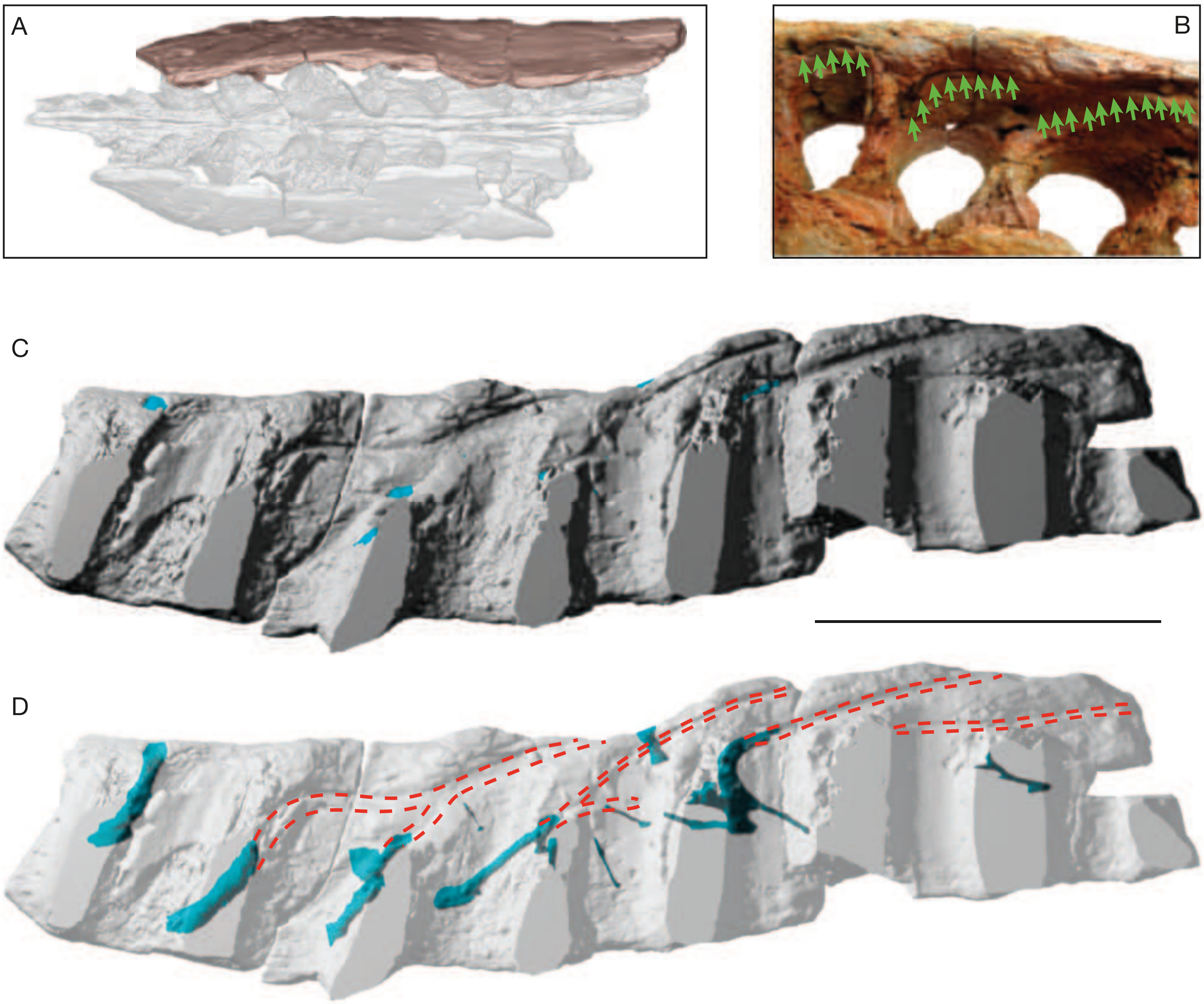


FIG. 16. — MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996, details on neurovascular grooves on the labial internal wall of the right maxilla: **A**, top view of the fossil with highlight of the very labial portion of the right maxilla; **B**, details of the fossil with highlighting of a passage of groove along the 3rd, 4th and 5th alveolus (**green arrows**); **C**, details on neurovascular grooves on the labial wall of the right maxilla (without teeth); **D**, general view of the internal labial wall of the right maxilla (without teeth) in transparency with the neurovascular network scanned with the interconnections of the grooves. Scale bar: 10 cm. Models by Frédéric Pittet and Florent Goussard.

COMPARISONS AND DISCUSSION

GENERAL CONSIDERATIONS

As we have seen in the descriptions of the premaxillae, the foramina are not only more and more numerous as we approache the rosette but also statistically wider. These two indices led to consider an important neurovascularization of the rosette in particular. In all extant taxa requiring increased sensitivity of the snout, this increasing density of foramina or pits towards the front is observed: birds (Gentle & Breward 1986; Cunningham *et al.* 2007, 2010; Hieronymus & Witmer 2010; Amendano *et al.* 2021), mammals (Manger *et al.* 1998; Pettigrew 1999; Miyamae *et al.* 2024), fishes (Vullo *et al.* 2016), crocodilians (Soares 2002; Di-Poï & Milinkovitch 2013), etc. This is also the case in several extinct groups such as pliosaurs (Sassoon *et al.* 2012; Foffa *et al.* 2014) or phytosaurs (Lees 1907; Anderson 1936; Hungerbühler *et al.* 2012; Datta *et al.* 2021). In addition, since the diameter of the nerves is proportional to the diameter of the bone foramina, it can be deduced that the nerve ramifications were dense on the surface of the dermis of the snout of Spinosauridae. Physiological studies demonstrate this aspect in many modern animals. DeGusta *et al.* (1999) already made the link between the size of foramina and that of the fiber to which it is attached in primates. George & Holliday (2013) concluded the same and showed by comparative analysis in several modern crocodilians that the size of foramina was a strong indicator to predict the size of the nerves they contain and for the number of axons present (Fig. 19). Clearly, the greater the diameter of the foramen is, the greater the diameter of the nerve is (so the number of axons also increases). The authors consider that this correlation can easily be used for fossil forms and that there is no reason to question this model. That is why we propose to apply it to dinosaurs and Spinosauridae in particular.

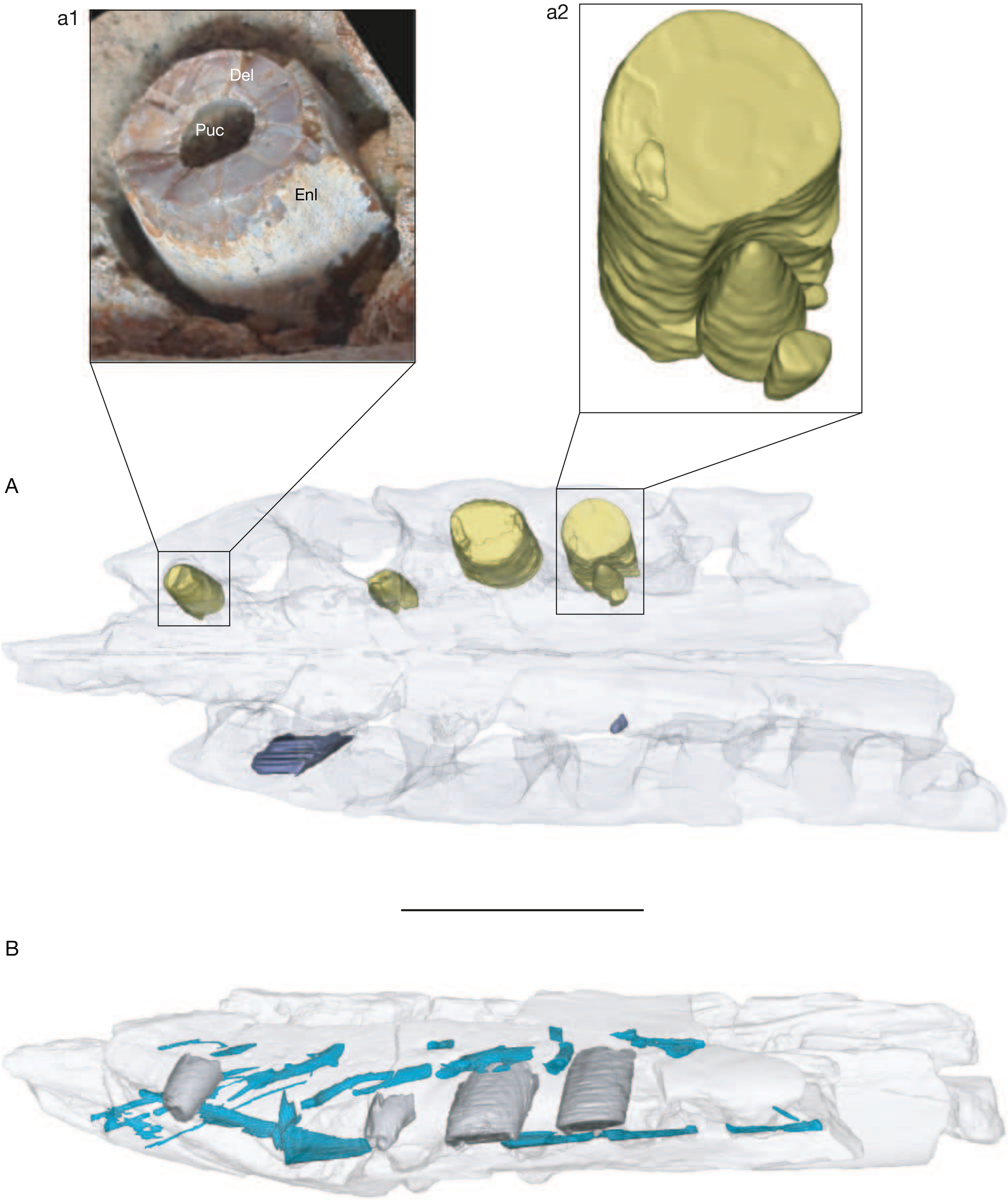


Fig. 17. — MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996: **A**, maxillae CT scans in transparency with teeth (ventral view) (right maxilla teeth in **purple**, left maxilla teeth in **yellow**); **a1**, details on the 2nd alveolus tooth from the left maxilla (**Enl**, enamel layer with longitudinal striations typical of Spinosaurinae; **Del**, dentine layer; **Puc**, pulp cavity); **a2**, details on the 6th alveolus of left maxilla with three generations of teeth and presence of demineralization; **B**, lateral view of the left maxilla in transparency with teeth and neurovascular complex. Scale bar: 10 cm. Models by Frédéric Pittet and Florent Goussard.

NEUROVASCULAR NETWORK AND SKIN SENSITIVITY IN MUZZLE OF SPINOSAURIDAE AND OTHER TETRAPODS

Non-avian theropods

Studies of potential integumentary sensory organs and other sensitive adaptations in theropods have been developing very rapidly in recent years. Most seem to converge in favor of a greater diversity of sensory adaptations than we previously thought in dinosaurs.

Following a comparative study of the teeth of several theropods, Rothschild & Naples (2017) suggested that the Albertosaurinae in particular must have had a chamber containing organs sensitive to the direction of the wind in their pronounced dental groove in order to orient themselves, like current weathervanes.

Series of foramina running along the nasal bones of the Cenomanian abelisaurid *Skorpiovenator* Canale, Scanferla, Agnolin & Novas, 2009 have also been described (Canale *et al.* 2009). The underlying channels are probably connected to the trigeminal nerve (Cerroni *et al.* 2022). The authors leave several hypotheses open as to the usefulness of these foramina, including the presence of sensory organs. The arrangement of these neurovascular branches which point to the roof of the bone recalls that we described in the premaxillae of *Cristatusaurus*.

Barker *et al.* (2017) revealed through tomographic study a well-developed neurovascular network in the premaxilla and maxilla of Allosauroidea *Neovenator salerii* Hutt, Martill & Barker, 1996 (Barremian, lower Cretaceous of UK). This theropod is considered to be a typically terrestrial predator and the authors also consider a link between this network and sensory structures on the animal's snout. A calculation of the ratio between the volume of the network and the bone was carried out: about 7.3% for the premaxilla and an average of 4.1% for the maxilla (which supports the hypothesis of a sensitivity increased as one approaches the apex of the snout). This ratio observed in the premaxillae of *Cristatusaurus lapparenti* is respectively 9.39 % for the juvenile MNHN.F.GDF366 and 9.99 % for the mature specimen MNHN.F.GDF365. That is, almost 10 % of the total volume of the premaxilla is "filled" with nerves and blood vessels, which is comparatively about a third more than observed in a "classic" terrestrial theropod as *Neovenator*. If we consider this ratio of neurovascular occupation as being the proportional reflection of sensory sensitivity, the Spinosauridae would undoubtedly be among the most successful non-avian dinosaurs in this field. Other comparative studies between theropods are, however, necessary to support or invalidate this hypothesis.

In Tyrannosauridae in general, the number of foramina is quite important on the jaws and more and more clues point to a sensory adaptation on the muzzle of these apex predators. In *Albertosaurus* Osborn, 1905 and *Alioramus* Kurzanov, 1976, there is a second horizontal row of large foramina above the traditional alveolar margin (Hurum *et al.* 2003). The bony surface of the skull of *Daspletosaurus horneri* Carr, Varricchio, Sedlmayr, Roberts & Moore, 2017 also suggests a scaly integument with what may look like integumentary sense organs (Carr *et al.* 2017).

In *Tyrannosaurus rex*, a row of foramina that follows the edge of the antorbital fenestra, called "circumfenestral row", have been identified on FMNH PR2081, "Sue" (Brochu 2003). Several other pits and foramina are visible between alveolar and circumfenestral rows (Fig. 18B). The right maxilla shows imprint of ramifying nerve between two foramina, which probably indicates that the axons and blood vessels connecting these openings should innervate and irrigate several structures. From the CT scans, Brochu (2003) was able to demonstrate that the foramina of the alveolar and circumfenestral rows joined in an internal ramus certainly belonging to the maxillary branch of the trigeminal nerve, which supports the sensory function of these openings, as in the other tetrapods.

The skull of *Tyrannosaurus rex* was recently scanned again, and the scans confirm an amazingly developed neurovascular network in both jaws (Carr *et al.* 2017; Bouabdellah *et al.* 2022).

Another interesting comparison between the Spinosauridae and the large Tyrannosauridae can be made by considering the effective surface of the supposedly sensitive epidermis: the longirostre strategy of the Spinosauridae makes it possible to gain in sensory surface due to the elongation of the muzzle itself, whereas the Tyrannosauridae, in addition to having the most massive skulls in theropods, developed a strongly convex maxillae on their lower margin, which induces by corollary a larger space for a sensory network, potentially. The same pattern is present in the Asian tyrannosaur *Tarbosaurus bataar* Maleev, 1955 (Hurum & Sabath 2003).

By comparison, the rostral neurovascular system of the maxillae is known to be primitively very stable in its configuration in the Diapsida: a broad main branch running horizontally along each maxilla, tubular, parallel to the alveolar margin and sending secondary branches at regular intervals leading directly to the row of typical and aligned labial foramina (Porter & Witmer 2015; Barker *et al.* 2017; Benoit *et al.* 2021). This configuration is different in *Tyrannosaurus rex* insofar as the main neurovascular root is not uniformly horizontal but operates at an angle to rise until it occupies a position superior to the large dental alveoli of the maxillae (Bouabdellah *et al.* 2022). We interpret this oblique and dorsal configuration of the maxillary branches in *Tyrannosaurus* as a possible adaptation of innervation and vascularization of mechanoreceptive sensory organs on almost all the surface of their enlarged maxillae, just as the Spinosauridae did with their premaxillae surface. Our interpretation of these results is that Tyrannosauridae must also have a high sensitivity in their snout and maybe even very sensitive lips. The work of Cullen *et al.* (2023) provides additional information on the probable presence of soft tissues covering the teeth of theropods.

Recent phylogenetic analyses suggest that physical characteristics typical of large tyrannosauroids are the result of a mosaic evolution (Brusatte & Carr 2016). The size of the body has gradually increased and with it, the power of bite, a more robust muzzle (in the shape of a U) or even asymmetric keels on the teeth to better bleed to death the prey in the late branching taxa such as *Tyrannosaurus rex* and *Tarbosaurus bataar*. All these developments show an improvement of the skull to kill more efficiently. Other adaptations such as the size and the number of the foramina on the bones of the two jaws (Fig. 18A-C), the well-developed neurovascular network, the large surface of the maxillae, and the configuration of the underlying neurovascular branches suggest a possible hyper-

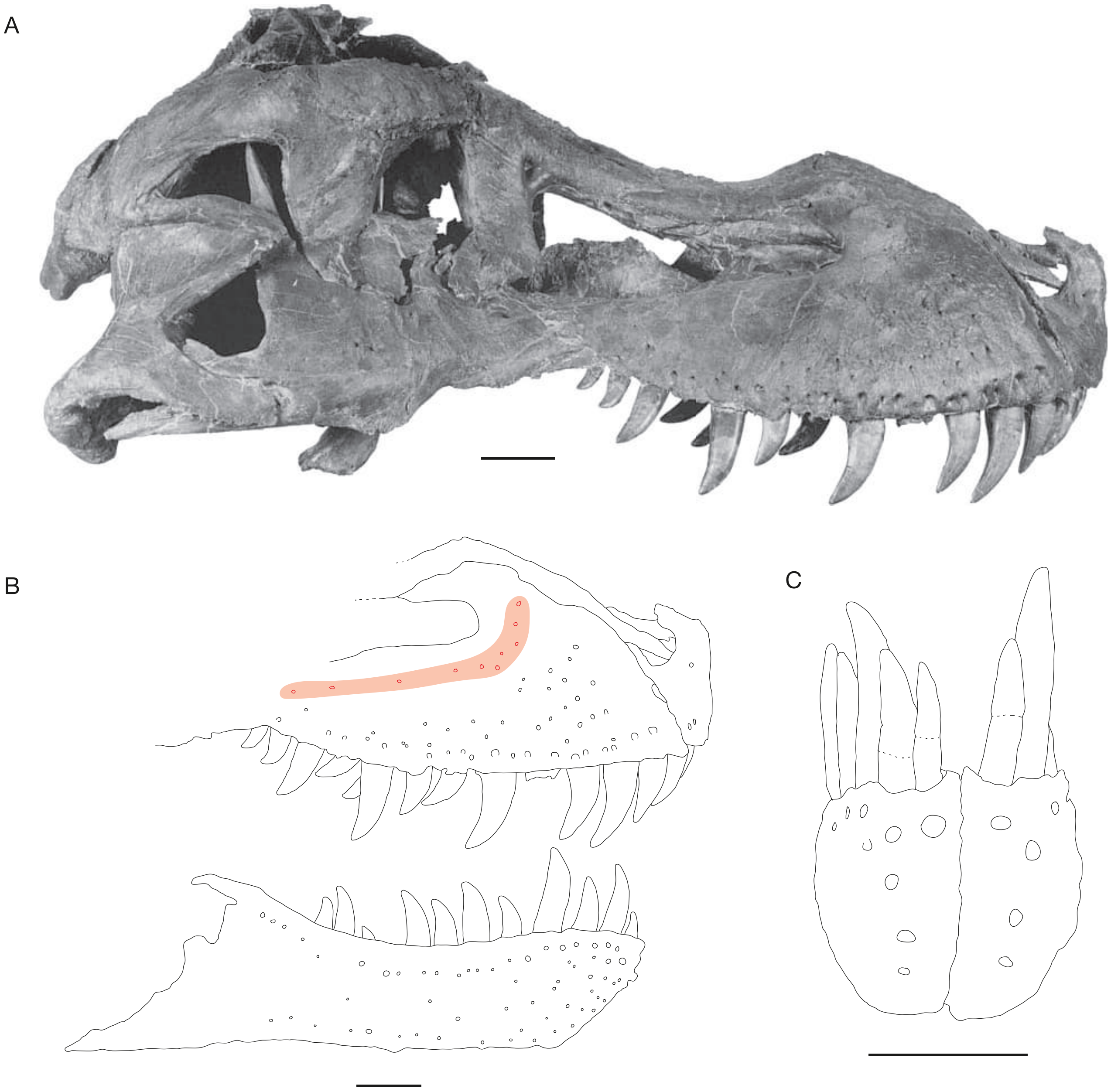


FIG. 18. — Overview of the distribution of foramina on the front of the skull of *Tyrannosaurus rex* Osborn, 1905: **A**, **B**, FMNH PR2081, *Tyrannosaurus rex* ("Sue"); **A**, photograph of the upper portion of the skull in right lateral view (from Brochu 2003 – photograph by J. Weinstein); **B**, highlighting of the foramina of the premaxilla/maxilla (**A**) with the "circumfenestral row" in **red** and of the dentary (**B**) in right lateral view (personal observations); **C**, BHI 3033, *Tyrannosaurus rex* ("Stan"); highlighting the size of the foramina on the dentary in anterior view (personal observations). Scale bars: 10 cm. Models by Frédéric Pittet and Florent Goussard.

sensitivity of the epidermis of the anterior half of the muzzle in *Tyrannosaurus rex*.

We suggest the hypothesis that theropods with very entangled forelegs and, like Tyrannosauridae or Abelisauridae, had to interact with their environment mainly with their muzzle. There are some indications that these reduced forelimbs were nevertheless robust and equipped with powerful muscles, certainly for an intraspecific display (Brochu 2003; Hutchinson *et al.* 2005; Lockley *et al.* 2008; Burch 2017).

It is quite reasonable to imagine these dinosaurs with more highly sensitive snout to interact with their congeners, their offspring, feel the pressure, temperature or even the variations of the wind as proposed by Rothschild and Naples (Rothschild & Naples 2017).

Their missing tactile information and compensated by sensitive integumentary structures on the snout should be compared with the way in which Spinosauridae compensated their olfactory sense and their sight (not very effective under water) by an ultrasensitive longirostrale strategy to feel the vibrations of their direct environment.

The cases of these frankly terrestrial theropods show us that it is not necessary to be long nosed to be "sensitive of the muzzle" (and even by looking at extant species). The longirostral character has more of a hydrodynamic utility and for the mode of nutrition (rapid lateral movements for catching fish, as observed in the gharial) rather than an obligatory sign of sensitivity.

In 2020, the holotype of the Compsognathidae *Juravenator* Göhlich & Chiappe, 2006 (Kimmeridgian, Late Jurassic) showed an astonishing diversity in the structure of the scales of the animal and in particular some strangely resembling the sensory domes of current crocodilians (Bell & Hendrickx 2020). The authors put forward the hypothesis of an increased cutaneous sensitivity for nocturnal aquatic hunting, its orbits being strongly developed.

Birds (avian dinosaurs)

The extant avian dinosaurs represent the closest relatives of the extinct theropod forms and, as such, are a good representation of the very wide range of sensory strategies developed in dinosaurs. Indeed, under the stratum corneum of their beak, the premaxillae and maxillae of birds sometimes have many foramina, like Spinosauridae, directly connected to the trigeminal network (Gentle & Breward 1986; Hieronymus & Witmer 2010; Amendano *et al.* 2021). The presence of very sensitive mechanoreceptive organs, such as Herbst or Merkel corpuscles, has been well documented on the rostrum of many avians (Gentle & Breward 1986; Cunningham *et al.* 2010; Rhinn *et al.* 2013). In several taxa, links have been made between the number of foramina on the jawbones and the density of the trigeminal sensory fibers. Ratites like the ostrich *Struthio camelus* Linnaeus, 1758 and the emu *Dromaius novaehollandiae* Latham, 1790 have an arrangement and a number of bony pits are comparable in both species and suggest increased extra and intraoral sensitivity (Crole & Soley 2017). These animals peck regularly and instinctively, so it is useful for them to quickly discriminate between the different elements that encounter their beak, vision not being able, once again, to suffice for this purpose.

The Anatidae also show a high density of foramina on the front of their premaxilla (Berkhoudt 1976). The nerve ramifications underlying these foramina are connected to the trigeminal nerve (Amendano *et al.* 2021). Ducks and swans must be able to rely more on the mechanoreception of their snout than on their vision to choose the right algae and other plant debris to ingest.

The example of probing birds (woodcocks, Apterygidae and Charadriiformes) is particularly interesting because, for these phylogenetically distant groups, the mechanisms for detecting prey found in mud or on the ground are similar. Recurrent sensory structures on the long snout of these birds reflect a new example of evolutionary convergence, the configuration of which is reminiscent of that found in Spinosauridae. In kiwis *Apteryx* Shaw, 1790, vision is extremely reduced and even useless in many respects, so much so that some individuals are blind. However, this does not prevent the animal from feeding and does not substantially impact its life expectancy. The sense of vision being compensated by other senses in these nocturnal animals: auditory, olfactory and, of course, tactile (Moore *et al.* 2017). While olfaction is widely used, prey on the ground can also be detected by the waves they propagate through the air as they move (Cunningham *et al.* 2007). These waves reach the fine vibrissae at the base of the beak and tell the animal's cortex the exact location of their origin (Martin *et al.* 2007). For probing of prey buried in the ground, on the other hand, it is the pressure-sensitive mechanoreceptors housed in the numerous foramina at the end of the snout that come into play (Cunningham *et al.* 2007, 2013). Again, the trigeminal branches transmit tactile information to the brain.

Some aquatic and semi-aquatic taxa

Phytosauria. Phytosaurs represent a well-known and long-studied sister group of Archosauria. They seem to have also adopted a strategy analogous to the longirostre species already described (Lees 1907; Anderson 1936; Hungerbühler *et al.* 2012) such as “grabbing” conical teeth, a developed rosette covered with numerous foramina, even in young individuals (Heckert *et al.* 2013), and trigeminal neurovascular network along the premaxilla, maxilla and dentary. This seems to correlate with the presence of sensory organs (Lessner & Stocker 2017).

Pliosauroidea. In pliosaurs, some specimens reveal a significant number of foramina on the premaxilla and the dentary (Sassoon *et al.* 2012). A neurovascular complex has also been described in the rostrum of a very large individual of *Pliosaurus kevani* Benson, Evans, Smith, Sassoon, Moore-Faye, Ketchum & Forrest, 2013 (Foffa *et al.* 2014). The authors considered that the strong neurovascular ramifications attached to the teeth and the foramina could suggest the presence of sensory organs, like the ISOs of crocodilians. They counted more than 200 foramina on the premaxillae and incomplete maxillae of this individual.

Other extinct aquatic Sauropterygia taxa show many foramina and pits on the front of the snout (Mosasauridae, Ichthyosauriformes, Plesiosauroidea, etc.) but more extensive comparative and tomographic studies still need to be carried out to make a solid link with any potential sensory organs. Some groups still represented today such as the Testudinata have many sensory corpuscles in their rhamphotheca, which certainly play a mechanoreceptive role in the coordination of movements under water (Buchtová *et al.* 2009).

Crocodilians. In crocodilians, a higher concentration of integumentary sensory organs (ISOs) is found near the teeth and on the anterior half of the skull. In Alligatoridae (Soares 2002), ISOs are only on the cranial region, while in *Crocodylus* Laurenti, 1768, *Tomistoma* Müller, 1838 and *Gavialis* Gmelin, 1789, they are also found on all scales of the animal's body (Leitch & Catania 2012). On Nile crocodile *Crocodylus niloticus*, most of scales have one ISO except for some scales of the face, which can have as many as thirty. This is an adaptation for higher sensitivity around the mouth (Di-Poï & Milinkovitch 2013). In mammals, chemoreceptors are all concentrated on the tongue and the mechanoreceptors diffused on all the surface of the skin. In crocodilians, these two types of receptors are within the ISOs themselves. Di-Poi and Milinkovitch (Di-Poï & Milinkovitch 2013) have even demonstrated that facial ISOs are the first cutaneous sensory structures devel-

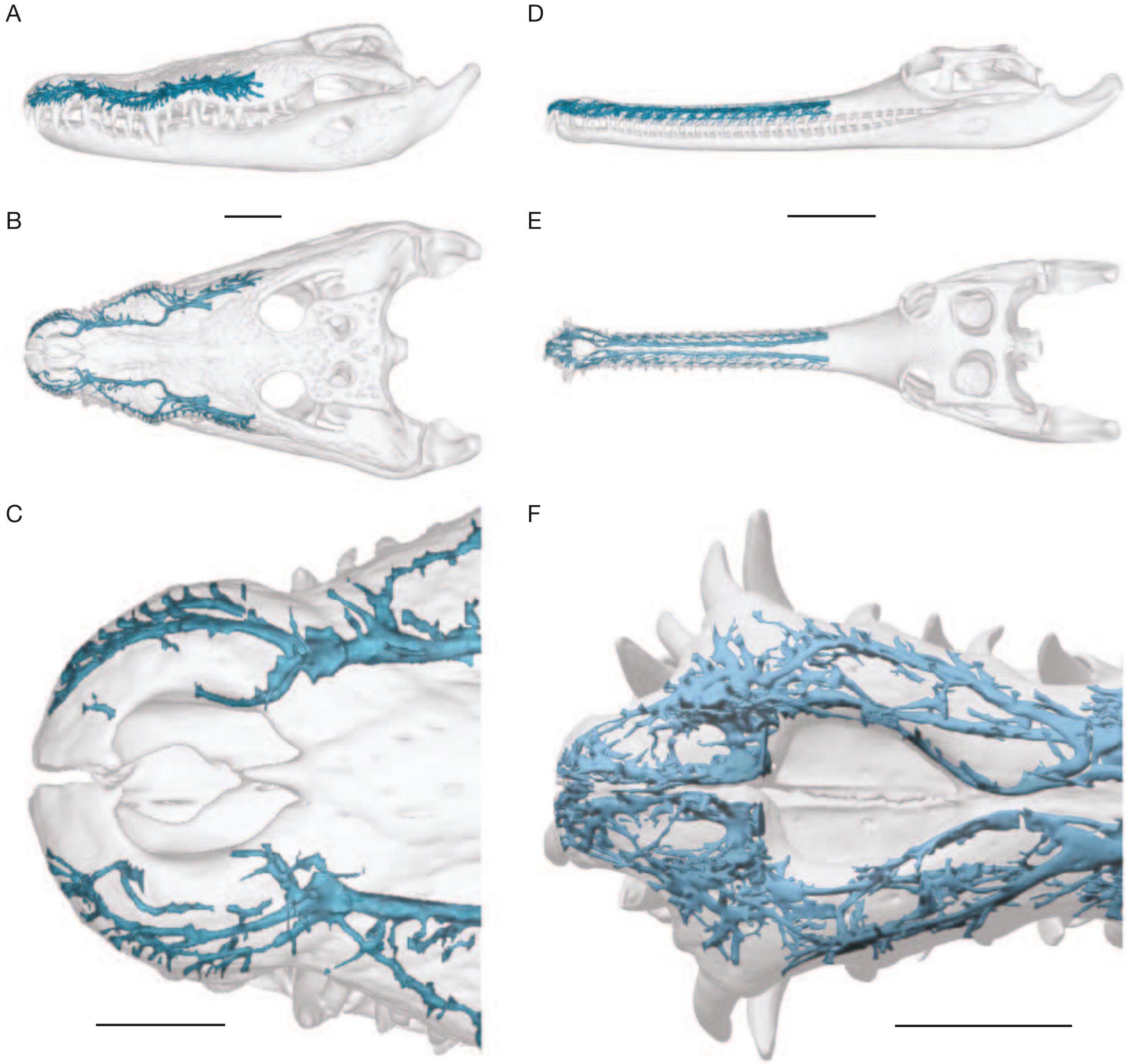


FIG. 19. — CT scans views of two crocodilians rostra in transparency with configuration of the neurovascular network: **A**-**C**, *Crocodylus moreletii* Duméril & Bibron, 1851 (TMM M-4980) in lateral left (**A**) and top (**B**) views with network highlighted in the rosette (**C**); **D**-**F**, *Gavialis gangeticus* Gmelin, 1789 (MHNG S14.25) in lateral left (**D**) and top (**E**) views with network highlighted in the rosette (**F**). Models by Frédéric Pittet and Florent Goussard. Scale bars: A, B, D, E, 10 cm; C, 5 cm; F, 2.5 cm.

oped in *Crocodylus niloticus* embryos, thus emphasizing their vital importance for the animal from an early development.

The comparison between Spinosauridae and crocodilians is historical and widely documented in the scientific literature (Taquet 1984; Holtz 1998; Rayfield *et al.* 2007; Cuff & Rayfield 2013). The very large number of foramina as well as the first indications of the presence of a neurovascular structure in the snout of *Spinosaurus aegyptiacus*, as in crocodilians, further prompted this comparison (Dal Sasso *et al.* 2009; Ibrahim *et al.* 2014). In addition, the long snouted morphology of these animals ended up portraying them as "crocodiles like" dinosaurs.

The fact that crocodilians ISOs have been particularly studied in recent years, coupled with the fact that Spinosauridae have often been compared to them because of their morphological analogies should not, however, lead us to conclude that they also have ISOs sensu stricto. Indeed, as we saw above, even if the neuronal integration of the sensory organs remains relatively stable during the evolution of the tetrapods (via the branches of the trigeminal nerve), there are no models of constant organizations of these sensory organs, each taxon having adopted a very sensitive snout having given birth to new sensory structures without synapomorphic link. We know, however, that it is indeed the maxillary branch of the trigeminal nerve (in addition to the blood vessels) which extends into the maxilla and premaxilla of crocodilians (Fig. 19), the ophthalmic branch being further back (Leitch & Catania 2012).

Our CT scans of the rostra of two Gavialidae (*Gavialis gangeticus* and *Tomistoma schlegelii*) and two Crocodylidae (*Crocodylus niloticus* and *Crocodylus moreletii* Duméril & Bibron, 1851) highlight this trigeminal network in a remarkable way (Fig. 19). The maxillary (and mandibular) branches are particularly ramified and developed and the evolutionary convergence with the Spinosauridae is once again evident, particularly if we compare this with the position of the nostrils (Fig. 19C, F). Note that the main branches along the maxillae of these crocodilians are mostly above the dental roots and send rami between each tooth to supply the lateral foramina and the neurovascular line running along the alveolar margin (Fig. 19A, B, D, E). This arrangement seems, as we described, to be different in *Cristatusaurus lapparenti* and *Spinosaurus maroccanus* where the main branches are in a labial position with respect to the teeth, at the level of the upper third of their height (Figs 8; 11; 14; 16; 17).

In addition, although sensitive integumentary structures are a definite asset for creatures living in water, it would be reductive to think that these sensory organs are the direct result of an amphibious behavior only (Leitch & Catania 2012). The link between the presence of ISOs or analogous structures with a specific diet (fish-eating) was precisely reinforced by the fact that spinosaurids have often been compared to crocodilians (specialized fish-eaters) due to their anatomical similarities. However, we find relatively similar structures in other taxa, not necessarily piscivorous, from theropods to mammals (Berkhoudt 1976; Andres *et al.* 1991; Brecht *et al.* 1997; Anjum *et al.* 2006; Cunningham *et al.* 2007; Crumpton & Thompson 2013; Crish *et al.* 2016; Crole & Soley 2017; Doneley & Sprohnle-Barrera 2021).

High sensitivity to changes in fluids (air, water) or surrounding solids having contact with the body (mud or earth) is in all cases of vital importance for these specialized animals. The speed of propagation of a (mechanical) sound wave in a fluid, due to the movement of prey for example, will only depend on the nature of the environment in which it evolves (Romagnan 2011). Air and water are the main fluids in which animals move. The speed of the wave will be greater as the density of the fluid is. Thus, the "quality" of the waves transmitted in an aqueous environment is much higher than that of the waves transmitted in the air (Ionescu 1924): about 340 m/s in the air against 1470 m/s in the water. Developing organs sensitive to the reception of these mechanical waves will therefore be a determining asset for fishing and an important driver of natural selection in the evolution of several taxa such as crocodilians or Spinosauridae.

Mammalia

Mechanoreceptors in the snout of mammals are present mostly in the shape of vibrissae or "sensory hairs". Like the ISOs of the crocodilians, mammalian vibrissae represent an interesting example of sensory anatomical structures attached to a complex and branched trigeminal network, as also seen in our Spinosauridae specimens. Vibrissae are mainly developed and abundant in three groups of mammals: 1) the terrestrial carnivorous/rodents; 2) the "burrowing" mammals; and 3) a lot of marine mammals (not only carnivorous). Brecht, Preilowski & Merzenich (Brecht *et al.* 1997) have shown that there are two main types of vibrissae in rodents: those responsible for tactile recognition of objects or prey in contact with the mouth, significantly more numerous at the tip of the snout and rather small, and those allowing spatial localization which are located further back and are usually larger. Dehnhardt & Kaminski (1995) found a correlation between mechanoreceptors density and sensibility in seals. In these animals, whiskers also play a role in locating prey by perception and analysis of water movement (Dehnhardt *et al.* 1998, 2001; Wieskotten *et al.* 2010, 2011; Gläser *et al.* 2011; Grant *et al.* 2013; Hanke *et al.* 2013). In the star-nosed mole *Condylura cristata* Linnaeus, 1758 a large concentration of mechanoreceptive domes is present on each of the 22 appendices of the snout. These mechanoreceptors (called here Eimer organs) are increasing in density from the proximal to the distal part of appendices, like the mechanoreceptor fingers in primates (Sawyer & Catania 2016). Moreover, the maxillary line (with the maxillary branch of the trigeminal nerve) is particularly wide in this species (Grand *et al.* 1998). In extreme situations in which mammals live exclusively underground (like the naked mole rat), where animals cannot rely on the vision, a complex system of vibrissae is developed on the face and extends over the rest of the body, like the ISOs of some crocodilians. Between these "somatic vibrissae", the skin is heavily innervated by sensory fibers in the naked mole rat (Crish *et al.* 2016). The shrew *Suncus etruscus* Savi, 1822 the smallest mammal in the world, measures less than 10 cm and weighs 1.8 g. This insectivorous shrew can catch a grasshopper in flight. Laboratory experiments demonstrated that the animal was using its whiskers vibrations covering its long snout to locate their prey more efficiently than no eye could do (Anjum *et al.* 2006). The mechanoreceptor sensitivity of the snout of many other specialized mammals has already been demonstrated by numerous studies, from the lips of the elephant shrew, manatees and dugong (Reep *et al.* 2001; Moore *et al.* 2022) to the vibrissae of hippopotamus (Springer *et al.* 2021).

Home (1802) noticed a long time first that the olfactory and optic nerves of the monotreme *Ornithorhynchus paradoxus* Blumenbach, 1800 were "abnormally large". Since a link between the volumes of the nervous system in the bill of Monotremes has been made with the specialized sensory organs located in it. The ability to electroreception in the platypus *Ornithorhynchus paradoxus* has been discovered in 1986 (Scheich *et al.* 1986) and demonstrated many times subsequently (Gregory *et al.* 1988; Manger & Pettigrew 1995; Langner & Scheich 2009). The animal can detect moving and still underwater preys as well. We now know that the mechanical-electrosensory system of Monotremes is as sophisticated as the vision in primates (Pettigrew *et al.* 1998). The muzzle of Monotremes is covered with highly specialized organs and strongly innervated large, myelinated nerve fibers joining the maxillary branch of the trigeminal nerve. In addition, the density of these sensory organs is again dependent of the animal's needs to feel the vibrations of the fluid around it. In *Ornithorhynchus* *anatinus* Shaw, 1799 from Australia (aquatic burrower), the number of electroreceptors is approximately 40 000; in the long snouted echidna *Zaglossus bruijnii* Peters & Doria, 1876 from the tropical forests of New Guinea (wetland burrower), the number rises to 2000; and in the short-snouted echidna *Tachyglossus* from Australia (burrowing in dry areas), there are 400 electroreceptors (Andres *et al.* 1991; Pettigrew 1999).

These animals are the only mammals capable of electroreception. It suggests that this sensory character is not inherited but phylogenetically appeared de novo, in association with this burrowing lifestyle quite unique in mammals (Proske *et al.* 1998), which requires efficient reception of electromagnetic waves propagated in a fluid. All these examples of sensitive structures in mammals show us that the sensory organs of the snout can have different appearances depending on the taxa but that they are always linked to a very developed vascular and trigeminal network, as in the Spinosauridae.

Sensory information from the vibrissae stimulation of all mammals is transmitted to the brain by the maxillary branch of the trigeminal nerve, which passes through a cranial opening present in most Eutheria Gill, 1872: the infraorbital foramen (Grand *et al.* 1998). There is a correlation between the size of the foramen and infraorbital mechanoreceptors density (not just those vibrissae) of the maxillary region (Muchlinski 2010; Crumpton & Thompson 2013). Thus, this character (diameter of the foramen/canal) is directly related to the amount of nerve fibers and blood vessels necessary for the functioning of this sensory network, and not a simply inherited feature. The interpretation of Muchlinski was tested on several small sized mammals, especially moles, because they show a wide range of behaviors and environmental adaptations. In 2013, Crumpton found that the size of the infraorbital foramen (IOF) varies according to the habitat of the animal. In other words, mammalian species having the same habitat preferences develop a comparable size of the IOF, independently of their phylogeny (Crumpton & Thompson 2013). This observation is important because it allows for a direct connection between the skeletal anatomy and sensory soft tissues of different taxa. It reminds us once again of the fact of evolutionary convergences for animals living in the same type of environment and having the same sensory detection needs. It is true that the more animals have burrowing lifestyle, the more tactile sensitivity is developed. The complex of the trigeminal branches is hypertrophied in these forms (Crumpton & Thompson 2013). The need to feel the vibrations from the environment may be responsible for the size and the density of some foramina, especially those related to the branches of the trigeminal nerve. This feature is so totally paraphyletic and could concern also fossil forms, as Spinosauridae, whether the animals were aquatic, semi-aquatic or terrestrial.

Spinosauridae

Due to the very rearward position of the nasal cavities in Spinosauridae, we can thus exclude senso strictu olfactory function from the premaxillary neurovascular network and reasonably assume a highly developed sensory need on the front of the muzzle. In Spinosauridae, a high density of neurovascular foramina, which open at the anterior extremity of the snout of *Spinosaurus aegyptiacus,* were interpreted as housing pressure receptors that detect water movement (Dal Sasso *et al.* 2009; Ibrahim *et al.* 2014). Based on computed tomographic scan of a specimen of *Spinosaurus aegyptiacus*, Ibrahim *et al.* (2014) observed that neurovascular foramina converge within the premaxilla and are separate from other spaces within the snout bones. The authors consider this arrangement close to that observed in some pliosaurs (Foffa *et al.* 2014) and which seems to be afferent trigeminal branches.

Our descriptions provide a more precise view of this trigeminal arrangement of neurovascular branches in the rostrum of *Spinosaurus*, despite the fragmentary condition of the Parisian specimen, MNHN.F.SAM124. In particular, the scans of the right upper portion of the premaxilla of *Spinosaurus maroccanus* show a grouping of secondary branches in dorsal position of the dental roots, following the shape of the latter and joining the main parallel branches just below the bony roof (Fig. 14A). Furthermore, the main branches, which continue to run along the rostrum in the maxillae, then show a more inferior position, running labially to the dental sockets on their upper third. This configuration is also found in the two specimens of *Cristatusaurus*, proof of a probable constancy of this arrangement in the Spinosauridae (Figs 8; 11; 14). The interconnections (or anastomoses) especially visible on the mature *Cristatusaurus* specimen sometimes involve one of the main branches with finer and secondary ramifications (Fig. 4B), proof of a common nerve and vascular nature (Savastano *et al.* 2015).

The three premaxillae studied here show a remarkable increase in the number of superficial foramina as one approaches the apex of the rosette. The underlying network perfectly follows what is observed on the surface, namely an increasing complexity of the network and ramifications towards the tip of the snout. A minority of the ramifications nourish and innervate the dental roots but the vast majority furrow between the alveoli to end in the foramina on the surface of the bone and join what could be non-olfactory sensitive cutaneous structures, perhaps resembling the ISOs described in crocodilians. We know that a very anterior orientation of the internal channels usually indicates a need for significant neurovascularization in this area of the muzzle, both in blood vessels and nerve endings. The size of the foramina fairly accurately reflects the width of the underlying canals, which are rather broad (DeGusta *et al.* 1999; George & Holliday 2013).

For some authors, dinosaurs, and theropods in particular, must have had lips (Reisz & Larson 2016) and support the statistical correlation between the density of extraoral foramina and the presence of soft structures that can precisely resembling lips (Morhardt 2009). In addition, the enamel must usually remain moist to avoid premature aging (Witmer *et al.* 2013; Zheng *et al.* 2013; Tamisiea 2023). We can note that the opening of the most anterior foramina of the rosette of *Spinosaurus maroccanus* present clearly visible furrows in the bone, extending the trajectory of the underlying neurovascular branches at an angle of inclination of 45° with respect to the bone surface. This configuration could support the hypothesis of innervation/nourishing of a soft structure along the anteroventral margin of the rosette.

Our descriptions have made it possible to highlight other remarkable common points in the three Spinosauridae specimens, as the parallel pairs of secondary branches, which pierce the convex bony roof of the rosette. Also, the presence of numerous superficial furrows directly in continuity with the inner network especially on posterodorsal regions (Figs 4C; 16B-D) is an additional clue for continuity of trigeminal nerve endings and blood vessels in skin structures. At this stage, it is important to recall the vascular role of the network, which has already been described as possibly important for the evacuation of excess heat, in large dinosaurs in particular (Porter & Witmer 2020). The indications of passage of furrows that we have described on the surface of the bones, and which extend the openings of certain foramina are all potential zones to innervate, of course, but also to vascularize, which makes them strategic points for heat exchanges (evacuate the heat accumulated in the body and cool the animal's blood if necessary). The superficial furrows with a "cross" shape that we described at the exit of the prenarial foramina of *Cristatusaurus* represents a good example. These grooves were probably linked to the nasal cavity of the animal's flesh nostrils, which were in this area. The nasal openings are in fact often a site of significant heat exchanges in amniotes and blood flow is sustained there (Langman *et al.* 1979; Hillenius 1992; Hillenius & Ruben 2004; Bourke *et al.* 2018).

About the teeth of the specimens

Although we believe that the two specimens of *Cristatusaurus* have sufficient characters to differentiate them from the European taxon *Baryonyx* (especially because of less diving anterior portion of the premaxillae and presence of the well-defined premaxillary crest), the characters linked to the teeth to differentiate taxa of Spinosauridae from each other, like the size of the alveoli, are not diagnostic. For example, to distinguish *Baryonyx* from *Cristatusaurus*, Hendrickx *et al.* (2016) noted that the first pair of alveoli was much smaller than the second in *Cristatusaurus* and that this is not the case in its European cousin. This observation is correct for the holotypic specimen of *Cristatusaurus* (MNHN.F.GDF366) but not for the more mature individual (MNHN.F.GDF365). Indeed, the tomographic study reveals a first pair of alveoli almost as large as the second in this specimen, which would therefore not differentiate it from the alveolar conformation of *Baryonyx*. Differences in the size of the alveoli and even the number of teeth is, in our opinion, not relevant diagnostic characters since they relate to ontogenetic, taphonomic and even intraspecific differences, which Hendricks also concludes (Hendrickx *et al.* 2016).

Our tomographic results highlight the large number of teeth in the alveoli of the three specimens, with often even three generations present per alveolus (Figs 5; 6; 9; 11; 14). The presence of a large number of dental crypts containing replacement teeth indicates a significant turnover rate and continued dental synthesis (Tucker & Fraser 2014). Alveolar chambers large enough to accommodate three generations of teeth have already been described in some theropods such as *Allosaurus*, *Gorgosaurus* (LeBlanc *et al.* 2017a) or *Tyrannosaurus* (Sattler & Schwarz 2021). The presence of three generations of teeth in each alveolus of the younger *Cristatusaurus* specimen is evidence of intense and uninterrupted dental development in these animals from an early age. The fact that there are fewer replacement teeth in the more mature individual of *Cristatusaurus* confirms that the rate of tooth replacement decreases as animals grow, as has already been suggested in tyrannosaurids (Erickson 1996; Sattler & Schwarz 2021).

Finally, note that the very deep rooting of the teeth in the jaws of *Cristatusaurus* gave them great robustness, particularly in the apical zone of the rosette. This series of teeth should in fact make it possible to firmly hold the prey, caught in the concavity of the rostrum, behind the rosette. It is here that the teeth are generally the smallest among the Spinosauridae because they had to leave space for the interlocking of the underlying dentary, with a series of teeth proportionally very large and fan shaped.

Although the shape of more or less conical teeth has become established among the Spinosauridae, this does not mean a strictly piscivorous diet for these dinosaurs. Indeed, certain clues seem to let us suppose a more generalist diet with the discovery of a spinosaur tooth between two cervical vertebrae of a pterosaur (Buffetaut *et al.* 2004) or the remains of what seems to be a young *Iguanodon* Mantell, 1825 in the stomach of *Baryonyx* (Charig & Milner 1997).

Comparison of *Cristatusaurus*, *Suchomimus* and *Baryonyx*

The curvature of the anterodorsal margin of the premaxilla in labial view has sometimes been used as a feature to differentiate the taxa of Spinosauridae (Hendrickx *et al.* 2016; Lakin & Longrich 2019), but their comparison by superimposition is complicated, in particular for *Cristatusaurus*, which lacks important posterior elements for such a comparison (external nostril, dorsoposterior blades of premaxillae, etc.). Thanks to the tomography, we propose here two interesting anatomical characters as reference points to help in the correct orientation of the bones and therefore in their comparison: first, the trajectory taken by the two main neurovascular branches for *Cristatusaurus* when they dive dorsoventrally (after the 7th alveolus) and then the location of the prenarial foramen in all specimens, indicating the onset of the prenarial depression (see description of MNHN.F.GDF365 and MNHN.F.GDF366). Unfortunately, the prenarial foramen is not preserved in the juvenile specimen, due to bone breakage, but the underlying neurovascular "bowl structure" tells us its approximate position. By homothety, we were able to superimpose the two specimens of *Cristatusaurus* considering the plunging angle of the neurovascular branches and we obtain a good correlation with the circumference of the two snouts (considering the slight bony erosion on the front and on the roof of the rosette of the younger specimen), including the curvature of the alveolar margin (Fig. 20). In the absence of tomographic data, it is difficult for us to accurately perform the same operation of neurovascular superimposition by adding *Baryonyx*

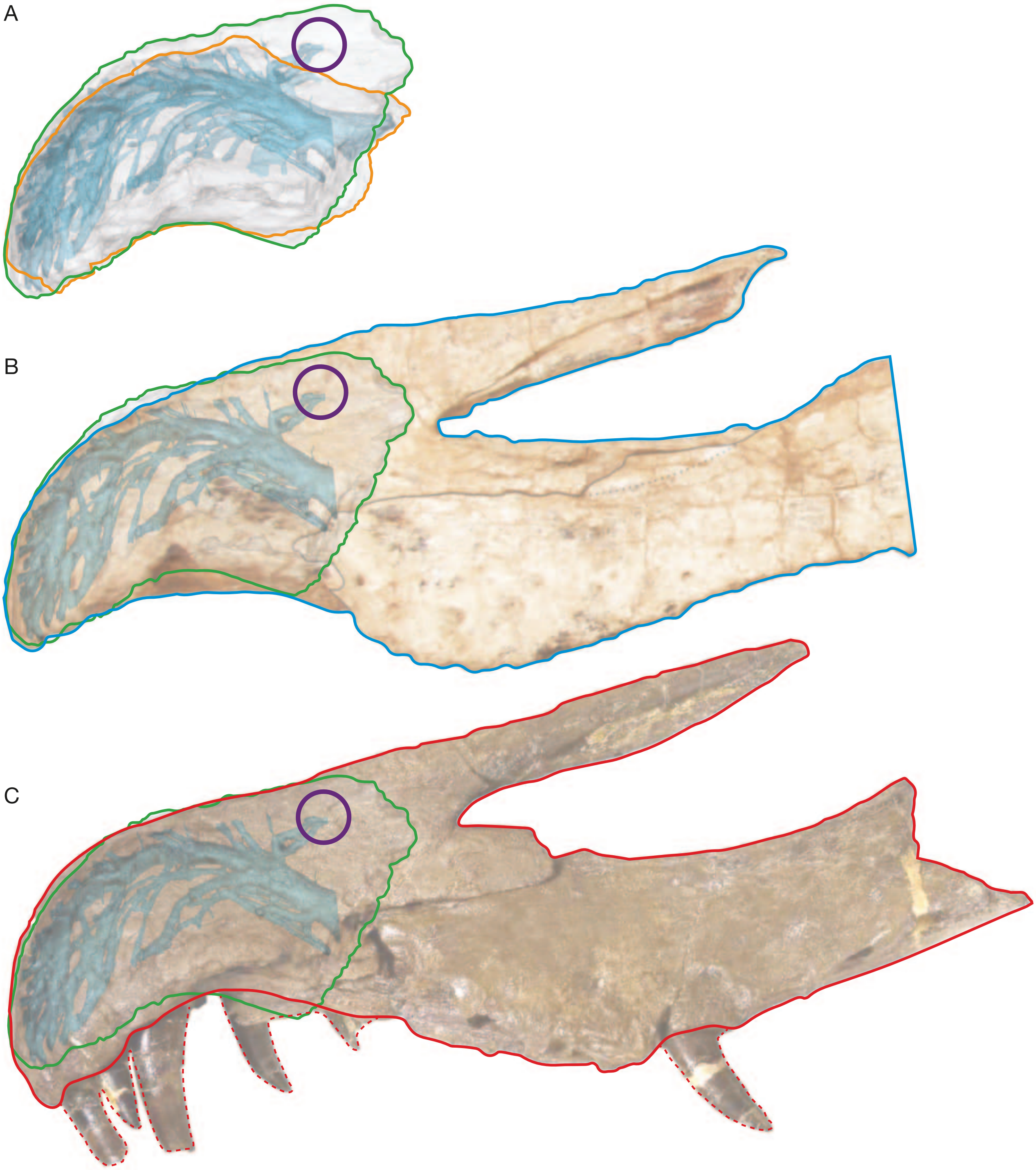


FIG. 20. — Left premaxillae of Baryonichinae *Cristatusaurus lapparenti* Taquet & Russell, 1998 (MNHN.F.GDF365 and MNHN.F.GDF366), *Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998 (MNN GDF501) and *Baryonyx walkeri* Charig & Milner, 1986 (BMNH R9951) all reduced to the same size by homothety and in transparency. The purple circle represents the location of the prenarial foramen: **A**, superimposition of left premaxillae of the two specimens of *Cristatusaurus lapparenti* (MNHN.F.GDF365 in **green** and MNHN.F.GDF366 in **orange** with eroded apex and bony roof) with the plunging angle of the main neurovascular branches and prenarial foramen location as references for comparison; **B**, superimposition of left premaxillae of *Suchomimus tenerensis* in **blue** (MNN GDF501, from Hendrickx *et al.* 2016) with *Cristatusaurus lapparenti* in **green** (MNHN.F.GDF365) with prenarial foramen location as landmarks for comparison; **C**, superimposition of left premaxillae of *Baryonyx walkeri* in **red** (BMNH R9951) with *Cristatusaurus lapparenti* in **green** (MNHN.F.GDF365) with prenarial foramen location as reference for comparison. Not to scale. Models by Frédéric Pittet and Florent Goussard.

and *Suchomimus*. However, considering the dorsal margin of their more complete premaxillae as well as the location of their conspicuous prenarial foramen, we see an almost perfect overlap between *Cristatusaurus* and *Suchomimus* (Fig. 20B) In *Baryonyx*, we can note a more developed anteroventral extension of the premaxillae than in the other specimens, giving the rosette a more hooked appearance (Fig. 20C). This is a clear differentiation between *Baryonyx* on the one hand and

Cristatusaurus/*Suchomimus* on the other. It should also be noted that the premaxilla of *Baryonyx* is much larger than that of the mature specimen MNHN.F.GDF365. However, the individual is nevertheless considered by its discoverers as an immature individual (Charig & Milner 1997) because of the lack of fusion between the bones of both skull and vertebrae on the specimen. This was observed on skulls of some other young theropods (Tsuihiji *et al.* 2011), where the internal surface between the two premaxillae is very smooth, like on MNHN.F.GDF366. A third point shared by *Cristatusaurus* and *Suchomimus* is the premaxillary crest (which originally gave its name to *Cristatusaurus*) due to the thinning of the upper margin of the premaxillae by the digging extending the narial fossa anteriorly. Even though the crest of the younger specimen is heavily damaged, we can get an idea of it by comparing the labial view of this individual with the more mature specimen MNHN.F.GDF 365, especially in relation to the location of his neurovascular network (Appendices 1F-H and 2F-H). Thus, as suggested in the original diagnosis of this taxon (Taquet 1984; Taquet & Russell 1998) and in the light of our tomographic results, we consider this character to be a diagnostic feature of *Cristatusaurus*, especially as it is not present in *Baryonyx*. Nor is this crest linked to ontogenic or intraspecific variability (Hendrickx *et al.* 2016), since it is present in two individuals at different stages of maturity. Finally, the presence of this crest in *Suchomimus tenerensis* suggests that the latter can be referred to *Cristatusaurus* and is indeed a junior synonym of *Cristatusaurus*. What is more, the two taxa are sympatric: all *Baryonyx* specimens are European (from England and Portugal) while *Suchomimus* and *Cristatusaurus* shared a relatively similar geographical distribution (Niger).

About the lifestyle and hunting techniques of Spinosauridae

Dinosaurs had scaly skin except for some avian theropods being covered with feathers on all or part of their body from the Middle Jurassic (Dhouailly 2009; Barrett *et al.* 2015; Hendrickx *et al.* 2022; Frank 2024; Wang *et al.* 2024). The Spinosauridae should not have been an exception. But thick and keratinized skin does not mean less sensitive skin.

A typical anatomical clue of the “fishing predator” is, of course, the terminal rosette of the snout of Spinosauridae. All members of this family share the longirostrine morphology, with a terminal rosette on the premaxillae and dentaries. These two characters are now interpreted as an adaptation to a predominantly fishing diet and to aquatic or semi-aquatic habits for several taxa like, of course, crocodilians but also pliosaurs (Foffa *et al.* 2014) or even some muraenesocids fishes such pike congers (Vullo *et al.* 2016). This analogous skull morphology could be very effective to grap and capture preys with high biting speed. Our descriptions of the premaxillae of the two specimens of *Cristatusaurus lapparenti* and *Spinosaurus maroccanus* revealed a higher concentration of foramina on the rosette (Figs 1; 4; 7; 12), which indicates a greater need for innervation and vascularization and therefore, by corollary, greater sensitivity, as we have seen. We have here defined the rosette as being the portion going from the apex of the snout to the point of maximum concavity of the alveolar margin. We note that 68% to 78% of the significant foramina (more than 1 mm in diameter) are in this apical zone (Table 1). The last statistical element in favor of a development of sensory organs on the rosette that we were able to highlight is the ratio between the volume of the neurovascular network contained in the premaxillae and that of the bone material itself (without considering the teeth), considering that the latter is proportional to the cutaneous sensory need of the area concerned (Table 2). Only the two specimens of *Cristatusaurus lapparenti* were considered here for the calculation of this ratio. Indeed, the specimen of *Spinosaurus maroccanus* being too fragmentary internally to make the measurement relevant.

In addition, note that the Spinosauridae were perhaps able to move their mandibular ramus laterally when they opened their jaws because their mandibular symphysis was mobile as in all theropods, since the teeth were connected by connective tissue (Hendrickx *et al.* 2016). Their enlarged pharynx would have made it possible to eat very large prey, like in Pelecanidae and some pterosaurs (Langston 1981; Witton & Naish 2013). Many fishes lived in mid-Cretaceous North African streams, some of modest sizes, such as *Serenoichtys* Dutheil, 1999 or *Erfoudichthys* Pittet, Cavin & Poyato-Ariza, 2010 and other rather large like *Aidachar* Nessov, 1981 (Mkhitaryan & Averianov 2011) or the 3-meter long cartilaginous fish *Onchopristis* Stromer, 1917. We know now these were at least part of the *Spinosaurus* regime (Sasso *et al.* 2005). Crocodiles currently mainly attack land animals by being in abundance in calm water on the banks (migrating wildebeest for example). For them, it is therefore a matter of catching their prey quickly, stunning them by spinning around and then drowning them so that they can devour them more easily. Unlike the crocodilians, the Spinosauridae probably hunted on the bank for large preys (and not in the water), but with the same system of detecting waves in an aqueous environment, with the front of their snout submerged in water. Here are some anatomical clues supporting this hypothesis.

Firstly, it has been shown that the skull of *Baryonyx walkeri* shared proportionally biomechanics characteristics like that of the current gharial (*Gavialis gangeticus*), with a long, compressed snout, a secondary palate and the loss or reduced antorbital fenestrae helping resist bending (Rayfield *et al.* 2007). Conversely, larger skulls with no secondary palate (find in other theropods) are more resistant to lateral torsion (but less on bending). Nevertheless, Cuff & Rayfield (Cuff & Rayfield 2013) also showed that considering the real size of the animal, *Baryonyx* was not so close to the gharial performance, because a large size can withstand more dorsoventral or mediolateral loads. They also included *Spinosaurus aegyptiacus* in their study and showed that this taxon was actually closer to the biomechanical performance of the gharial. Anyway, both *Baryonyx* and *Spinosaurus* (but especially *Spinosaurus*) better support ventrodorsal than mediolateral stress or torsion in their jaws. Plunging the mouth open into the water to capture a large prey was to cause a huge ventrodorsal resistance. Indeed, water being a fluid much denser than air, the effort required to maintain

TABLE 1. — Summary table of the distribution of foramina on the premaxillae of specimens MNHN.F.GDF365 and GDF366 (*Cristatusaurus lapparenti* Taquet & Russell, 1998) and MNHN.F.SAM124 (*Spinosaurus maroccanus* Russell, 1996) with highlighting the percentage of foramina counted on their respective rosettes. Symbol: *, indicates the number of "significant" foramina, with a diameter greater than or equal to 1 mm.

Taxon	Specimen	Number of foramina – right premaxilla	Number of foramina – left premaxilla	Total number of foramina	Number of foramina on the rosette (with percentage of total)
Cristatusaurus lapparenti	MNHN.F.GDF366 (juvenile)	50 (38*) 49 (43*)	54 (36*)	104 (74*)	55 (52.88%) 51 (68.92%)*
Cristatusaurus lapparenti	MNHN.F.GDF365 (adult)	49 (43*)	42 (42*)	91 (85*)	71 (78.02%) 67 (78.82%)*
Spinosaurus maroccanus	MNHN.F.SAM124	36 (34*)	28 (27*)	64 (61*)	44 (68.75%) 43 (70,49%)*

TABLE 2. — Summary table highlighting the importance of the neurovascular volume occupying the bone material of the premaxillae (without the alveoli) of specimens MNHN.F.GDF365 and GDF366 (*Cristatusaurus lapparenti* Taquet & Russell, 1998).

Taxon	Specimen	Volume of bone (without alveoli) – Premaxillae	Volume of the neurovascular network – Premaxillae	Percentage of neurovascular network in the bones (without alveoli volume)
Cristatusaurus lapparenti	MNHN.F.GDF366 (juvenile)	79.1727 cm^3	7.4281 cm^3	9.39 %
Cristatusaurus lapparenti	MNHN.F.GDF365 (adult)	339.90 cm^3	33.96 cm^3	9.99 %

and extract the prey was gigantic. This is an interesting clue to the hypothesis of heron-like fishing from the bank to come up and "throw" the prey onto dry land to devour it (Draulans 1987; Cuff & Rayfield 2013). Secondly, it is also suggested that the median crest on the top of the *Spinosaurus* (and *Cristatusaurus*) skull must have reduced friction in the water and made the dorsoventral movements of the head more hydrodynamic (Gimsa & Gimsa 2021). Thirdly, the study of the semicircular canals of the Brazilian Spinosaurinae *Irritator challengeri,* with their inclination of 45° relative to the cranial roof, indicates that this dinosaur must have been particularly precise in its downward head movements, giving it a great ability to catch its prey by quickly lowering its head (Schade *et al.* 2020), as many piscivorous predators do from the shores like herons, storks, egrets (Draulans 1987; TOJO 1996; Papakostas *et al.* 2005; Choi *et al.* 2007; Matsinos *et al.* 2012) or bears (Gende *et al.* 2001; Gende 2002; Klinka 2004; Gende & Quinn 2004; Lincoln & Quinn 2019). Although recent anatomical clues such as the elongation of caudal neural spines suggest that some Spinosauridae could propel themselves efficiently in water, particularly *Spinosaurus aegyptiacus* (Ibrahim *et al.* 2020), this does not, however, discredit the theory of fishing from the bank (Hone & Holtz 2021). The three clues that we provided above also support this theory. Perhaps small prey could have been captured underwater by active swimming (Ibrahim *et al.* 2014, 2020), although this has not been demonstrated so far (Myhrvold *et al.* 2024). In any case, we believe that this would not have been the case for large prey, which had to be removed from the water quickly. These larger preys undoubtedly offer a more interesting yield in terms of energy input versus the energy deployed by active hunting.

We know from ethological observations that crocodilians preferentially hunt large terrestrial prey from the water, in the flood below the surface (like the wildebeest during their migration). We believe that Spinosauridae did the opposite: they must have preferentially hunted large aquatic prey from the bank. The goal for the dinosaurs, like the crocodilians, was certainly to kill their prey as efficiently as possible. The crocodilians try to drown them by stunning them and spinning around during the attack. Spinosauridae had to deprive large prey living in the water of oxygen, therefore, in our opinion, to get them out of the water as quickly as possible with a rapid movement of the head ventrodorsally, like herons, since, let us remember, these dinosaurs were not adapted to lateral cranial tensions but rather ventrodorsally.

Thus, we advance the hypothesis that, Spinosauridae had to hunt their prey more by executing not only fast but also with vertical movements when they were on the shore, the front of the snout in the water and the nostrils above the water surface (Fig. 21). Indeed, it is likely that the developed neural spines of some of these animals (like *Spinosaurus*) and the long hypapophyses of the last cervical/ first dorsal vertebrae (Gomani 1997; Evers *et al.* 2015) should be used primarily to link the tendons of the powerful neck muscles to quickly extract their prey once identified by their ultra-sophisticated sensory organs by literally "lifting" them out of the water. A complex system of ligaments can also explain the elongation of neural spines, as in other vertebrates such as the giraffe *Giraffa camelopardalis* Linnaeus, 1758 which has a particular ligament with striated fibers reminiscent of those found in muscles and which also participate in movements (Murie 1872; Holdrege 2005). When watering, the animal's head is in fact level with the surface of the water

FIG. 21. — Life restoration of two adult individuals of *Cristatusaurus lapparenti* Taquet & Russell, 1998, fishing from the bank and using their snout sensitive receptors to hunt small coelancanths, *Mawsonia gigas* Mawson & Woodward, 1907. Bottom left, three *Erfoudichtys rosae* Pittet, Cavin & Poyato-Ariza, 2010 try to escape the attacks of the dinosaurs. Original illustration by Alain Bénéteau.

point and it can raise its long neck quickly in the event of danger (Williams 2016). Other taxa share this paraphyletic character of neural spines developed on the thoracic vertebrae when the animals must have strengthened muscles in their neck (buffalos, bison, gorillas, etc.).

About the behavior of young Spinosauridae individuals: The rosette of young Spinosauridae was already highly innervated and vascularized, with more interconnected branches, as we showed in the description of the smaller premaxilla of *Cristatusaurus*. In addition, tooth replacement was more active in young individuals, given that MNHN.F.GDF366 has three generations of teeth in each of its alveoli, which is not the case in the mature specimen. It must indeed have been common for teeth to break or fall out for all young theropod dinosaurs. If the animal was hunting aquatic prey, it must also be remembered that the density of the water caused more stress on the teeth than for prey in the open air.

Finally, the remains of several *Spinosaurus* individuals proportionally smaller than those previously discovered were described in 2019 (Lakin & Longrich 2019). These remains (vertebrae, a portion of premaxilla and a quadrate) were acquired from traders in the Erfoud region (Morocco). The authors estimate that they would come from the Ifezouane Formation rather than the Aoufous Formation, based on taphonomic data (Krassilov & Bacchia 2013). Adult *Spinosaurus* were indeed present in the Ifezouane Formation, especially based on teeth and other remains found in this area (Stromer 1914; Kellner & Campos 1996; Dal Sasso *et al.* 2005; Ibrahim *et al.* 2014; Benyoucef *et al.* 2015; Hendrickx *et al.* 2016; Lakin & Longrich 2019). Young animals therefore seemed to evolve in the same environments after having reached a respectable size of a few meters and had to live and hunt in the same way as adults. Only very young individuals (estimated at less than two meters in length) do not seem to be represented in these same deposits, due to the absence of bone remains and teeth of a size proportionally adapted to these stages of development (Lakin & Longrich 2019). Hunting for fishing undoubtedly requires significant and complex learning, as observed today on several Archosaurians such as crocodilians and aquatic birds (Coombs 1989; Whitaker 2007; Campos *et al.* 2012; Lakin 2022). This parental care may be a primitive character for archosaurians in general (Brazaitis & Watanabe 2011). Mechanically, it must also have been important for young

Spinosauridae to fine-tune the coordination between the sensory electrical signals received from their trigeminal nerve to the cerebral cortex and the contraction of their muscles to correctly execute the downward-upward movements of the snout to avoid any unnecessary injury or trauma and ultimately ensure the best possible chance of survival.

Given the biomechanical, anatomical and paleoenvironmental indices described above, we argue that at least some Spinosauridae must have been able to hunt underwater for small preys, especially the most recent forms like *Spinosaurus*. They were perhaps, however, more adapted to lying in wait on the banks or standing motionless in any case for largest preys like *Onchopristis*, their muzzle just below the surface of the water, using their sensory organs, prepared for rapid, coordinated movements to catch their prey.

CONCLUSION

The amazing quality of preservation of the neurovascular network of the premaxillae of both *Cristatusaurus lapparenti* and *Spinosaurus maroccanus* finally gives us a precise idea of its anatomy. No complete representation of the neurovascular network of a Spinosauridae rosette has ever been described before. Our tomographic results show one of the best-preserved premaxillary neurovascular complex discovered in a dinosaur and the very first complete in a spinosaur with the mature specimen of *Cristatusaurus lapparenti*. We found that the volume of the network, the size of the foramina admirably coinciding with that of the underlying scanned branches, as well as the comparison with other extinct and extant animals that have developed efficient sensory structures represent as many additional indices supporting the hypothesis of a hypersensitivity of the rosette of Spinosauridae. In addition, the tomographic analysis of the premaxilla of the young individual of *Cristatusaurus lapparenti* reveals a neurovascular network just as dense (or even denser) and more generations of teeth than in the mature specimen. We believe that these indices underline a sustained sensory need and a significant dental replacement rate from a very young age.

The idea that animals using their snout as an anatomical part “exploring the environment” have strong sensory innervation in this area and have therefore developed a trigeminal nervous system is commonly accepted. Whether it is a shark, an alligator, a platypus or a Spinosauridae, we observe the same thing. The evolutionary convergences, widely documented, between Spinosauridae and extant crocodilians is legitimate but must be considered now as highly reductive, in particular by the presence of structures similar to the ISOs found in crocodilians *sensu stricto* on the snout of these dinosaurs. Numerous strategies leading to the development of non-olfactory sensory organs on the snout have been described in this article and underline the paraphyletic nature of the presence of such structures. This sensitivity of the snout depends neither on the environment (because it is found in aquatic, semi-aquatic, terrestrial and even underground taxa), nor on the animal’s diet. In our opinion, it is predominately linked to the animal’s need to feel the vibrations of the fluids in its environment when one or more of its senses is lacking (the senses of sight or touch in particular). Even the longirostral aspect is not necessarily due to increased sensitivity; it is simply a more efficient way of catching prey mechanically underwater. Non-longirostrum skulls may also be sensitive (tyrannosaurs, rats, cats, horses, proboscideans, etc.). An aquatic or semi-aquatic lifestyle can encourage certain taxa to adopt efficient non-olfactive sensitive structures, because waves travel faster in water than in air. But we saw that many other animals, even clearly terrestrial, could need a “sensitive muzzle”. Finally, even if you have a sensitive nose, this does not mean a strict fish-eating diet. Several clues such as the shape of the teeth, the environments frequented or even the oxygen isotopic ratios analyzed in certain bones tend to support the thesis of a fish-eating diet. But other fossil evidence shows a possibly broader diet (small dinosaurs, pterosaurs, etc.). That said, it seems to us that when these animals fished, they must have done so from the bank, at least for large prey, with the rosette of their muzzle in the water, according to the morphological and biomechanical clues. An overview of several taxa that are phylogenetically distant but have adopted such sensory structures through evolutionary convergence allows us to have a better appreciation of the situation. The skin sensitivity of dinosaurs (and of the snout in particular) seems more complex than previously thought. This work should open new interpretative perspectives of future tomographic studies on the premaxillary and maxillary neurovascular network that will teach us more about the sensory degree of the snout of Spinosauridae and dinosaurs in general.

Supplementary data

3D data and CT scans accessible on MorphoMuseuM (Pittet & Goussard 2025): https://doi.org/10.18563/journal.m3.272

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REFERENCES

Ahlberg P. E. 1991. — A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society* 103 (3): 241-287. https://doi.org/10.1111/j.1096-3642.1991.tb00905.x

Amendano B., Spriggs S. & Cost I. 2021. — A comparative description of the maxillary and mandibular divisions of the trigeminal nerve in birds. *Journal of the Pennsylvania Academy of Science* 95 (2): 121-134. https://doi.org/10.5325/jpennacadscie.95.2.0121

Anderson H. T. 1936. — The jaw musculature of the phytosaur, machaeroprosopus. *Journal of Morphology* 59 (3): 549-587. https://doi.org/10.1002/jmor.1050590307

Andres K. H., Düring M., Iggo A. & Proske U. 1991. — The anatomy and fine structure of the echidnaTachyglossus aculeatus snout with respect to its different trigeminal sensory receptors including the electroreceptors. *Anatomy and Embryology* 184 (4): 371-393. https://doi.org/10.1007/BF00957899

Anjum F., Turni H., Mulder P. G. H., Van Der Burg J. & Brecht M. 2006. — Tactile guidance of prey capture in Etruscan shrews. *Proceedings of the National Academy of Sciences* 103 (44): 16544-16549. https://doi.org/10.1073/pnas.0605573103

Barker C. T., Naish D., Newham E., Katsamenis O. L. & Dyke G. 2017. — Complex neuroanatomy in the rostrum of the Isle of Wight theropod Neovenator salerii. *Scientific Reports* 7 (1): 3749. https://doi.org/10.1038/s41598-017-03671-3

Barrett P. M., Evans D. C. & Campione N. E. 2015. — Evolution of dinosaur epidermal structures. *Biology Letters* 11 (6): 20150229. https://doi.org/10.1098/rsbl.2015.0229

Bell P. R. & Hendrickx C. 2020. — Crocodile-like sensory scales in a Late Jurassic theropod dinosaur. *Current Biology* 30 (19): R1068-R1070. 10.1016/j.cub.2020.08.066

Benoit J., Ford D. P., Miyamae J. A. & Ruf I. 2021. — Can maxillary canal morphology inform varanopid phylogenetic affinities? *Acta Palaeontologica Polonica* 66 (2): 389-393. https://doi.org/10.4202/app.00816.2020

Benyoucef M., Läng E., Cavin L., Mebarki K., Adaci M. & Bensalah M. 2015. — Overabundance of piscivorous dinosaurs (Theropoda: Spinosauridae) in the mid-Cretaceous of North Africa: The Algerian dilemma. *Cretaceous Research* 55: 44-55. https://doi.org/10.1016/j.cretres.2015.02.002

Berkhoudt H. 1976. — Taste buds in the bill of the mallard (Anas platyrhynchos L.). *Netherlands Journal of Zoology* 27 (3): 310-331. https://doi.org/10.1163/002829677X00180

Bleckmann H. 2006. — The lateral line system of fish. *Fish physiology* 25: 411-453. https://doi.org/10.1016/S1546-5098(06)25010-6

Bleckmann H. & Zelick R. 2009. — Lateral line system of fish. *Integrative Zoology* 4 (1): 13-25. https://doi.org/10.1111/j.1749-4877.2008.00131.x

Bonaparte C. L. 1837. — A New Systematic Arrangement of Vertebrated Animals. *Transactions of the Linnean Society of London 18*: 247-304. https://doi.org/10.1111/j.1095-8339.1838.tb00177.x

Bonaparte C. L. 1841. — *A New Systematic Arrangement of Vertebrated Animals.*2 volumes. R. Taylor. https://doi.org/10.5962/bhl.title.49547

Bouabdellah F., Lessner E. & Benoit J. 2022. — The rostral neurovascular system of *Tyrannosaurus rex*. https://doi.org/10.26879/1178

Bourke J. M., Porter W. R. & Witmer L. M. 2018. — Convoluted nasal passages function as efficient heat exchangers in ankylosaurs (Dinosauria: Ornithischia: Thyreophora). *PLoS One* 13 (12): e0207381. https://doi.org/10.1371/journal.pone.0207381

Bowman C. I. W., Young M. T., Schwab J. A., Walsh S., Witmer L. M., Herrera Y., Choiniere J., Dollman K. N. & Brusatte S. L. 2022. — Rostral neurovasculature indicates sensory trade-offs in Mesozoic pelagic crocodylomorphs. *The Anatomical Record* 305 (10): 2654-2669. https://doi.org/10.1002/ar.24733

Brazaitis P. & Watanabe M. E. 2011. — Crocodilian behaviour: a window to dinosaur behaviour? *Historical Biology* 23 (1): 73-90. https://doi.org/10.1080/08912963.2011.560723

Brecht M., Preilowski B. & Merzenich M. M. 1997. — Functional architecture of the mystacial vibrissae. *Behavioural brain research* 84 (1-2): 81-97. https://doi.org/10.1016/S0166-4328(97)83328-1

Brochu C. A. 2003. — Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology* 22 (suppl. 4): 1-138. https://doi.org/10.1080/02724634.2003.10010947

Brusatte S. L. & Carr T. D. 2016. — The phylogeny and evolutionary history of tyrannosauroid dinosaurs. *Scientific Reports* 6 (1): 20252. https://doi.org/10.1038/srep20252

Buchtová M., Pá L., Knotek Z. & Tichý F. 2009. — Complex sensory corpuscles in the upper jaw of Horsfield's Tortoise (Testudo horsfieldii). *Acta Veterinaria Brno* 78 (2): 193-197. https://doi.org/10.2754/avb200978020193

Budney L. A., Caldwell M. W. & Albino A. 2006. — Tooth socket histology in the Cretaceous snake *Dinilysia*, with a review of amniote dental attachment tissues. *Journal of Vertebrate Paleontology* 26 (1): 138-145. https://doi.org/10.1671/0272-4634(2006)26[138:TSHITC]2.0.CO;2

Buffetaut E., Martill D. & Escuillié F. 2004. — Pterosaurs as part of a spinosaur diet. *Nature* 430 (6995): 33-33. https://doi.org/10.1038/430033a

Burch S. H. 2017. — Myology of the forelimb of *Majungasaurus crenatissimus* (Theropoda, Abelisauridae) and the morphological consequences of extreme limb reduction. *Journal of Anatomy* 231 (4): 515-531. https://doi.org/10.1111/joa.12660

Butler A. B. & Hodos W. 2005. — *Comparative Vertebrate Neuroanatomy: Evolution and Adaptation*. John Wiley & Sons, 715 p. https://doi.org/10.1002/0471733849

Butler R. J., Porro L. B., Galton P. M. & Chiappe L. M. 2012. — Anatomy and cranial functional morphology of the small-bodied dinosaur Fruitadens haagarorum from the Upper Jurassic of the USA. *PloS One* 7 (4): e31556. https://doi.org/10.1371/journal.pone.0031556

Caldwell M. W., Budney L. A. & Lamoureux D. O. 2003. — Histology of tooth attachment tissues in the Late Cretaceous mosasaurid *Platecarpus*. *Journal of Vertebrate Paleontology* 23 (3): 622-630. https://doi.org/10.1671/0272-4634(2003)023[0622:HOTATI]2.0.CO;2

Campos Z., Sanaiotti T., Muniz F., Farias I. & Magnusson W. E. 2012. — Parental care in the dwarf caiman, *Paleosuchus palpebrosus* Cuvier, 1807 (Reptilia: Crocodilia: Alligatoridae). *Journal of Natural History* 46 (47-48): 2979-2984. https://doi.org/10.1080/00222933.2012.724723

Canale J. I., Scanferla C. A., Agnolin F. L. & Novas F. E. 2009. — New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften* 96 (3): 409-414. https://doi.org/10.1007/s00114-008-0487-4

Carr T. D., Varricchio D. J., Sedlmayr J. C., Roberts E. M. & Moore J. R. 2017. — A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Scientific Reports* 7 (1): 44942. https://doi.org/10.1038/srep44942

Cerroni M. A., Canale J. I., Novas F. E. & Paulina Carabajal A. 2022. — An exceptional neurovascular system in abelisaurid theropod skull: new evidence from *Skorpiovenator bustingorryi*. *Journal of Anatomy* 240 (4): 612-626. https://doi.org/10.1111/joa.13258

Charig A. J. & Milner A. C. 1986. — *Baryonyx*, a remarkable new theropod dinosaur. *Nature* 324: 359-361. https://doi.org/10.1038/324359a0

Charig A. J. & Milner A. C. 1997. — *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin-Natural History Museum Geology Series* 53: 11-70. https://www.biodiversitylibrary.org/page/36949178

Choi Y.-S., Kwon I.-K. & Yoo J.-C. 2007. — Foraging habitat preferences of herons and egrets. *Journal of Ecology and Environment* 30 (3): 237-244. https://doi.org/10.5141/JEFB.2007.30.3.237

Coombs W. P. 1989. — Modem analogs for dinosaur nesting and parental behavior, *in* Farlow J. O. (ed.), Paleobiology of the Dinosaurs. *Geological Society of America, Special Papers* 238: 21. https://doi.org/10.1130/SPE238-p21

Coombs S., Bleckmann H., Fay R. R. & Popper A. N. (eds) 2014. — *The Lateral Line System*. Vol. 48. Springer Handbook of Auditory Research, Springer, New York. https://doi.org/10.1007/978-1-4614-8851-4

Cope E. D. 1889a. — On a new genus of Triassic Dinosauria. *American Naturalist* 23 (271): 626. https://doi.org/10.1086/274979

Cope E. D. 1889b. — Synopsis of the families of Vertebrata. *The American Naturalist* 23 (274): 849-877. https://doi.org/10.1086/275018

Crish C. M., Crish S. D. & Comer C. 2016. — Tactile Sensing in the Naked Mole Rat, *in* Prescott T., Ahissar E. & Izhikevich E. (eds), *Scholarpedia of Touch*. Atlantis Press, Paris: 95-101.

Crole M. R. & Soley J. T. 2017. — Bony pits in the Ostrich (*Struthio camelus*) and Emu (*Dromaius novaehollandiae*) bill tip. *The Anatomical Record* 300 (9): 1705-1715. https://doi.org/10.1002/ar.23594

Crowe-Riddell J. M. & Lillywhite H. B. 2023. — Sensory Systems, *in* Warwick C., Arena P. C. & Burghardt G. M. (eds), *Health and Welfare of Captive Reptiles*. Springer International Publishing, Cham: 45-91. https://doi.org/10.1007/978-3-030-86012-7_3

Crumpton N. & Thompson R. S. 2013. — The Holes of Moles: Osteological Correlates of the Trigeminal Nerve in Talpidae. *Journal of Mammalian Evolution* 20 (3): 213-225. https://doi.org/10.1007/s10914-012-9213-2

Cuff A. R. & Rayfield E. J. 2013. — Feeding mechanics in spinosaurid theropods and extant crocodilians. *PLoS One* 8 (5): e65295. https://doi.org/10.1371/journal.pone.0065295

Cullen T. M., Larson D. W., Witton M. P., Scott D., Maho T., Brink K. S., Evans D. C. & Reisz R. 2023. — Theropod dinosaur facial reconstruction and the importance of soft tissues in paleobiology. *Science* 379 (6639): 1348-1352. https://doi.org/10.1126/science.abo7877

Cunningham S., Castro I. & Alley M. 2007. — A new prey-detection mechanism for kiwi (*Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. *Journal of Anatomy* 211 (4): 493-502. https://doi.org/10.1111/j.1469-7580.2007.00786.x

Cunningham S. J., Alley M. R., Castro I., Potter M. A., Cunningham M. & Pyne M. J. 2010. — Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. *The Auk* 127 (2): 308-316. https://doi.org/10.1525/auk.2009.09117

Cunningham S. J., Corfield J. R., Iwaniuk A. N., Castro I., Alley M. R., Birkhead T. R. & Parsons S. 2013. — The anatomy of the bill tip of kiwi and associated somatosensory regions of the brain: comparisons with shorebirds. *PLoS One* 8 (11): e80036. https://doi.org/10.1371/journal.pone.0080036

Dagenais P., Hensman S., Haechler V. & Milinkovitch M. C. 2021. — Elephants evolved strategies reducing the biomechanical complexity of their trunk. *Current Biology* 31 (21): 4727-4737. https://doi.org/10.1016/j.cub.2021.08.029

Dal Sasso C., Maganuco S. & Cioffi A. 2009. — A neurovascular cavity within the snout of the predatory dinosaur *Spinosaurus, in* North African vertebrate palaeontology NAVEP1 at Marrakech, abstract volume: 30-31.

Dal Sasso C., Maganuco S., Buffetaut E. & Mendez M. A. 2005. — New information on the skull of the enigmatic theropod *Spinosaurus* , with remarks on its size and affinities. *Journal of Vertebrate Paleontology* 25 (4): 888-896. https://doi.org/10.1671/0272-4634(2005)025[0888:NIOTSO]2.0.CO;2

Datta D., Sharma K. & Ray S. 2021. — Cranial evolution of the Late Triassic phytosaurs (Diapsida, Archosauria): preliminary observations from landmark-based morphometric analysis. *Historical Biology* 33 (11): 2683-2705. https://doi.org/10.1080/08912963.2020.1822831

DeGusta D., Gilbert W. H. & Turner S. P. 1999. — Hypoglossal canal size and hominid speech. *Proceedings of the National Academy of Sciences* 96 (4): 1800-1804. https://doi.org/10.1073/pnas.96.4.1800

Dehnhardt G. & Kaminski A. 1995. — Sensitivity of the mystacial vibrissae of harbour seals (*Phoca vitulina*) for size differences of actively touched objects. *Journal of Experimental Biology* 198 (11): 2317-2323

Dehnhardt G., Mauck B. & Bleckmann H. 1998. — Seal whiskers detect water movements. *Nature* 394 (6690): 235-236. https://doi.org/10.1242/jeb.198.11.2317

Dehnhardt G., Mauck B., Hanke W. & Bleckmann H. 2001. — Hydrodynamic trail-following in Harbor seals (*Phoca vitulina*). *Science* 293 (5527): 102-104. https://doi.org/10.1126/science.1060514

Deiringer N., Schneeweiss U., Kaufmann L. V., Eigen L., Speissegger C., Gerhardt B., Holtze S., Fritsch G., Göritz F. & Becker R. 2023. — The functional anatomy of elephant trunk whiskers. *Communications Biology* 6 (1): 591. https://doi.org/10.1038/s42003-023-04945-5

Dhouailly D. 2009. — A new scenario for the evolutionary origin of hair, feather, and avian scales. *Journal of Anatomy* 214 (4): 587-606. https://doi.org/10.1111/j.1469-7580.2008.01041.x

Di-Poï N. & Milinkovitch M. C. 2013. — Crocodylians evolved scattered multi-sensory micro-organs. *EvoDevo* 4 (1): 19. https://doi.org/10.1186/2041-9139-4-19

Doneley R. & Sprohnle Barrera C. 2021. — Cutaneous botryomycosis in a free-living short-beaked echidna (*Tachyglossus aculeatus*). *Australian Veterinary Journal* 99 (10): 427-431. https://doi.org/10.1111/avj.13105

Draulans D. 1987. — The effect of prey density on foraging behaviour and success of adult and first-year grey herons (Ardea cinerea). *The Journal of Animal Ecology*: 479-493. https://doi.org/10.2307/5062

Duméril C. & Bibron. 1851. — *Catalogue méthodique de la collection des reptiles*. Volume 2. Gide et Baudry, Paris, 224 p. https://gallica.bnf.fr/ark:/12148/bpt6k883907t

Dutheil D. B. 1999. — The first articulated fossil cladistian: *Serenoichthys kemkemensis* , gen. et sp. nov., from the Cretaceous of Morocco. *Journal of Vertebrate Paleontology* 19 (2): 243-246. https://doi.org/10.1080/02724634.1999.10011138

Edmund G. 1960. — 4. Evolution of dental patterns in the lower vertebrates, *in* Cameron T. W. M. (ed.), *Evolution*. University of Toronto Press: 45-62.

Elzanowski A. & Wellnhofer P. 1993. — Skull of Archaeornithoides from the upper Cretaceous of Mongolia. *American Journal of Science* 293 (A): 235-252. 10.2475/ajs.293.A.235

Erickson G. M. 1996. — Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement ratex using growth line counts. *Proceedings of the National Academy of Sciences* 93 (25): 14623-14627. https://doi.org/10.1073/pnas.93.25.14623

Erudaitius A. P., Pruett J. A., Campos S. M., Ossip-Drahos A. G., Lannoo S. J., Zúñiga-Vega J. J., Vital-García C., Hews D. K., Martins E. P. & Romero-Diaz C. 2024. — Vomeronasal organ volume increases with body size and is dissociated with the loss of a visual signal in Sceloporus lizards. *Journal of Evolutionary Biology* 37 (1): 89-99. https://doi.org/10.1093/jeb/voad002

Evers S. W., Rauhut O. W., Milner A. C., McFeeters B. & Allain R. 2015. — A reappraisal of the morphology and systematic position of the theropod dinosaur Sigilmassasaurus from the “middle” Cretaceous of Morocco. *PeerJ* 3: e1323. https://doi.org/10.7717/peerj.1323

Fitzinger L. J. 1843. — *Systema reptilium: fasciculus primus: Amblyglossae*. Vol. 1. Braumüller & Seidel, Vienna, 106 p. https://doi.org/10.5962/bhl.title.4694

Foffa D., Sassoon J., Cuff A. R., Mavrogordato M. N. & Benton M. J. 2014. — Complex rostral neurovascular system in a giant pliosaur. *Naturwissenschaften* 101 (5): 453-456. https://doi.org/10.1007/s00114-014-1173-3

Fong R. K., LeBlanc A. R., Berman D. S. & Reisz R. R. 2016. — Dental histology of Coelophysis bauri and the evolution of tooth attachment tissues in early dinosaurs. *Journal of Morphology* 277 (7): 916-924. https://doi.org/10.1002/jmor.20545

Frank R. M. 2024. — When feathered dinosaurs engage in conversations with humans: talking with a parrot named Chaucer. https://doi.org/10.17077/pp.006728

Funston G. F., Powers M. J., Whitebone S. A., Brusatte S. L., Scannella J. B., Horner J. R. & Currie P. J. 2021. — Baby tyrannosaurid bones and teeth from the Late Cretaceous of western North America1. *Canadian Journal of Earth Sciences* 58 (9): 756-777. https://doi.org/10.1139/cjes-2020-0169

Gauthier J. 1986. — Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8: 1-55. https://www.biodiversitylibrary.org/page/15651737

Gende S. M. & Quinn T. P. 2004. — The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology* 82 (1): 75-85. https://doi.org/10.1139/z03-226

Gende S. M. 2002. — *Foraging Behavior of Bears at Salmon Streams: Intake, Choice, and the Role of Salmon Life History*. Phd thesis, University of Washington, 24 p.

Gende S. M., Quinn T. P. & Willson M. F. 2001. — Consumption choice by bears feeding on salmon. *Oecologia* 127 (3): 372-382. https://doi.org/10.1007/s004420000590

Gentle M. J. & Breward J. 1986. — The bill tip organ of the chicken (Gallus gallus var. domesticus). *Journal of Anatomy* 145: 79. https://pubmed.ncbi.nlm.nih.gov/3429310/

George I. D. & Holliday C. M. 2013. — Trigeminal nerve morphology in *Alligator mississippiensis* and its significance for crocodyliform facial sensation and evolution. *The Anatomical Record* 296 (4): 670-680. https://doi.org/10.1002/ar.22666

Gill T. 1872. — Arrangement of the families of mammals. With analytical tables. Prepared for the Smithsonian Institution. *Smithsonian Miscellaneous Collections 230* (I-VI): 1-98. https://www.biodiversitylibrary.org/page/14512573

Gimsa J. & Gimsa U. 2021. — Contributions to a discussion of *Spinosaurus aegyptiacus* as a capable swimmer and deep-water predator. *Life* 11 (9): 889. https://doi.org/10.3390/life11090889

Gläser N., Wieskotten S., Otter C., Dehnhardt G. & Hanke W. 2011. — Hydrodynamic trail following in a California sea lion (Zalophus californianus). *Journal of Comparative Physiology A* 197 (2): 141-151. https://doi.org/10.1007/s00359-010-0594-5

Gmelin J. F. 1789 — *Caroli a Linné Systema naturae*. ed. 13. Tome 1 Pars 3. G. E. Beer, Lipsiae: 1033-1516. https://doi.org/10.5962/bhl.title.36932

Gomani E. M. 1997. — A crocodyliform from the Early Cretaceous Dinosaur Beds, northern Malawi. *Journal of Vertebrate Paleontology* 17 (2): 280-294. https://doi.org/10.1080/02724634.1997.10010975

Göhlich U. B., Tishlinger H. & Chiappe L. M. 2006. — *Juravenator starki* (Reptilia, Theropoda), ein neuer Raubdinosaurier aus dem Oberjura der Südlichen Frankenalb (Süddeutschland): Skelettanatomie und Weichteilbefunde [*Juravenator starki* (Reptilia), a new Theropod dinosaur from the Upper Jurassic of the Southern Franconian Alb (Southern Germany): skeletal anatomy and soft tissue]. *Archaeopteryx: Jahreszeitschrift der Freunde des Jura-Museums in Eichstätt* 24: 1-26.

Grand T., Gould E. & Montali R. 1998. — Structure of the proboscis and rays of the star-nosed mole, Condylura cristata. *Journal of Mammalogy* 79 (2): 492-501. https://doi.org/10.2307/1382980

Grant R., Wieskotten S., Wengst N., Prescott T. & Dehnhardt G. 2013. — Vibrissal touch sensing in the harbor seal (Phoca vitulina): how do seals judge size ? *Journal of Comparative Physiology A* 199 (6): 521-533. https://doi.org/10.1007/s00359-013-0797-7

Gregory J. E., Iggo A., McIntyre A. K. & Proske U. 1989. — Responses of electroreceptors in the snout of the echidna. *The Journal of Physiology* 414 (1): 521-538. https://doi.org/10.1113/jphysiol.1989.sp017701

Gregory J. E., Iggo A., McIntyre A. K. & Proske U. 1988. — Receptors in the bill of the platypus. *The Journal of Physiology* 400 (1): 349-366. https://doi.org/10.1113/jphysiol.1988.sp017124

Haeckel E. 1866. — *Generelle Morphologie der Organismen.* Georg Reimer, Berlin, 632 p. https://gallica.bnf.fr/ark:/12148/bpt6k679173

Halpern M. & Frumin N. 1979. — Roles of the vomeronasal and olfactory systems in prey attack and feeding in adult garter snakes. *Physiology & Behavior* 22 (6): 1183-1189. https://doi.org/10.1016/0031-9384(79)90274-9

Hanai T. & Tsuihiji T. 2019. — Description of Tooth Ontogeny and Replacement Patterns in a Juvenile *Tarbosaurus bataar* (Dinosauria: Theropoda) Using CT-Scan Data. *The Anatomical Record* 302 (7): 1210-1225. https://doi.org/10.1002/ar.24014

Hanke W., Wieskotten S., Marshall C. & Dehnhardt G. 2013. — Hydrodynamic perception in true seals (Phocidae) and eared seals (Otariidae). *Journal of Comparative Physiology A* 199 (6): 421-440. https://doi.org/10.1007/s00359-012-0778-2

Heckert A. B., Jenkins H. S., Lucas S. G. & Hunt P. 2013. — Mandibles of juvenile phytosaurs (Archosauria: Crurotarsi) from the Upper Triassic Chinle Group of Texas and New Mexico, USA. *Bulletin of the New Mexico Museum of Natural History and Science* 61: 228-236.

Hendrickx C., Bell P. R., Pittman M., Milner A. R. C., Cuesta E., O'Connor J., Loewen M., Currie P. J., Mateus O., Kaye T. G. & Delcourt R. 2022. — Morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avialan theropod dinosaurs. *Biological Reviews* 97 (3): 960-1004. https://doi.org/10.1111/brv.12829

Hendrickx C., Mateus O. & Buffetaut E. 2016. — Morphofunctional analysis of the quadrate of Spinosauridae (Dinosauria: Theropoda) and the presence of *Spinosaurus* and a second spinosaurine taxon in the Cenomanian of North Africa. *PLoS One* 11 (1): e0144695. https://doi.org/10.1371/journal.pone.0144695

Hieronymus T. L. & Witmer L. M. 2010. — Homology and evolution of avian compound rhamphothecae. *The Auk* 127 (3): 590-604. https://doi.org/10.1525/auk.2010.09122

Hillenius W. J. 1992. — The evolution of nasal turbinates and mammalian endothermy. *Paleobiology* 18 (1): 17-29. https://doi.org/10.1017/S0094837300012197

Hillenius W. J. & Ruben J. A. 2004. — The evolution of endothermy in terrestrial vertebrates: who? when? why? *Physiological and Biochemical Zoology* 77 (6): 1019-1042. https://doi.org/10.1086/425185

Holdrege C. 2005. — *The Giraffe's Long Neck. From Evolutionary Fable to Whole Organism*. The Nature Institute, Ghent, 104 p.

Holtz T. R. 1998. — Spinosaurs as crocodile mimics. *Science* 282 (5392): 1276-1277. https://doi.org/10.1126/science.282.5392.1276

Home E. 1802. — IV. A Description of the anatomy of the ornithorhynchus paradoxus. *Philosophical Transactions of the Royal Society of London* 92: 67-84. https://doi.org/10.1098/rstl.1802.0006

Hone D. W. & Holtz T. R. Jr 2021. — Evaluating the ecology of *Spinosaurus*: shoreline generalist or aquatic pursuit specialist? https://doi.org/10.26879/1110

Hungerbühler A., Mueller B., Chatterjee S. & Cunningham D. P. 2012. — Cranial anatomy of the Late Triassic phytosaur *Machaeroprosopus*, with the description of a new species from West Texas. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103 (3-4): 269-312. https:doi.org/10.1017/S1755691013000364

Hurum J. H., Sabath K. & Currie P. J. 2003. — Skull structure and evolution in tyrannosaurid dinosaurs. *Acta Palaeontologica Polonica* 48: 227-234. https://doi.org/10.7939/R31Z41S6Z

Hurum J. H. & Sabath K. 2003. — Giant theropod dinosaurs from Asia and North America: skulls of Tarbosaurus bataar and Tyrannosaurus rex compared. *Acta Palaeontologica Polonica* 48 (2): 161-190.

Hutchinson J. R., Anderson F. C., Blemker S. S. & Delp S. L. 2005. — Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: implications for stance, gait, and speed. *Paleobiology* 31 (4): 676-701. https://doi.org/10.1666/0094-8373(2005)031[0676:AOHMMA]2.0.CO;2

Hutt S., Martill D. M. & Barker M. J. 1996 — The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch für Geologie und Paläontologie-Monatshefte* 1996 (10): 635-644. https://doi.org/10.1127/njgpm/1996/1996/635

Huxley T. H. 1864. — *Lectures on the Elements of Comparative Anatomy: On the Classification of Animals and on the Vertebrate Skull*. J. Churchill, London, 303 p. https://doi.org/10.5962/bhl.title.4164

Huxley T. H. 1880. — On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 43: 649-662. https://www.biodiversitylibrary.org/page/28522869

Ibrahim N., Maganuco S., Dal Sasso C., Fabbri M., Auditore M., Bindellini G., Martill D. M., Zouhri S., Mattarelli D. A. & Unwin D. M. 2020. — Tail-propelled aquatic locomotion in a theropod dinosaur. *Nature* 581 (7806): 67-70. https://doi.org/10.1038/s41586-020-2190-3

Ibrahim N., Sereno P. C., Dal Sasso C., Maganuco S., Fabbri M., Martill D. M., Zouhri S., Myhrvold N. & Iurino D. A. 2014. — Semiaquatic adaptations in a giant predatory dinosaur. *Science* 345 (6204): 1613-1616. https://doi.org/10.1126/science.1258750

Ionescu T. V. 1924. — Sur la vitesse du son dans les liquides et sur ses relations avec les chaleurs de vaporisation. *Journal de Physique et le Radium* 5 (12): 377-383. https://doi.org/10.1051/jphysrad:01924005012037700

Josberger E. E., Hassanzadeh P., Deng Y., Sohn J., Rego M. J., Amemiya C. T. & Rolandi M. 2016. — Proton conductivity in ampullae of *Lorenzini jelly*. *Science Advances* 2 (5): e1600112. https://doi.org/10.1126/sciadv.1600112

Kalmijn A. J. 1972. — Bioelectric fields in sea water and the function of the ampullae of *Lorenzini* in elasmobranch fishes. https://escholarship.org/uc/item/62q699rw

Kellner A. W. & Campos D. de A. 1996. — First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae; First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen* 199 (2): 151-166. https://doi.org/10.1127/njgpa/199/1996/151

Klinka D. R. 2004. — *Sensory Modes, Foraging Profitability, Colour Polymorphism and Behavioural Plasticity in Coastal Bear Populations*. M.Sc. Thesis, University of Victoria, British Columbia.

Krassilov V. & Bacchia F. 2013. — New Cenomanian florule and a leaf mine from southeastern Morocco: Palaeoecological and climatological inferences. *Cretaceous Research* 40: 218-226. https://doi.org/10.1016/j.cretres.2012.07.005

Kurzanov S. M. 1976. — A new Late Cretaceous carnosaur from Nogon-Tsav, Mongolia. *Soviet-Mongolian Paleontological Expedition, Transactions* 20: 93-104.

Lamarck J. B. 1801. — *Système des Animaux sans Vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux.* Édition par l'auteur, Paris, 432 p. https://doi.org/10.5962/bhl.title.14255

Lambe L. M. 1914. — On a new genus and species of carnivorous dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Stephanosaurus marginatus* from the same horizon. *Ottawa Naturalist* 28: 13-20. https://www.biodiversitylibrary.org/page/5739477

Lakin R. 2022. — *The Evolution of Parental Care in Archosaurs*. PhD Thesis, University of Bath [retrieved from https://purehost.bath.ac.uk/ws/portalfiles/portal/237797342/University_of_Bath_Thesis_5_1_compressed.pdf].

Lakin R. J. & Longrich N. R. 2019. — Juvenile spinosaurs (Theropoda: Spinosauridae) from the middle Cretaceous of Morocco and implications for spinosaur ecology. *Cretaceous Research* 93: 129-142. https://doi.org/10.1016/j.cretres.2018.09.012

Langman V. A., Maloiy G. M. O., Schmidt-Nielsen K. & Schroter R. C. 1979. — Nasal heat exchange in the giraffe and other large mammals. *Respiration Physiology* 37 (3): 325-333. https://doi.org/10.1016/0034-5687(79)90079-3

Langner G. & Scheich H. 2009. — Electric senses in monotremes: electroreception and electrolocation in the *Platypus* and the *Echidna*, *in* Encyclopedia of Neuroscience. Springer, Cham: 1056-1060. https://doi.org/10.1007/978-3-540-29678-2_2919

Langston W. 1981. — Pterosaurs. *Scientific American* 244 (2): 122-137. https://www.jstor.org/stable/24964287

Latham J. 1790. — *Index ornithologicus, sive, Systema ornithologiae: complectens avium divisionem in classes, ordines, genera, species, ipsarumque varietates: adjectis synonymis, locis, descriptionibus*. Vol. 2. *Sumptibus authoris.* Londini Sumptibus authoris. https://doi.org/10.5962/bhl.title.131313

LeBlanc A. R., Reisz R. R., Evans D. C. & Bailleul A. M. 2016. — Ontogeny reveals function and evolution of the hadrosaurid dinosaur dental battery. *BMC Evolutionary Biology* 16: 1-13. https://doi.org/10.1186/s12862-016-0721-1

LeBlanc A. R. H., Brink K. S., Cullen T. M. & Reisz R. R. 2017a. — Evolutionary implications of tooth attachment versus tooth implantation: A case study using dinosaur, crocodilian, and mammal teeth. *Journal of Vertebrate Paleontology* 37 (5): e1354006. https://doi.org/10.1080/02724634.2017.1354006

LeBlanc A. R. H., Lamoureux D. O. & Caldwell M. W. 2017b. — Mosasaurs and snakes have a periodontal ligament: timing and extent of calcification, not tissue complexity, determines tooth attachment mode in reptiles. *Journal of Anatomy* 231 (6): 869-885. https://doi.org/10.1111/joa.12686

Lees J. H. 1907. — The skull of *Paleorhinus*: a Wyoming phytosaur. *The Journal of Geology* 15 (2): 121-151. https://doi.org/10.1086/621382

Leitch D. B. & Catania K. C. 2012. — Structure, innervation and response properties of integumentary sensory organs in crocodilians. *Journal of Experimental Biology* 215 (23): 4217-4230. https://doi.org/10.1242/jeb.076836

Lessner E. J. & Stocker M. R. 2017. — Archosauriform endocranial morphology and osteological evidence for semiaquatic sensory adaptations in phytosaurs. *Journal of Anatomy* 231 (5): 655-664. https://doi.org/10.1111/joa.12668

Lessner E. J., Dollman K. N., Clark J. M., Xu X. & Holliday C. M. 2023. — Ecomorphological patterns in trigeminal canal branching among sauropsids reveal sensory shift in suchians. *Journal of Anatomy* 242 (5): 927-952. https://doi.org/10.1111/joa.13826

Linnaeus C. 1758. — Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Editio Decima, Reformata. Tomus I. Holmiæ (Stockholm): impensis direct. Laurentii Salvii*: 824. https://doi.org/10.5962/bhl.title.542

Lincoln A. E. & Quinn T. P. 2019. — Optimal foraging or surplus killing: selective consumption and discarding of salmon by brown bears. *Behavioral Ecology* 30 (1): 202-212. https://doi.org/10.1093/beheco/ary139

Lockley M., Kukihara R. & Mitchell L. 2008. — Why *Tyrannosaurus rex* had puny arms: an integral morphodynamic solution to a simple puzzle in theropod paleobiology, *in* Larson P. L. & Carpenter K. (eds), *Tyrannosaurus rex, the Tyrant King.* Indiana University Press, Bloomington: 131-164. https://archive.org/details/tyrannosaurusrex0000unse_z2m5

Maleev E. A. 1955. — New carnivorous dinosaurs from the Upper Cretaceous of Mongolia. *Doklady Akademii Nauk SSSR* 104 (5): 779-782.

Manger P. R. & Pettigrew J. D. 1995. — Electroreception and the feeding behaviour of platypus (*Ornithorhynchus anatinus*: Monotremata: Mammalia). *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 347 (1322): 359-381. https://doi.org/10.1098/rstb.1995.0030

Manger P. R., Keast J. R., Pettigrew J. D. & Troutt L. 1998. — Distribution and putative function of autonomic nerve fibres in the bill skin of the platypus (*Ornithorhynchus anatinus*). *Philosophical Transactions of the Royal Society of London*, series B, *Biological Sciences* 353 (1372):1159-1170. https://doi.org/10.1098/rstb.1998.0273

Marsh O. C. 1877. — Notice of new dinosaurian reptiles from the Jurassic Formation. *American Journal of Science* 3 (84): 514-516. https://doi.org/10.2475/ajs.s3-14.84.514

Marsh O. C. 1881. — Principal characters of American Jurassic dinosaurs. Part V. *The American Journal of Science and Arts* S3-21 (125): 417-423. https://doi.org/10.2475/ajs.s3-21.125.417

Martill D. M., Cruickshank A. R. I., Frey E., Small P. G. & Clarke M. 1996. — A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil. *Journal of the Geological Society* 153 (1): 5-8. https://doi.org/10.1144/gsjgs.153.1.0005

Martin G. R., Wilson K.-J., Wild J. M., Parsons S., Kubke M. F. & Corfield J. 2007. — Kiwi forego vision in the guidance of their nocturnal activities. *Plos One* 2 (2): e198. https://doi.org/10.1371/journal.pone.0000198

Matsinos Y. G., Wolff W. F. & Moustakas A. 2012. — Adapting foraging to habitat heterogeneity and climate change: an individual-based model for wading birds. *Ethology Ecology & Evolution* 24 (3): 209-229. https://doi.org/10.1080/03949370.2011.601762

Meyer H. von. 1861 — *Archaeopteryx lithographica* (Vogel-Feder) und *Pterodactylus* von Solenhofen (Brief an Prof. Bronn vom 30. September 1861). *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 5: 678-679.

Miyamae J. A., Benoit J., Ruf I., Sibiya Z. & Bhullar B. S. 2024. — Synapsids and sensitivity: Broad survey of tetrapod trigeminal canal morphology supports an evolutionary trend of increasing facial tactile specialization in the mammal lineage. *The Anatomical Record*: ar.25604. https://doi.org/10.1002/ar.25604

Mkhitaryan T. G. & Averianov A. O. 2011. — New material and phylogenetic position of *Aidachar paludalis* Nessov, 1981 (Actinopterygii, Ichthyodectiformes) from the Late Cretaceous of Uzbekistan. *Proceedings of the Zoological Institute RAS* 315 (2): 181-192

Moore A. M., Hartstone Rose A. & Gonzalez Socoloske D. 2022. — Review of sensory modalities of sirenians and the other extant Paenungulata clade. *The Anatomical Record* 305 (3): 715-735. https://doi.org/10.1002/ar.24741

Moore B. A., Paul-Murphy J. R., Tennyson A. J. D. & Murphy C. J. 2017. — Blind free-living kiwi offer a unique window into the ecology and evolution of vertebrate vision. *BMC Biology* 15 (1): 85. https://doi.org/10.1186/s12915-017-0424-0

Morhardt A. C. 2009. — *Dinosaur Smiles: do the Texture and Morphology of the Premaxilla, Maxilla, and Dentary Bones of Sauropsids Provide Osteological Correlates for Inferring Extra-Oral Structures Reliably in Dinosaurs?* Western Illinois University, Macomb, Illinois.

Muchlinski M. N. 2010. — A comparative analysis of vibrissa count and infraorbital foramen area in primates and other mammals. *Journal of Human Evolution* 58 (6): 447-473. https://doi.org/10.1016/j.jhevol.2010.01.012

Müller S. 1838. — Waarnemingen over de Indische Krokodillen en Beschrijving van Eene Nieuwe Soort. (Observations of the Indonesian crocodiles and description of a new species). *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie* 5: 61- 87. https://www.biodiversitylibrary.org/page/13474839

Müller R. 2009. — Hierarchical microimaging of bone structure and function. *Nature Reviews Rheumatology* 5 (7): 373-381. https://doi.org/10.1038/nrrheum.2009.107

Murakami Y. & Kuratani S. 2008. — Brain segmentation and trigeminal projections in the lamprey; with reference to vertebrate brain evolution. *Brain Research Bulletin* 75 (2-4): 218-224. https://doi.org/10.1016/j.brainresbull.2007.10.057

Murie J. 1872. — XX. On the horns, viscera, and muscles of the Giraffe; with a record of the post mortem examination of two specimens killed by a fire. *Annals and Magazine of Natural History* 9 (51): 177-195. https://doi.org/10.1080/00222937208696563

Murray R. W. 1960. — The response of the ampullae of Lorenzini of elasmobranchs to mechanical stimulation. *Journal of Experimental Biology* 37 (2): 417-424. https://doi.org/10.1242/jeb.37.2.417

Myhrvold N. P., Baumgart S. L., Vidal D., Fish F. E., Henderson D. M., Saitta E. T. & Sereno P. C. 2024. — Diving dinosaurs? Caveats on the use of bone compactness and pFDA for inferring lifestyle. *Plos One* 19 (3): https://doi.org/10.1371/journal.pone.0298957

Nessov L. A. 1981. — Amfibii i reptilii v ekosistemakh Mela sredney Azii [Amphibia and reptiles in Cretaceous ecosystems of central Asia], *in* The Problems of Herpetology. Fifth Herpetological Conference, abstract volume: 91-92.

Norell M. A., Clark J. M., Demberelyin D., Rhinchen B., Chiappe L. M., Davidson A. R., McKenna M. C., Altangerel P. & Novacek M. J. 1994. — A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266 (5186): 779-782. https://doi.org/10.1126/science.266.5186.779

Osborn H. F. 1905. — *Tyrannosaurus* and other Cretaceous carnivorous dinosaur. *Bulletin of American Museum of Natural History* 21 (14): 259-265. http://hdl.handle.net/2246/1464

Owen R. 1842. — Report on British fossil reptiles, part 2. *Report of the British Association for the Advancement of Science* 11: 60. https://www.biodiversitylibrary.org/page/33377524

Papakostas G., Kazantzidis S., Goutner V. & Charalambidou I. 2005. — Factors affecting the foraging behavior of the Squacco Heron. *Waterbirds* 28 (1): 28-34. https://doi.org/10.1675/1524-4695(2005)028[0028:FATFBO]2.0.CO;2

Peters W. C. H. & Doria G. 1876. — *Descrizione di una nuova specie di tachglossus, proveniente dalla Nuova Guinea settentrionale. Annali del Museo Civico Storia Naturale di Genova* 9: 183-185. https://www.biodiversitylibrary.org/page/29875915

Pettigrew J. D. 1999. — Electroreception in monotremes. *Journal of Experimental Biology* 202 (10): 1447-1454. https://doi.org/10.1242/jeb.202.10.1447

Pettigrew J. D., Manger P. R. & Fine S. L. B. 1998. — The sensory world of the platypus. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 353 (1372): 1199-1210. https://doi.org/10.1098/rstb.1998.0276

Peyer B. & Zangerl R. 1968. — *Comparative Odontology*. University of Chicago Press, Chicago, 475 p. https://archive.org/details/comparativeodont0000peye

Pittet F. & Goussard F. 2025. — 3D models related to the publication: Neurovascular system and dental renewal in the rostrum of Spinosauridae: new descriptions and implications on non-olfactive snout sensitivity of dinosaurs. *MorphoMuseuM* e272. https://doi.org/10.18563/journal.m3.272

Pittet F., Cavin L. & Poyato-Ariza F. J. 2010. — A new teleostean fish from the early Late Cretaceous (Cenomanian) of SE Morocco, with a discussion of its relationships with ostariophysans. *Gonorynchiformes and Ostariophysan Relationships: A Comprehensive Review. Enfield (New Hampshire): Science Publishers*: 339-62. https://doi.org/10.1201/b10194

Porter W. R. & Witmer L. M. 2015. — Vascular patterns in iguanas and other squamates: blood vessels and sites of thermal exchange. *PLoS One* 10 (10): e0139215. https://doi.org/10.1371/journal.pone.0139215

PORTER W. R. & WITMER L. M. 2020. — Vascular Patterns in the Heads of Dinosaurs: Evidence for Blood Vessels, Sites of Thermal Exchange, and Their Role in Physiological Thermoregulatory Strategies. *The Anatomical Record* 303 (4): 1075-1103. https://doi.org/10.1002/ar.24234

PROSKE U., GREGORY J. E. & IGGO A. 1998. — Sensory receptors in monotremes. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 353 (1372): 1187-1198. https://doi.org/10.1098/rstb.1998.0275

RASMUSSEN L. E. L. & MUNGER B. L. 1996. — The sensorineural specializations of the trunk tip (finger) of the asian elephant,elephas maximus. *The Anatomical Record* 246 (1): 127-134. https://doi.org/10.1002/(SICI)1097-0185(199609)246:1<127::AID-AR14>3.0.CO;2-R

RAYFIELD E. J., MILNER A. C., XUAN V. B. & YOUNG P. G. 2007. — Functional morphology of spinosaur 'crocodile-mimic' dinosaurs. *Journal of Vertebrate Paleontology* 27 (4): 892-901. https://doi.org/10.1671/0272-4634(2007)27[892:FMOSCD]2.0.CO;2

REEP R. L., STOLL M. L., MARSHALL C. D., HOMER B. L. & SAMUELSON D. A. 2001. — Microanatomy of facial vibrissae in the Florida manatee: the basis for specialized sensory function and oripulation. *Brain Behavior and Evolution* 58 (1): 1-14. https://doi.org/10.1159/000047257

REISZ R. R. & LARSON D. 2016. — Dental anatomy and skull length to tooth size ratios support the hypothesis that theropod dinosaurs had lips, *in* Canadian Society of Vertebrate Palaeontology Annual Meeting IV, Mississauga, Canada, 2016: 49-50.

RHINN M., MIYOSHI K., WATANABE A., KAWAGUCHI M., ITO F., KURATANI S., BAKER C. V. H., MURAKAMI Y. & RIJLI F. M. 2013. — Evolutionary divergence of trigeminal nerve somatotopy in amniotes. *Journal of Comparative Neurology* 521 (6): 1378-1394. https://doi.org/10.1002/cne.23236

RIEPPEL O. & KEARNEY M. 2005. — Tooth replacement in the Late Cretaceous mosasaur Clidastes. *Journal of Herpetology* 39 (4): 688-692. https://doi.org/10.1670/119-05A.1

ROMAGNAN J.-P. 2011. — *Comprendre la mécanique*. EDP sciences, Paris, 347 p.

ROMER A. S. 1956. — *Osteology of the Reptiles*. Harvard University Press, Cambridge, 300 p. https://doi.org/10.5962/bhl.title.6573

ROTHSCHILD B. M. & NAPLES V. 2017. — Apparent sixth sense in theropod evolution: The making of a Cretaceous weathervane. *Plos One* 12 (11): e0187064. https://doi.org/10.1371/journal.pone.0187064

RUSSEL D. A. 1996. — Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. *Bulletin du Muséum national d'Histoire naturelle, 4ème série, section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie* 18 (2-3): 349-415. https://www.biodiversitylibrary.org/page/55870551

SASSO C. D., MAGANUCO S., BUFFETAUT E. & MENDEZ M. A. 2005. — New information on the skull of the enigmatic theropod *Spinosaurus* , with remarks on its size and affinities. *Journal of Vertebrate Paleontology* 25 (4): 888-896. https://doi.org/10.1671/0272-4634(2005)025[0888:NIOTSO]2.0.CO;2

SASSOON J., NOÈ L. F. & BENTON M. J. 2012. — Cranial anatomy, taxonomic implications and palaeopathology of an Upper Jurassic Pliosaur (Reptilia: Sauropterygia) from Westbury, Wiltshire, UK. *Palaeontology* 55 (4): 743-773. https://doi.org/10.1111/j.1475-4983.2012.01151.x

SATTLER F. & SCHWARZ D. 2021. — Tooth replacement in a specimen of *Tyrannosaurus rex* (Dinosauria, Theropoda) from the Hell Creek Formation (Maastrichtian), Montana. *Historical Biology* 33 (7): 949-972. https://doi.org/10.1080/08912963.2019.1675052

SAVASTANO M. C., LUMBROSO B. & RISPOLI M. 2015. — In vivo characterization of retinal vascularization morphology using optical coherence tomography angiography. *Retina* 35 (11): 2196-2203. https://doi.org/10.1097/iae.0000000000000635

SAVI P. 1822. — Osservazioni sopra il mustiello, o mustiolo nuova specie di toporagno Toscano: *Sorex etruscus. Nuovo Giornale dei Litterati, Pisa* 1: 60-71.

SAWYER E. K. & CATANIA K. C. 2016. — Somatosensory organ topography across the star of the star-nosed mole (*Condylura cristata*). *Journal of Comparative Neurology* 524 (5): 917-929. https://doi.org/10.1002/cne.23943

SCHADE M., RAUHUT O. W. & EVERS S. W. 2020. — Neuroanatomy of the spinosaurid Irritator challengeri (Dinosauria: Theropoda) indicates potential adaptations for piscivory. *Scientific Reports* 10 (1): 9259. https://doi.org/10.1038/s41598-020-66261-w

SCHEICH H., LANGNER G., TIDEMANN C., COLES R. B. & GUPPY A. 1986. — Electroreception and electrolocation in platypus. *Nature* 319 (6052): 401-402. https://doi.org/10.1038/319401a0

SCHNEIDER C., RASBAND W. & ELICEIRI K. 2012. — NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671-675. https://doi.org/10.1038/nmeth.2089

SEELEY H. G. 1888. — I. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London, 43* (258-265): 165-171. https://doi.org/10.1098/rspl.1887.0117

SERENO P. C., BECK A. L., DUTHEIL D. B., GADO B., LARSSON H. C. E., LYON G. H., MARCOT J. D., RAUHUT O. W. M., SADLEIR R. W., SIDOR C. A., VARRICCHIO D. D., WILSON G. P. & WILSON J. A. 1998. — A Long-Snouted Predatory Dinosaur from Africa and the Evolution of Spinosaurids. *Science* 282 (5392): 1298-1302. https://doi.org/10.1126/science.282.5392.1298

SHAW G. 1790. — Vivarium Naturæ or the Naturalist's Miscellany Vol. 11. Nodder & Company, London. https://doi.org/10.5962/bhl.title.79941

SHAW G. 1792. — *Myrmecophaga aculeata*. The Porcupine Anteater. *Naturalists' Miscellany* 3: 36. https://www.biodiversitylibrary.org/page/59564684

SHAW G. & NODDER F. P. 1799. — The duck-billed platypus. *The Naturalists' Miscellany* 10: https://www.biodiversitylibrary.org/page/59339870

SOARES D. 2002. — An ancient sensory organ in crocodilians. *Nature* 417 (6886): 241-242. https://doi.org/10.1038/417241a

SPRINGER M. S., GUERRERO-JUAREZ C. F., HUELSMANN M., COLLIN M. A., DANIL K., MCGOWEN M. R., OH J. W., RAMOS R., HILLER M. & PLIKUS M. V. 2021. — Genomic and anatomical comparisons of skin support independent adaptation to life in water by cetaceans and hippos. *Current Biology* 31 (10): 2124-2139.e3. https://doi.org/10.1016/j.cub.2021.02.057

STROMER E. 1915. — *Das original des theropoden* Spinosaurus aegyptiacus *nov. gen., nov. spec.* Königlich Bayerische Akademie der Wissenschaften, München.

STROMER E. 1917. — Ergebnisse der Forschungsreisen Prof. Stromers in den Wüsten Ägyptens. Die Säge des Pristiden Onchopristis numidus Haug sp. und über die Sägen der Sägehaie. *Abhandlungen der Bayerisch Akademie der Wissenschaften* 28: 1-28.

TAKAMI S. 2002. — Recent progress in the neurobiology of the vomeronasal organ. *Microscopy Research and Technique* 58 (3): 228-250. https://doi.org/10.1002/jemt.10094

TAMISIEA J. 2023. — Imagine *T. Rex*. Now imagine it with lips. *International New York Times*.

TAQUET P. 1984. — Une curieuse spécialisation du crâne de certains Dinosaures carnivores du Crétacé : le museau long et étroit des Spinosauridés. *Comptes-rendus des séances de l'Académie des sciences. Série 2, Mécanique-Physique, Chimie, Sciences de l'univers, Sciences de la Terre* 299 (5): 217-222. https://gallica.bnf.fr/ark:/12148/bpt6k6139155c/f223.item

TAQUET P. & RUSSELL D. A. 1998. — New data on spinosaurid dinosaurs from the Early Cretaceous of the Sahara. *Comptes Rendus de l'Académie des Sciences-Series IIA, Earth and Planetary Science* 327 (5): 347-353. https://doi.org/10.1016/S1251-8050(98)80054-2

TOJO H. 1996. — Habitat selection, foraging behaviour and prey of five heron species in Japan. *Japanese Journal of Ornithology* 45 (3): 141-158. https://doi.org/10.3838/jjo.45.141

TSUIHIJI T., WATABE M., TSOGTBAATAR K., TSUBAMOTO T., BARSBOLD R., SUZUKI S., LEE A. H., RIDGELY R. C., KAWAHARA Y. & WITMER L. M. 2011. — Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* 31 (3): 497-517. https://doi.org/10.1080/02724634.2011.557116

TUCKER A. S. & FRASER G. J. 2014. — Evolution and developmental diversity of tooth regeneration. *Seminars in Cell & Developmental Biology* 25-26: 71-80. https://doi.org/10.1016/j.semcdb.2013.12.013

VON LINNÉ C. 1788. — *Caroli a Linné systema naturae.* Vol. 1. Impensis Georg. Emanuel. Beer., Leipzig. https://doi.org/10.5962/bhl.title.545

VULLO R., ALLAIN R. & CAVIN L. 2016. — Convergent evolution of jaws between spinosaurid dinosaurs and pike conger eels. *Acta Palaeontologica Polonica* 61 (4): 825-828. https://doi.org/10.4202/app.00284.2016

WANG X., O'CONNOR J., ZHENG X., WANG Y. & KIAT Y. 2024. — Earliest evidence of avian primary feather moult. *Biology Letters* 20 (7): 20240106. https://doi.org/10.1098/rsbl.2024.0106

WEBB J. F. 2023. — Structural and functional evolution of the mechanosensory lateral line system of fishes. *The Journal of the Acoustical Society of America* 154 (6): 3526-3542. https://doi.org/10.1121/10.0022565

WELLNHOFER P. 1994. — New data on the origin and early evolution of birds. *Comptes rendus de l'Académie des sciences. Série 2. Sciences de la terre et des planètes* 319 (3): 299-308. https://gallica.bnf.fr/ark:/12148/bpt6k61389174/f303.item

WHITAKER N. 2007. — Extended parental care in the Siamese crocodile (Crocodylus siamensis). *Russian Journal of Herpetology* 14 (3): 203-206.

WIESKOTTEN S., DEHNHARDT G., MAUCK B., MIERSCH L. & HANKE W. 2010. — Hydrodynamic determination of the moving direction of an artificial fin by a harbour seal (Phoca vitulina). *Journal of Experimental Biology* 213 (13): 2194-2200. https://doi.org/10.1242/jeb.041699

WIESKOTTEN S., MAUCK B., MIERSCH L., DEHNHARDT G. & HANKE W. 2011. — Hydrodynamic discrimination of wakes caused by objects of different size or shape in a harbour seal (Phoca vitulina). *Journal of Experimental Biology* 214 (11): 1922-1930. https://doi.org/10.1242/jeb.053926

WILLIAMS E. M. 2016. — Giraffe stature and neck elongation: Vigilance as an evolutionary mechanism. *Biology* 5 (3): 35. https://doi.org/10.3390/biology5030035

WITMER L. M., ABLER W. L., MURPHY N., CARPENTER K., FARLOW J. O., CHAPMAN R. E., LARSON P. L., KEILLOR T., ROTHSCHILD B. M. & KOPPELHUS E. B. 2013. — *Tyrannosaurid Paleobiology*. Indiana University Press, Bloomington. https://muse.jhu.edu/book/23718

WITTON M. P. & NAISH D. 2013. — Azhdarchid pterosaurs: water-trawling pelican mimics or "terrestrial stalkers"? *Acta Palaeontologica Polonica* 60 (3): 651-660. https://doi.org/10.4202/app.00005.2013

WUERINGER B. E., WINTHER JANSON M., RAOULT V. & GUTTRIDGE T. L. 2021. — Anatomy of the mechanosensory lateral line canal system and electrosensory ampullae of L orenzini in two species of sawshark (fam. P ristiophoridae). *Journal of Fish Biology* 98 (1): 168-177. https://doi.org/10.1111/jfb.14567

ZHENG J., WENG L. Q., SHI M. Y., ZHOU J., HUA L. C., QIAN L. M. & ZHOU Z. R. 2013. — Effect of water content on the nanomechanical properties and microtribological behaviour of human tooth enamel. *Wear* 301 (1-2): 316-323. https://doi.org/10.1016/j.wear.2012.12.043

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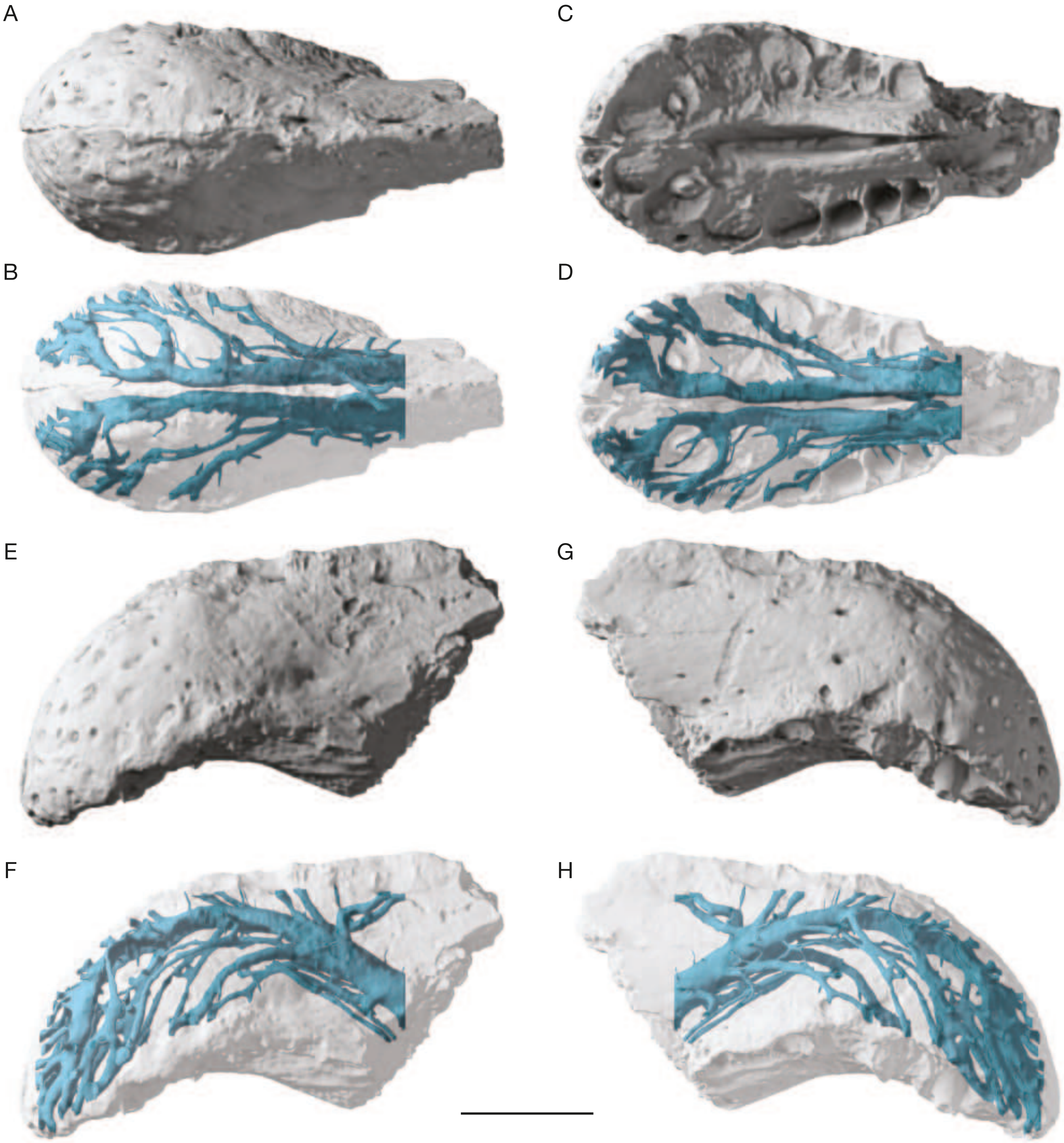
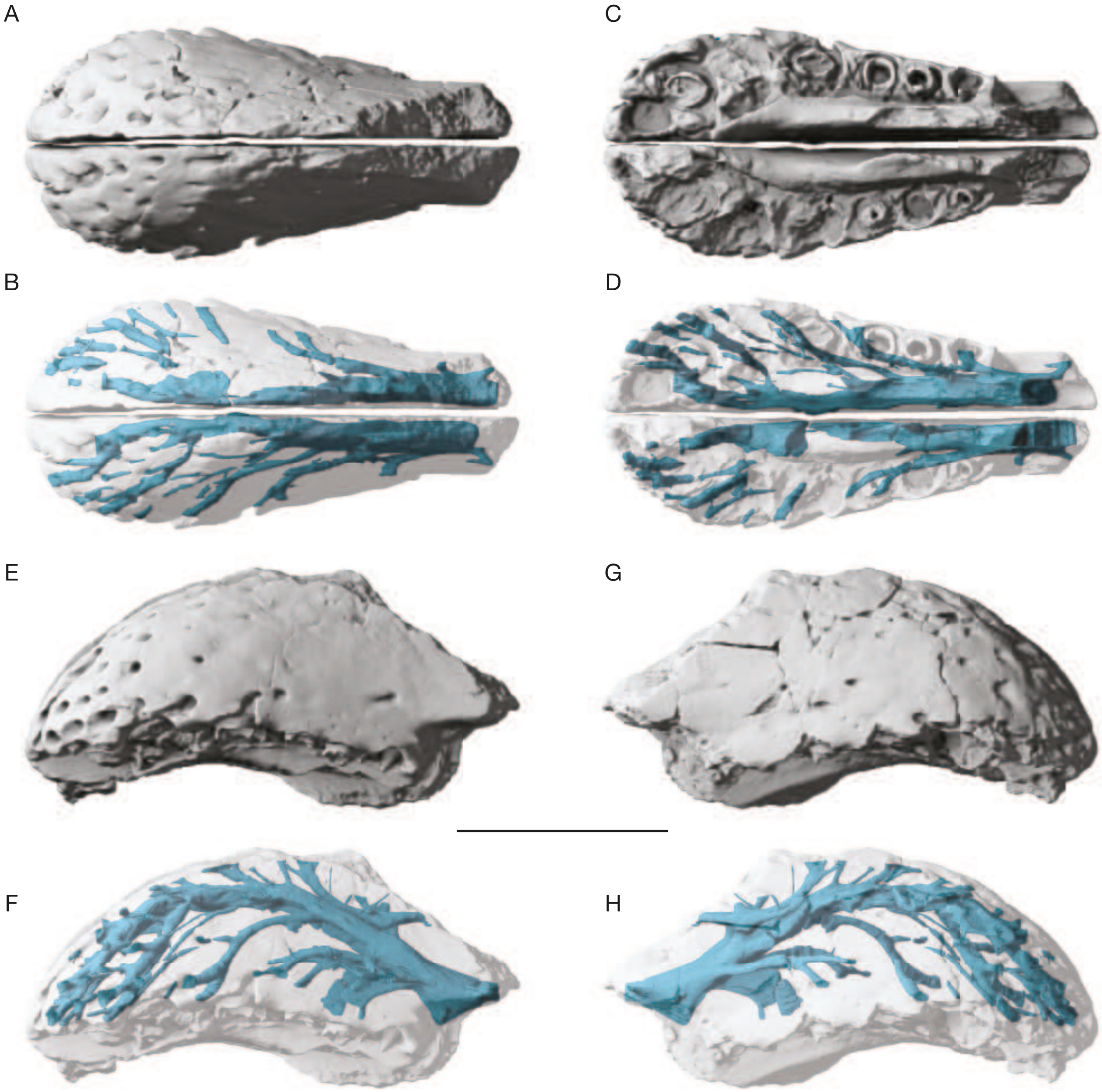
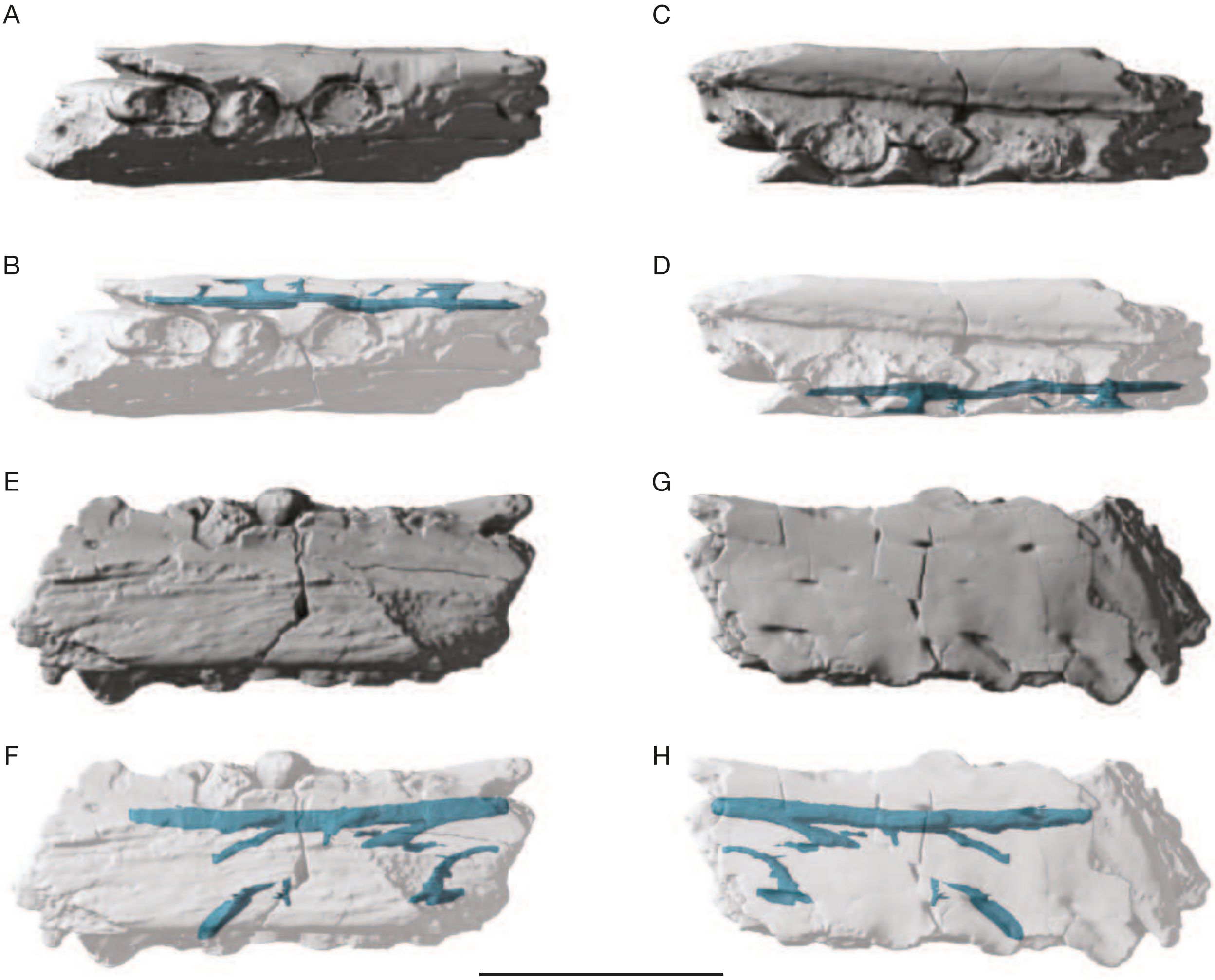


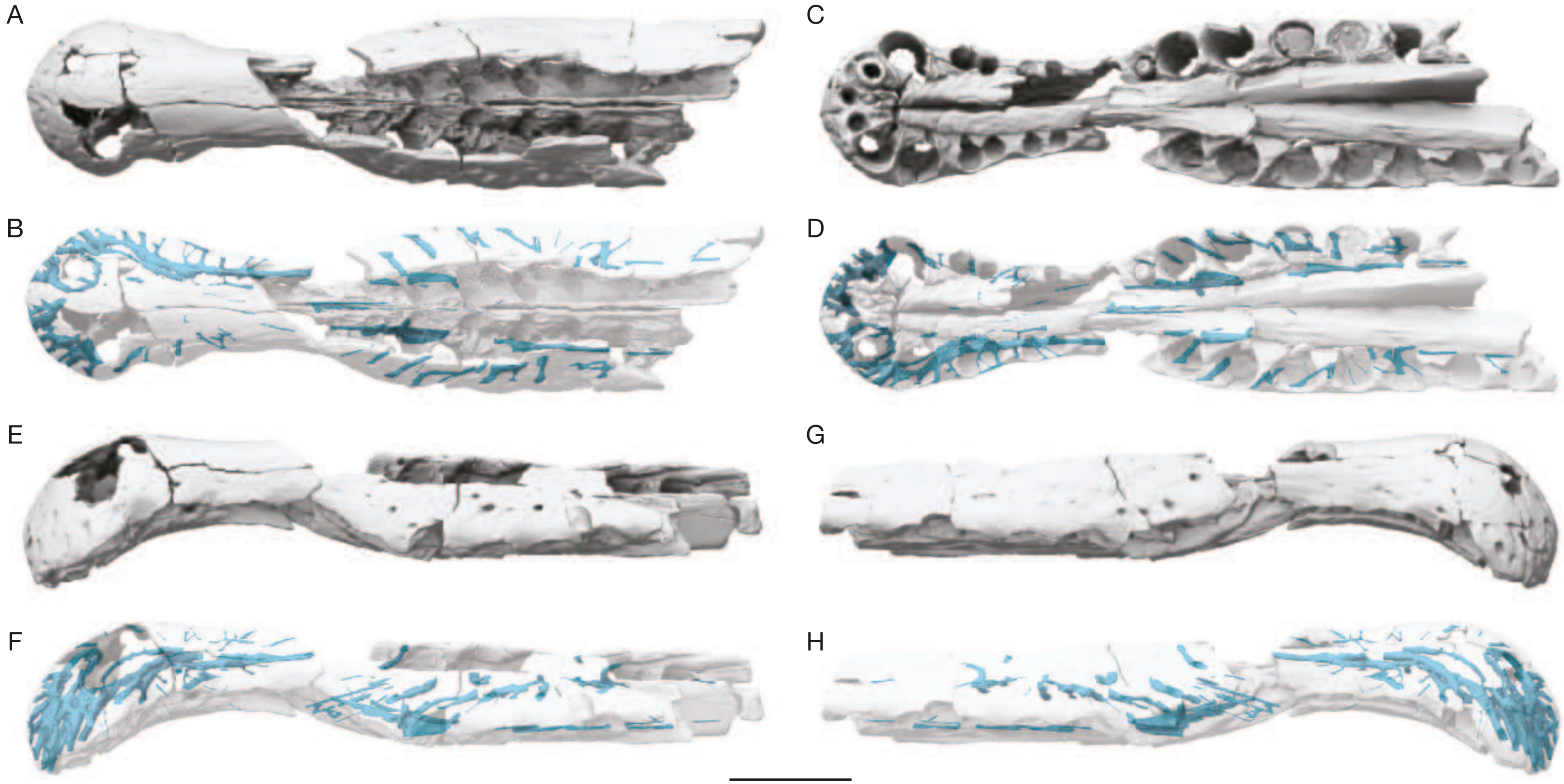
Appendix 1. — MNHN.F.GDF365 premaxillae, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **A**, dorsal superficial view of the premaxillae; **B**, dorsal view in transparency with neurovascular network in the premaxillae; **C**, ventral superficial view of the premaxillae; **D**, ventral view in transparency with neurovascular network in the premaxillae; **E**, left labial view of the premaxilla; **F**, left labial view in transparency with neurovascular network in the premaxilla; **G**, right labial view of the premaxilla; **H**, right labial view in transparency with neurovascular network in the premaxilla. Scale bar: 5 cm. Models by Frédéric Pittet & Florent Goussard.



Appendix 2. — MNHN.F.GDF366 premaxillae, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **A**, dorsal superficial view of the premaxillae; **B**, dorsal view in transparency with neurovascular network in the premaxillae; **C**, ventral superficial view of the premaxillae; **D**, ventral view in transparency with neurovascular network in the premaxillae; **E**, left labial view of the premaxilla; **F**, left labial view in transparency with neurovascular network in the premaxilla; **G**, right labial view of the premaxilla; **H**, right labial view in transparency with neurovascular network in the premaxilla. Scale bar: 5 cm. Models by Frédéric Pittet & Florent Goussard.



Appendix 3. — MNHN.F.GDF366 part of right maxilla, *Cristatusaurus lapparenti* Taquet & Russell, 1998: **A**, dorsal superficial view of the maxilla; **B**, dorsal view in transparency with neurovascular network in the maxilla; **C**, ventral superficial view of the maxilla; **D**, ventral view in transparency with neurovascular network in the maxilla; **E**, left labial view of the maxilla; **F**, left labial view in transparency with neurovascular network in the maxilla; **G**, right labial view of the maxilla; **H**, right labial view in transparency with neurovascular network in the maxilla. Scale bar: 5 cm. Models by Frédéric Pittet & Florent Goussard.



Appendix 4. — MNHN.F.SAM124, *Spinosaurus maroccanus* Russell, 1996: **A**, dorsal superficial view of the premaxillae and maxillae; **B**, dorsal view in transparency with neurovascular network in the premaxillae and maxillae; **C**, ventral superficial view of the premaxillae and maxillae; **D**, ventral view in transparency with neurovascular network in the premaxillae and maxillae; **E**, left labial view of the premaxillae and maxillae; **F**, left labial view in transparency with neurovascular network in the premaxilla and maxilla; **G**, right labial view of the premaxillae and maxillae; **H**, right labial view in transparency with neurovascular network in the premaxillae and maxillae. Scale bar: 10 cm. Models by Frédéric Pittet & Florent Goussard.