Skull and brain anatomy of Late Carboniferous Sibyrhynchidae (Chondrichthyes, Iniopterygia) from Kansas and Oklahoma (USA)

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ABSTRACT

Recent gnathostomes are composed of two major clades, the chondrichthyans, or cartilaginous fishes, and the osteichthyans, or bony fishes and tetrapods. Recent chondrichthyans include about 1200 elasmobranch (sharks and rays) species, but only about 40 holocephalan (ratfish) species. Nevertheless, an important radiation of chondrichthyans took place in the Carboniferous (360-300 Myr), and gave rise to an important diversity of odd and poorly understood taxa, such as the iniopterygians, that are considered as related to extant holocephalans. However, the relationships between these taxa and the two extant chondrichthyan clades remain controversial. The material studied here by means of computed microtomography scanning using synchrotron radiation X-ray, consists of neurocrania from the Upper Carboniferous of Kansas and Oklahoma (USA), which are remarkably well preserved in three dimensions, and which belong to one of the two families of iniopterygians, the Sibyrhynchidae Zangerl & Case, 1973. A detailed description of these specimens provides more information about the cranial and brain anatomy of this taxon. No three-dimensionally preserved skull of any stem-holocephalan was known in detail to date, contrary to fossil elasmobranchs. The data presented here show the three-dimensionally preserved braincase of a possible stem-holocephalan as these new specimens share with extant chimaeroids some key neurocranial characters. This may provide means for a comparative study of skull anatomy in Paleozoic representatives of the main two chondrichthyan clades.

KEY WORDS
Chondrichthyes,
Iniopterygia,
Sibyrhynchidae,
gnathostomes,
holocephalans,
neurocranium,
brain,
Paleozoic,
Synchrotron,
X-ray,
USA.

RÉSUMÉ

Anatomie du crâne et du cerveau des Sibyrhynchidae (Chondrichthyes, Iniopterygia) du Carbonifère supérieur du Kansas et de l'Oklahoma (USA).

Les gnathostomes actuels sont représentés par deux clades majeurs, les chondrichthyens, ou poissons cartilagineux, et les osteichthyens, ou poissons osseux et tétrapodes. Les chondrichthyens modernes comprennent environ 1200 espèces d'élasmobranches (requins et raies), mais seulement une quarantaine d'espèces d'holocéphales (chimères). Cependant, une importante radiation de chondrichthyens a eu lieu durant le Carbonifère (360-300 Ma) et a généré une importante diversité de taxons étranges et mal connus, comme les inioptérygiens qui sont considérés comme phylogénétiquement proches des holocéphales actuels. Néanmoins, les relations de parenté entre ces taxons et les deux clades actuels de chondrichthyens demeurent controversées. Le matériel, étudié ici grâce à la microtomographie assistée par ordinateur utilisant la lumière Synchrotron, consiste en des neurocrânes du Carbonifère supérieur du Kansas et de l'Oklahoma (USA), parfaitement conservés en trois dimensions et qui appartiennent à une des deux familles d'inioptérygiens, les Sibyrhynchidae Zangerl & Case, 1973. Une description détaillée de ces spécimens fournit des informations supplémentaires quant à l'anatomie du crâne et du cerveau de ce taxon. Contrairement aux élasmobranches, il n'existait jusqu'à ce jour aucun crâne conservé en trois dimensions d'holocéphale fossile. Les spécimens étudiés ici nous fournissent un neurocrâne préservé en trois dimensions d'un possible holocéphale souche, tant ils partagent avec les chimères actuelles des caractères neurocrâniens caractéristiques. Ils permettent donc des études comparatives de l'anatomie crânienne chez les représentants paléozoïques des deux clades majeurs de chondrichthyens.

MOTS CLÉS
Chondrichthyes,
Iniopterygia,
Sibyrhynchidae,
gnathostomes,
holocéphales,
neurocrâne,
cerveau,
Paléozoïque,
lumière Synchrotron,
rayons X,
États-Unis.

INTRODUCTION

Recent gnathostomes are represented by two major clades, the Chondrichthyes Huxley, 1880, or cartilaginous fishes, and osteichthyans, or bony fishes and tetrapods. The interrelationships of the two subclasses (Elasmobranchii Bonaparte, 1838, i.e. sharks, skates, rays and Holocephali Bonaparte, 1932, i.e. ratfish, chimaera, spookfish) of recent chondrichthyans are far from satisfactorily elucidated and this situation is even worse when fossil chondrichthyans are considered, in particular the Paleozoic ones (Woodward 1889; Lund 1977; Zangerl 1981; Maisey 1984; Didier 1995; Janvier 1996; De Carvalho 1996; Grogan & Lund 2004). This results from the high degree of morphological disparity in the Paleozoic forms that far exceeds that observed in living forms, as well as from a generally poor preservation and the difficulty to observe crucial features.

Crown-group holocephalans could be followed through the fossil record as far back as the Jurassic (e.g., *Ischyodus* Egerton, 1843; Stahl 1999). Association of earlier forms with this group is unclear. According to Coates & Sequeira (2001a, b), a number of Paleozoic chondrichthyans could be resolved as stem-holocephalans, such as the Symmoriiformes Zangerl, 1981, but there is no consensus about these relationships to date (Maisey 2007). The description of new three-dimensional braincases of possible stem-holocephalans, including consideration of the cranial blood vascular system, cranial nerve pattern and endocranial cavity, may provide information that could support these relationships, as the description of Paleozoic three-dimensionally shark braincases already did for the total-group elasmobranchs and early gnathostomes phylogeny (Schaeffer 1981; Maisey 2001a, 2005; Maisey & Anderson 2001).

Zangerl & Case (1973) first described a new order of chondrichthyan fishes from the Pennsylvanian of Indiana (USA), the Iniopterygia Zangerl & Case, 1973, which contain two families: the Iniopterygidae Zangerl & Case, 1973, and the Sibyrhynchidae Zangerl & Case, 1973. Other iniopterygids from Indiana and the Mississippian of Montana (USA) were respectively discovered and described by Zangerl (1997) and Grogan & Lund (2009). M. Coates (pers. comm.) recently discovered some elements of an iniopterygian in the Lower Carboniferous of Beardsen (Scotland).

Iniopterygians were assumed to belong to the subclass Subterbranchialia Zangerl, 1979, as stem-holocephalans (Zangerl 1981; Stahl 1999). Nevertheles, recent cladistic analysis on the neurocranium of the new iniopterygid specimens from Montana, brings them in a stemward position, before the divergence between the elasmobranchs and holocephalans (Grogan & Lund 2009), whereas the sibyrhynchids share derived characters with the living chimearoids (e.g., a palatoquadrate that is fused to the neurocranium). In addition, the iniopterygians also display many characters, which are shared with other Paleozoic chondrichthyans, and a relatively large number of autapomorphies, notably the dorsal position of the pectoral fins. Consequently, the phylogenetic status of the Iniopterygia is still in question.

Unfortunately, all the iniopterygian specimens previously described are flattened (Zangerl & Case 1973; Zangerl 1997; Grogan & Lund 2009). Consequently, they do not allow any extensive description, in particular concerning the braincase. Recently, a short paper based on new material from the Pennsylvanian of Kansas and Oklahoma put an emphasis on a new technique of observation, the quantitative phase contrast tomography that revealed the first three-dimensionally preserved Sibyrhynchidae neurocrania known to date. In addition, one of these new sibyrhynchid braincases houses exceptionally preserved parts of the brain itself (Pradel *et al.* 2009).

These three dimensionally preserved skulls and the fossilized brain provide new information about the external and internal morphology of the braincase. They allow a comparative study of skull and brain anatomy with other three-dimensionally preserved neurocrania of Paleozoic and extant chrondrichthyans as well. According to the importance of these three-dimensionally preserved skulls and this unique case of fossilized brain, a detailed description of the braincases, dentition, and dermal denticles of the head and the preserved brain is provided in this paper, prolonging their initial publication with further anatomical details.

MATERIALS AND METHODS

The manual preparation of the specimens is very difficult because of the extreme fragility of the fossilized calcified cartilage. Consequently, and because it is necessary to investigate the internal anatomy of the braincases, computerized X-ray microtomography (XR-μCT scan), X-ray synchrotron microtomography (SR-μCT scan) and quantitative phase contrast tomography (holotomography) were performed. These techniques provide an ideal non-invasive technology to investigate structures of the fossil that are otherwise inaccessible.

ABBREVIATIONS

aa	anterior ampulla;
ala	acoustico-lateral area;
alc	anterior lobe of the corpus cerebelli;
am	articular zone of the mandible;
amf	anterior median fissure;
antjc	anterior opening of the jugular canal;
arf	articular facet of the palatoquadrate;
asc	anterior semicircular canal;
basa	basilar artery;
bmc	bucco-maxillary complex;
br	mineralized brain;
bso	possible branch of a spino-occipital nerve innervating the epaxial musculature;
ca	cerebellar auricle;
cc	crus commune;
ccer	corpus cerebelli;
ceps	canal for the efferent pseudobranchial artery;
cerc	cerebellar commissure;
cerch	cerebellar chamber;
cha	connection between the horizontal ampulla and the utricular recess;
cora	canal for the orbital artery;
cpcv	canal for the posterior cerebral vein;
cpitv	canal for the pituitary vein;

cpr	canal for the profoundus ramus of the trigeminal nerve;
cso	canal for spino-occipital nerve;
csoph	canal for the superficial ophthalmic complex;
ctz	central tectal zone;
cVmx	canal for the maxillary ramus of the trigeminal nerve;
cVI	canal for the abducens nerve;
cVII	canal for the main trunk of the facial nerve;
cVIIapal	canal for the anterior ramule of the palatine ramus of the facial nerve;
cVIIpal	canal for the palatine ramus of the facial nerve;
cVIIppal	canal for the posterior ramule of the palatine ramus of the facial nerve;
cIX	canal for the glossopharyngeus nerve;
cX+lcX	canal for the vagus nerve and its lateralis component;
dd	dermal denticle;
dor	dorsal otic ridge;
dp	dorsal part of the postorbital wall;
dppr	dorsal paroccipital process;
d.r.	diencephalic region;
ds	dorsum sellae;
end	endolymphatic duct;
endc	endocranial cavity;
eps	efferent pseudobranchial artery;
fam	fossa for the adductor musculature of the mandible;
flcX	foramen for the lateralis component of the vagus nerve;
fm	foramen magnum;
fmop	foramen situated in the medial otic process;
folfcap	floor of the olfactory capsule;
fot	foramen for the olfactory tract;
fp	point of fusion of the parachordals;
fpcv	foramen for the posterior cerebral vein;
fpitv	foramen for the pituitary vein;
fsoph	foramen for the superficial ophthalmic complex;
fv	facial vein;
fII	foramen for the optic nerve;
fIII	foramen for the oculomotor nerve;
fIV	foramen for the trochlear nerve;
fVmd	foramen for the mandibular ramus of the trigeminal nerve in the mandible;
fVmx	foramen for the maxillary ramus of the trigeminal nerve;
fVI	foramen for the abducens nerve;
fVII	foramen for the main trunk of the facial nerve;
fVIIpal	foramen for the palatine ramus of facial nerve;
fIX	foramen for the glossopharyngeus nerve;
fX	foramen for the vagus nerve;
gas	Gasser's ganglion;
ghr	groove for the mandibular-hyoidean ramus of the facial nerve;
gjv	groove for the jugular vein;
ha	horizontal ampulla;
hsc	horizontal semicircular canal;
hyp	hypophysis;
hypch	hypophyseal chamber;
ic	intertectal commissure;
il	inner layer of the endocranium;
ilh	inferior lobe of the hypothalamus;
imz	intermuscular elevated cranial zone;
ing	internasal groove;
inp	internasal plate;
inw	internasal wall;
is	isthmus rhombencephali;
jc	jugular canal;
jv	jugular vein;
lap	lateral articular process of the mandible;
lcm	lateral crest of the mandible probably supporting tooth whorl;
lcX	lateralis component of the vagus nerve;
ld	lateral depression housing gills and abductor musculature;
lpm	lateral process of the mandible probably supporting tooth whorl;
ls	lateral sulcus;
map	medial articular process of the mandible;
mcv	middle cerebral vein;
med	medulla oblongata;
mi	muscular insertion;
mop	medial otic process;
ntl	nucleus tegmentalis lateralis;
obmc	orbital foramen for the bucco-maxillary complex;
occh	occipital chamber;
occot	occipital cotylus;
occr	occipital crest;
oeps	orbital foramen for the efferent pseudobranchial artery;
ofp	orbital foramen for the ophthalmic profondus ramus of the trigeminal nerve;
ol	outer layer of the endocranium;
olfc	olfactory canal;
olfcap	olfactory capsule;
onc	orbitonasal canal;
oonc	orbital foramen for the orbitonasal canal;
oora	orbital foramen for the orbital artery;
opa	optic retinal artery;
opch	optic chiasm;
optec	optic tectum;
ora	orbital artery;
P-1	first tooth whorl ("vomerine");
P-2	second tooth whorl ("vomerine");
P-4	fourth tooth whorl or "canine" ("vomerine");
P-5	fifth tooth whorl (palatine);
pa	posterior ampulla;

palc	palatine crest;
parc	parachordal cartilage;
pcv	posterior cerebral vein;
pdd	patch of dermal denticles;
pdf	posterior dorsal fontanelle;
pdob	posterior dorsal otic bulges;
pf	preoccipital fossa;
pitv	pituitary vein;
plc	posterior lobe of the corpus cerebelli;
pms	posterior median sulcus;
postc	posterior commissure;
postjc	posterior opening of the jugular canal;
pow	postorbital wall;
pq	palatoquadrate;
pr	ophthalmic profundus ramus of the trigeminal nerve;
prefc	prefacial commissure;
prefp	preorbital foramen for the ophthalmic profundus ramus of the trigeminal nerve;
proo	prootic foramen;
prp	preorbital process;
psc	posterior semicircular canal;
ptf	primary transverse fissure;
ptz	periventricular tectal zone;
pwo	posterior wall of the olfactory capsule;
rX	root of the vagus nerve;
sac	saccular chamber;
sdp	symphysial dentigerous plate;
smc	somatic motor column;
so	spino-occipital nerve;
sof	spino-occipital nerve foramen;
soph	superficial ophthalmic complex;
ss	sinus superior;
ssc	somatic sensory column;
stz	superficial tectal zone;
sups	supraorbital shelf;
teg	tegmentum;
th	thalamus;
tpf	trigemino-pituitary fossa;
tr	transverse dentigerous ridge on the symphysial dental plate;
ur	utricular recess;
vc	cerebellar ventricle;
vbmc	ventral foramen for the bucco-maxillary complex;
veps	ventral foramen for the efferent pseudobranchial artery;
vm	ventricular mesencoelia;
vmc	visceral motor column;
vonc	ventral opening of the orbitonasal canal;
vora	ventral foramen for the orbital artery;
vppr	ventral paroccipital process;
vs	vascular sac;
vsc	visceral sensory column;
vIII	third ventricle;
vIV	fourth ventricle;
II	optic nerve;
III	oculomotor nerve;
IIId	dorsal ramus of the trochlear nerve;
IIIv	ventral ramus of the trochlear nerve;
IV	trochlear nerve;
Vmd	mandibular ramus of the trigeminal nerve;
Vmx	maxillary ramus of the trigeminal nerve;
VI	abducens nerve;
VII	main trunk of the facial nerve;
VIIapal	anterior ramule of the palatine ramus of the facial nerve;
VIIh	hyoidean ramule of the mandibular-hyoidean ramus of the facial nerve;
VIIhym	mandibular-hyoidean ramus of the facial nerve;
VIImd	mandibular ramule of the mandibular-hyoidean ramus of the facial nerve;
VIIpal	palatine ramus of the facial nerve;
VIIppal	posterior ramule of the palatine ramus of the facial nerve;
IX	glossopharyngeus nerve;
X	vagus nerve.

MATERIALS

The specimens under investigation come from the Upper Carboniferous (Pennsylvanian) of Kansas and Oklahoma and are referred to the family Sibyrhynchidae (Chondrichthyes, Iniopterygia). The examined material consists of four three-dimensionally preserved braincases, plus one isolated three-dimensionally preserved symphysial dentigerous plate. In some cases, these neurocrania are articulated with some postcranial elements, teeth and dermal denticles. These elements are preserved in ovoid phosphatic nodules, the size of which varies from 3 to 5 cm in width and height (Fig. 1).

Kansas material

The material from Kansas studied here comprises a total of four specimens belonging to the Kansas University Natural History Museum, Lawrence (KUNHM 22060, KUNHM 21894, KUNHM 56360 and KUNHM 12492).

The nodules were collected in a fish-bearing nodule outcrop, which was first reported and studied by Twenhofel & Dunbar (1914). An extensive paleoecological, stratigraphical and geochemical study of these nodules was later made by Miller & Swineford (1957), and the following information are mainly based on this work.

The nodules crop out approximately 150 km southeast of Kansas City, between the towns of Lawrence and Baldwin, in about 30 different localities. They occur in a thin bed of yellow-gray shale deposited in a near shore environment, probably within shallow marine basins formed in a semitropical and wet area. Stratigraphically, they occur at the limit between the marine Haskell Limestone Member and the overlying Robbins Shale of the Stranger Formation, deposited in brackish water. This sequence is part of the Douglas Group, dated as late Virgilian, Upper Pennsylvanian (305-299 Myr). Similar conditions were present in the black shale, where the first described iniopterygians of the Mecca fauna were found (Zangerl & Richardson 1963).

The matrix of the nodules is mainly composed of apatite and also displays quartz grains and organic matter. The crystalline calcite may fill the endocranial cavity of the specimen, while the prismatic calcified cartilage is calcium phosphate (see below) as in KUNHM 22060.

Beside the chondrichthyan remains, the fossil record is mostly represented by actinopterygian remains and some cephalopods (goniatites, nautiloids, orthocerids), brachiopods (Orbiculoidea d'Orbigny, 1849), arthropods (Idiotheca Girty, 1909), fossil wood and fish coprolites.

KUNHM 22060 (Fig. 1A). This specimen is a complete neurocranium articulated with teeth in natural position, the mandible slightly removed from its original position, part of the branchial apparatus almost in its natural position and some dermal denticles. It has been previously prepared superficially and mechanically, thereby exposing some features, such as the mandible and the anterior part of the braincase.

KUNHM 21894 (Fig. 1B, B'). This specimen is an almost complete neurocranium, only lacking its anterodorsal part, and associated with the pectoral girdle and fin almost in natural position, as well as other postcranial elements, teeth and dermal denticles.

KUNHM 56360 (Fig. 1C, C'). This specimen consists of the mid posterior part of the braincase.

KUNHM 12492 (Fig. 1D-D"). This specimen is an isolated ethmoid plate showing the entire symphysial dentigerous plate.

Oklahoma material

OKM 38 (Fig. 1E, E'). This specimen comes from Oklahoma and was loaned by Dr John Maisey (Curator in charge, American Museum of Natural History, New York). It was collected by Dr Royal Mapes (Geology Department, Ohio University, Athens, Ohio, USA) from the Coffeyville Formation (dated as Pennsylvanian, Missourian, *c.* 307 Myr), at a roadcut in Tulsa County, Oklahoma (Center of NW sec. 2., T. 18 N, R. 12 E, Sapulpa North 7 ½ Quadrangle). Numerous paleoniscoid braincases were also recovered from small nodules at this site.

This specimen is an almost complete braincase lacking the ventral part of the orbit, which has been displaced, however, at some distance in the nodule. It is associated with some elements of the pectoral girdle and fin, teeth and dermal denticles.

Remarks

Only KUNHM 22060 bears the entire internal part of the braincase undoubtedly because of its complete matrix filling. All the other braincases merely show part of the endocranial cavity and skeletal labyrinth, and consequently, they only display the external surface of the neurocranium in the part where the endocranial cavity is not preserved. The different cranial foramina are thus very difficult to locate in this region because there are no structural differences between a real foramen and a small gap in the cartilage. Only the foramina that are observed in relation with their corresponding internal canals are mentioned in the present work. The other ones are speculative and are not described.

All the neurocrania studied in the present work have almost the same proportions and size as the adult specimens studied by Zangerl & Case (1973). Therefore, it is assumed that these are adult individuals.

METHODS

OKM 38 (Fig. 2)

This specimen has been scanned by µCT scan at the University of Texas High-Resolution X-ray CT

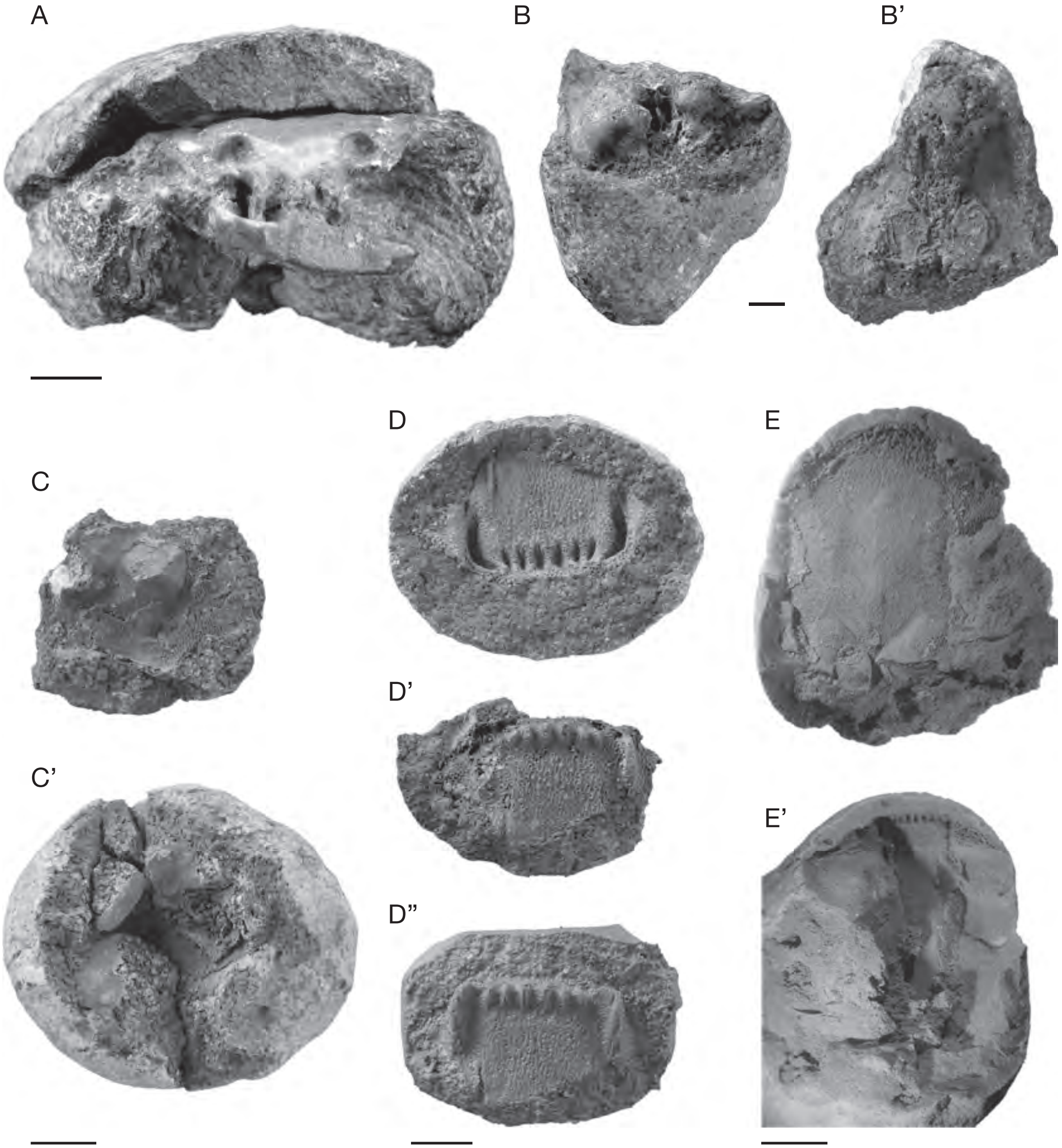

FIG. 1. — Photograph of the different nodules studied in the present work: **A**, KUNHM 22060 in anterior view; **B**, **B'**, KUNHM 21894, part (**B**) and counterpart (**B'**); **C**, **C'**, KUNHM 56360, part (**C**) and counterpart (**C'**); **D**-**D"**, KUNHM 12492, part (**D**), counterpart (**D'**) and silicone cast (**D"**); **E**, **E'**, OKM 38, part (**E**) and counterpart (**E'**). Scale bars: 5 mm.

Facility, Austin. Scan parameters were as follows: 1024 × 1024 16-bit TIFF images. II, 180 kV, 0.12 mA, no filter, air wedge, no offset, slice thickness 2 lines (= 0.04872 mm), S.O.D. 70 mm, 1400 views, 2 samples per view, inter-slice spacing 2 lines (= 0.04872 mm), field of reconstruction 22.8 mm (maximum field of view 23.17 mm), reconstruction offset 8000, reconstruction scale 3200. Acquired with 19 slices per rotation and 15 slices per set. Flash and ring-removal processing done based on correction

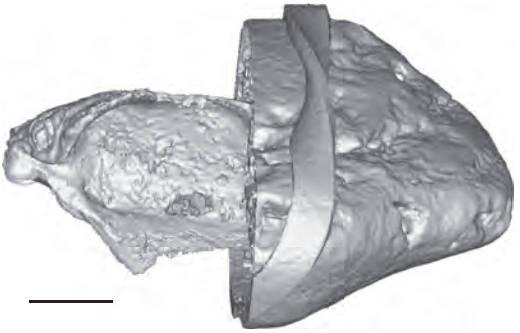

Fig. 2. — Volume and surface rendering generated from XR-μCT scan slices of the specimen OKM 38 partially cleaned virtually, left side. Scale bar: 5 mm.

of raw sinogram data by Alison Mote using IDL routines “RK_SinoDeSpike” and “RK_SinoRingProcSimul,” both with default parameters. Deleted first four duplicate slices of each rotation except for slices 1-4. Rotation correction processing has done using IDL routine “DoRotationCorrection.” Total final slices = 649.

KUNHM 56360
This specimen has been scanned at the University of Poitiers, France by Arnaud Mazurier by means of a Viscom model X8050-16 facility. Scan parameters were as follows: 1004 × 1004 12-bit TIFF images. 125 kV, 0.350 mA, CCD camera, slice thickness 2 lines (= 0.028 mm), 32 integration per projections, 1800/360° projections. The reconstruction was performed with DigiCT v1.15 (Digisens) by Arnaud Mazurier. Total final slices = 984 with the format 8-bits, 678 × 678 pixels.

KUNHM 22060 (Fig. 3) and KUNHM 21894
They were imaged using X-ray based synchrotron microtomography (SR-μCT) (Tafforeau *et al.* 2006) on the beamline ID19 of the European Synchrotron Radiation Facility, Grenoble, France, by Paul Tafforeau. Scan parameters were as follows: monochromatic X-ray beam of 60 keV energy. The detector was a FReLoN (Fast Readout Low Noise) (Labiche *et al.* 2007) CCD camera coupled with an optical magnification system, yielding an isotropic pixel size of 30.3 μm. 1200/180° projections with 0.4 s of exposure time. Data were reconstructed using the filtered backprojection algorithm (PyHST software, ESRF) by Paul Tafforeau. Reconstructed slices were converted from 32 bits to 8 bits in order to reduce the data size for 3D processing.

Because the posterior part of the orbit of KUNHM 22060 concentrates many important features, such as the fossilized brain and different foramina, it was also imaged using quantitative phase tomography (holotomography) (Cloetens *et al.* 1999; Pradel *et al.* 2009), which is more powerful than a synchrotron acquisition (Fig. 3B). Scan parameters were as follow: monochromatic X-ray beam of 60 keV energy, isotropic pixel size of 14.92 μm. 1500/180° projections with 0.3 s of exposure time. Two holotomographic acquisitions were necessary to cover the whole structure. The propagation distances were 50 mm (absorption), 400 mm and 950 mm, respectively. After phase retrieval, the slices were duplicated and reconstructed using the filtered backprojection algorithm, then converted into 8-bit TIFF files. Finally, the two holotomographic scans were combined to one volume where the common slices were removed.

KUNHM 12492
This specimen was studied by means of manual preparation and silicone cast (Fig. 1D”).

Segmentation and 3D rendering were performed with MIMICS® software (Materialise® Inc. NV, Leuven, Belgium) by myself. MIMICS® (Materialise’s Interactive Medical Image Control System) is of great interest to deal with such a large amount of data, as those generated from μCT scan. The MIMICS® 64 bits version runs on a Dell 690 Windows XP 64 workstation with 16 GB of RAM.

MIMICS® allows different types of measurement and segmentation to be performed. Regions of interest can be selected with accuracy using threshold method to create segmentation masks. With this method, selections depend on a range of defined grey values, and not on manual outlining operations. 3D models have been calculated from segmentation masks and combined through Boolean operations.

Many of the illustrations in this work represent views captured from MIMICS® surface renderings.

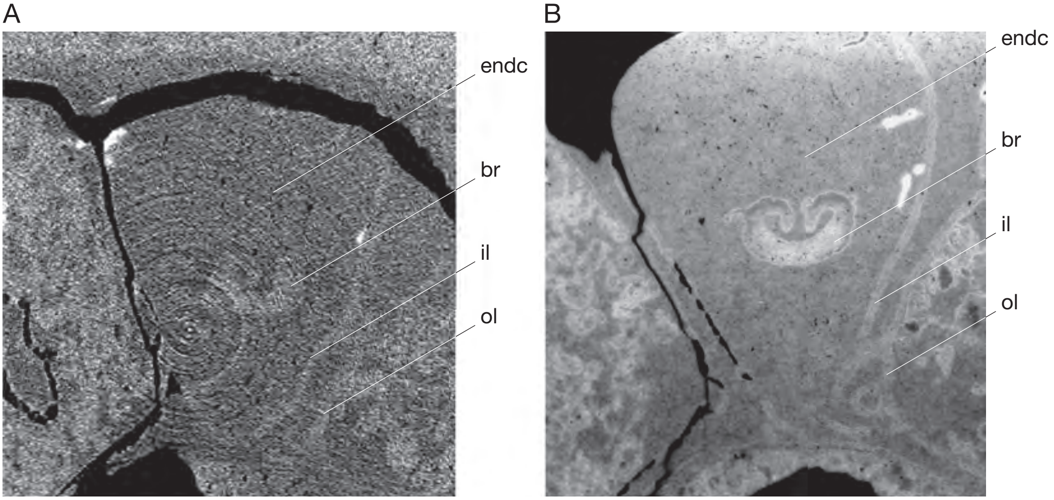

FIG. 3. — Transverse microtomographic slices of KUNHM 22060 through the posterior end of the optic nerve foramen showing the difference of contrast and precision between a Synchrotron Radiation microtomographic (absorption contrast) acquisition (**A**) and a Synchrotron Radiation holotomographic (phase contrast) acquisition (**B**). Abbreviations: see Materials and methods.

Adobe Photoshop CS3 extended v.10.0.1 was used to increase the contrast of the MIMICS® surface renderings and to make the final illustration.

The operation of virtual crushing made on the contour-based rendering of KUNHM 22060 was performed with Autodesk Maya 2008 x64 software.

Microprobe analysis was performed to reveal the mineral composition of the fossilized brain, the preserved skull and the surrounding matrix. This provides information that help for understand the mode of fossilization. It was operated by Omar Boudouma at the Electron Microscopy Service of the UFR 928, University Paris 6, by using a field effect gun (FEG) scanning electron microscope ZEISS SUPRA55VP, with a nominal resolution of 1.0 nm (at 15 kV and 2 mm distance). The analyzer was a detector SDD SAHARA of PGT including the SPIRIT software.

TAPHONOMY

The remarkable abundance and exceptional three-dimensional preservation of the fish remains from Kansas could be explained by their deposition in a quiet anoxic environment, without strong currents nor overturning condition.

The palaeoniscoid braincases found in these concretions have been extensively studied by Poplin (1974) and Hamel & Poplin (2008). According to Poplin (1986), the fact that the actinopterygian remains are almost exclusively isolated braincases, suggests that the latter are the result of chondrichthyan regurgitation. It is also possible that, previous to burial, the endocrania resulting from scattered carcasses were "sorted" by currents. However the presence of the phosphatic fossilized brain in one specimen (KUNHM 22060) (Pradel *et al.* 2009) and the fact that several nodules contain, in addition to the neurocranium, some teeth and postcranial elements almost in natural position, suggests that the diagenesis occured immediately after the death of the animal.

The microprobe analysis was performed where the mineralized brain material reaches the surface of KUNHM 22060: the right optic nerve foramen, where the natural cast of the orbital cavity was separated from the rest of the nodule (Fig. 4A, B), and at the level of an almost transverse break through the nodule, which shows the calcite filling of the brain cavity and the rearmost end of the presumably preserved spinal cord. In both cases, they reveal for the brain a crystalline structure that radically differs from that of the surrounding calcite (almost pure calcium carbonate), and proved to be composed of calcium phosphate (Fig. 4C-E).

Among the soft tissues that were present in the head during life, only the brain is fossilized. The eyes and muscles, which are external to the skull, are not preserved. Moreover, the optic nerve, which is preserved inside the endocranial cavity, is completely absent after reaching the surface of its foramen. This suggests that the brain was preserved because of a locally confined environment that was favourable to rapid phosphatization (Briggs & Kear 1993; Briggs *et al.* 1993), such as the endocranial cavity of the braincase. This almost completely closed space may have generated an anoxic environment where authigenic mineralization was possible. Such an anoxic environment, plus a possible increase of CO_2 and volatile fatty acids (present in the brain) generate a fall in pH that would have shifted the equilibrium of precipitation in favour of calcium phosphate rather than calcium carbonate (Wilby 1993; Briggs *et al.* 1993; Trinajstic *et al.* 2007). This required a high concentration of phosphorus inside the endocranial cavity, and the brain itself contains much phosphorus, because the latter participates to the cellular metabolism of the brain. According to Briggs (2003), a microbial film may concentrate and protect the phosphorus. Nevertheless, there is no evidence of preserved microbes inside the iniopterygian specimen here. This suggests that if authigenic mineralization has occured, the mineral precipitation is microbially induced rather than the result of autolithification of the microbes proper (Briggs 2003).

Another mode of soft-tissue fossilization is permineralization, which is the result of early infiltration and permeation of tissues by mineral-charged water (Briggs 2003). The organic material is subsequently replaced by mineral. The Kansas nodules studied here occur in a thin bed of yellow-gray shale deposited in a near shore environment, probably within shallow marine basins formed in a semitropical and wet area. Such an environment allows a high concentration of phosphorus. Nevertheless, permineralization of soft animal tissues is rare (Briggs 2003) and most permineralizations involve silica (Voigt 1988; Wuttke 1992).

Consequently, it is more probable that the brain underwent a microbially induced phosphatization shortly after the beginning of decay (the environment being probably saturated with calcium phosphate, hence the concretions). It could have been rapidly surrounded by diagenetic calcite after the phosphatization. Some shrinking of the tissues may have occurred before phosphatization (Briggs 2003), which is suggested by the position of the cerebellum far anterior to the otic capsule. Nevertheless, the optic nerve reaches its foramen in a natural position, like the other nerves, which emerge from the brain and reach perfectly to their respective foramina. Consequently, the shrinking of the brain may not have been very significant.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Order INIOPTERYGIA Zangerl & Case, 1973

Family SIBYRHYNCHIDAE Zangerl & Case, 1973

TYPE GENUS. — *Sibyrhynchus* Zangerl & Case, 1973.

INCLUDED GENERA. — *Sibyrhynchus*, *Iniopera* Zangerl & Case, 1973, *Inioxyele* Zangerl & Case, 1973.

ETYMOLOGY. — From sibyne (= hunting spear) and rhynchos (= snout).

DIAGNOSIS. — The Sibyrhynchidae are holostylic Iniopterygia in which the labio-lingual tooth rows (tooth families) are basally fused to form tooth whorls of different size and shape.

Sibyrhynchidae gen. et sp. indet.

MATERIAL EXAMINED. — KUNHM 22060, KUNHM 21894, KUNHM 56360, KUNHM 12492 and OKM 38.

REMARKS

The braincases described here (KUNHM 22060, KUNHM 21894, KUNHM 56360, KUNHM 12492 and OKM 38) are very close to those in all three genera described by Zangerl & Case (1973) (see discussions). Nevertheless, the diagnosis of the latter is incomplete principally because of the flatness and the split of the specimens. It is therefore difficult to assign the new specimens described here to known genera with accuracy. The teeth, the overall morphology and the different structures

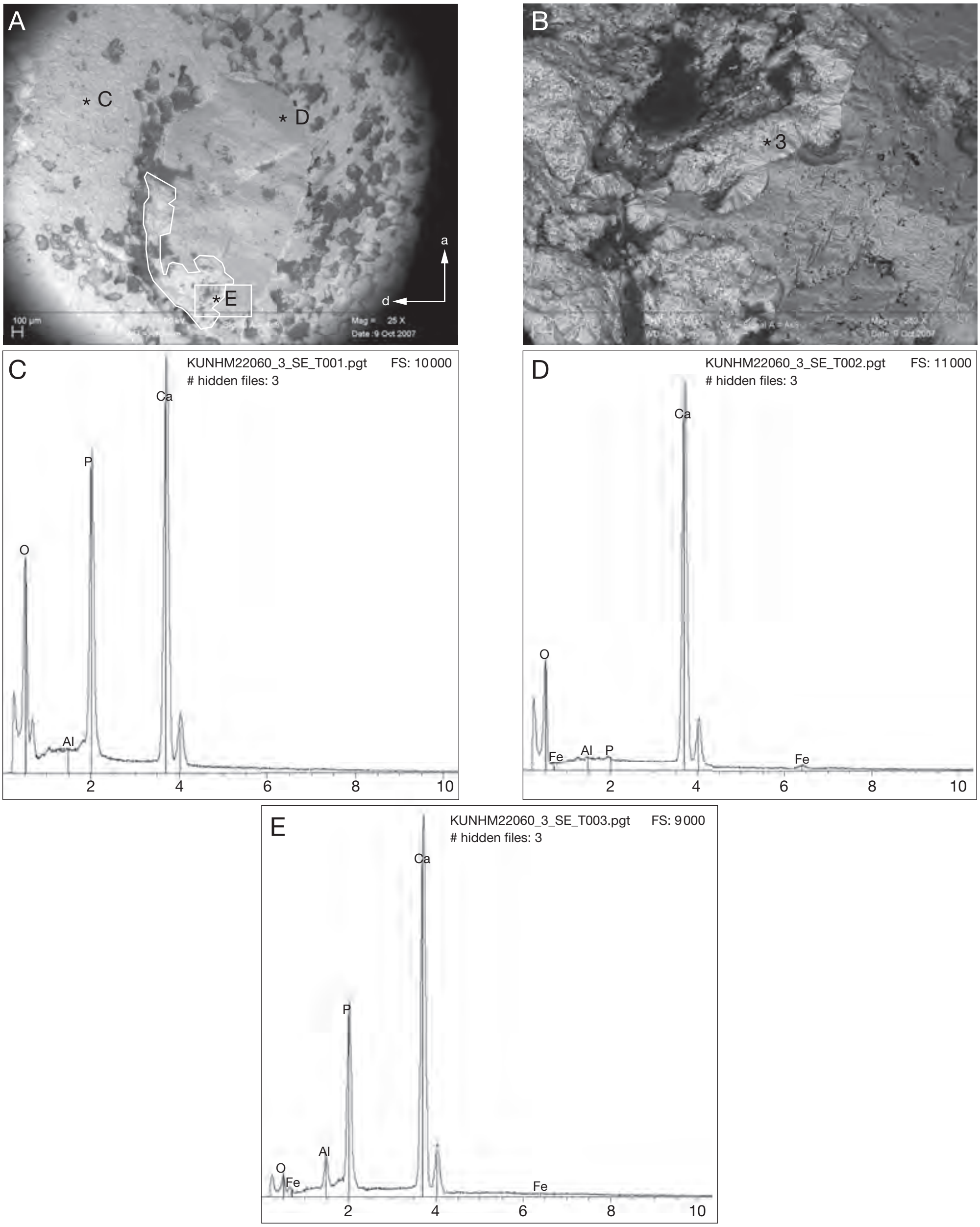

FIG. 4. — SEM micrograph and microprobe analyses of the surface of the calcite-filled right optic foramen of KUNHM 22060; the asterisks in A, B indicate the location of the microprobes analyses corresponding to the respective diagrams in C-E: **A**, general view of the optic foramen and surrounding prismatic calcified cartilage; arrows point anteriorly (a) and dorsally (d); the area delimited by a bold line corresponds to the emergence of the preserved optic nerve; calcium phosphate dominates in the light grey areas and calcium carbonate dominates in the dark grey areas; **B**, detail of the area framed in A, showing the finely crystalline structure of calcium phosphate of the preserved optic nerve; **C**-**E**, microprobe analyses for P, O, Al, Fe, and Ca at the level of the optic foramen and optic nerve of KUNHM 22060 (C-E in A, B); **C**, external surface of the prismatic calcified cartilage (mostly calcium phosphate); **D**, surface of the calcite filling the brain cavity and cranial nerve canals (calcium carbonate); **E**, surface of the emerging preserved optic nerve (mostly calcium phosphate with traces of Al and Fe).

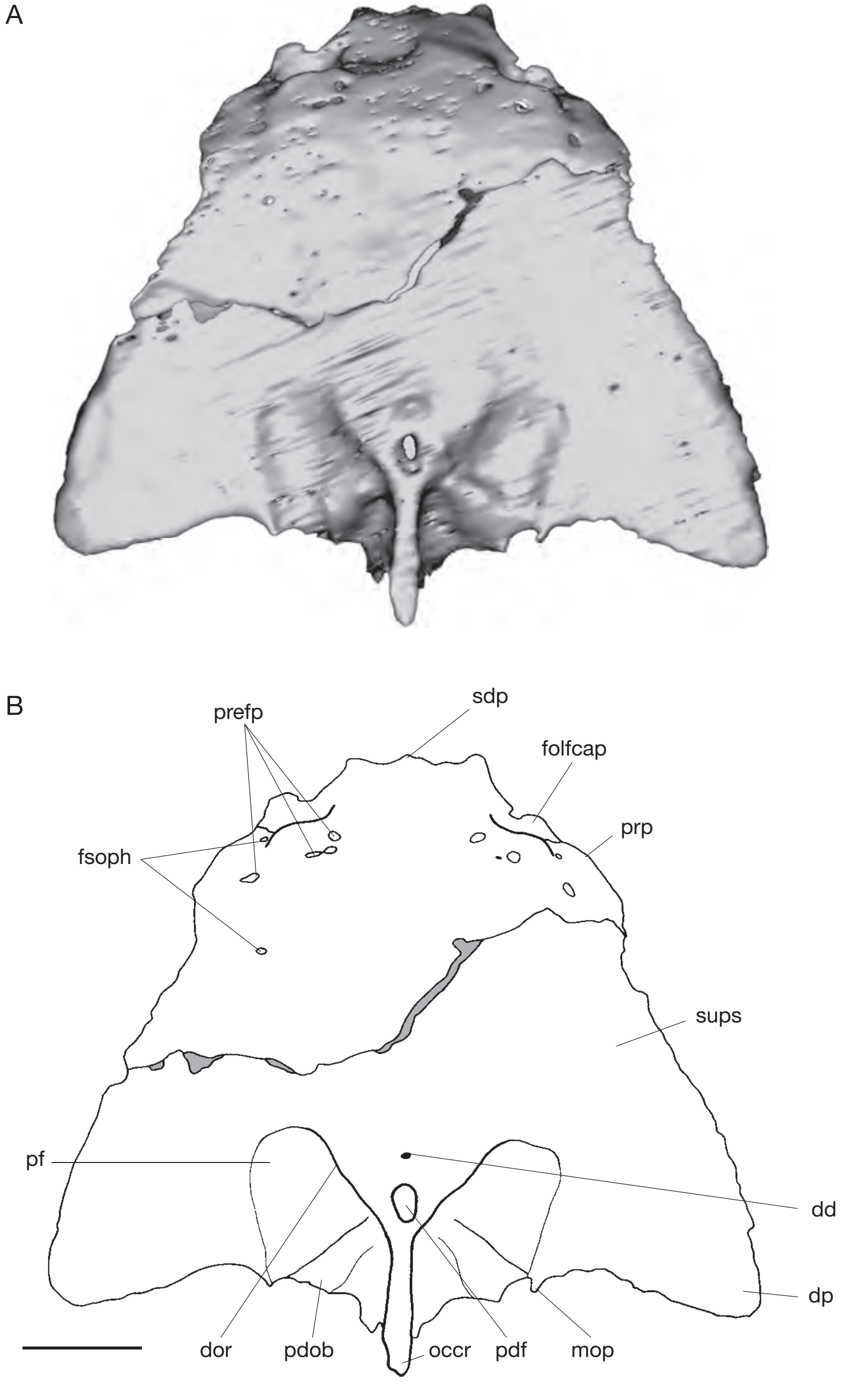

FIG. 5. — Dorsal view of the braincase of KUNHM 22060: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

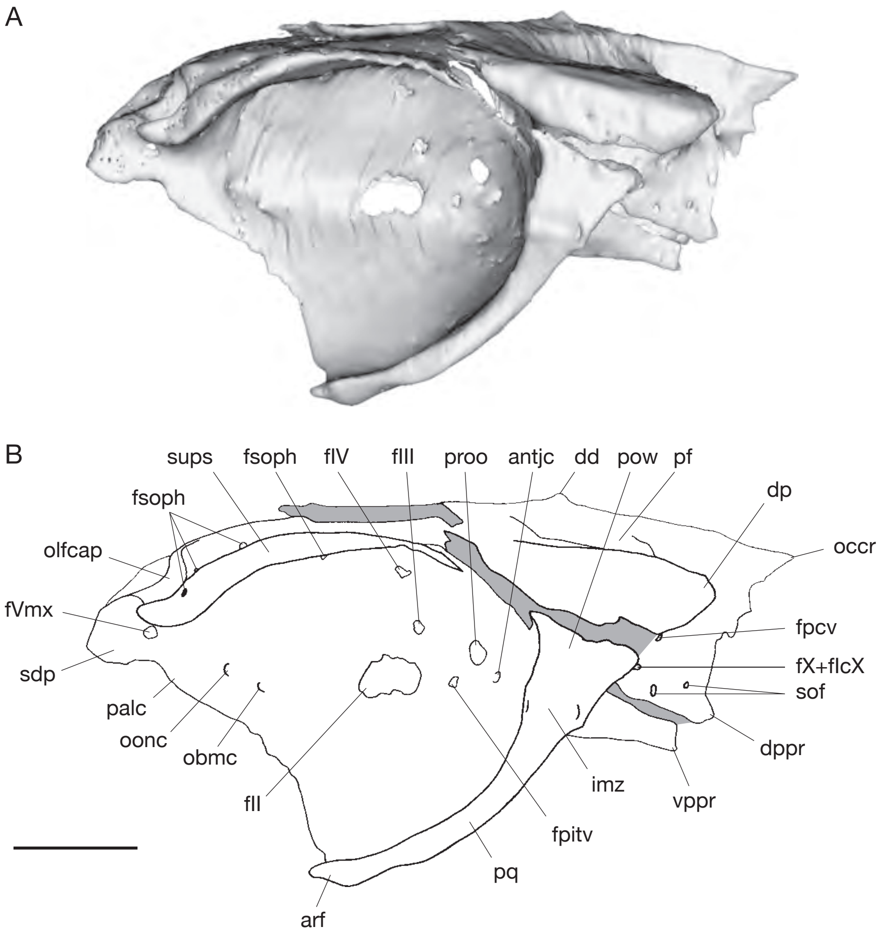

FIG. 6. — Lateral view of the braincase of KUNHM 22060, left side: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

of the neurocranium are smilar in all these new specimens. They are thus considered as belonging to the same genus.

DESCRIPTION OF THE BRAINCASES

GENERAL FEATURES

The five neurocrania studied here are not complete. The most complete one is KUNHM 22060 (Figs 5-13), it will be described in more detail in the present work. Nevertheless, the other specimens provide some supplementary data missing in KUNHM 22060.

KUNHM 22060 (Fig. 5) and KUNHM 21894 (Fig. 14A) show in dorsal view the same broad, delta-shaped outline, with the larger part in the posterior end of the braincase.

They have very large orbits, bordered posteriorly and ventrally by an expanded postorbital wall confluent with the supraorbital shelf dorsally and a large suborbital shelf mainly formed by the palatoquadrate (pow, sups, pq, Figs 6; 14B; 16). Despite the large orbits, there is no interorbital septum and the endocranial cavity extends between the orbits (Figs 8; 29; 30), suggesting that the neurocranium is platybasic (*sensu* Maisey 2007). In the posterior part of the orbit are gathered various foramina for the blood vessels and cranial nerves (Figs 12; 13).

The otic and occipital regions are both short, as in the symmoriiforms elasmobranchs and *Pucapampella* Janvier & Suarez-Riglos, 1986 (Zangerl & Case 1976; Coates & Sequeira 1998; Maisey & Anderson 2001; Maisey 2007).

Deep postorbital depressions flank the ventral part of the occipital region (ld, Fig. 10). Dorsomedial to these depressions are the otic capsules. There is no persistent otico-occipital fissure that separates the otic region from the occipital arch.

Anterior to the narrow ventral occipital region, the outline of the ventral part of the braincase is parallel-sided, as far as an anterior rectangular cartilage plate (Figs 7; 17). Contrary to elasmobranchs, the floor of the basicranium below the otic capsules is not formed by the hypotic lamina. The ventral surface of the braincase is flat and does not display any indication of the basal angle retained in some recent adult elasmobranchs.

ETHMOID REGION AND SYMPHYSIAL DENTIGEROUS PLATE

Nasal region

The ethmoid region includes the part of the braincase located anterior to the orbit and surrounding the nasal capsules. This region is well preserved in OKM 38 and KUNHM 22060 although the former lacks its right nasal capsule (Fig. 19) and the latter a small portion of its dorsal part between the two nasal capsules (Fig. 11). In KUNHM 21894, the anterodorsal part of the braincase is not preserved (Fig. 14A). The entire ethmoid region of KUNHM 56360 is lacking.

In the specimens described here, the ethmoid region is broad but very short. The ventral internasal plate does not merge anteriorly with a rostral process (Figs 5; 15; inp, Figs 7; 17) and there is no evidence of a precerebral fontanelle at the anterior end of the neurocranium. In addition, there is no evidence of a separate pineal opening, and the endocranial cavity is not opened anteriorly. There is also no evidence of a ventral ethmoidal keel.

There is no septum between the nasal capsules and the olfactory capsules are well apart. This indicates a broad internasal wall (inw, Figs 11; 19), as in many other Paleozoic chondrichthyans (e.g., *Stethacanthus altonensis* St John & Worthen, 1875, *S.* cf. *S. productus* Newberry, 1897, *Cobelodus aculeatus* Cope, 1894 and *Akmonistion zangerli* Coates & Sequeira, 2001 [Lund 1974: fig. 3; 1985: fig. 1; Zangerl & Case 1976: figs 2, 3, 7; Coates & Sequeira 1998: fig. 5]).

The nasal capsules are well preserved in KUNHM 22060 and OKM 38, oval in shape, and with well marked borders (olfcap, Figs 11; 19). The olfactory canals open posteromedially in the posterior wall of the nasal capsule (fot, pwo, Figs 8; 11; 19). The nasal capsules are also pierced by several foramina. One of them is situated dorsal to the foramen for the olfactory tract and is connected by canals to a set of dorsal and orbital foramina (prefp, ofp, cpr, Figs 5; 7-9; 11; 15; 16; 19). These foramina were probably for the profundus ramus of the trigeminal nerve. OKM 38 displays other foramina in the nasal region, which were probably also for the branches of the profundus ramus of the trigeminal nerve.

The olfactory chambers exhibit a complete cartilaginous floor (folfcap, Fig. 5), possibly formed from the cornua trabecularum that are trabeculae-derived embryonic structures (De Beer 1937). The incurrent and excurrent narial openings must have been situated in the uncalcified or non-chondrified portion of the capsule and were probably directed frontally, contrary to most other chondrichthyans. There is no indication of basal communicating canals.

In frontal view, between the nasal capsules, a V-shaped groove, only observable in OKM 38 (ing, Fig. 19), probably marks the boundary between the internasal wall and the dorsal surface of the braincase. Two symmetrical large foramina seem to be present between this groove, which is not preserved in KUNHM 22060, and the dorsal limit of the symphysial dentigerous plate (see below) (fVmx, Figs 11; 19). Each foramen is connected by canals to a foramen situated laterally to the symphysial dentigerous plate and above the palatine crest (see below) (fVmx, cVmx, Figs 6; 8; 9). All these foramina are thus located near the teeth and may have given passage to maxillary ramules of the trigeminal nerve.

The nasal capsules are bordered ventrolaterally by a preorbital process that projects backward and laterally into the supraorbital shelf (prp, sups, Figs 7; 11; 19). The preorbital process meets the upper part of the symphysial dentigerous plate

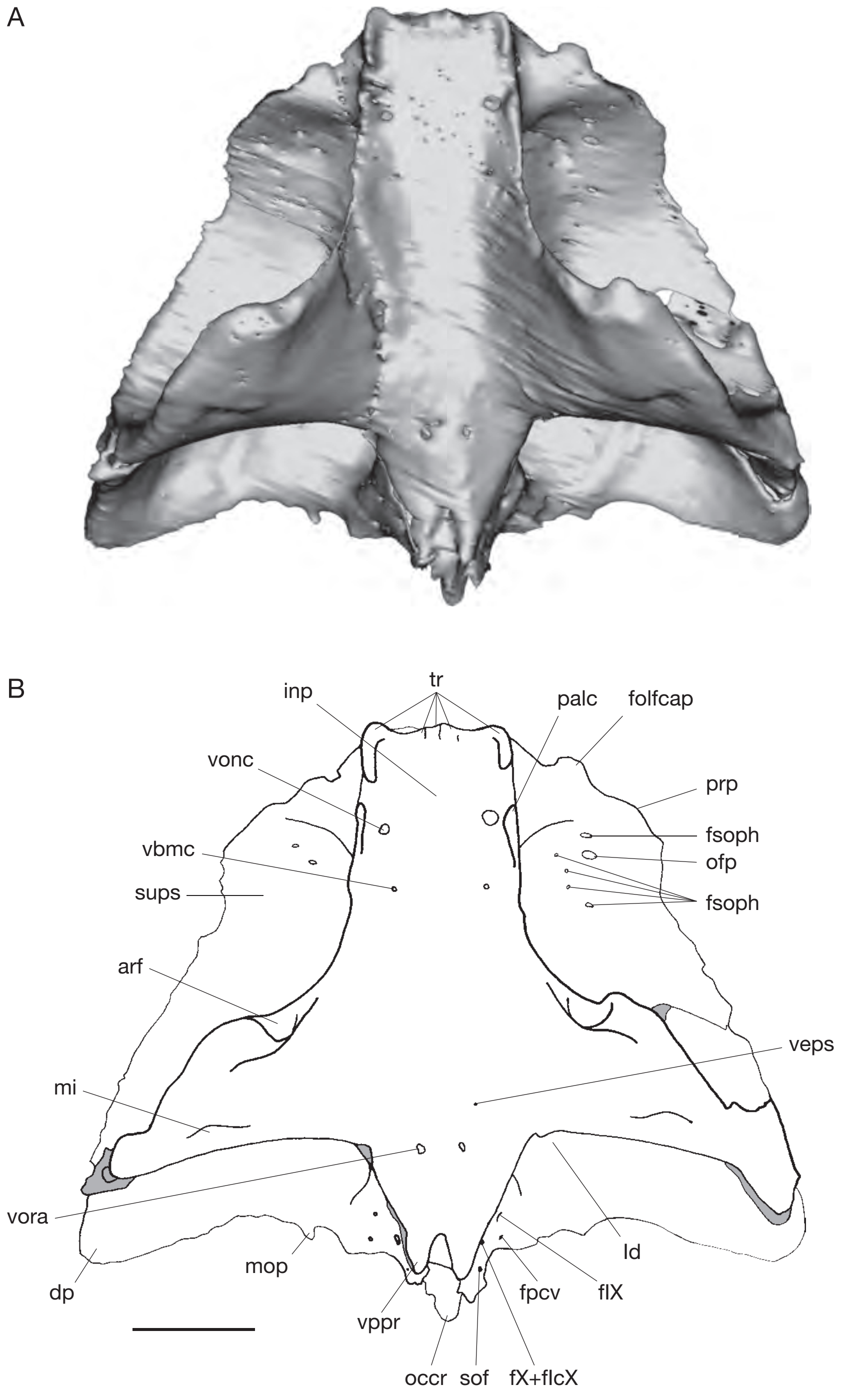

Fig. 7. — Ventral view of the braincase of KUNHM 22060: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

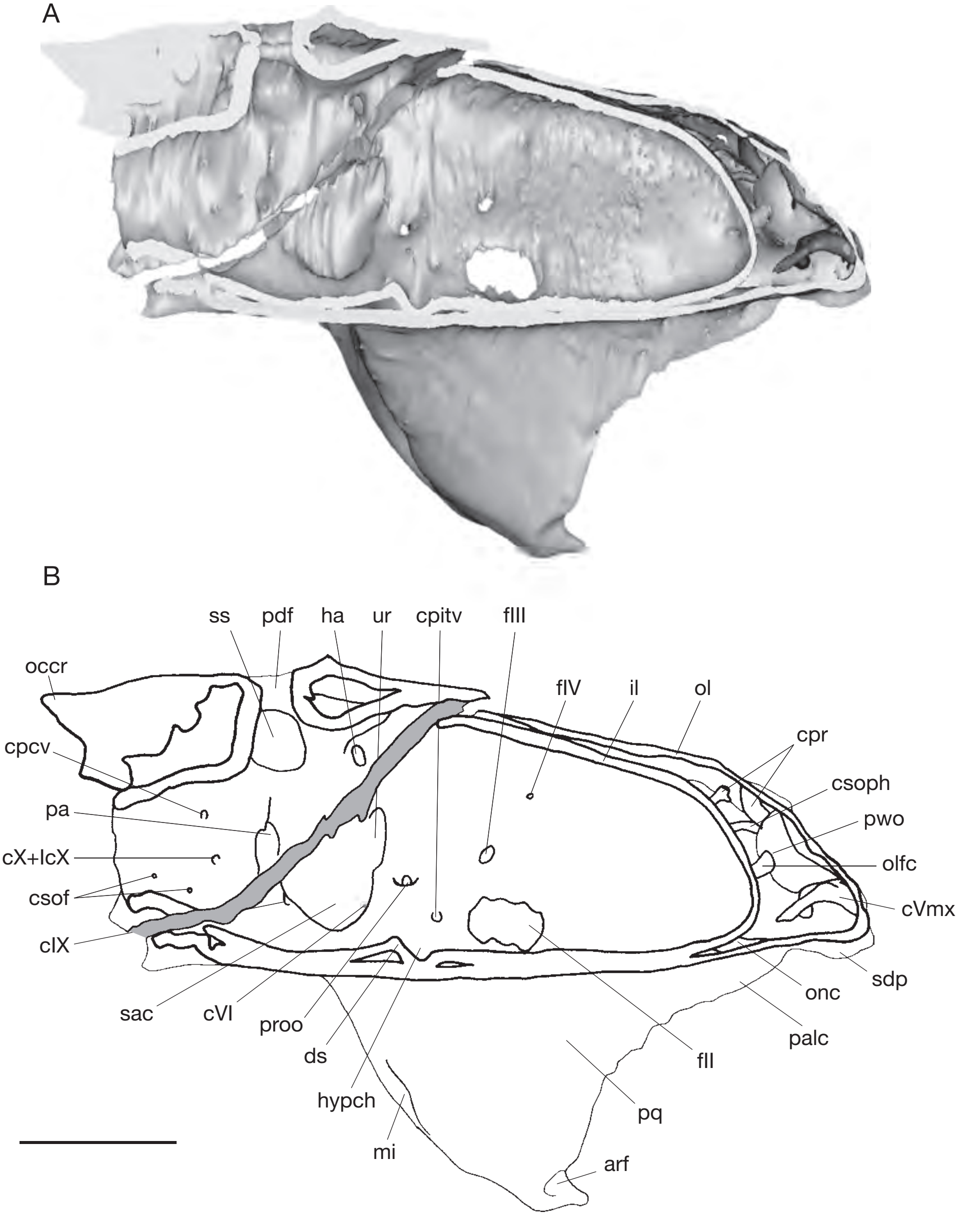

FIG. 8. — Medial view of the braincase of KUNHM 22060, left side: **A**, sagittal section of surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

ventromedially to the nasal capsules at the level of their medial wall.

Lateral to the olfactory capsules, two foramina for the superficial ophthalmic complex reach the preorbital process (fsoph, csoph, Figs 5; 8; 9; 11; 15; 19).

At the anteroventral extremity of the orbit is a foramen (oonc, Figs 6; 16), which may have housed

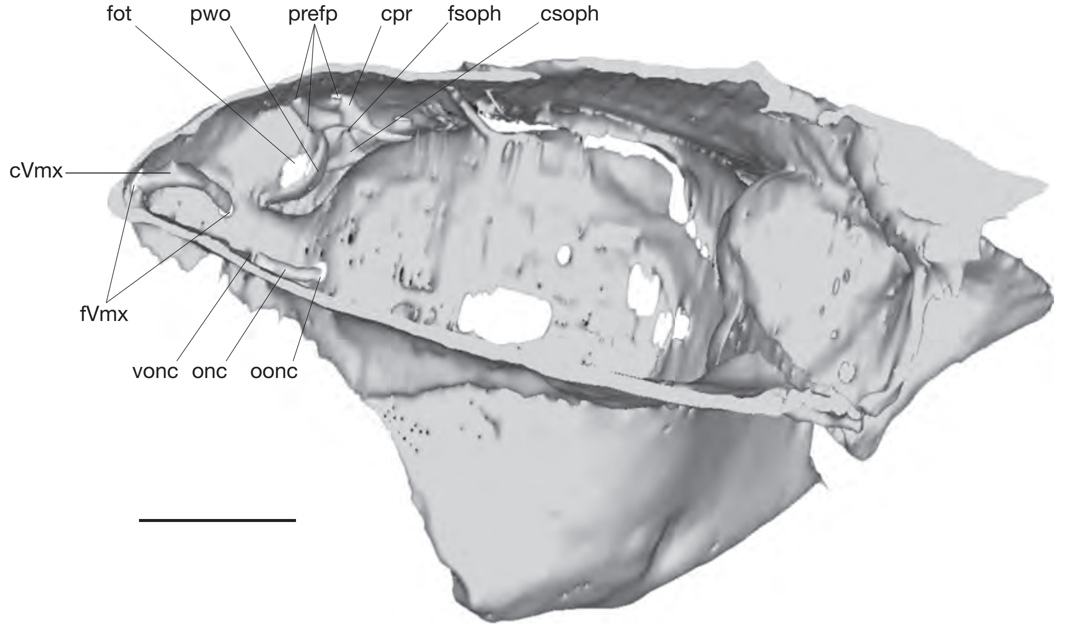

FIG. 9. — Oblique medial view of the surface rendering generated from Synchrotron Radiation microtomographic slices of the outer layer of the braincase of KUNHM 22060 showing the different canals inside the ethmoid region, right side. Abbreviations: see Materials and methods. Scale bar: 5 mm.

the facial vein (an anterior prolongation of the jugular vein) (fv, Fig. 21), since the orbital opening of the orbitonasal canal of chondrichthyans is commonly situated in this region. The orbitonasal canal runs forward obliquely through the neurocranium (onc, Figs 8; 9) and its ventral exit reaches the lateral border of the internasal plate medially to the nasal capsules (vonc, Figs 7; 17). The foramina located immediately posterior to the orbital and ventral foramina of the orbitonasal canal probably represent the exit of a canal through which the bucco-maxillary complex passed together with the buccal and possibly the palatine ramus of the facial nerve (obmc, Figs 6; 16; see below). Another foramen for the maxillary ramus of the trigeminal nerve is situated ventral to the nasal capsules (fVmx, Fig. 6; see below).

Symphysial dentigerous plate

The neurocranium ends anteriorly with a steep rectangular cartilage plate bearing a parallel series of grooves and ridges, which have an anteroposteriorly elongated axis. This plate is continuous ventrally with the internasal plate (inp, Figs 7; 17) and dorsally with the internasal wall (inw, Figs 11; 19). It is marked ventrally by a transverse ridge from which arises the base of the dental ridges (Fig. 17). It is also marked frontally by a horizontal V-shaped groove (ing, Fig. 19). The palatoquadrates are fused to the neurocranium in the iniopterygians studied here (see below) and are separated from each other by the broad internasal plate. The anterior end of the presumed palatoquadrates forms a crest marking of the anteroventral margin of the orbits (palc, Figs 7; 11; 17; 19). The crest supports lateral tooth whorls (see below).

The symphysial dentigerous plate (sdp, Figs 17; 19) displays three pairs of central ridges plus one pair of lateral ridges (tr, Figs 7; 17; 19). The two lateral, medially concave ridges are much larger than the six central ones, in which the two medialmost ridges are much larger than the others.

KUNHM 22060 shows the natural association between the teeth and these ridges (Fig. 32). Each

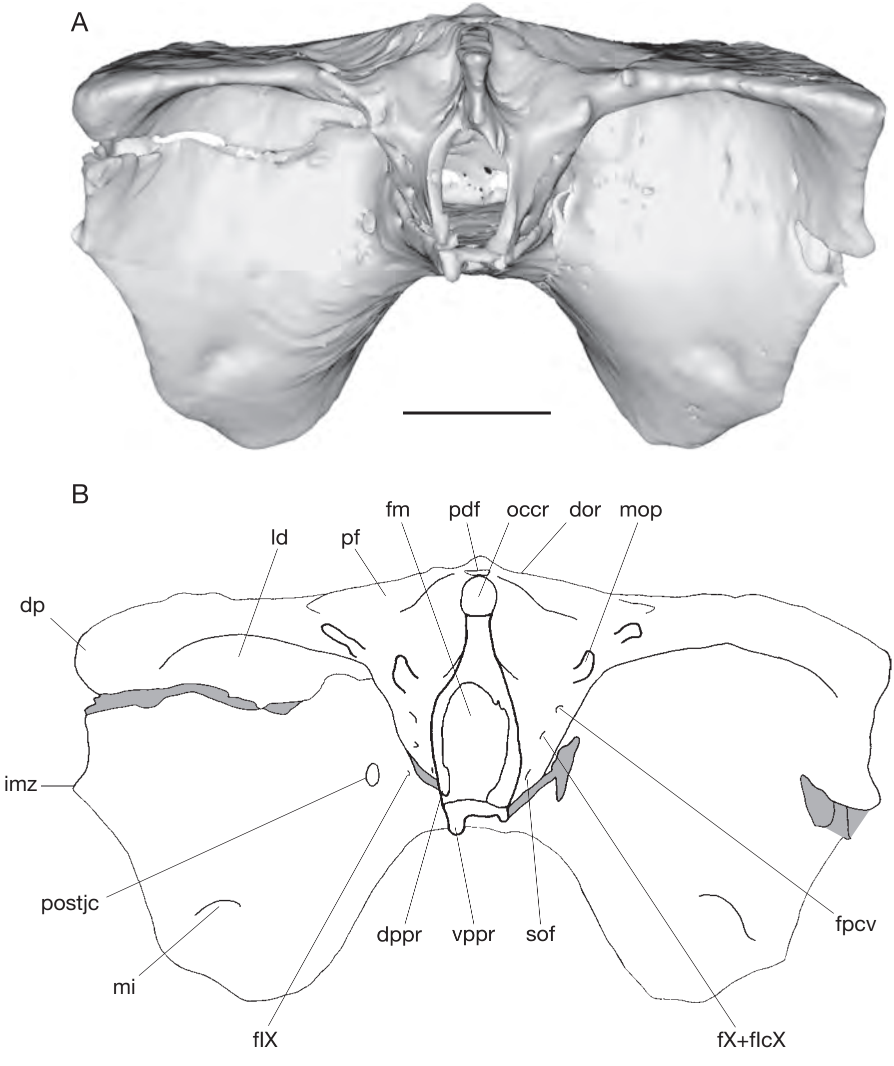

FIG. 10. — Posterior view of the braincase of KUNHM 22060: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

ridge supports a tooth whorl, which differs from other ones in the shape of the whole structure, the size and number of teeth, according to their labiolingual position into the mouth (see below for the description of the teeth and dermal denticles). Consequently, the dental arcade is continuous despite the absence of palatoquadrate symphysis.

ORBITO-TEMPORAL REGION

Orbit

The orbits of the iniopterygians described here are remarkably large and represent half the length of the entire braincase (Figs 6; 14B; 16). They are almost circular in shape in lateral view and are separated by a comparatively large cranial cavity.

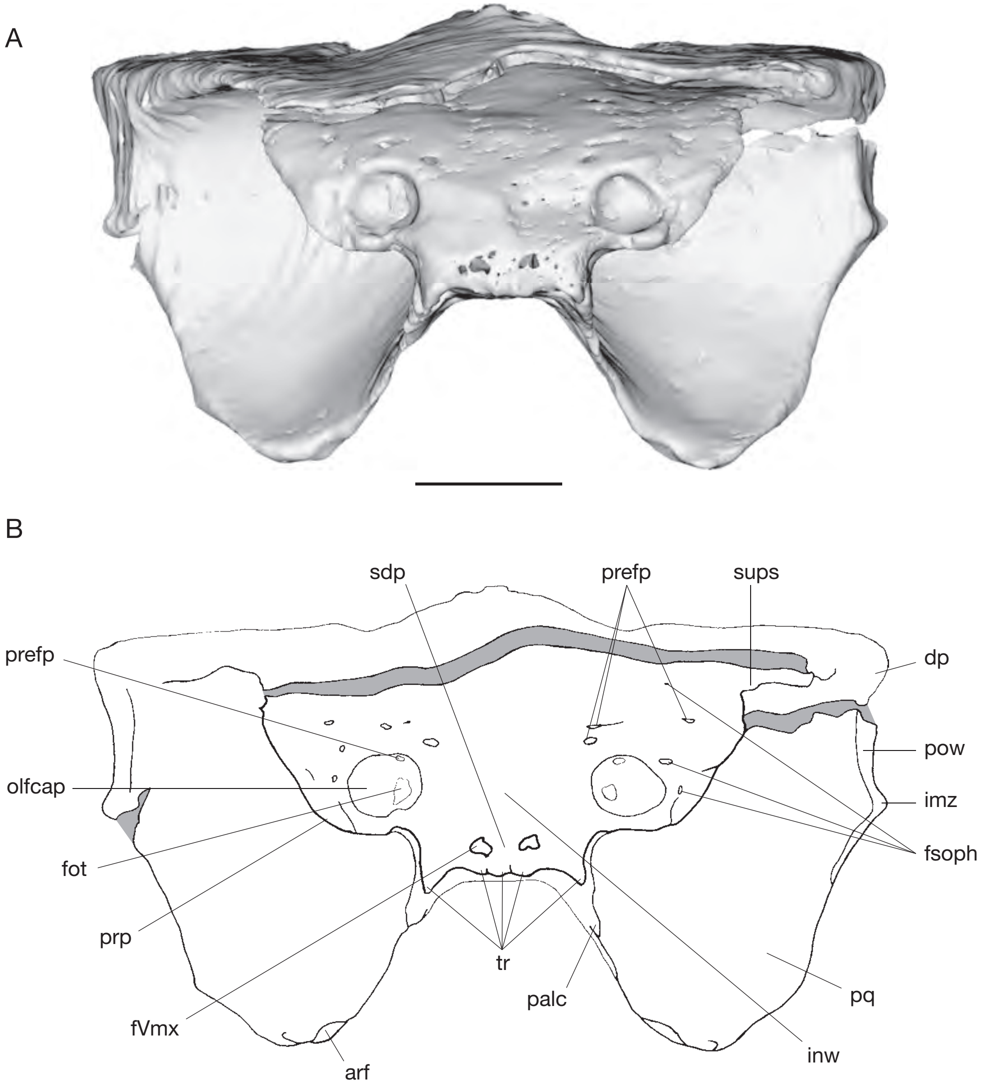

FIG. 11. — Anterior view of the braincase of KUNHM 22060: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

There is no evidence of any ring of sclerotic cartilage or any ring of numerous small presumed bony plates. There is also no evidence for an optic pedicel attachment in the orbit.

Supraorbital shelf

The orbital cavity is delimited dorsally by a very broad supraorbital shelf (sups, Figs 5-7; 11; 14-17; 19). A series of foramina is present all along the dorsal margin of the orbit (fsoph, Figs 5-7; 11-13; 15-17; 20). In modern elasmobranchs, the limit between the embryonic supraorbital cartilage and the orbital cartilage is marked by several foramina in similar position (De Beer 1937). These are for the ascending branches of the superficial ophthalmic complex (supplying the supraorbital sensory canal above the braincase). This nerve complex includes the superficial ophthalmic components of the anterodorsal lateral line (including the superficial ophthalmic and buccal branches of the facial nerve [Northcutt & Bemis 1993]) and trigeminal nerves (Maisey 2005) when these components are combined.

Consequently, this series of foramina present in the specimens described here may be for the superficial ophthalmic complex and may determine the hypothetical original medial boundary of the supraorbital shelf.

In dorsal view, the preorbital process flares laterally, but tapers slightly to a blunt point when it becomes the supraorbital shelf posteriorly (Figs 5; 14A). Then, the supraorbital shelf flares laterally as far as the distal extremity of the postorbital wall. This morphology is comparable to that of *Clodoselache* Dean, 1894 (Maisey 2007) and *Akmonistion* Coates & Sequeira, 2001 (Coates & Sequeira 1998) altough the blunt point between the preorbital process and the supraorbital shelf is situated more posteriorly in the sibyrhynchids.

Palatoquadrate, suborbital shelf and extent of the inferred embryonic polar cartilage

The first description of iniopterygian braincases (Zangerl & Case 1973) showed a holostylic jaw suspension, similar to that of extant holocephalans, where the palatoquadrate is fused to the neurocranium. Further investigations demonstrated that not all iniopterygians possess a holostylic jaw suspension (Stahl 1980). Indeed, only the Sibyrhynchidae possess a palatoquadrate which is fused to the neurocranium.

The two most complete Kansas specimens clearly show a pair of articular facets at the anterior end of what is provisionally referred to as the ventral suborbital shelf (arf, Figs 7; 11; 14B). The skull OKM 38 is broken at the level of the suborbital shelf and the latter, which shows the same articular facets, is found free in the nodule.

KUNHM 22060 shows the mandible (Fig. 31A, B), which has been slightly displaced during the fossilization (see below for the description of the mandible). The mandible possesses at its posterior ends a pair of articular facets complementary to those of the anterior end of the suborbital shelf (am, Fig. 31D). When virtually placed in front of the suborbital shelf, it perfectly articulates with the latter (Fig. 31B).

As seen previously, the anterior end of the neurocranium displays ventrolaterally a pair of pronounced crests (palc, Figs 6; 7; 11; 14B; 16; 17; 19; 32), which form with the symphysial dentigerous plate a continuous dental arcade. The orbital foramen for the orbitonasal canal is located immediately above the lateral crest (oonc, palc, Figs 6; 14B; 16) and the ventral foramen is situated at the medial junction of this crest and the internasal plate (vonc, inp, Figs 7; 17). This recalls the condition present in extant chimaeroids, in which the anterior part of the palatoquadrate also supports palatine teeth and its dorsal margin is approximately indicated by orbitonasal canal foramina (Grogan *et al.* 1999). This relative disposition in the specimens described here between the palatine crest supporting different tooth whorls and the orbitonasal canal, as well as the presence of articular facets at the anterior extremity of the suborbital shelf in perfect position for the articulation with the lower jaw, suggests that the palatoquadrate is fused to the neurocranium, as in extant chimaeroids. So considered, the anteroventral extremity of the suborbital shelf displaying articular facets corresponds to the quadrate process, which was in connection with the mandible, whereas the anterior crest corresponds to the palatine part of the palatoquadrate. The anterior margin of the palatoquadrate may be indicated by the foramen for the maxillary ramus of the trigeminal nerve (fVmx, Fig. 6).

If fusion of the palatoquadrate with the neurocranium in sibyrhynchids was the same as in modern chimaeroids, the palatoquadrate probably extended backward as far as the posterior limit of the orbits, where the orbital foramen for the efferent pseudobranchial artery is situated (oeps, Figs 12; 13; 16). Indeed, the hind limit of the palatoquadrate of extant chimaeroids is marked by the path of the efferent pseudobranchial artery and defined by the fusion of the palatoquadrate to the embryonic basitrabecular cartilage, which in extant chimaeroids is said to be derived from the polar cartilage (Grogan *et al.* 1999). Consequently, the suborbital shelf of the iniopterygian described here is mainly made up by the palatoquadrate, secondarily fused to the neurocranium and is therefore probably of visceral arch origin and not derived from the primary cranial cartilage.

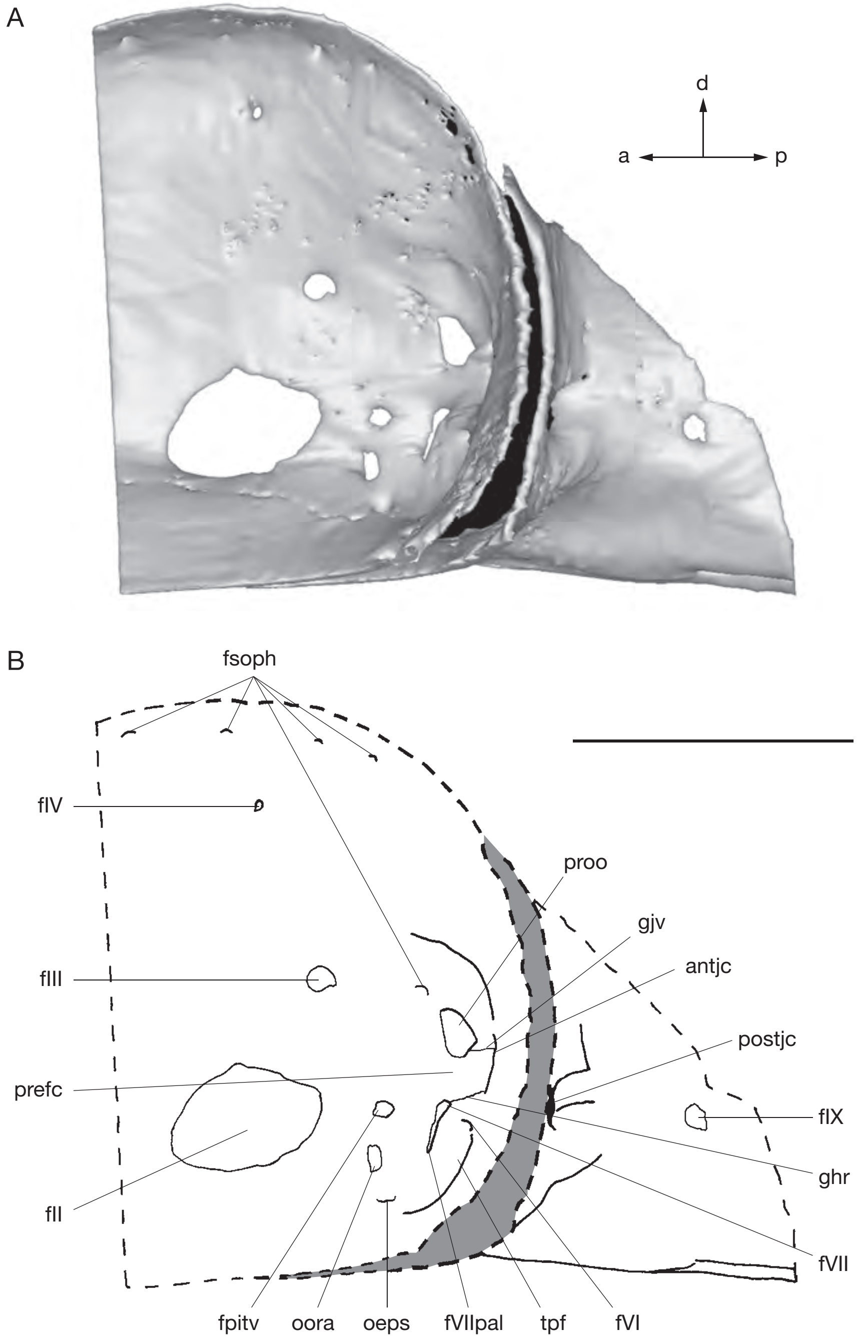

FIG. 12. — Detail of the posterior part of the orbit of KUNHM 22060 in lateral view, left side: **A**, surface rendering generated from Synchrotron Radiation holotomographic slices; **B**, corresponding drawing. Arrows point anteriorly (a), posteriorly (p) and dorsally (d). Abbreviations: see Materials and methods. Scale bar: 5 mm.

In the iniopterygians described here, the foramina for the efferent pseudobranchial artery and the pituitary vein are almost at the same level (oeps, fpitv, Figs 12; 13). This may indicate the presence of very small embryonic polar cartilages, since these two foramina generally mark respectively the anterior and the posterior margin of the embryonic polar cartilage in extant elasmobranchs (De Beer 1931, 1937). In addition, the hypophyseal chamber and dorsum sellae are comparatively small (hypch, ds, Figs 8; 26B-D), also suggestive of small embryonic polar cartilages, since the dorsum sellae arise from the polar cartilages during the chondrichthyan ontogeny.

Nevertheless, in extant chimaeroids, the embryonic polar cartilages elaborate structures, which contribute to the suborbital shelf cartilages, and consequently, they extend from the foramen for the efferent pseudobranchial artery to the anterior foramen of the jugular canal. The suborbital shelf of extant chimaeroids is thereby formed from the fusion of the palatoquadrate, the basitrabecular process and posteriorly the otic process (Grogan *et al.* 1999).

By comparison, the polar cartilages in iniopterygians may also extend from the foramen for the efferent pseudobranchial artery, ventrally, to rather the anterior foramen of the jugular canal situated more posterodorsally than the foramen for the pituitary vein, thereby indicating a more important polar cartilage, which forms a laterally extended basitrabecular process. The latter may have formed with the palatoquadrate the suborbital shelf.

A lateral extension of the basitrabecular cartilage forming thereby a prominent basitrabecular process, which is connected to the palatoquadrate, is inferred in Paleozoic autodiastylic chondrichthyans, such as cochliodonts (Lund & Grogan 1997a).

The orbital artery foramen is present between the efferent pseudobranchial artery foramen and the pituitary vein foramen (oora, oeps, fpitv, Figs 11; 12). This disposition suggests that the orbital artery canal passes through the inferred extent of the embryonic polar cartilage (ora, Fig. 21). In modern holocephalans, the orbital artery canal is situated between the foramen for the efferent pseudobranchial artery and foramen for the pituitary vein, thus running also through the embryonic polar cartilage.

In posterior view, the palatoquadrate displays in its underside a small cavity, which may have housed hyoidean muscles (mi, Fig. 10), as in extant chimaeroids (e.g., the muscle *levator hyoideus*; Didier 1995).

Postorbital wall and jugular canal

A complete and massive postorbital wall, dorsally continuous with the supraorbital shelf and ventrally with the palatoquadrate, is present in the iniopterygians described here (pow, Figs 6; 14B; 16). This postorbital wall is located lateral to the saccular chamber and anterior ampulla. The prootic and facial foramina of the specimens studied here are closely set in front of the postorbital wall (proo, fVII, Figs 11; 12). The posterior end of the supraorbital shelf merges posteriorly with the dorsal part of the postorbital wall (dp, Figs 5-7; 10; 11; 14), which is situated lateral to the otic capsule. The latter is extremely large and projects posterolaterally from the braincase. It surrounds quite a small jugular canal near its medial connection with the braincase. The orbital (anterior) opening of the jugular canal is located behind the prootic foramen at the postorbital wall (antjc, Figs 12; 13). A shallow groove between the prootic foramen and the orbital opening of the jugular canal may have supported the jugular vein (gjv, Figs 12; 13; jv, Fig. 21). The canal bends slightly upwards anteriorly near the lateral wall of the saccular chamber (jc, Figs 27; 28) and opens posteriorly in front of the foramen for the glossopharyngeus nerve (postjc, Figs 10; 11). The posterior end of the jugular canal is therefore situated farther ventrally than its anterior end. Such a massive and complete postorbital wall surrounding the jugular canal recalls that of Paleozoic sharks, such as *Orthacanthus* Agassiz, 1843, *Tamiobatis* Eastman, 1897, *Akmonistion*, *Cladodoides* Jaeckel, 1921 and “*Cobelodus*” (Schaeffer 1981; Coates & Sequeira 1998; Maisey 2005, 2007).

The lateral border of the postorbital wall is flattened. A prominent horizontal ridge is present at mid length on the surface of the postorbital wall (imz, Figs 6; 10; 11). It may correspond to a zone that have separated on one side a mandibular muscle, such as the *adductor mandibulae posterior* muscle, and on the other side a branchial muscle, such as the *cucullaris superficialis* muscle. These two muscles are described by Didier (1995) in extant holocephalans. In the latter, the *ad-*

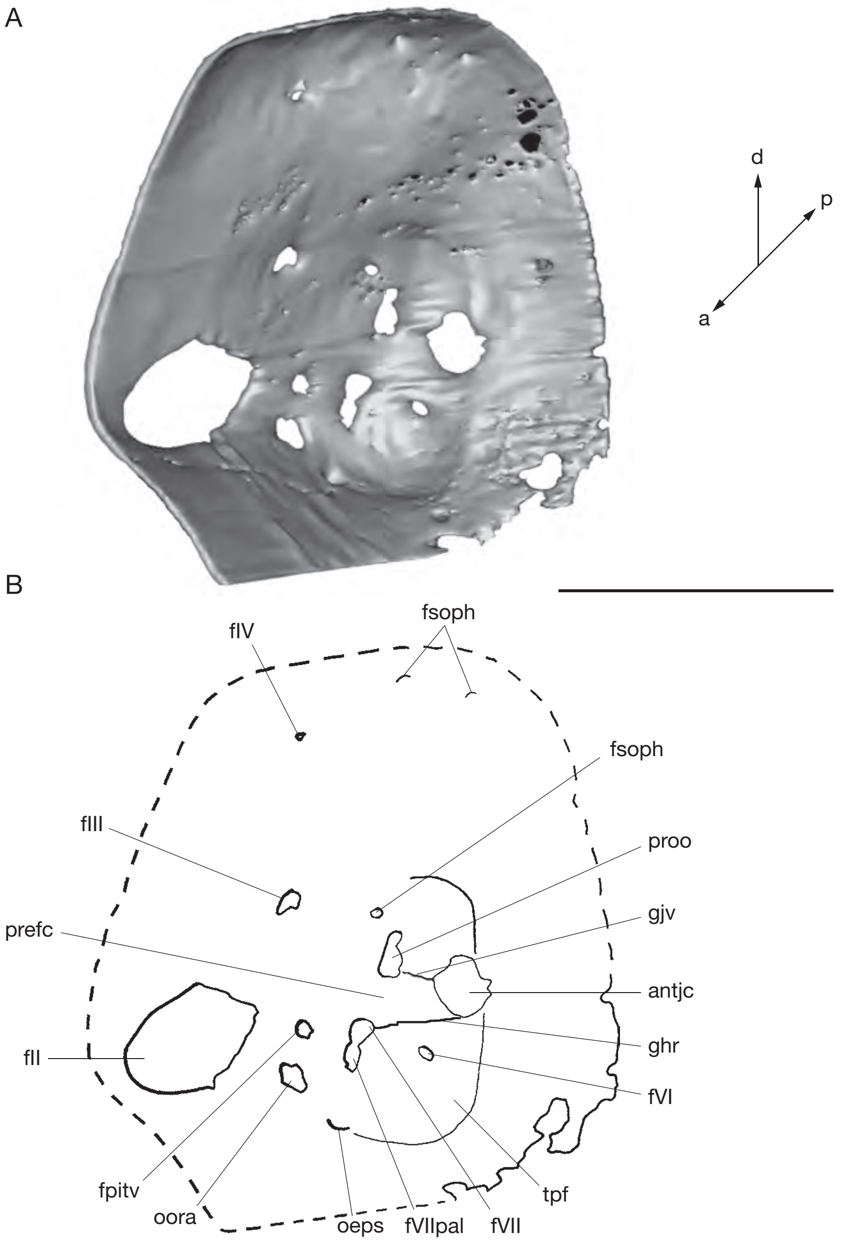

Fig. 13. — Detail of the posterior part of the orbit of KUNHM 22060 in anterolateral view, left side: **A**, surface rendering generated from Synchrotron Radiation holotomographic slices; **B**, corresponding drawing. Arrows point anteriorly (a), posteriorly (p) and dorsally (d). Abbreviations: see Materials and methods. Scale bar: 5 mm.

ductor mandibulae posterior muscle originates from the suborbital shelf and the *cucullaris superficialis* muscle originates more posterodorsally from the postorbital crest. The cranial surface between these two muscle insertions remains directly in contact with the overlying skin (Didier 1995: fig. 41; amp, cs).

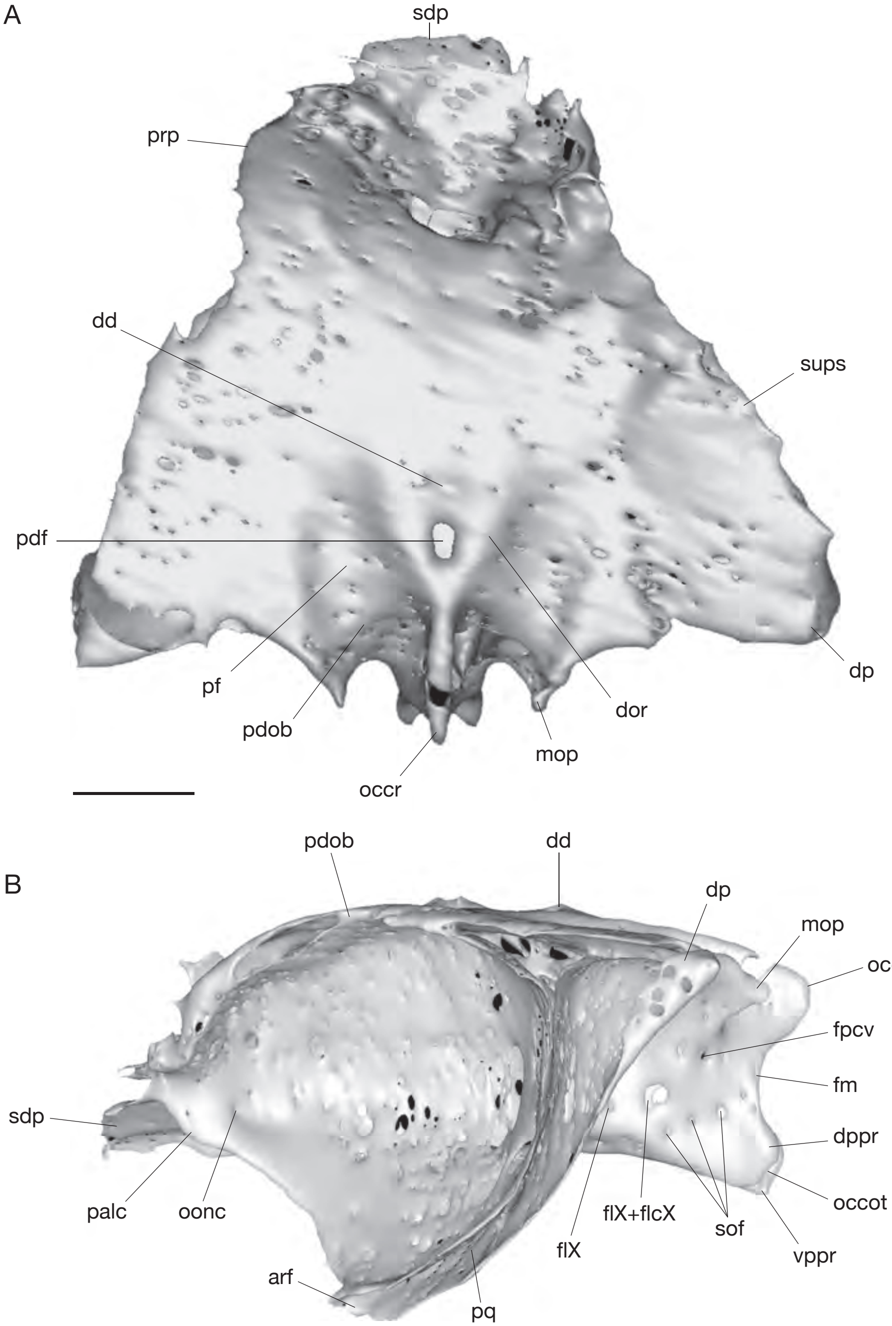

FIG. 14. — Surface rendering generated from Synchrotron Radiation microtomographic slices of the braincase of KUNHM 21894: **A**, dorsal view; **B**, lateral view. Abbreviations: see Materials and methods. Scale bar: 5 mm.

Optic nerve (II), oculomotor nerve (III), and pituitary vein

The orbital wall displays the largest ovoid foramen centrally (fII, Figs 6; 12; 13; 16). According to the relation between this foramen and the brain and nerves preserved in the endocranial cavity (fII, II, Fig. 26), it contained the optic nerve (Pradel *et al.* 2009) and probably the optic (retinal) artery (opa, Fig. 21), as in *Cladodoides* (Maisey 2005) and *Chlamydoselachus* Garman, 1884 (Allis 1923). It is also through this foramen that the efferent pseudobranchial artery supplied the blood to the brain (see below).

In chondrichthyans, the oculomotor nerve leaves the brainstem near the midline of the mesencephalon (Jollie 1962; Maisey 2005). In the preserved brain (Pradel *et al.* 2009) a pair of nerves leaves the ventral part of the mesencephalon at the midline (III, Fig. 26) and passes through a foramen situated dorsal to the optic foramen at the level of its posterior end (fIII, Figs 6; 8; 12; 13; 16; 26), suggesting that it is the oculomotor nerve foramen. As suggested by the shape of the nerve, the oculomotor nerve seems to have been divided into a dorsal ramus, which may have innervated the superior and internal rectus muscles, and a ventral ramus, which innervated the inferior rectus and inferior oblique eye muscles (IIId, IIIv, Fig. 21).

The pituitary vein foramen is located immediately behind the optic foramen, below the oculomotor nerve foramen (fpitv, Figs 12; 13; pitv, Fig. 21).

Trochlear nerve (IV)

In modern elasmobranchs as well as in modern holocephalans, the trochlear nerve emerges from the dorsal aspect of the brainstem at the level of the caudal mesencephalon, just before the cerebellum, and it innervates the superior oblique eye muscle. In the preserved brain, only the root of this nerve is observable (IV, Fig. 26) and runs upward toward a foramen located far dorsally in the posterior part of the orbit, directly above the oculomotor nerve foramen (fIV, Figs 6; 8; 12; 13; 16; 26), as in extant chondrichthyans, *Cladodoides*, *Orthacanthus* and "*Cobelodus*" (Schaeffer 1981; Maisey 1983, 2005, 2007).

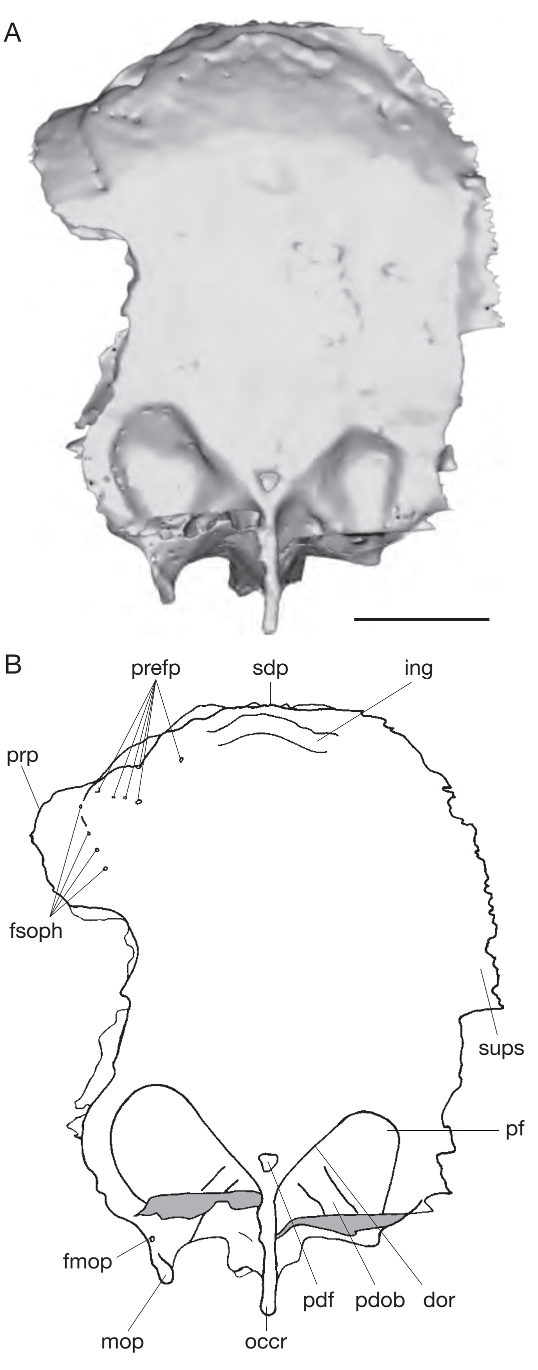

FIG. 15. — Dorsal view of the braincase of OKM 38: **A**, surface rendering generated from XR-µCT scan slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

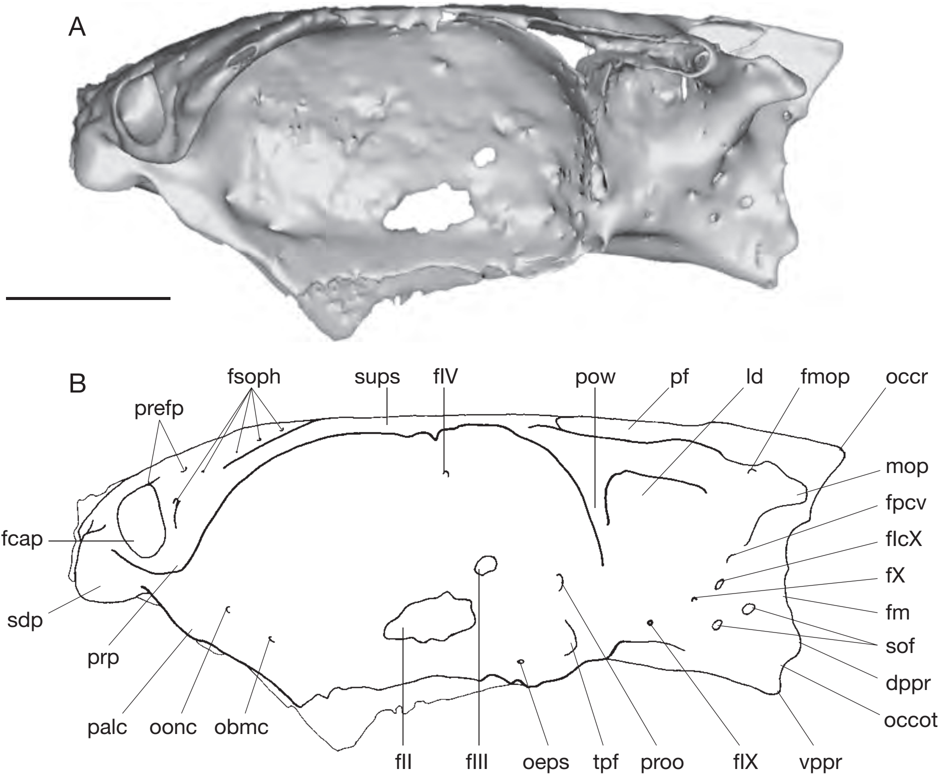

FIG. 16. — Lateral view of the braincase of OKM 38, left side: **A**, surface rendering generated from XR-µCT scan; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

Trigeminal (V), profundus ramus and anterodorsal lateral line nerves

The trigeminal nerve passed through a prootic foramen (proo, Figs 6; 8; 12; 13; 16; 26). The middle cerebral vein may also have left the braincase through this foramen (mcv, Fig. 21), as in modern elasmobranchs and "*Cobelodus*" (Maisey 2007).

In many modern chondrichthyans, the profundus ramus of the trigeminal nerve, the superficial ophthalmic ramus of trigeminal and anterodorsal lateral line nerves leave the braincase together. In the iniopterygians studied here, there is no evidence of a separate foramen for the anterodorsal lateral line nerve and superficial ophthalmic ramus of the trigeminal nerve in the inner wall of the braincase (proo, Fig. 28). This suggests that these nerves left the braincase through the same (prootic) foramen, and formed a dorsal superficial ophthalmic complex, as inferred in other Paleozoic chondrichthyans (Maisey 2005, 2007). Nevertheless, a notch is present in the anterodorsal margin of the prootic foramen in the inner endocranial wall (Fig. 28), and there is a small foramen anterodorsal to this notch in the external orbital wall of the braincase (fsoph, Figs 12; 13). This suggests a separate opening for the dorsal superficial ophthalmic complex through the outer wall of the braincase. The profundus ramus of the trigeminal nerve (pr, Fig. 21) may have left the braincase separately from the superficial ophthalmic complex (soph, Fig. 21), through the prootic foramen.

A foramen is situated ventrolaterally, immediately posterior to the orbital foramen for the orbitonasal canal and the palatine tooth whorl, at the junction between the palatoquadrate and the ethmoidal plate (obmc, Figs 6; 16). This foramen is linked to a ventral foramen (vbmc, Figs 7; 17), which is situated posterior to the ventral foramen of the orbitonasal canal, by a short canal. A ventral bucco-maxillary complex (the maxillary ramus of the trigeminal nerve plus the buccal ramus of the anterodorsal lateral line nerve) is inferred in many Paleozoic chondrichthyans (Maisey 2007) and may be also present in the iniopterygians studied here. If present, it probably ran through the orbit (bmc, Fig. 21) and probably left the neurocranium through the foramina described just above.

A more anterior foramen is present ventral to the nasal capsule (fVmx, Figs 6; 9). A foramen in a similar position is present in other holostylic fishes. In the upper jaw of extant chimaeroids a foramen for a branch of the maxillary ramus is situated "near the dorsal extremity of the lateral set of teeth" (Cole 1896). An anterior foramen for the maxillary ramus of the trigeminal nerve is also present in the posterior part of the preorbital wall and below the foramen for the superficial ophthalmic ramus of the facial nerve and the ophthalmic profundus ramus of the trigeminal nerve in holostylic Devonian dipnoans (Pridmore *et al.* 1994; Campbell & Barwick 2000). This suggests that the foramen described above in the specimens studied here was probably for a branch of the maxillary ramus of the trigeminal nerve of the bucco-maxillary complex (Vmx, Fig. 21).

The mandibular ramus of the trigeminal nerve may also have run ventrally in the orbit as far as the articulation between the mandible and the palatoquadrate (Vmd, Fig. 21), as in extant chimaeroids (Cole 1896; De Beer & Moy-Thomas 1935).

Abducens nerve (VI)

The posteroventral part of the orbit displays a fossa (see below), where a foramen pierces the neurocranium (fVI, Figs 12; 13). This foramen was probably for the exit of the abducens nerve (VI, Fig. 21), which supplied the external (= posterior) rectus muscle. Since the dorsum sellae is very short in the iniopterygians described here, the abducens nerve probably left the neurocranium above and behind the dorsum sellae (cVI, ds, Figs 8; 26), which represents an autapomorphic condition in chondrichthyans (Gardiner 1984). In the endocranial cavity, the canal for the abducens nerve is located between the utricular recess and the saccular chamber (cVI, Figs 27; 28).

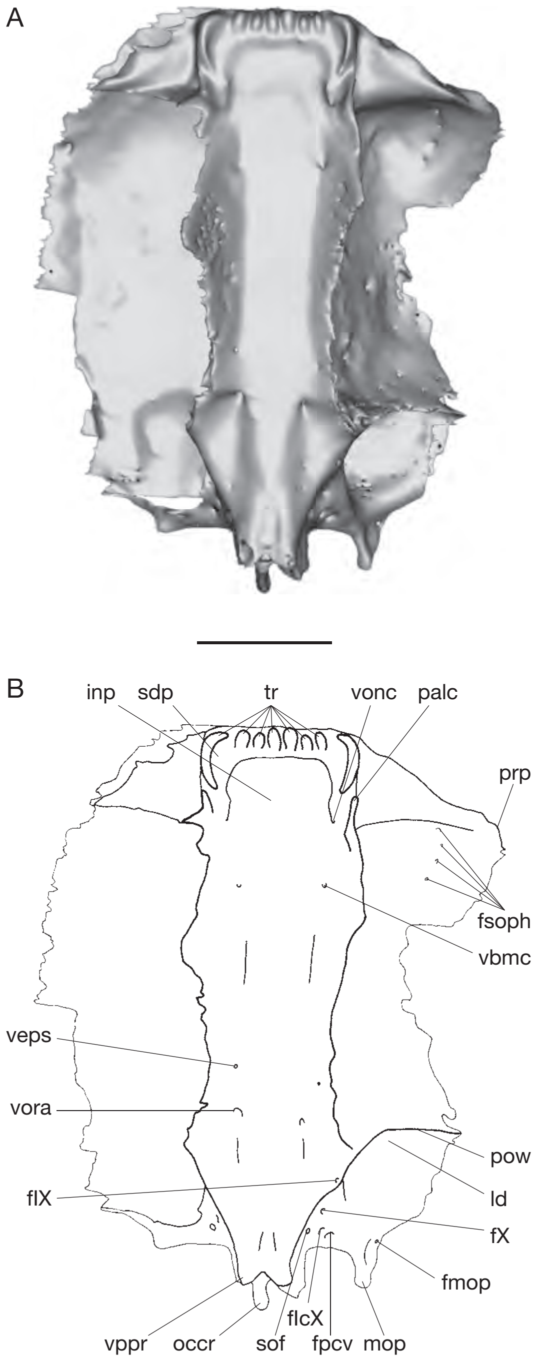

FIG. 17. — Ventral view of the braincase of OKM 38: **A**, surface rendering generated from XR-µCT scan slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

Facial nerve (VII)
The foramen for the main trunk of the facial nerve is located in the surface of the orbital cartilage, between the foramina for the pituitary vein and abducens nerve (fVII, Figs 12; 13). This foramen is followed ventrally by another one (fVIIpal, Figs 12; 13), which is connected to the canal for the orbital artery ventrally (cora, Fig. 28) by an almost vertical canal (cVIIpal, Fig. 28). Same foramina are present in "*Cobelodus*" in which the main facial trunk is assumed to divide into anterior (palatine) and posterior (mandibular-hyoidean) rami after leaving the braincase. The palatine ramus shared ventrally the same groove as the orbital artery after passing through the floor of the postorbital arcade, while the mandibular-hyoidean ramus presumably passed through the jugular canal posteriorly (Maisey 2007). Consequently, in the specimens studied here, the anatomy of the facial nerve may have been the same. The palatine and mandibular-hyoidean rami may have given off from the main trunk of the facial nerve when the latter appears to surface (VII, VIIpal, VIIhym, Fig. 21).

Then, the palatine ramus probably entered the neurocranium just below the main facial foramen (fVII, fVIIpal, Figs 12; 13) and ran through the vertical canal until the canal for the orbital artery ventrally (cora, Fig. 28). The latter is directed anterodorsally and its orbital opening is located immediately below the foramen for the pituitary vein (oora, Figs 12; 13), while its ventral opening is situated behind the ventral foramen (vora, Figs 7; 17) for the efferent pseudobranchial artery (veps, Figs 7; 17).

Two hypotheses concerning the course of the palatine ramus of the facial nerve (VIIpal, Fig. 21) of sibyrhynchids can be proposed: 1) the palatine ramus entered the orbital artery canal and ran backwards. After exiting from the braincase through the ventral opening of orbital artery canal, it divided into the anterior and posterior ramules; and 2) the palatine ramus entered the orbital artery canal and divided into the anterior and posterior ramules inside it. The anterior ramule (VIIapal, Fig. 21) ran forward (cVIIapal, Fig. 28) and exited from the braincase through the orbital opening of the orbital artery canal, whereas the posterior one (VIIppal, Fig. 21) ran backwards (cVIIppal, Fig. 28) and exited from the braincase through the ventral opening of the orbital artery canal. Then, the anterior ramule ran in the ventral part of the orbit as far as the foramen for the bucco-maxillary complex.

In extant adult chimaeroids, the palatine ramus divides into the anterior and posterior ramules after exiting from the orbital artery canal through its ventral foramen. This pattern corresponds to the first hypothesis proposed here. Nevertheless, in extant chimaeroids the orbital artery canal is more vertical than in sibyrhynchids, in which this canal is oriented anterodorsally (cora, Fig. 28). If the same arrangement was present in iniopterygians, the anterior ramule is far from the palatoquadrate and must have made a loop to innervate the palatine muscles. In addition, the palatine ramus of extant chimaeroids enters the orbital artery canal through its orbital foramen, whereas in iniopterygians, as seen previously, it probably entered the neurocranium just below this facial foramen and ran through a canal, which meets ventrally the canal for the orbital artery intracranially.

In *Cladodoides* and "*Cobelodus*" (Maisey 2005, 2007), the palatine ramus enters a canal, and then divides into the anterior and posterior ramules before exiting from the neurocranium. The division presumably occurs within the lateral commissure, which formed a part of the postorbital wall. Consequently, there are two different foramina for the anterior ramule and the posterior ramule respectively. In *Cladodoides*, the anterior ramule enters the orbit ventrolaterally through the orbital artery groove. In "*Cobelodus*", the foramina for the anterior and posterior ramule reach ventrally the braincase in the groove housing the orbital artery. This pattern corresponds to the second hypothesis proposed here, which appears to be the most probable.

The mandibular-hyoidean ramus presumably passed posteriorly via the jugular canal (VIIhym, Fig. 21), as suggested by the presence of a shallow groove between the foramen for the main trunk of the facial nerve and the orbital opening of the jugular canal (ghr, fVII, antjc, Figs 12; 13), as in extant chimaeroids (De Beer & Moy-Thomas 1935: fig. 1) and "*Cobelodus*" (Maisey 2007). Then, the hyomandibular ramus may have divided into

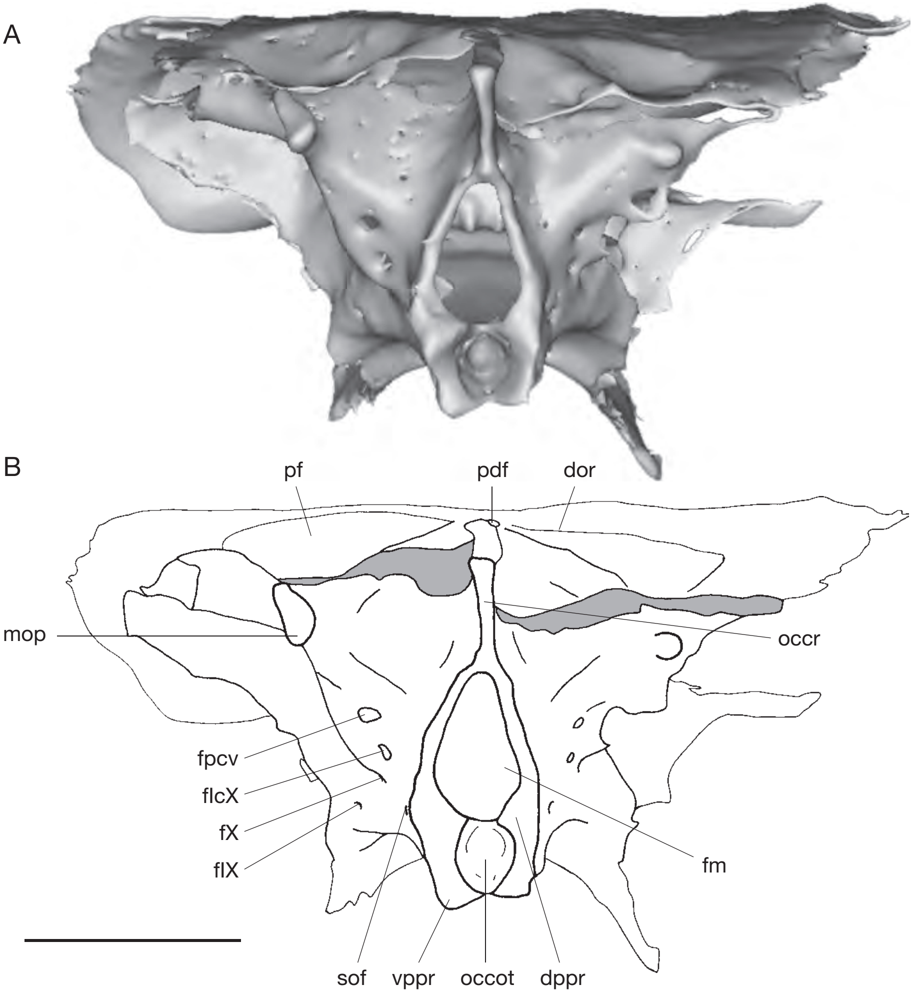

FIG. 18. — Posterior view of the braincase of OKM 38: **A**, surface rendering generated from CT scan slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

mandibular and hyoidean ramules when it passed lateral to the epihyal (VIImd, VIIh, Fig. 21), again as in extant chimaeroids (De Beer & Moy-Thomas 1935). It is also possible that only the hyoidean ramule passed through the jugular canal and that the mandibular ramule accompanied the maxillary ramus of the trigeminal nerve.

Prefacial commissure and trigemino-pituitary fossa
The prootic foramen and the foramen for the main trunk of the facial nerve (proo, fVII, Fig. 12) are separated by a bar of cartilage, which is assumed to be a prefacial commissure (prefc, Figs 12; 13).

In the iniopterygians described here, the posteroventral corner of the orbit displays a large trigemino-pituitary fossa (*sensu* Allis 1918, 1923, 1928) (tpf, Figs 12; 13) delimited anteriorly by the foramina for the pituitary vein and for the orbital artery (fpitv, oora, Figs 12; 13) and ventrally by the foramen for the efferent pseudobranchial artery (oeps, Figs 12; 13). This fossa also contains the prootic foramen in its dorsal part (proo, Figs 12; 13), and the fo-

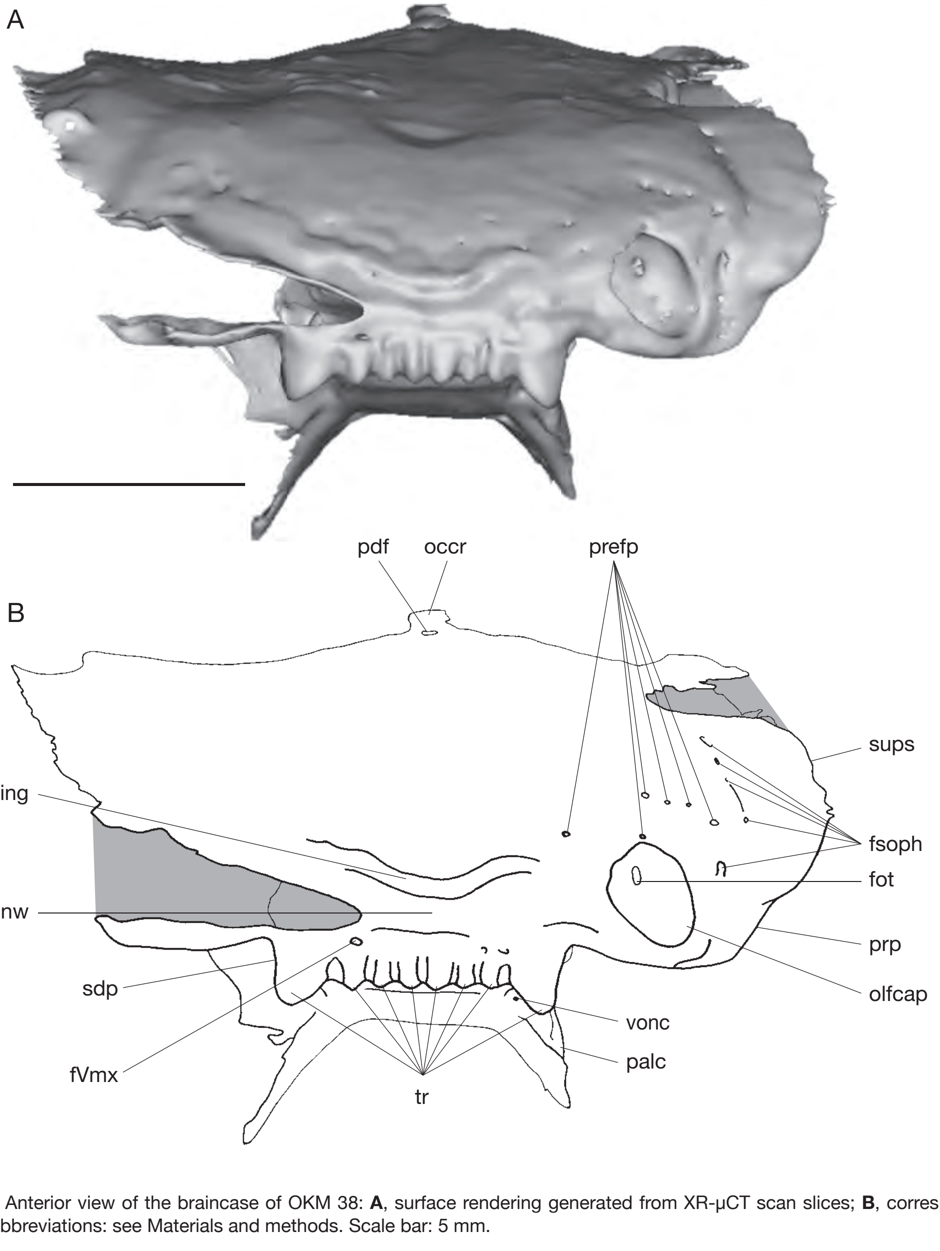

FIG. 19. — Anterior view of the braincase of OKM 38: **A**, surface rendering generated from XR-µCT scan slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

ramen for the facial nerve (fVII, Figs 11; 12). The trigemino-pituitary fossa is much more pronounced in its posteroventral part, where the foramen for the abducens nerve pierces the braincase wall (fVI, Figs 12; 13).

The palatine and mandibular-hyoidean rami of the facial nerve of the iniopterygians studied here probably diverged within the facial foramen (see above). Consequently, the facial nerve ganglion was probably situated partially inside and partially outside

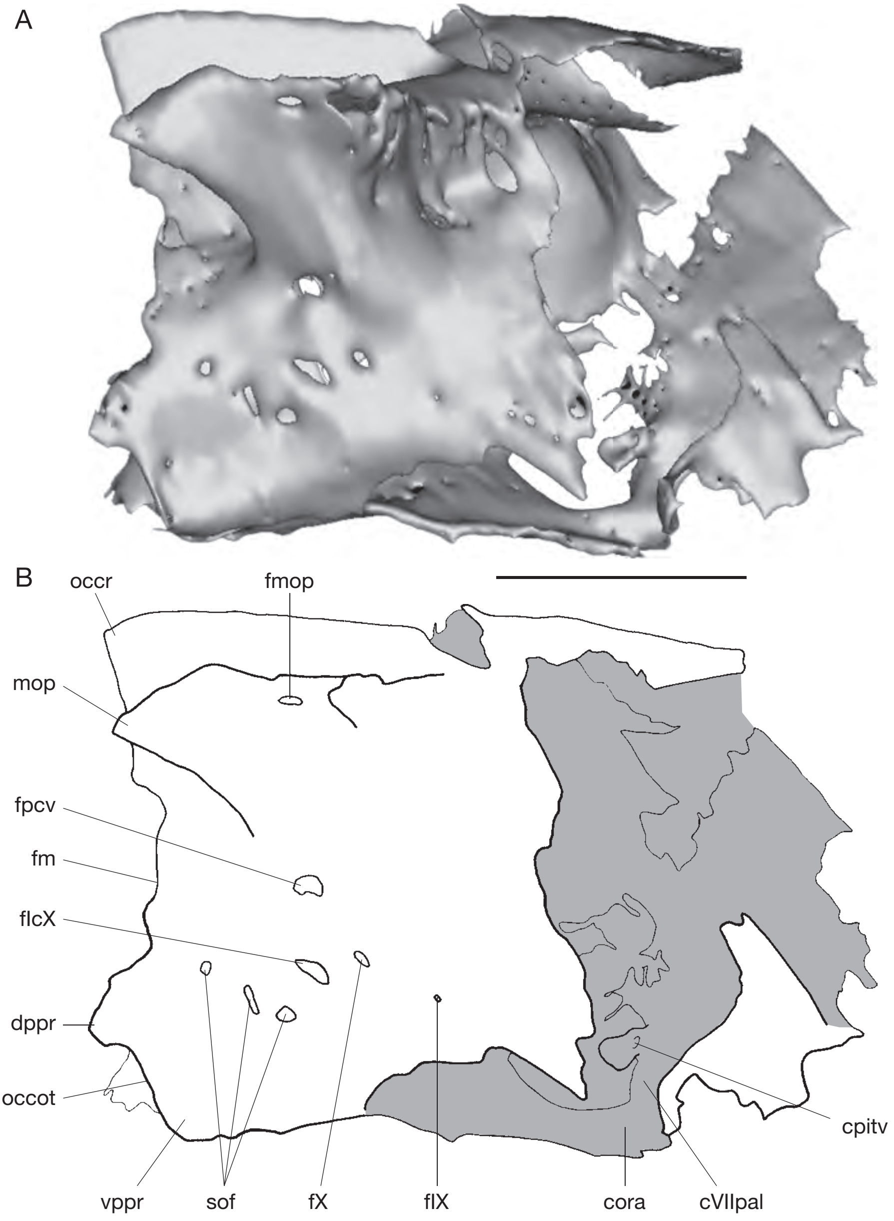

Fig. 20. — Lateral view of the braincase of KUNHM 56360, right side; **A**, surface rendering generated from XR-µCT scan slices. **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

the neurocranium in the trigemino-pituitary fossa. The trigeminal ganglion (Gasser's ganglion; gas, Fig. 21) was probably situated in part lateral to the posterior part of the orbit, in the trigemino-pituitary fossa, and partly internally because the superficial ophthalmic ramus probably exited the braincase with the anterodorsal lateral line nerve through a foramen that is distinct from the prootic one.

Arterial supply to the head

At the level of the posterior attachment of the postorbital wall of the braincase, the basicranium displays a pair of foramina (vora, Figs 7; 17), which corresponds to the ventral foramina for the orbital artery canal. There is neither a basicranial fenestra, nor a hypophyseal fenestra. Consequently, there is no evidence of foramina for the internal carotid arteries, which thus probably did not supply blood to the brain.

A small canal (ceps, Fig. 28) passing through the suborbital shelf, with its orbital opening (oeps, Figs 12; 13; 16) situated ventral to the orbital foramen of the orbital artery canal and its ventral opening (voeps, Fig. 17) located in front of the ventral foramen of the orbital artery canal, is present anterior to the internal hypophyseal chamber. It may have housed the efferent pseudobranchial artery. In such a case, the efferent pseudobranchial artery (eps, Fig. 21) probably entered the brain cavity through the large optic foramen. Then, it may have divided into an optical (retinal) artery (opa, Fig. 21), which re-entered into the orbits, and a basilar artery (basa, Fig. 21), which supplied blood to the brain.

Otic region

The short otic region of the iniopterygians described here is pierced dorsally by a median posterior dorsal fontanelle (pdf, Figs 7; 14A; 15).

As in many Paleozoic sharks, the otic region shows a posterolaterally directed lateral process on either side of the braincase (dp, Figs 5-7; 10; 11; 14). It extends very far laterally from the loop of the posterior semicircular canal and from the preoccipital fossa (pf, Figs 5; 6; 10; 14A; 15; 16; 18) that probably represents insertion area for the epaxial musculature.

An other pair of processes encloses the loop of each posterior semicircular canal and overlies on a short distance the horizontal semicircular canal (mop, Figs 5; 7; 10; 14-18; 20). They are located more medially, on either sides of the occipital crest, at the lateral margin of the dorsal preoccipital fossae. There is a foramen at the extremity of the medial otic process (fmop, Figs 15-17; 20). The attribution of this foramen to either blood vessels or cranial nerves is unclear (see below).

A pair of posterior dorsal otic bulges (pdob, Figs 5; 14; 15) originates from the medial otic processes of either sides and converges anteriorly toward the posterior dorsal fontanelle. They enclose the dorsal part of the posterior semicircular canal. A similar pair of posterior dorsal otic bulges is present in many extinct chondrichthyans, such as *Akmonistion* (Coates & Sequeira 1998: fig. 5).

Low dorsal otic ridges, which overly the anterior semicircular canals and flank the endolymphatic fossa (or posterior dorsal fontanelle), as that of "*Cobelodus*", are present in iniopterygians (dor, Figs 5; 10; 14A; 15; 18).

The course of the horizontal semicircular canal in iniopterygians is delimited by the lateral margin of the preoccipital fossae and the course of the posterior part of the anterior semicircular canal is delimited by the anteromedial margin of the fossa. These fossae are anteriorly divergent and their position corresponds to the vacuity delimited by the dorsal part of the three semicircular canals (pf, Figs 5; 6; 10; 14A; 15; 16; 18).

Consequently, the dorsal otic ridges seen in some other Paleozoic chondrichthyans (e.g., *Tamiobatis*, *Cladodoides*, "*Cobelodus*") are represented here by the medial margin of the preoccipital fossae. The lateral otic ridge of these Paleozoic chondrichthyans may be also represented in iniopterygian by the lateral margin of the preoccipital fossae. In these Paleozoic sharks, the dorsal and lateral otic ridges delimit a dorsolateral otic fossa, which may be represented in iniopterygians by the preoccipital fossae, even though the latter are completely dorsal in position. This dorsal, rather than dorsolateral position is probably due to the extreme lateral extent of the postorbital wall.

The semicircular canals are restricted to the dorsal part of the posterior half of the neurocranium, in a region that is very shallow (Fig. 10). Such a condition is otherwise found only in the strongly flattened braincases of certain arthrodire placoderms (Stensiö 1969; Goujet 1984) and perhaps *Helodus* Agassiz, 1838 (Moy-Thomas 1936; Patterson 1965). Ventrolateral to the otic region are very deep postorbital depressions (ld, Figs 7; 10; 16; 17) that probably accommodated the jaw and visceral musculature (e.g., the *cucullaris profundus*,

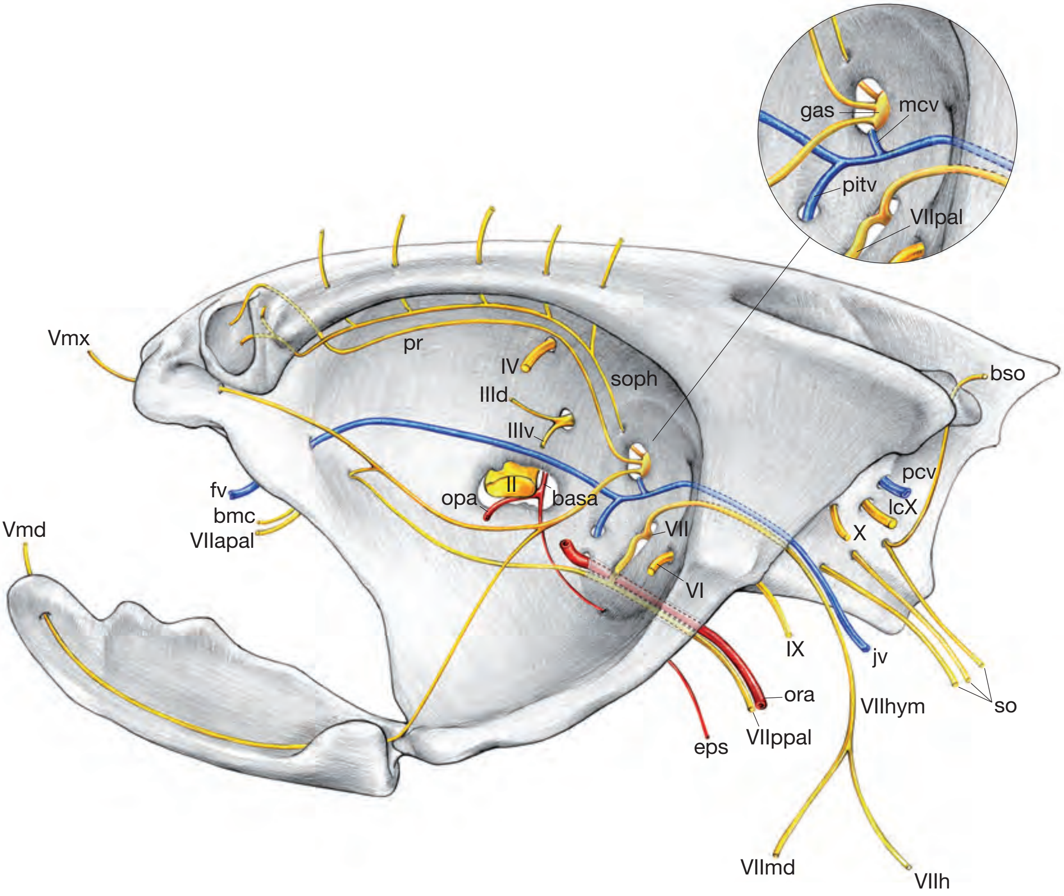

FIG. 21. — Hypothetical arrangements of arteries (in red), veins (in blue) and nerves (in yellow) in the chondrocranium of a reconstructed Sibyrhynchidae based on the different 3D reconstructions of the braincase. Abbreviations: see Materials and methods. Not to scale.

subspinalis, and *levator hyoideus* muscles, as in extant chimaeroids; Didier 1995) and gills. The branchial apparatus was thus situated beneath the braincase, instead of extending behind it. This position of the gills relative to the neurocranium is similar to that of chimaeroids. Therefore, iniopterygians were first classified among the Subterbranchialia (Zangerl 1981), a taxon including also the extant chimaeroids. In addition, like in extant chimaeroids, there is no evidence of an articular facet for the hyomandibula in the otico-occipital region, as well as on the postorbital wall. Nevertheless, more data on the branchial skeleton are needed to know whether a hyomandibula is present or not. "*Cobelodus*" lacks a distinct hyomandibular facet on the neurocranium although the presence of a hyomandibula suggests a weak ligamentous attachment, probably with the periotic process (Maisey 2007).

OCCIPITAL REGION

General features

Posterior to the postorbital wall, the ventral part of the braincase is narrow (Figs 7; 17). The occipital part of the braincase is relatively short and is flanked by the postorbital depressions (ld, Figs 7; 10; 16; 17). According to Romer (1964) and Coates & Sequeira (1998), a relatively elongated otico-occipital region is presumably a plesiomorphic condition among gnathostomes. Consequently, a comparatively short otico-occipital region may represent a derived condition. Nevertheless, a relatively short otico-occipital region commonly occurs in actinopterygians, sarcopterygians, *Acanthodes* Agassiz, 1833, *Pucapampella*, chimaeroids, neoselachians, Symmoriiformes and hybodonts.

Behind the posterior dorsal fontanelle and between the preoccipital fossae is a prominent crest, which extends far posteriorly (occr, Figs 7-8; 10; 14-16; 18). Below this crest, the occipital arch surrounds dorsally the foramen magnum, and ventrally the notochordal canal (fm, occot, Figs 10; 18). The notochordal canal forms a deep fovea commonly called occipital cotylus, as in many other Paleozoic chondrichthyans (e.g., *Cladodoides*, "*Cobelodus*"). This suggests a strong connection with the vertebral column. In life, the occipital cotylus is assumed to have enclosed the anterior end of the notochord, which is usually persistent in the adult in modern cyclostomes, chondrichthyans, sturgeons, lungfishes and coelacanths. In all iniopterygians studied here, the occipital cotylus merges anteriorly into the rear of the braincase about as far as the level of the anteriormost spino-occipital foramen (sof, Figs 6; 8; 14B; 16; 20) and there is no evidence of a hemicentrum.

A similar cotylus is present in hybodonts and many Paleozoic sharks (Maisey 1983, 2005, 2007). Nevertheless, contrary to many Paleozoic sharks in which the occipital cotylus is larger than the foramen magnum (e.g., *Cladodoides*), these two structures are about the same width, as in "*Cobelodus*". The dorsolateral and ventrolateral part of the rim of the occipital cotylus protrudes posteriorly to form the dorsal and ventral paroccipital processes of the occipital cotylus (dppr, vppr, Figs 6; 7; 10; 14B; 16-18; 19). These processes presumably contributed to the craniovertebral joint and are generally absent in Paleozoic sharks with an elongated occipital region (e.g., *Cladodoides*, *Orthacanthus*, *Tamiobatis*). They are present in *Cobelodus aculeatus*, *Stethacanthulus* Zangerl, 1990, *Akmonistion* and "*Cobelodus*" (Zangerl & Case 1976: fig. 5; Williams 1985: figs 3, 6; Zidek 1992: fig. 4; Coates & Sequeira 1998: fig. 4; Maisey 2007: fig. 11).

There is a posterior cartilage ridge that joins the two dorsal paroccipital processes. It separates the notochordal canal from the foramen magnum at the posterior extremity of the occipital region (occot, fm, Fig. 22A). Then, the inner wall of the braincase separates the notochordal canal from the endocranial cavity more anteriorly. Therefore, the notochord was completely enclosed (presumably by the parachordal cartilages), contrary to the condition in extant chimaeroids, where the notochord is free above the basal plate. The notochord was also enclosed by cartilage (perhaps derived from the parachordals) in placoderms, primitive actinopterygians, and primitive chondrichthyans. This suggests that an enclosed notochord in the adult is a plesiomorphic condition among the gnathostomes.

The occipital cotylus generally separates posteriorly the paired parachordal cartilages in chondrichthyans. In the iniopterygians studied here, between the ventral paroccipital processes is a median posterior notch that extends anteriorly as far as the level of the anteriormost foramen for the spino-occipital nerves (Figs 7; 17). This suggests that the two parachordals are incompletely fused posteriorly (parc, Fig. 22A). When the notochordal canal tapers anteriorly, a vertical septum connects the notochordal canal to the basicranium and marks the beginning of the embryonic fusion of the paired parachordal cartilages. At this level, the basal plate is not yet well defined (fp, Fig. 22B). On each side of the septum is an occipital chamber, which is delimited at the level of the spino-occipital nerve by the correspondent canals (occh, sof, Fig. 22B).

This septum is thus not primary homologous to the vertical subnotochordal septum, which connects the notochordal canal to a well-defined basal plate in *Cladodoides* (Maisey 2005: fig. 30). In addition, there is no evidence, in iniopterygians, of paired subnotochordal "chambers" present in *Cladodoides* when the septum disappears anteriorly at the level of the anterior end of the notochordal septum.

Glossopharyngeus nerve (IX)

In the iniopterygians described here, there is neither a persistent ventral metotic part of the otico-occipital fissure, nor a posterior basicapsular commissure separating the otic capsules from a hypotic lamina, and

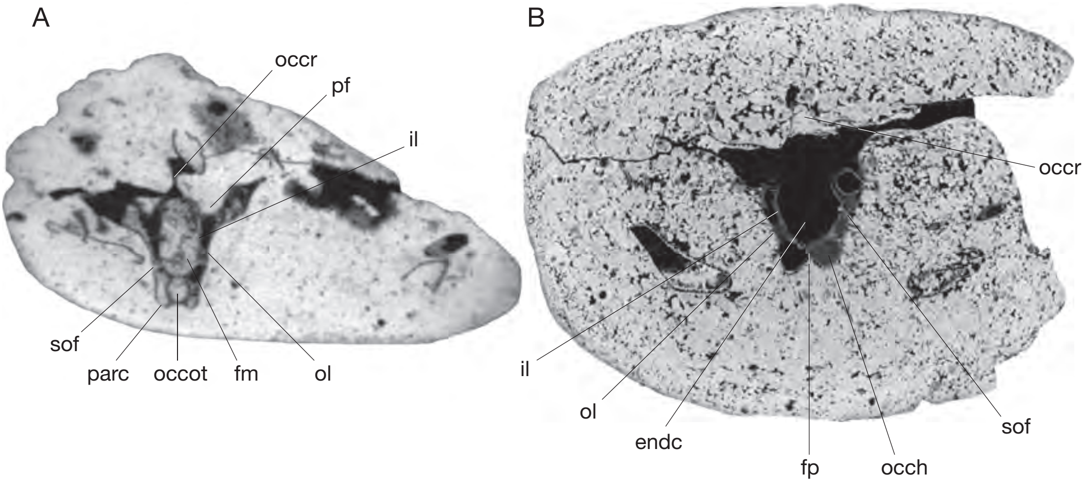

Fig. 22. — Transverse XR-μCT scan slice at the level of the mid occipital cotylus of OKM 38 (**A**) and transverse Synchrotron Radiation microtomographic slice at the level of the anterior end of the occipital cotylus of KUNHM 21894 (**B**). Abbreviations: see Materials and methods. Not to scale.

the glossopharyngeus nerve does not pass in a canal floored by the ventral hypotic lamina (cIX, Figs 27; 28). There is also no evidence of a persistent dorsal otico-occipital fissure, which initially separates the occipital pila from the otic capsules in Recent embryonic elasmobranchs. Consequently, a hypotic lamina seems to be absent in sibyrhynchids

The glossopharyngeus nerve (IX, Fig. 21) emerged via a short canal originating in the posteroventral part of the saccular chamber (cIX, Figs 8; 27; 28), and is anterior to the vagus nerve (fIX, fX, Figs 7; 10; 14B; 15; 17; 18; 20), as in extant chimaeroids. It seems to pass through the vestibular chamber, since there is no evidence of a medial wall separating the vestibular chamber from the endocranial cavity (Fig. 8).

Spino-occipital nerves

The occipital arch in the iniopterygians described here is relatively short, with three spino-occipital foramina being well visible externally and oriented posterodorsally in KUNHM 21894 (sof, Fig. 14B) and KUNHM 56360 (sof, Fig. 20). It is obscured by a break at the level of the putative anteriormost foramen in KUNHM 22060 (sof, Fig. 6), and by the absence of infilling matrix in OKM 38 (sof, Fig. 6).

The number of spino-occipital foramina is highly variable among chondrichthyans (Maisey 2007). In addition, there may be a difference between the number of externally visible foramina and the real number of spino-occipital nerves (e.g., "*Cobelodus*": Maisey 2007). In iniopterygians, there is no difference between the number of spino-occipital canals showing in the endocast of the endocranial cavity (cso, Fig. 27) and the externally visible foramina.

Since there may be a relatively large number of spino-occipital nerves (more than three) located in the occipital region even in forms that have a short occipital region (e.g., "*Cobelodus*"), and conversely, a lower number is sometimes present in forms with a long occipital region (e.g., *Orthacanthus*), there is no simple correlation between the number of nerves in the occipital region and the length of this region. Nevertheless, three or more canals may represent a plesiomorphic condition in chondrichthyans, and a lower number is probably a derived condition. According to Bemis & Forey (2001), three foramina may represent the primitive condition for gnathostomes.

As mentioned above, a foramen pierces the posterodorsal part of the median otic process (fmop, Figs 15-17; 20). It is possible that a branch of a spino-occipital nerve ran through it medially to innervate the epaxial musculature located in the preoccipital fossae (so, bso, Fig. 21). However, this foramen may have housed a blood vessel as well.

Vagus nerve (X) and other foramina

Immediately above the spino-occipital foramina are one or two closely-set foramina (fX, flcX, Figs 6; 14B; 16; 20). These foramina are connected to the endocranial cavity below the posterior ampulla by a canal, which probably housed different branches of the vagus nerve (cX+lcX, Fig. 27). The vagus nerve was therefore posterior to the glossopharyngeus nerve. The octavolateral nerves also include the lateralis component of the vagus nerve and, in *Notorynchus* Péron, 1807 (Maisey 2004b: fig. 6) there is a foramen for the supratemporal lateral line branch of the vagus nerve located above the vagus foramen and behind the glossopharyngeus nerve. Consequently, one of the two foramina seen in iniopterygians may be for the passage of a lateralis component of the vagus nerve (flcX, Figs 16-18; 20; lcX, Fig. 21). In specimens presenting only one foramen for the vagus nerve, the different branches of this nerve probably ran through a same canal (fX+flcX, cX+clcX, Figs 6-8; 10; 14). The number of foramina for the vagus nerve depends on whether the division of the different branches occurs before their exit from the braincase, in the endocranial cavity, or after.

Dorsally to these foramina and at the base of the medial otic process is another foramen (fpcv, Figs 6; 7; 10; 14B; 16-18; 20), which is connected to the endocranial cavity by a canal at the level of the posterior semicircular canal, behind and above its ampulla (cpcv, Fig. 27). In extant chimaeroids, a corresponding foramen located farther dorsally carries the posterior cerebral vein. It is possible that this foramen contained a similar vein in iniopterygians (pcv, Fig. 21).

Posterior dorsal fontanelle (or endolymphatic fossa) and posterior tectum

Iniopterygians have an anteroposteriorly elongated opening in the posterior part of the roof of the braincase (pdf, Figs 5; 14A; 15). It lies between the otic capsules and is flanked by the preoccipital fossae.

In the Sibyrhynchidae studied here, there is no persistent otico-occipital fissure but the endolymphatic fossa (or posterior dorsal fontanelle) is well defined. Therefore, it is unclear whether the iniopterygians have or not a posterior tectum, but if it is present it may be reduced.

There is no evidence of either endolymphatic ducts or endolymphatic foramina, and the medial wall of the otic capsule is unmineralized (Figs 8, 23B). However the endolymphatic ducts were probably present and passed from the posterior dorsal fontanelle through the unmineralized medial wall of the otic capsule, as suggested in *Cladodoides* (Maisey 2005) and seen in extant chimaeroids (end, Fig. 23A; De Beer & Moy-Thomas 1935; Schaeffer 1981). There is no evidence of perilymphatic fenestra at the level of posterior semicircular canal.

The median occipital crest borders the fontanelle posteriorly. This medial occipital crest and the preoccipital fossae could be the insertion areas for epaxial trunk musculature. In front of this fontanelle is a small pointed elevation (dd, Figs 5; 6; 14) present in the iniopterygians studied here. The latter may correspond to the position of a dermal denticle that is firmly tied to the skull, as other dermal denticles are present, free in the nodules.

DESCRIPTION OF THE BRAIN

The new holotomographic approach adapted to absorbing objects allows the observation of a presumed mineralized brain and some nerves, preserved in their natural position in the endocranial cavity of KUNHN 22060 (Pradel *et al.* 2009) (Figs 3; 24-26). Consequently, several foramina that open on the surface of the braincase could be identified thanks to the preserved nerves leading to them (Fig. 26). This unique case of fossilized brain among fossil vertebrates allows a comparative study with that of extant chondrichthyans. Nevertheless, only the morphology of the different structures of the brain is comparable, even though the slices through the brain (Fig. 25) show different structures that may recall histological features. These are more likely to be the result of differences in contrast due to differential mineralization that occurred during diagenesis.

The neuroaxis of the iniopterygian studied here shows the typical fish-brain organization, being composed, from back to front of the myelencephalon, metencephalon, mesencephalon (or midbrain), diencephalon below the mesencephalon, and telencephalon, even though the latter is not preserved

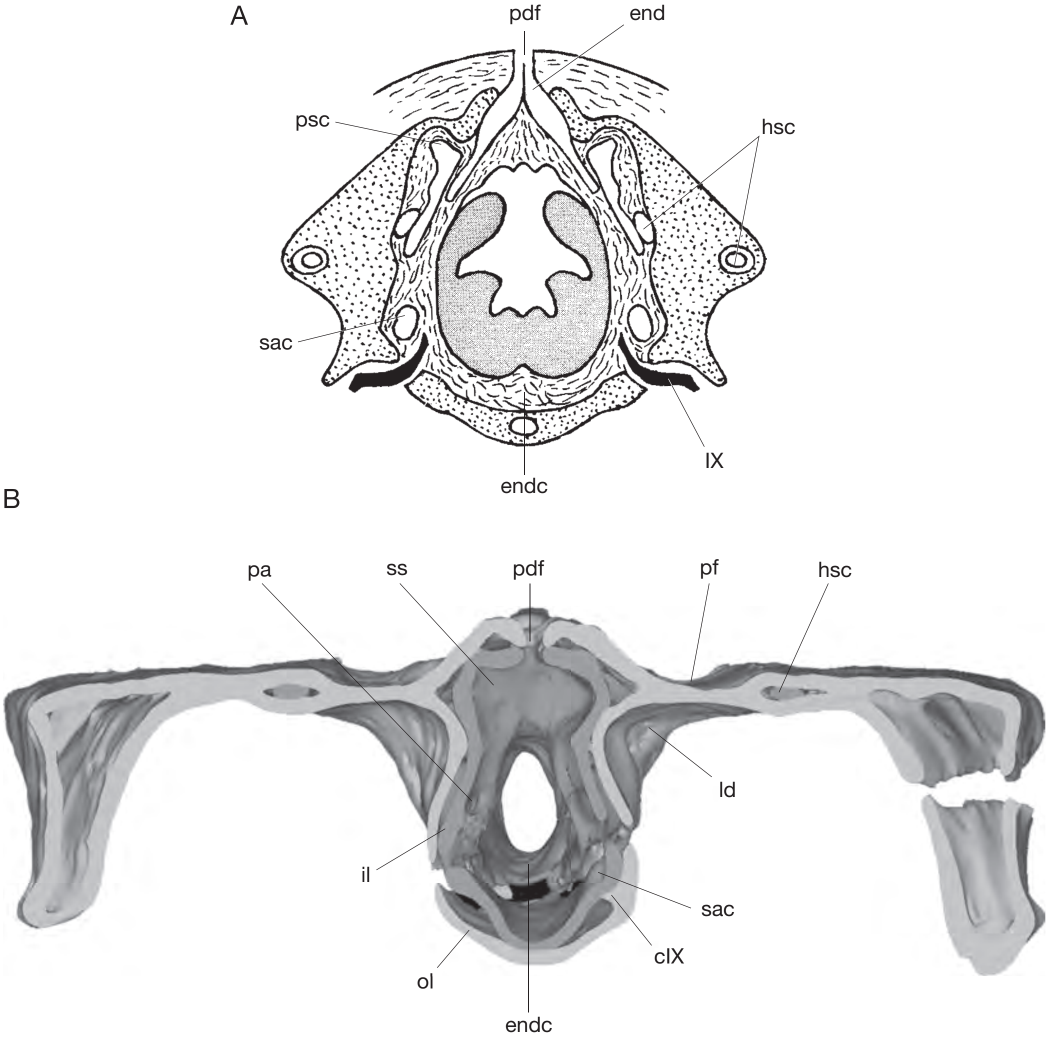

FIG. 23. — Transverse section through the endolymphatic pouches and labyrinth: **A**, in the chimaeroid *Callorhinchus* (modified after De Beer & Moy-Thomas 1935 in Schaeffer 1981); **B**, in KUNHM 22060. Abbreviations: see Materials and methods. Not to scale.

in the studied specimen. The myelencephalon and metencephalon are classically gathered under the term rhombencephalon (or hindbrain), whereas the diencephalon and the telencephalon constitute the prosencephalon (or forebrain).

The extant chimaeroids and elasmobranchs have very similar brains but they clearly differ from each other in a number of neural characters, especially concerning the telencephalic region (Northcutt 1978) and the deformation of it and the mesencephalon in parallel with the presence of an interorbital septum in chimaeroids.

RHOMBENCEPHALON

The cerebellum of the iniopterygian studied here consists of a relatively small, ovoid, median structure, the rostral corpus cerebelli (ccer, Figs 24A, C; 25C, F), and of a slightly laterally expanding caudal part, the paired cerebellar auricle (ca, Figs 24A, C; 25B, C, F). The latter also slopes

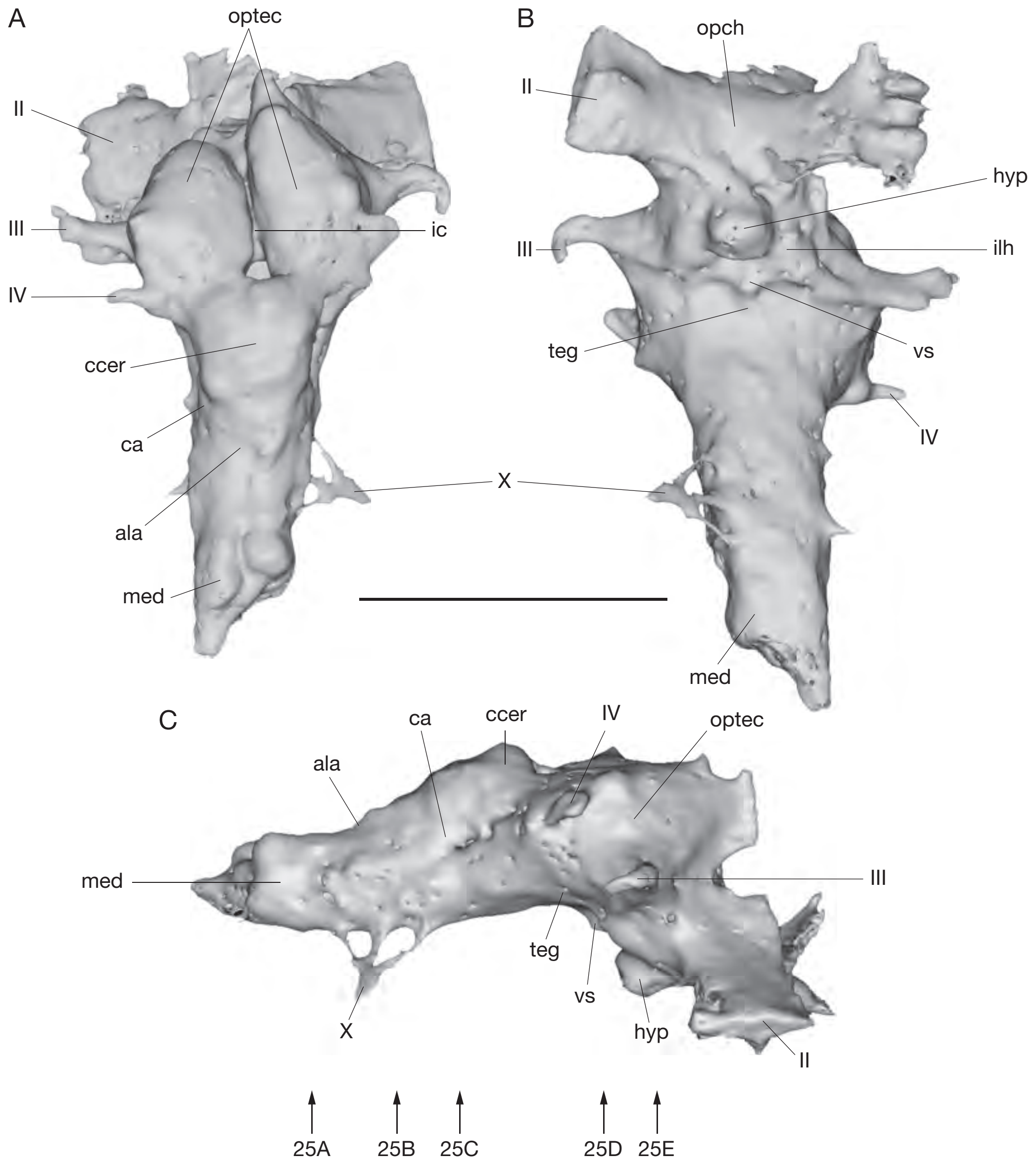

FIG. 24. — Surface rendering generated from Synchrotron Radiation holotomographic slices of the brain of KUNHM 22060; **A**, dorsal view; **B**, ventral view; **C**, right lateral view; the transverse microtomographic slices of Fig. 25 are indicated. Abbreviations: see Materials and methods. Scale bar: 1 mm.

backward behind the corpus cerebelli and is continuous posteriorly with the acoustico-lateral area (ala, Figs 24A, C; 25F), which is commonly covered by the crista cerebelli in extant chondrichthyans.

The cerebellum appears relatively small and the anterior part of the corpus does not protrude over the optic tectum (ccer, optec, Fig. 24A), contrary to the condition in extant holocephalans (Kuhlenbeck & Niimi 1969; Yopak *et al.* 2007; Ari &

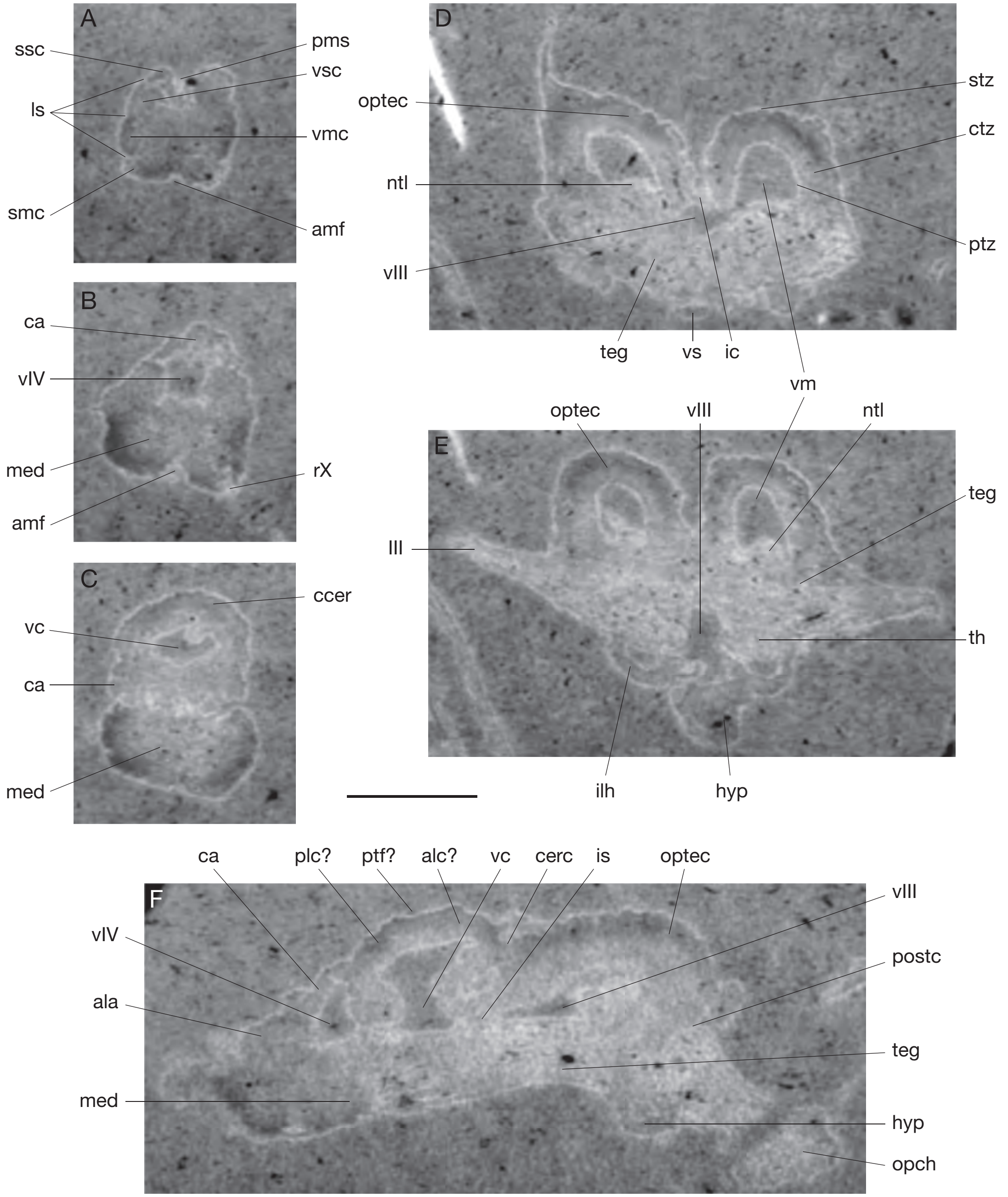

FIG. 25. — Transverse (**A**-**E**) and saggital (**F**) microtomographic slices generated from Synchrotron Radiation holotomographic through different part of the brain of KUNHM 22060 (levels of the transverse slices indicated by arrows on Figure 24C): **A**, through the posterior medulla oblongata; **B**, through the cerebellar auricles; **C**, through the corpus cerebelli; **D**, through the caudal part of the mesencephalon; **E**, through the diencephalon and the rostral part of the mesencephalon; **F**, through the longitudinal mid-line of the brain. Abbreviations: see Materials and methods. Scale bar: 1 mm.

Kálmán 2008; Yopak & Montgomery 2008) and galeomorph sharks (Yopak *et al.* 2007). Nevertheless, the optic tectum of the former appears more ventral in position, situated almost below the cerebellum, probably because of the general ventral displacement of the mesencephalon in parallel with the presence of the interorbital septum immediately anterior to it, whereas in galeomorph sharks, this is due to the hypertrophy of the cerebellum.

The corpus cerebelli is non-convoluted, as in hexanchiform, squaliform, pristiophoriform, squatinomorph sharks and holocephalans, even though the latter have a rather large cerebellum (Northcutt 1978; Ari & Kálmán 2008). However, it is difficult to know whether or not the corpus is divided into lobes in the sibyrhynchid brain. The presence of anterior and posterior pouches of the cerebellar ventricle (vc, Fig. 25C, F) may suggest that the corpus cerebelli is actually divided into anterior and posterior lobes (alc?, plc?, Fig. 25F), as in chimaeroids, squatiniforms, squalomorphs and some galeomorphs, such as heterodontids and scyliorhinids (Northcutt 1978), whereas other galeomorph sharks have a hypertrophied and convoluted corpus divided into three lobes. Nevertheless, these putative lobes are not clearly visible externally, and the so-called primary transverse fissure (ptf?, Fig. 25F) that usually separates the corpus in anterior and posterior lobes, is barely visible contrary to the condition in most neoselachians. However, extant chimaeroids also have a corpus divided into two lobes with a less developed primary transverse fissure than that of neoselachians (Kuhlenbeck & Niimi 1969). A smooth corpus divided into anterior and posterior lobes is considered as an ancestral condition for chondrichthyans by Northcutt (1978).

The corpus is connected ventrally with the medulla oblongata immediately anterior to the cerebellar auricles (med, Fig. 25C, F). The auricles also appear relatively small, as in osteichthyans (Bertin 1958), and it is unfortunately not possible to distinguish their folds.

The medulla oblongata (med, Figs 24; 25A-C, F), which seems to be relatively narrow, extends forward as far as the root of the trochlear nerve (IV, Figs 24; 26A-D) below the cerebellum. The fourth ventricle (vIV, Fig. 25B, F), which corresponds to the open division of the medulla, is preserved from approximately the posterior end of the corpus cerebelli to the posteriormost root of the presumed vagus nerve (X, Fig. 24; rX, Fig. 25B). It seems to be continuous anteriorly with the cerebellar ventricle (vc, Fig. 25C, F), as in extant chimaeroids (Ari & Kálmán 2008). Its roof is formed rostrally by the cerebellum and more caudally by probably a choroid tissue, which is thinner than the floor of the ventricle, so that even though the fourth ventricle is commonly called "open part of the rhombencephalon", there is no evidence of a real opening. The floor of the fourth ventricle is the closed part of the medulla oblongata. At the level of the fourth ventricle, it clearly displays only one median groove, which certainly corresponds to the anterior median fissure (amf, Fig. 25B). However, posterior to the posteriormost root of the presumed vagus nerve, the medulla has a different morphology that recalls the morphology of the spinal chord (Fig. 25A). Indeed, there is no fourth ventricle and the medulla oblongata displays in transverse section four longitudinal columns, which are separated from each other by rather shallow grooves that correspond to the different sulci. The dorsomedial one represents probably the posterior median sulcus (pms, Fig. 25A), the ventromedial one may correspond to the anterior median fissure (amf, Fig. 25A) and there are three additional lateral sulci (ls, Fig. 25A). The longitudinal column comprised between the anterior median fissure and the lateral sulcus situated immediately dorsolateral to the anteriomedian fissure may correspond to the spinal somatic motor column (smc, Fig. 25A), whereas the immediately next dorsal column is probably the spinal visceral motor column (vmc, Fig. 25A). The following two dorsalmost column may be the spinal visceral sensory column (vsc, Fig. 25A) and the spinal somatic sensory column (ssc, Fig. 25A), respectively. Three branches leave the brainstem in its ventral part. The anteriormost branch is situated at the level of the cerebellar auricles and the posteriormost one is located posterior to the acoustico-lateral area. The anteroposterior disposition of these branches recalls the pattern of the different roots of the vagus nerve (rX, Fig. 25B). Nevertheless, the roots of the vagus nerve normally originate from the visceral motor column, whereas

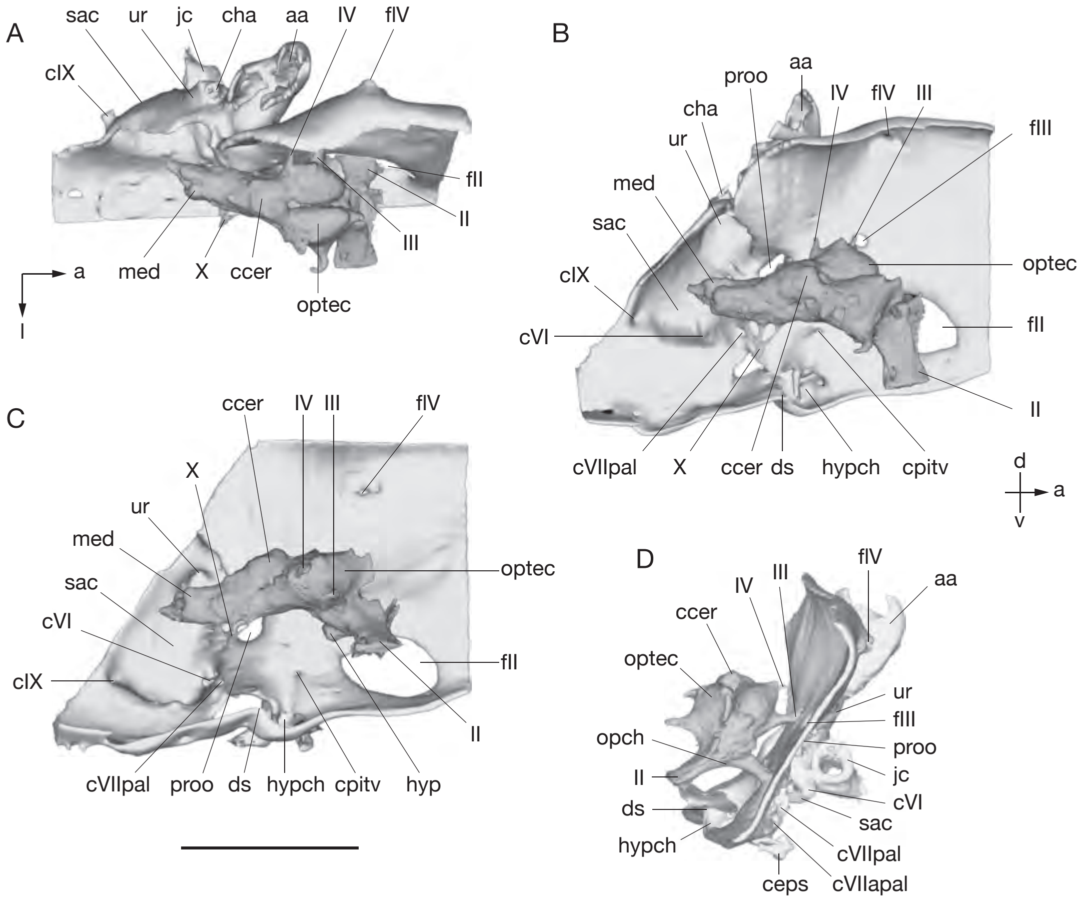

FIG. 26. — Surface rendering generated from Synchrotron Radiation holotomographic slices of the phosphatized brain, presumed preserved nerves and internal surface of a part of the endocranial cavity of KUNHM 22060: **A**, dorsal view; **B**, dorsolateral view; **C**, lateral view; **D**, anterior view. Line and arrows point anteriorly (a), laterally (l), ventrally (v) and dorsally (d). Abbreviations: see Materials and methods. Scale bar: 5 mm.

they seem to originate here more ventrally, in the somatic motor column. However, at this level the different columns are not well defined and a slight distortion of the roots due to the fossilization may have occured. In addition, in extant chimaeroids, there are dorsal and more ventral roots of the vagus nerve (Kuhlenbeck & Niimi 1969: figs 5; 8).

MESENCEPHALON

The brain displays a constriction between the rhombencephalon and the mesencephalon, which represents the isthmus rhombencephali that connects these two brain regions (is, Fig. 25F).

Anterodorsally to the corpus cerebelli are two large ovoid lobes, which represent the optic tectum of the mesencephalon (optec, Figs 24A, C; 25D-F). The latter is separated from the metencephalon by a cerebelar commissure (cerc, Fig. 25F). The caudal part of the optic tectum is not overlapped by the corpus cerebelli (see above), and the two lobes appear comparatively very large, perhaps in correlation to the important size of the eyes in iniopterygians. The optic lobes are well separated from each other dorsally, and an intertectal commissure (ic, Figs 24A; 25D) unites them ventrally, except on their caudal part. A ventricular mesencoelia (vm, Fig. 25D) is present inside each lobe and seems to be continuous with the cerebellar ventricle and the third ventricle (vIII, Fig. 25D-F). Moreover, it is open dorsally and communicates with the surrounding endocranial cavity immediately anterior to the corpus, at the caudal extremity of the mesencephalon (Fig. 24A). Such a condition is unknown among extant chondrichthyans.

The optic tectum of Recent chondrichthyans consists of multiple laminae, which Northcutt (1978) grouped into three zones: periventricular, central and superficial. There is considerable variation concerning the histology of the different zones between extant holocephalans and elasmobranchs, especially concerning their relative concentration of cells (Northcutt 1978).

Unfortunately, these zones are not clearly well defined in the material studied here, and the different contrasts observed in the tectum must be interpreted with great reservations. They could represent indication of fossilized laminae or merely a diagenetic bias. Nevertheless, I suggest here a possible correspondance between these laminae and the zones observed in the fossilized brain (ptz, ctz, stz, Fig. 25D). Unfortunately no comparative description of the histology within the extant elasmobranchs and holocephalans is possible. At the level of the caudal part, the lateral wall of the optic tectum displays a lateral projection, which corresponds in position to the root of the trochlear nerve (III, Figs 24; 25E). At mid-length of the mesencephalon, a dorsally-oriented projection emerges from the dorsal part of the optic tectum (Fig. 25D). This position does not correspond to that of any cranial nerve in known brain fishes. Nevertheless, it could be either a blood vessel or an artefact. The rostral part of the mesencephalon shows a rather deep median infolding of the optic tectum (optec, Fig. 25E), as seen in extant chimaeroids.

The midbrain floor, or tegmentum (teg, Figs 24B, C; 25D-F), is continuous posteriorly with the medulla oblongata. Its external and internal caudal morphology appears regular as far as its mid-region, where the root of oculomotor nerve emerges laterally. At this level, a pair of bulges lays the floor of the paired ventricle (ntl, Fig. 25D, E). These may represent the location of the nucleus tegmentalis lateralis, present at the same position in extant chimaeroids (Ari & Kálmán 2008). The rostral end of the tegmentum is prolonged ventrally by the diencephalon.

PROSENCEPHALON

The diencephalon is situated below the rostral part of the mesencephalon, posterior to the optic chiasm (opch, Figs 24B; 25F). It is separated from the mesencephalon by the posterior commissure (postc, Fig. 25F).

The epithalamus, which corresponds to its dorsal part, and the thalamus, which forms its lateral walls, are not clearly distinct from each other, but its floor is well preserved. The thalamus (th, Fig. 25E) seems to be continuous caudally with the tegmentum (teg, Fig. 25E) of the mid-brain, as in extant chondrichthyans.

The floor of the diencephalon comprises, from front to rear, the optic chiasm (opch, Figs 24B; 25F), the inferior lobes of the hypothalamus (ilh, Figs 24B; 25E), the infundibulum containing the hypophysis (hyp, Figs 24B, C; 25E) and the vascular sac (vs, Figs 24B, C; 25D). The central third vesicle (vIII, Figs 25E, F) is also well defined, flanked by the inferior lobe of the hypothalamus, and floored by the hypophysis. The vesicle of each inferior lobe of the hypothalamus is therefore continuous with the third vesicle at the level of the anterior end of the hypophysis.

The inferior lobes of the hypothalamus have extensive lateral recesses, as in chimaeroids, sharks and primitive batoids (Northcutt 1978). Between them is a bulb that most probably represents the hypophysis. Posterior to the hypophysis is a small median process, which may correspond to the vascular sac. Anterior to the inferior lobes of the hypothalamus and the hypophysis is the optic chiasm, which illustrates the decussation of very large optic nerves that are a diencephalic derivative.

The telencephalon is unfortunately missing in the sibyrhynchid specimen that displays the fossilized brain. Nevertheless, the optic nerve is situated very far from the olfactory canals of the endocranial cavity (olfc, Figs 27; 29; 30), which are assumed to house the olfactory tracts. This suggests a very long telencephalon, similar to that of Recent chimaeroids.

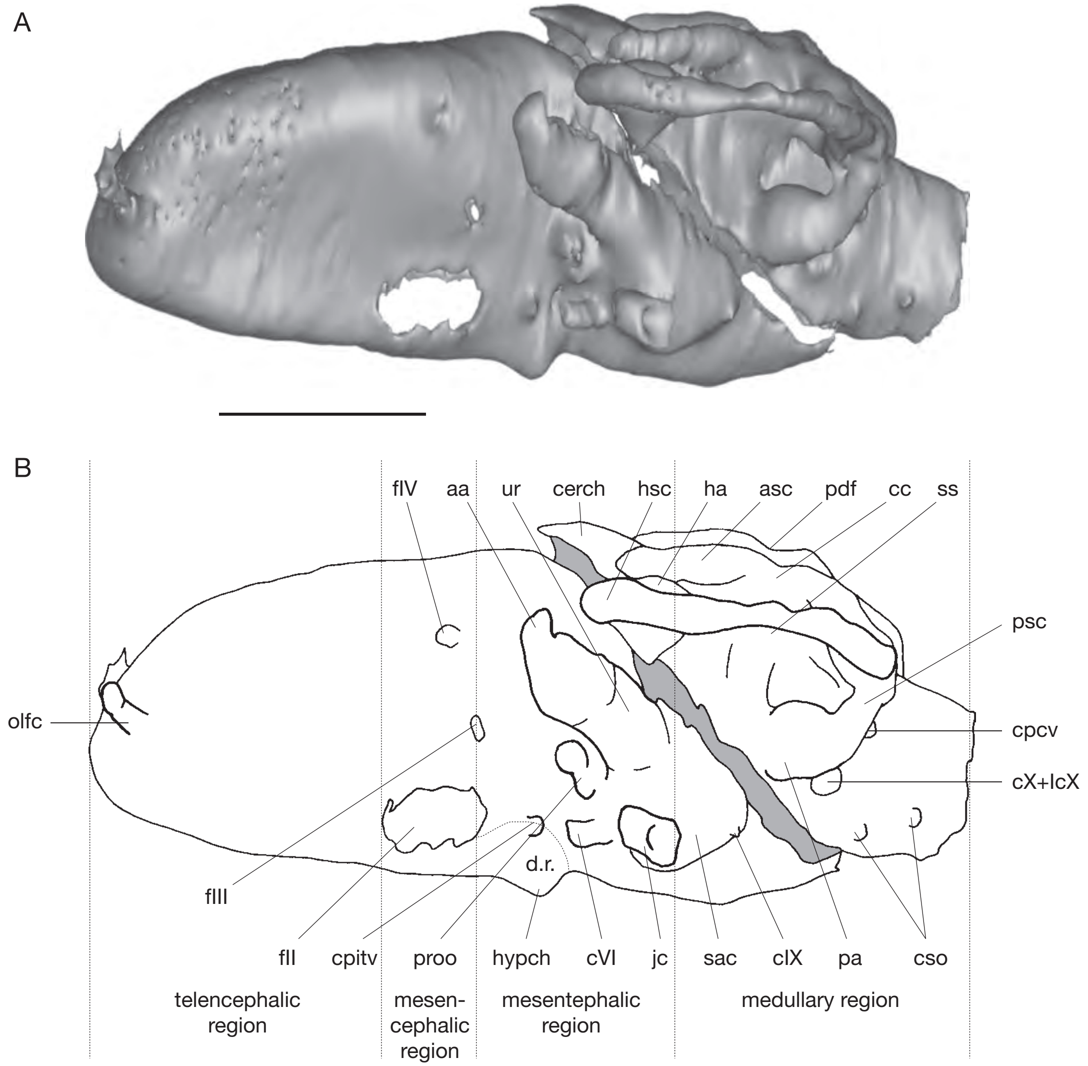

FIG. 27. — Lateral view of the endocranial cavity of KUNHM 22060, left side; **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

DESCRIPTION OF THE ENDOCRANIAL CAVITY

GENERAL FEATURES

The braincase of chondrichthyans displays two layers of calcified cartilage forming the inner and the outer surfaces of a single wall. The outer layer forms the external outline of the neurocranium and the inner one lines the endocranial cavity (ol, il, endc, Figs 5; 8; 22). The morphology of the endocranial cavity may not be reflected by the external outline of the braincase. Therefore, since the morphology of the endocranial cavity has considerable phylogenetic potential (Maisey 2004a), it must be studied, but apart from the external braincase morphology. Fossilized brains are exceptional, and it is useful to use terms of brain morphology to describe the endocranial cavity, because the different regions of the brain may be inferred from the endocranial cavity by using, as landmarks, the position of the foramina or canals for the exit of the respective nerves.

There is no evidence of dorsal opening or dorsal protuberance for a pineal organ that reaches the roof of the braincase (Figs 8; 27). Since the medial capsular wall of the otic capsule is unmineralized, the labyrinth chamber is therefore confluent with the brain cavity (Figs 8; 23; 26B, C), as in *Cladodoides*,"*Cobelodus*" (Maisey 2005: figs 22-25; Maisey 2007: figs 24-30), extant chimaeroids and osteichthyans.

The general width of the endocranial cavity regularly increases anteriorly as far as the opening for the trochlear nerve (fIV, Figs 29; 30). Then it tapers forward. The anterior end of the brain cavity confirms that there is no precerebral fontanelle (Fig. 29).

In the endocranial cavity, the anterior margin of the optic foramen is assumed to mark the limit between the telencephalic region and the diencephalic/mesencephalic region (Fig. 27). Consequently, the telencephalic region in iniopterygians appears relatively elongated, as also observed in extant chimaeroids.

The telencephalic region of the endocranial cavity of iniopterygians is relatively large and deep (Figs 27; 29; 30). Posteriorly, it merges imperceptibly with the diencephalic and mesencephalic region, as in *Heterodontus* Blainville, 1816, *Squatina* Duméril, 1806, *Hexanchus* Rafinesque, 1810, *Notorynchus* and *Cladodoide*s (Maisey 2004a: figs 1B, D-F; 2B; Maisey 2005: figs 22; 23). Anteriorly, it ends with a pair of narrow canals for the olfactory tract (olfc, Figs 29; 30) that reach the olfactory capsules. There is no evidence of a presphenoid process along the inner wall of the telencephalic chamber. The posterior end of the telencephalic region is marked on either side by a broad and ovoid opening for the optic nerve and arteries (fII, Figs 26B, C; 27; 28; 30).

The mesencephalic region, comprised between the optic foramen and trochlear nerve foramen (fII, fIV, Figs 26B, C; 27; 28), appears to be the broadest part of the endocranial cavity, but is particularly short. The oculomotor nerve enters the cartilage immediately above the posterior limit of the large optic foramen (III, fIII, fII, Figs 26-28). This arrangement is peculiar because in chondrichthyans, it usually reaches the wall of the endocranial cavity more posteriorly. The trochlear nerve enters the cartilage far dorsally, at the level of the roof of the endocranial cavity. It is situated more dorsal than in other Paleozoic chondrichthyans, but a similar condition is observed in *Notorynchus* (Maisey 2004b: fig. 7C). The trochlear nerve foramen of the endocranial cavity is located dorsal and anterior to the oculomotor nerve. This condition is seen in modern chimaeroids and hybodonts among chondrichthyans and is considered as a derived character of these taxa (Coates & Sequeira 1998).

The metencephalic region is approximately indicated by the trochlear nerve foramen anteriorly and, posteriorly, by the beginning of the elevation of the sinus superior leading to the posterior dorsal fontanelle (fIV, ss, Figs 27; 29). The cerebellar chamber (cerch, Figs 27; 29), which constitutes this metencephalic region, is narrower than the mesencephalic region. Dorsally, the cerebellar chamber does not seem to form paired vestibulolateral (auricular) chambers. Dorsally to the foramen for the trigeminal, facial and anterodorsal lateral line nerves, the cerebellar chamber slopes abruptly as seen in *Chlamydoselachus* (Allis 1923: fig. 12).

The prootic foramen is broad and situated immediately in front of the utricular recess (ur, Figs 27; 28). The main trunk of the facial nerve, not yet differentiated into anterior and posterior rami, passed through an anterodorsally-oriented canal (cVII, Fig. 28). The junction of the latter to the endocranial cavity is located ventral and slightly posterior to the prootic foramen, at the base of the anterior end of the saccular chamber (proo, sac, Fig. 28).

The canal for the facial nerve is anteriorly connected to a more ventral canal (cVIIapal, cVIIppal, cora, Fig. 28) by a vertical canal (cVIIpal, Fig.28), which presumably leads the palatine ramus into it. The ventral canal, which also houses the orbital artery, is directed anterodorsally and is much larger than the canal for the facial nerve. It is situated below the latter and lateral to the hypophyseal chamber (hypch, Fig. 28).

An acustico-trigemino-facial recess was defined by Allis (1914, 1923) as an internal recess located

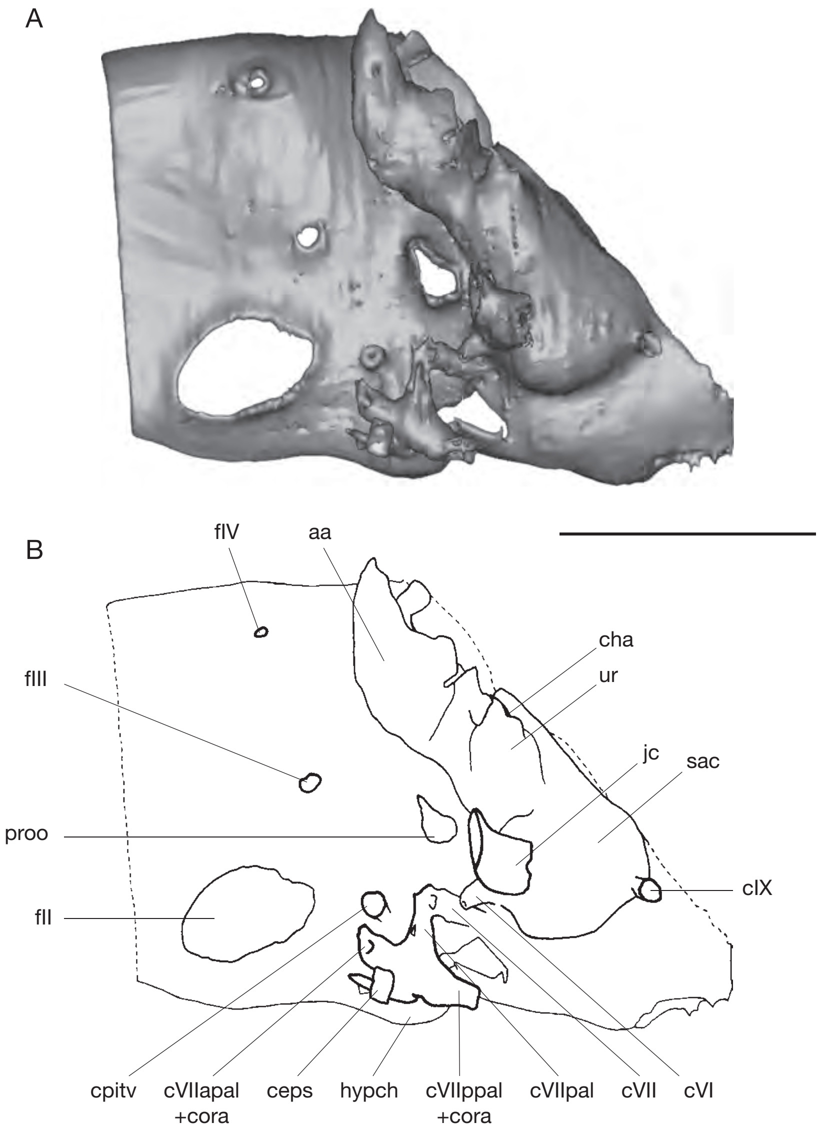

FIG. 28. — Detail of the endocranial cavity at the level of the posterior part of the orbit of KUNHM 22060 in lateral view, left side; **A**, surface rendering generated from Synchrotron Radiation holotomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

immediately anterior to the otic capsule within the prefacial commissure, and containing the roots of the trigeminal, facial and abducens nerves. The ganglia of the trigeminal and facial nerves lie partly in this recess and partly in the trigemino-pituitary fossa for the trigeminal one. Such an acustico-trigemino-facial recess may thus be present within the prefacial commissure in the iniopterygians studied here. The prootic foramen is situated in a depression in the internal wall of the endocranial cavity, in which was probably housed at least part of the trigeminal ganglion (see above).

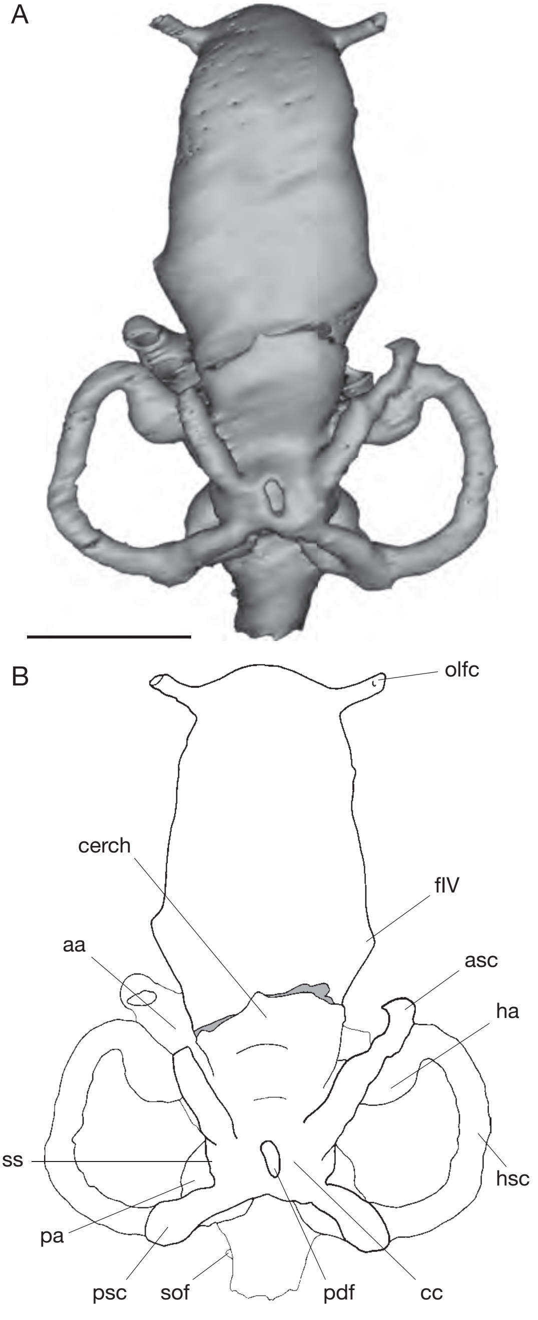

FIG. 29. — Dorsal view of the endocranial cavity of KUNHM 22060: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

Such an acustico-trigemino-facial recess, or at least a trigemino-facial recess (containing only the facial and trigeminal foramina) is present in neoselachians (e.g., *Chlamydoselachus*, *Squalus* Linnaeus, 1758, *Notorhynchus* [Allis 1914, 1923; El-Toubi 1949; Maisey 2004b]) and probably in some Paleozoic elasmobranchs, such as *Cladodoides* (Maisey 2005).

In extant chimaeroids, it seems to be absent (Jollie 1962: figs 5-19D; pers. obs.), since there is no evidence of a prefacial commissure and the ganglia for trigeminal and facial nerves lie within the prootic foramen and the trigemino-pituitary fossa. Nevertheless, the antotic foramen is situated in a depression in the internal wall of the endocranial cavity, as does the prootic foramen of iniopterygians.

At the posterior margin of the hypophyseal chamber is the interorbital canal for the pituitary vein (cpitv, Fig. 28). The jugular canal is situated close to the lateral wall of the anterior part of saccular chamber (jc, sac, Fig. 28), and it is also directed anterodorsally. Medial to it is a small canal that transmitted the abducens nerve (cVI, Fig. 28) from the saccular chamber to the posterior part of the orbit.

Canals for the spino-occipital nerves are represented in the endocast by a series of short bridges oriented posterodorsally in the myelencephalic region (cso, Fig. 27).

The diencephalic region (d.r., Fig. 27) includes the hypophyseal chamber underneath the mesencephalic region. The latter is very short in sibyrhynchids, since the trochlear nerve foramina are very close to the optic ones. The hypophyseal chamber is also short (hypch, Figs 26B, C; 27; 28; 31). Behind the hypophyseal chamber, the floor of the endocranial cavity is formed by the dorsum sellae, which is oriented posterodorsally (ds, Figs 8; 26B, C). The latter is very small. These characteristics also indicate a small diencephalic region. There is no evidence of an opening on the ventral surface of the basicranium for a hypophyseal pit.

GENERAL FEATURES OF THE SKELETAL LABYRINTH

The skeletal labyrinth is seen here in views of the endocast (Figs 27; 29; 30). The otic capsules are shallow and they display the general gnathostomes features, including the anterior, posterior and horizontal semicircular canals with their respective ampullae, and the vestibular chamber ventrally. Behind the cerebellar chamber and between the otic capsules, the crus commune rises and merges dorsally with the posterior dorsal fontanelle (cc, pdf, Figs 27; 29). This has been considered a primitive gnathostome character.

The endocranial cavity appears more constricted in this region below the sinus superior.

The vestibular chamber is almost entirely confluent with the cranial cavity (sac, ur, Figs 8; 23; 26B, C). The medial capsular wall is unchondrified as in extant chimaeroids and most of Paleozoic chondrichthyans. The vestibular chamber is subdivided into two regions. The dorsal region is the utricular chamber (ur, Figs 27; 28; 30) and the ventral one is the saccular chamber (sac, Figs 27; 28; 30). There is no evidence of a prominent lagenar chamber. The utricular and saccular chambers are relatively small and meet medially. The utricular recess is represented by a low bulge that is constricted at the level of its junction to the dorsal anterior ampulla and the ventral saccular chamber. The anterior ampulla (aa, Figs 27; 28) is connected to the anterodorsal part of the utricular recess, while the horizontal ampulla (ha, Fig. 27) seems to have a separate ventral projection (cha, Fig. 28) connecting the posterodorsal part of the utricular recess. Unfortunately there is a crack just at this level.

Since there is no chondrified medial wall, the octaval nerve passes presumably directly into the utricular recess.

The horizontal semicircular canal (hsc, Figs 27; 29) lies just above the deep depressions housing the gills, and lies along the dorsal part of the postorbital wall. The anterior (asc, Figs 27; 29) and posterior (psc, Figs 27; 29) semicircular canals meet dorsally at a crus commune (cc, Figs 27; 29), below which is a sinus superior (ss, Figs 27; 29) connecting the crus commune and the saccular chamber. The posterior ampulla (pa, Figs 8; 27; 29) is confluent with the saccular chamber and there is no evidence of a preampullary canal (*sensu* Maisey 2001b). The horizontal canal is strongly curved. It enters the sinus superior just below the crus commune after meeting the posterior canal. It is unclear if the horizontal canal passes inside the loop of the pos-

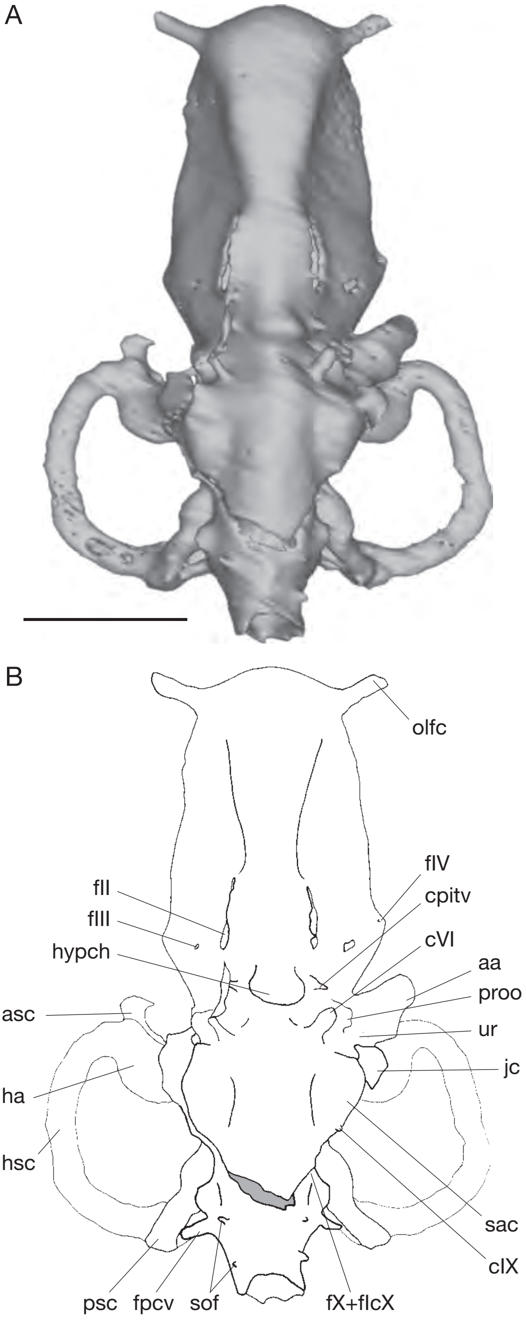

FIG. 30. — Ventral view of the endocranial cavity of KUNHM 22060: **A**, surface rendering generated from Synchrotron Radiation microtomographic slices; **B**, corresponding drawing. Abbreviations: see Materials and methods. Scale bar: 5 mm.

terior canal, as it generally does in gnathostomes, or if the two canals are confluent in this area. In "*Cobelodus*" (Maisey 2007: figs 24; 25), the two canals approach each other very closely, whereas in *Cladodoides* they are well separated. The ampulla of the horizontal canal, situated behind and slightly above the anterior ampulla, seems to meet ventrally the utricular recess.

As in *Notorynchus* and *Squalus*, the plane of the horizontal semicircular canal (hsc, Fig. 27) of the iniopterygians studied here is almost parallel to the long axis of the braincase, the hypophyseal chamber (hypch, Fig. 27) is ventral to the level of the saccular chamber (sac, Fig. 27) and the vestibular chamber does not extend much below the level of the floor of the medullary region.

The three ampullae are located above a longitudinal axis passing through the occipital region, because of the lack of depth of the otic capsules.

The semicircular canals are narrow, and the horizontal semicircular canal has a relatively marked radius of curvature (hsc, Fig. 29).

DESCRIPTION OF THE LOWER JAW AND ITS ARTICULATION WITH THE PALATOQUADRATE

The lower jaw is preserved in KUNHM 22060 (Fig. 31). It has been slightly displaced during the fossilization (Fig. 31A), but by means of MIMICS® software it is possible to place it virtually in its natural position (Fig. 31B).

The Meckelian cartilages are fused at the symphysis, so that the mandible has the same shape as that described in *Iniopera* by Zangerl & Case (1973: figs 68; 70). The mandible forms a massive rectangular and slightly convex cartilage anteriorly that recalls the mandible of dipnoans (e.g., *Melanognathus* Jarvik, 1968). The anterodorsally curved rostral end of the mandible is blunt. The anterior corners display two large lateral processes (lpm, Fig. 31C, F, G), which could have borne correspondingly "canine" tooth whorls to those on the symphysial dentigerous plate of the braincase (see below). Behind these two processes are crests (lcm, Fig. 31C, F, G), which may have supported a tooth whorl similar to the palatine one. Nevertheless, there is no evidence of the central ridges similar to those present in the upper jaw.

One foramen is present at the lingual base of each anterolateral process, and is connected to another foramen present on the labial side of the processes by a short, dorsally oriented canal (fVmd, Fig. 31F, G). These foramina and canal could be the passage for the mandibular ramus of the trigeminal nerve, which innervated the inferior lip. On the lateral side of the mandible, anterior to the articular zone, there is a distinct depression, which sits in the corner and occupies half of each branch of the mandible. This may have housed the adductor musculature (fam, Fig. 31C, F, G). The mandible ends posteriorly by a massive articular zone with medial and lateral articular processes, which flank a concave facet (map, lap, am, Fig. 31D-G). As in all extant chimaeroids (Didier 1995), the iniopterygians described here have a double-articulating jaw joint. The quadrate process shows a lateral process and medial fossa that perfectly interlock with the concave facet and medial process of the Meckelian cartilage. This type of jaw joint is interpreted as a primitive condition in gnathostomes by Hotton (1952) and Miles (1964).

The lateral process of the mandible, similar to the "retroarticular process" of the extant *Callorhinchus milii* Bory de Saint-Vincent, 1823 (Didier 1995: 33, 34), passes laterally to the lateral process of the quadrate process.

DENTITION AND DERMAL DENTICLES

Dentition

The tooth whorls in the Sibyrhynchidae have been previously described by Zangerl & Case (1973). Nevertheless, their relative position inside the mouth was essentially speculative. Since there is no evidence of mandibular tooth whorls in natural position in the mandible of KUNHM 22060, the comparison of the dentition will be made only on the basis of the dentition of the upper jaw of the Sibyrhynchidae described by Zangerl & Case and the new material studied in the present work.

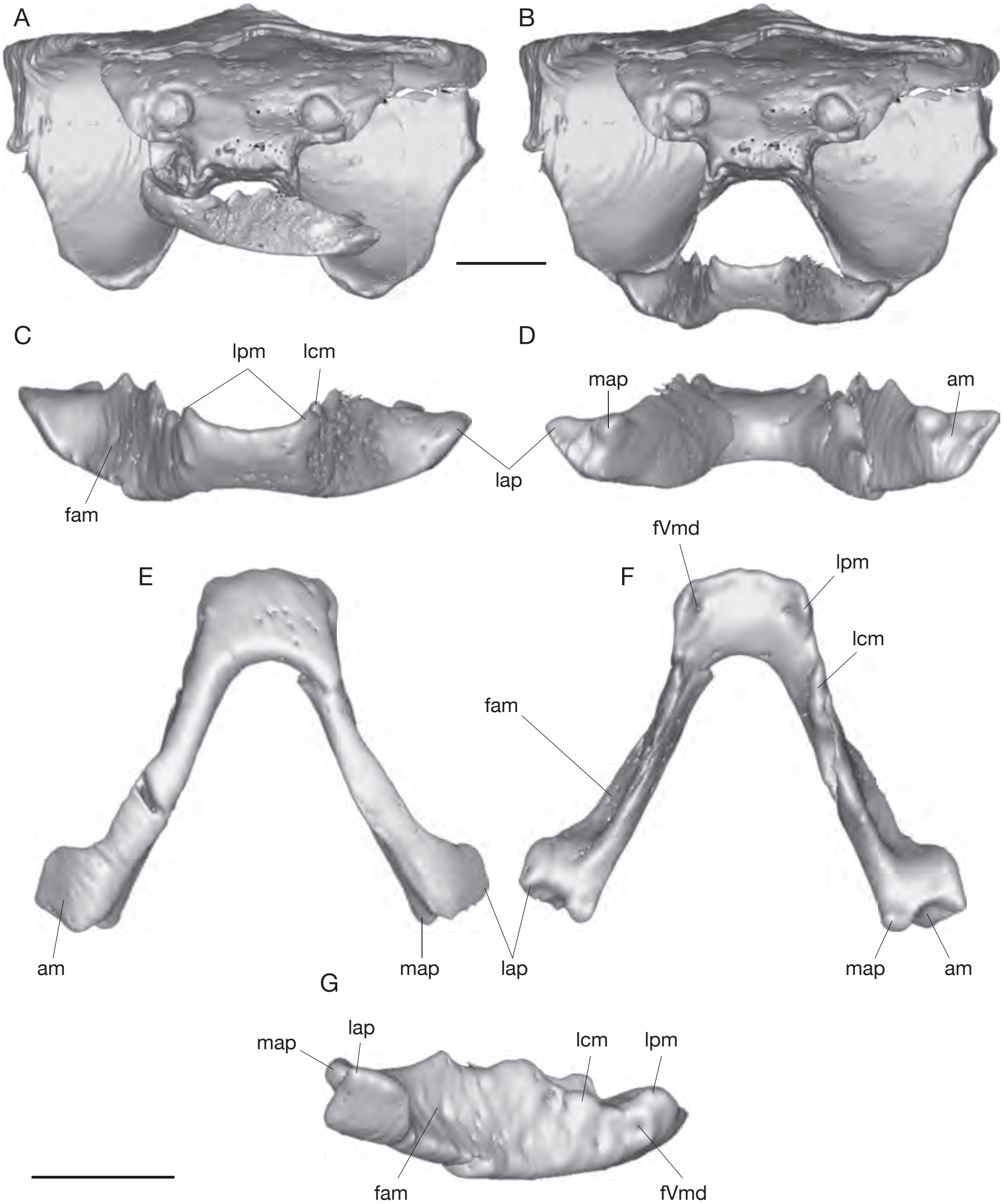

FIG. 31. — Surface rendering generated from Synchrotron Radiation microtomographic slices of braincase and lower jaw of KUNHM 22060: **A**, relative position of the lower jaw as found inside the nodule; **B**, lower jaw virtually placed to its supposed natural position; **C**-**G**, lower jaw in anterior (**C**), posterior (**D**), ventral (**E**), dorsal (**F**), and right lateral (**G**) views. Abbreviations: see Materials and methods. Scale bar: 5 mm.

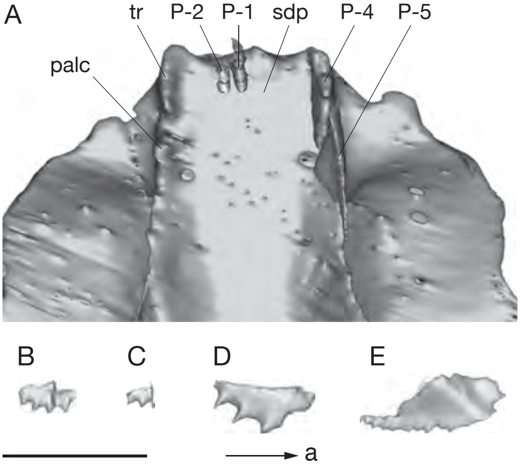

FIG. 32. — The upper jaw dentition in KUNHM 22060: **A**, ventral view of the anterior extremity of the skull showing the natural disposition of the different kinds of tooth whorls; **B**, lateral view of the P-1; **C**, lateral view of the P-2; **D**, lateral view of the "canine" or P-4; **E**, lateral view of the palatine tooth whorl or P-5. Arrow points anteriorly (a). Scale bar: 5 mm. Abbreviations: see Materials and methods.

KUNHM 22060 displays the natural association between the teeth and these ridges (Fig. 32A), whereas the other nodules contained scattered teeth, beside the neurocranium. Each ridge supports a tooth whorl that is oriented anteroposteriorly and they are parallel to each other, as in *Inioxyele* (Zangerl & Case 1973: fig. 82).

OKM 38 clearly shows four pairs of transverse ridges in the dental symphysial plate, and one lateral pair of palatine crest (tr, Fig. 17). The lateralmost two ridges are more developed than the six central ones, in which the centralmost two ridges are quite significantly larger than the others.

However, KUNHM 22060 clearly displays only three pairs of transverse ridges in the dental symphysial plate (tr, Fig. 7). For each pair, one of the two ridges is associated with its corresponding tooth whorls (tr, P-1, P-2, P-4, Fig. 32). One pair of palatine crests is also present and the left one supports its respective tooth whorls (palc, P-5, Fig. 32). Nevertheless, on each side, a space is present between the lateralmost preserved ridge of the dental symphysial plate and the palatine crest. It may correspond to a fourth pair of transverse ridges, not preserved in this specimen. Therefore, it is assumed that there are also four pairs of transverse ridges in the symphysial dentigerous plate, plus one pair of lateral palatine crests that support tooth whorls in the upper jaw in the iniopterygians studied here. There is no evidence of a single symphysial tooth whorls flanked by a series of paired tooth whorl, as previously described in *Iniopera*. The number of pairs of tooth whorls differs from what was previously described in *Sibyrhynchus*.

The palatine tooth whorl (P-5, Fig. 32A, E) is the largest one, and located on the palatine crest of the palatoquadrate. In its anterior part, the tooth crown is not clearly distinguishable. The palatine tooth whorls may thus correspond to the lateral tooth whorls or P-6 described by Zangerl & Case (1973: figs 47; 50) in *Sibyrhynchus*.

The fourth tooth whorl (P-4, Fig. 32A, D) from the symphysis is attached to the lateral large ridge of the dental symphysial plate just in front of the palatine tooth whorl and interlocks perfectly with the latter. It is the largest tooth whorl and the tooth crown is quite massive and the teeth are well separated. It may correspond to the "canine" tooth whorl described by Zangerl & Case (1973: fig. 50).

The third tooth whorl is lacking on KUNHM 22060. The first and second one are present (P-1, P-2, Fig. 32A-C) and the first one is larger than the second one. They are similar to the P-1 and P-2 described by Zangerl & Case (1973: fig. 50) in *Sibyrhynchus*.

In the specimen described by Zangerl & Case (1973: fig. 50), only the P-1, P-2 and P-3 are *in place* and the size of the tooth whorls decreases from P-1 to P-3. Thus it is assumed that the P-3 in the iniopterygians described here may be the same as that mentioned by Zangerl & Case.

DERMAL DENTICLES COVERING THE HEAD

Zangerl & Case (1973: 53; fig. 63) mentioned the presence of "a patch of dermal denticles that form a pavement presumably on the dorsal (or ventral) side of the head of *Iniopera richardsoni*". A similar patch of small dermal denticles clearly covers the posterior and lateral part of the dorsal surface of the skull in KUNHM 22060 (pdd, Fig. 33A). They are extremely difficult to observe in SRµ-CT scan slices, and manual preparation on this specimen was necessary for observing them. The other neurocrania are not filled with matrix, so that manual preparation is not possible.

The Sibyrhynchidae previously described are assumed to bear in the snout and lower jaw strong tubercles consisting mostly of trabecular dentine (Zangerl & Case 1973: figs 47; 50; 65). Similar tubercles are present free in the different nodules housing the neurocrania (except KUNHM 56360), but unfortunately none of them are in natural position (Fig. 33B).

There is no evidence of similar plates that cover the floor or the roof of the mouth cavity in *Sibyrhynchus* or *Iniopera* (Zangerl & Case 1973: figs 47; 70; 71) in the nodules. However, additional tubercles are present in the roof of the skull (Fig. 33C, D). One is clearly present in natural position just in front of the posterior dorsal fontanelle and another one is observed resting on the posterolateral edge of the dorsal surface of KUNHM 21894 (dd, Figs 5; 6; 14). They are sharper and narrower than those which presumably cover the snout. Similar tubercles are found free in nodules, suggesting that they are present in different places on the skull during life.

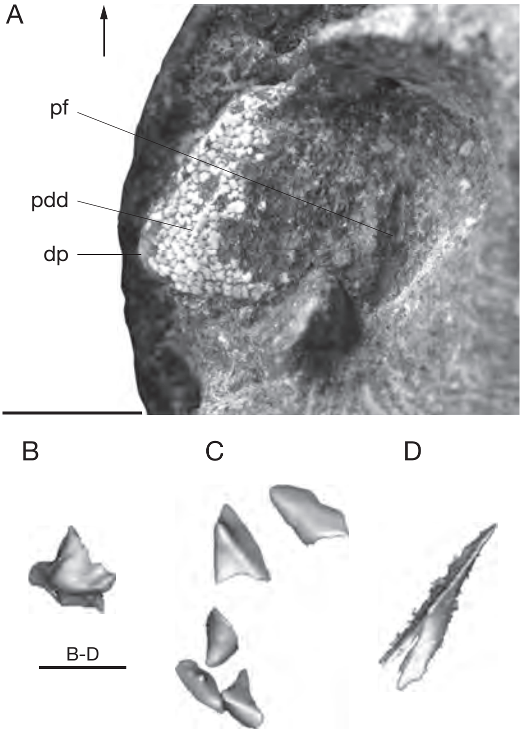

Fig. 33. — The different types of dermal denticles: **A**, photograph of the posterolateral end of KUNHM 22060, showing a patch of small dermal denticles; **B**, surface rendering of similar denticles (scattered in KUNHM 21894) as that previously described by Zangerl & Case (1973) in the snout and lower jaw of the Sibyrhynchidae; **C**, surface rendering of dermal denticles scattered in KUNHM 22060; **D**, surface rendering of dermal denticles found either scattered or attached in the lateral margin of the skull in KUNHM 21894. Scale bars: A, 5 mm; B-D: 2 mm. Abbreviations: see Materials and methods.

DISCUSSIONS

The previous interpretation by Zangerl & Case (1973) and systematics of the new specimens

The iniopterygian specimens studied by Zangerl & Case (1973) are strongly compressed dorsoventrally, therefore the authors used stereoradiographs for reconstructing their anatomy.

In order to compare the specimens described by Zangerl & Case (1973), the new material described here was virtually compressed. This assumed that the braincase in previously described specimens was originally as deep as in the material described here.

The digital contour-based surface rendering of KUNHM 22060 was therefore virtually compressed by reducing its y-axis dimension by 95% (Fig. 34) following the technique used by Maisey (2007) in his work on "*Cobelodus*". Nevertheless, although only 5-10% of the original depth is available for stereographic analysis of the radiographs, Zangerl & Case reconstructed a deep braincase in the Sibyrhynchidae (Zangerl & Case 1973: figs 56; 78), although with narrower orbits. They also mentioned a holostylic jaw suspension in this family, which is confirmed in the present work, as to the general hang-glider-like shape of the braincase. In the iniopterygians studied in the present work, the outline of the basicranium and suborbital shelf of the digitally flattened model is similar to that of *Sibyrhynchus*. Nevertheless, the specimen preserved in three dimensions displays a strong suborbital shelf that extends far ventrally to the basicranium. The strong demarcation between the ventral plate and the lateral suborbital shelf seen in *Iniopera* may represent the difference in level between the basicranium and the suborbital shelf. In addition, the specimens studied here clearly display a preorbital process, as in *Iniopera*. However the anterior end of the skull of *Sibyrhynchus* is not well preserved in the specimen described by Zangerl & Case (1973) and it could possibly be present. In sum, based on the braincase alone, it is difficult to refer the new material to either *Sibyrhynchus* or *Iniopera*.

The Meckelian cartilages are fused at the symphysis in both genera but that of *Iniopera* appears more rectangular at its anterior end (Zangerl & Case 1973: fig. 45 for *Sibyrhynchus* and figs 68 and 70 for *Iniopera*). The mandible of KUNHM 22060 displays much the same morphology as that of *Iniopera* (Fig. 31). Moreover, the skull of *Iniopera* bears at its posterior zone the same pavement of dermal denticles as seen in KUNHM 22060 (Fig. 33A).

Regarding the dentition, it is difficult to compare the arrangement of the tooth whorls, since the previous material of Sibyrhynchidae does not allow the observation of the morphology of the ethmoid part of the braincase, which bears the tooth whorls. In addition, the organization of the tooth whorls remains speculative in Zangerl & Case's (1973) work since only few specimens show clearly the natural position of the teeth in the upper jaw. Indeed, only one *Sibyrhynchus* specimen clearly has the P-1, P-2 and P-3 in place. Moreover, the three genera are supposed to have possessed similar tooth whorls (even though the teeth crowns are sharper in *Iniopera*).

The dentition of KUNHM 22060 is a combination of what was assumed by Zangerl & Case to be the condition in the Sibyrhynchidae. Nevertheless, the arrangement of the teeth in parallel is similar to what is assumed to be the condition in *Inioxyele* (Fig. 32A). Unfortunately, no braincase of this taxon is figured and described.

In conclusion, the specimens described here are very close to those in all three genera described by Zangerl & Case (1973). The strong differences between them are not at the level of the braincase or teeth (yet the braincase of *Inioxyele* is still unknown). Nevertheless, the lower jaw and the patch of dermal denticles of *Iniopera* are similar to those of KUNHM 22060.

Match between the morphology of the endocranial cavity and the brain

For a long time, the brain morphology in fossils was inferred from the shape of the endocranial cavity. Actually, only few works dealed with a match between the morphology of the brain and that of the cavity that houses it (Maisey 2004a). The brain fills much of the endocranial cavity in some elasmobranchs (e.g., batoids, lamniformes), but not in others (e.g., squaloids: Maisey 2004a). The adult coelacanth *Latimeria chalumnae* Smith, 1939 also possesses a brain that does not completely fill the endocranial cavity (Anthony & Robineau 1976), although it does so during its early growth stages. Generally, the brain of the juvenile or embryonic individuals of the most inclusive recent vertebrates fills out the entire endocranial cavity (Stensiö 1963), but during development, the brain may grow slower in size than the endocranium. Consequently, the endocranial cavity is larger (and sometimes much longer) than the brain and may differ from it in shape.

The brain of the iniopterygian studied here is the first fossilized brain (Pradel *et al.* 2009), and it therefore allows a comparative study between its morphology and that of the endocranial cavity. It appears very small compared to the endocranial cavity (br, Fig. 3; Fig. 26). Nevertheless, the preserved nerves correspond perfectly with their respective foramina, so that a possible post-mortem shrinking of the brain was probably not important.

Maisey (2004a: 158) noted that a correspondence between the length of some parts of the brain and that of their respective regions in the endocranial cavity may be absent in extant elasmobranchs: "the olfactory passage in the elasmobranch ethmoid region may significantly under-represent the original length of the olfactory tract". Nevertheless, nothing is said concerning the overall morphology.

As mentionned above, the telencephalon of the iniopterygians studied here was probably elongated. Nevertheless, the olfactory canals appear much less developed (olfc, Fig. 29), so that they may not reflect the original length of the olfactory tracts. It is also possible that the olfactory tracts were as long as the olfactory canals, so that a long telencephalon medium may have extended anteriorly approximately as far as the base of the olfactory canals. Yet according

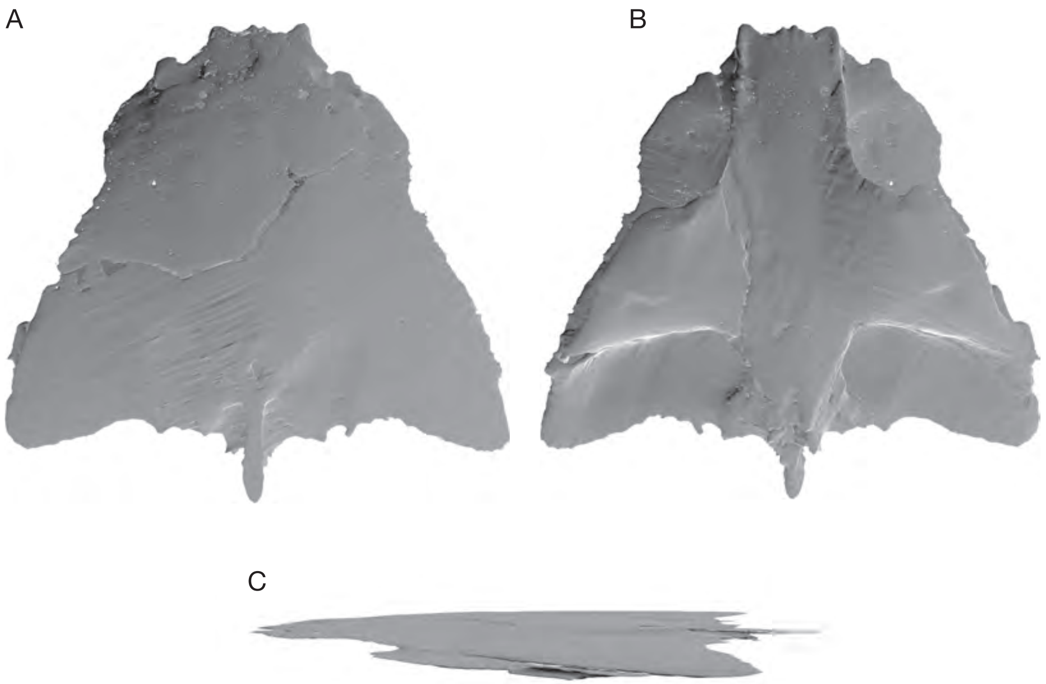

FIG. 34. — Digitally flattened contour-based surface rendering of the braincase of KUNHM 22060 (95 % along the y-axis, unaltered dimensions along x and z axes): **A**, dorsal view; **B**, ventral view; **C**, slightly tilted lateral view.

to the different landmark, the telencephalic region appears also relatively elongated (see above). Actually, in this example, the telencephalic region of the endocranial cavity may approximate the original length of the telencephalon of the brain, but it does not indicate its general morphology.

However, one can notice that some parts of the endocranial cavity may reflect the morphology of the corresponding parts of the brain. For instance, the cerebellar chamber does not seem to form paired vestibulolateral (auricular) chambers (cerch, Fig. 29), probably in correlation with the relatively small corpus cerebelli and auricles of the brain (cerch, ca, Fig. 24A).

Conversely, the mesencephalic region of the iniopterygians studied here appears to be the broadest part of the endocranial cavity, but is particularly short (Fig. 29), while the mesencephalon proper is comparatively longer (optec, Fig. 24C).

In "*Cobelodus*" and *Cladodoides*, the trochlear foramen is situated far behind the optic foramen, and near the nerve foramina related to the otic capsule, thereby suggesting a long mesencephalic region. According to Maisey (2007), this condition implies the elongation of the tegmentum of the mesencephalon and the anterior displacement of the hypothalamus in the brain, perhaps in correlation with the hypertrophy of the polar cartilages.

In iniopterygians, since the mesencephalic region of the endocranial cavity is short, but the mesencephalon of the brain relatively elongated, there is no general match, as suggested by Maisey (2007). A correlation between the outline of the endocranial cavity and the extent of the embryonic cartilages is probably correct, but a correlation between the outline of the endocranial cavity and the morphology of the brain remains doubtful for some regions.

In modern chondrichthyans, the hypothalamus fills most of the hypophyseal chamber. In *Orthacanthus* (Schaeffer 1981: fig. 14C), hybodonts (e.g., *Tribodus limae* Brito & Ferreira, 1989: Maisey

2004a: fig. 5) and modern elasmobranchs (e.g., *Notorynchus*: Maisey 2004b: fig. 7; *Squalus*: Jollie 1962: fig. 13-12), the hypothalamus (for extant species) and the hypophyseal chamber (for extinct species) respectively lie ventral to the cerebellum and the cerebellar chamber. In "*Cobelodus*" and *Cladodoides* (Maisey 2007: fig. 31A, B), the hypophyseal chamber is located completely anterior to the level of the cerebellar chamber. In iniopterygians, the hypophyseal chamber is also anterior to the cerebellar chamber (hypch, cerch, Fig. 27), and the preserved brain displays a hypothalamus that lies below the anterior extremity of the optic lobe, as in extant chimaeroids (hyp, optec, Fig. 26C; Pradel *et al.* 2009). Maisey (2007) supposed that the relative anterior disposition of the hypophyseal chamber, which is formed by the polar cartilages that fused posteriorly with the parachordals to contribute to the formation of the dorsum sellae, is also due to the hypertrophy of the polar cartilage. This suggests that iniopterygians possessed great embryonic polar cartilage, and confirms that there is an extensive basitrabecular process rather than small polar cartilage (see above).

In sum, the problem of the correspondence between the different regions of the endocranial cavity and the different regions of the brain is more complex than previously supposed. The relative length of a region of the endocranial cavity may reflect the original length of its corresponding part of the brain, but not its morphology (e.g., telencephalic region), or there may be no match (e.g., mesencephalic region). Nevertheless, the relative disposition of the different parts of the endocranial cavity probably reflects the relative disposition of the corresponding parts of the brain (e.g., hypophyseal and cerebellar chambers). In all these cases, the overall morphology of the endocranial cavity does not reflect that of the brain, but in the case of the cerebellar chamber, the morphology of the latter may provide some indication about the overall morphology of the cerebellum and cerebellar auricles.

Mode of life

Iniopterygians are retrieved from localities of North America and western Europe: The Mississippian of Montana (USA), the Serpukovian of Bearsden (Scotland), the Pennsylvanian of Kansas, Oklahoma and Indiana (USA), which all represent marine, epicontinental basins in a semitropical and wet area (Miller & Swineford 1957; Zangerl & Richardson 1963; Clark 1989; Grogan & Lund 2002). The general habitus of iniopterygians is assumed to be similar to that of the modern chimaeroids (Zangerl 1981), i.e. bottom-dwellers. The nature of their dentition suggests they were predators (Zangerl & Case 1973), and they were probably durophagous, feeding on hard-shelled prey.

The morphology of the brain may provide some indications about the life style of these fishes (Northcutt 1978). The sibyrhynchids described here possess a relatively small cerebellum compared to extant predator sharks, such as the galeomorphs. In addition, they display a large mesencephalon. Actually, an increased cerebellar volume is "very likely related to an increase in sensory inputs involved in motor control" (Northcutt 1978), so that the animals move more rapidly (Northcutt 1989; Yopak *et al.* 2007). Consequently, a small cerebellum indicates slow movement. Moreover, according to Yopak *et al.* (2007), a relatively average-sized cerebellum and medulla, and enlarged mesencephalon characterize sluggish, demersal benthic or benthopelagic extant chondrichthyans. In addition, the horizontal semicircular canal has a relatively marked radius of curvature (hsc, Fig. 29), whereas the highly maneuvrable fishes have a relative small one (Maisey 2001b). This suggests that the Sibyrhynchidae were slow bottom-dweller predators.

Comparative anatomy and phylogenetic relationships

Zangerl & Case (1973) previously pointed out several crown-holocephalan-like characters in iniopterygians, such as a palatoquadrate fused to the neurocranium, a cartilage ray-supported opercular flap, the slender tail, the presence of tenacular hooks (on the basipterygium of the pelvic fin), the general nakedness of the skin, the tendency toward dental fusion, the elaborate clasper mechanisms in males. Zangerl (1979) latter erected the subclass Subterbranchialia to gather iniopterygians and extant holocephalans on the basis of the subcranial position of the gill arches, while Lund & Grogan (1997b) proposed to gather these taxa under the Euchondrocephali.

The present description provides additional comparative anatomical data. The iniopterygians described here confirms the previous observation of the holocephalan-like characters relative to the palatoquadrate, position of the gill arches and the teeth. It also provides new characters, which are only shared with extant holocephalans among modern chondrichthyans. Nevertheless, it is necessary to decide whether these characters are apomorphic or plesiomorphic.

Absence of a precerebral fontanelle

The precerebral fontanelle is absent in placoderms, extant chimaeroids, osteichthyans and jawless fishes (except perhaps in lampreys) and this probably represents a chondrichthyan plesiomorphy. The presence of a precerebral fontanelle has been regarded as an elasmobranch synapomorphy (Maisey 1984; Gaudin 1991). However, some authors have suggested that the ethmoid canal of holocephalans, which encloses the profundus ramus of the trigeminal nerve and the superficial ophthalmic complex, is homologous to the precerebral fontanelle (e.g., Holmgren 1942; Schaeffer 1981).

Since the brain is separated from the precerebral fontanelle by the dura mater in modern elasmobranchs, the fontanelle is considered as an extracranial structure. Nevertheless, the boundary between the internal cranial and extracranial spaces may be difficult to determine. For instance, in *Notorynchus* and *Chlamydoselachus* the pineal organ (which is an intracranial feature) is not enclosed by cartilage and lies instead within the fontanelle (Allis 1923; Maisey 2004b). The embryo of the holocephalan *Callorhinchus* possesses a pineal foramen that De Beer & Moy-Thomas (1935) considered as a remnant of a precerebral fontanelle in chimaeroids, obstructed by the formation of the ethmoid canal. In addition, contrary to Holmgren (1942), who considered that the ethmoid canal is intracranial, De Beer & Moy-Thomas (1935) and later Didier (1995) demonstrated that this canal is also extracranial, since it is separated, ventrally to the dura mater, by a cartilaginous floor. Moreover, the pineal organ, as well as the anterodorsal part of the dura mater, is situated behind the orbital opening of the ethmoid canal (De Beer & Moy-Thomas 1935: fig. 15).

Nevertheless, the origin of the floor of the ethmoid canal and of the precerebral fontanelle differs slightly. The floor of the former is made up by a posterior extension of the roof of the olfactory capsules (De Beer 1937), whereas the floor of the latter is formed from the internasal plate. It is thus difficult to elaborate a hypothesis of primary homology between these two structures.

Presence of an internasal plate separating the two palatoquadrates and supporting teeth

Extant elasmobranchs display both a continuous dental arcade and a palatoquadrate symphysis, which may be well developed between the two palatoquadrates (e.g., *Squalus*) or more flexible (e.g., *Chlamydoselachus*). This arrangement has been considered as a primitive feature of crown-group gnathostomes (Jarvik 1980).

In many Paleozoic sharks (i.e. *Hybodus* Agassiz, 1837, *Egertonodus* Maisey, 1987 [Maisey 1980, 1983], *Cladodoides* [Maisey 2005; Gross 1937], *Doliodus* Woodward, 1892 [Maisey *et al.* 2009], *Pucapampella* [Maisey & Anderson 2001], xenacanths [Schaeffer 1981], *Tristychius* Agassiz, 1837 [Dick 1978], *Akmonistion* [Coates & Sequeira 2001a, b]), as well as in osteichthyans (Poplin 1974; Gardiner 1984), placoderms (Goujet 1984; Young 1986) and *Acanthodes* (Miles 1964, 1968, 1973b), there is no palatoquadrate symphysis, and the two palatoquadrates are separated by an internasal plate (or trabecular plate). In taxa where the palatoquadrates are not known, the presence of a lateral process for the orbital articulation of the palatoquadrate situated anteriorly on both sides of the internasal plate indicates that the anterior part of the palatoquadrates were separated by the internasal plate (e.g., *Cladoselache*, *Akmonistion*, "*Cobelodus*", *Cladodoides*).

Moreover, the internasal plate that separates the two palatoquadrates may support teeth in stem-elasmobranchs, so that a continuous dental arcade is present (e.g., *Egertonodus*, *Doliodus*; Maisey 1983; Maisey *et al.* 2009).

In modern holocephalans the palatoquadrates are anteriorly fused with the nasal capsules and the internasal plate medially, which separates the two palatoquadrates from each other (Dean 1906; De

Beer & Moy-Thomas 1935; Grogan *et al.* 1999). The internasal plate directly supports a pair of "vomerine" tooth plates while a pair of "palatine" more laterally situated tooth plates are supported by the palatoquadrates (De Beer & Moy-Thomas 1935; Didier 1995), thereby forming a continuous dental arcade. The same condition is present in the stem-holocephalan *Helodus* (Moy-Thomas 1936).

In placoderms, the anterior superognathals are situated on the ethmoidal plate (e.g., *Dicksonosteus* Goujet, 1975; Goujet 1984), and in osteichthyans, the anterior teeth of the inner arcade are located on the vomer. In acanthodians, such as *Ptomacanthus* Miles, 1973 (Miles 1973; Brazeau 2009), a continous upper dorsal dental arcade is present, and this probably represents a general feature for acanthodians.

A continuous dental arcade seems to be a plesiomorphic character for chondrichthyans, whereas a palatoquadrate symphysis is probably unique to neoselachians.

Absence of a hypotic lamina.
The glossopharyngeus nerve crosses the otic capsule to reach the ventrolateral side of the braincase.
The embryonic parachordal plate of modern elasmobranchs gives rise laterally to the hypotic lamina, which extends entirely beneath the otic capsule. It fuses secondarily with the otic capsule at the anterior and posterior basicapsular commissure to close more or less the metotic fissure. The ontogenetic obliteration of the fissure leaves only a canal for the glossopharyngeus nerve in adult neoselachians (De Beer 1931). The extent of the metotic fissure, and the formation of a distinct glossopharyngeus canal, is therefore apparently governed by the degree to which the hypotic lamina becomes secondarily fused to the otic capsule during the development. In fossils, the presence of a hypotic lamina is inferred when a canal for the glossopharyngeus nerve is bordered ventrally by a lateral expansion of the inferred embryonic parachordal cartilage, or when the metotic fissure is still open and the glossopharyngeus nerve passes through it. In taxa where there is no hypotic lamina, the glossopharyngeus nerve seems to pass through the posterior part of the saccular chamber and exits the neurocranium by a short canal which is more ventrolaterally directed (see Schaeffer 1981: fig. 10 for an illutration of these conditions).

In most Paleozoic chondrichthyans and Recent elasmobranchs (e.g., *Orthacanthus*, *Tamiobatis*, *Akmonistion*, *Cladodoides*, "*Cobelodus*": Schaeffer 1981; Cotes & Sequeira 1998; Maisey 2005, 2007), a hypotic lamina is assumed to be present. A hypotic lamina was present in many placoderms (e.g., acanthothoracids, rhenanids, petalichthyids: Young 1986). Nevertheless, in *Dicksonosteus* (Goujet 1984), the condition is uncertain, since it may have possessed no hypotic lamina, and the glossopharyngeus nerve may have passed through the otic capsule.

The adult extant chimaeroids have neither persistent embryonic fissures, nor a hypotic lamina. However, after De Beer (1937), the embryo of extant chimaeroids possesses a fissure between the auditory capsule and the occipital arch. De Beer also added "the glossopharyngeus nerve does not pass (or appear to pass) through the cavity of the auditory capsule" (De Beer 1937: 72). Nevertheless, personal observations on *Chimaera monstrosa* Linnaeus, 1758 show that the glossopharyngeus nerve passes through a short canal that reaches internally the posteroventral border of the saccular chamber. Its external opening is anterior to that of the vagus nerve. Such a condition is assumed to be present in *Helodus* (Patterson 1965; Maisey 2001a) and in sibyrhynchids (see above).

A hypotic lamina is also absent in osteichthyans, but the latter sometimes show either a persistent embryonic metotic fissure, or a remnant of this fissure (such as the vestibular fontanelle; Gardiner 1984; Maisey 2005). In osteichthyans, the glossopharyngeus nerve generally exits via a short canal anterior to the vagus, ventrally, and the nerve passes through the otic capsule.

In *Acanthodes*, the presumed embryonic parachordal cartilage does not seem to flare laterally beneath the otic capsule (Miles 1973b). Moreover, in the lateral wall of the otic region is a distinct foramen for the glossopharyngeus nerve, which is situated anterior to the metotic part of the continous cranial fissure (otico-occipital fissure plus ventral otic fissure). Consequently, the latter does not reach the fissure, and is thus not floored by the parachordal plate. There is therefore no clear evidence of a hypotic lamina. The condition in *Acanthodes* is thus similar to that in osteichthyans.

In the osteostracan *Norselaspis* Janvier, 1981, there is no hypotic lamina and the glossopharyngeus nerve passed through the saccular chamber of the otic capsule and then ran into a canal situated ventrally to the otic capsule to reach the ventral surface of the braincase anterior to the foramen for the vagus nerve. Nevertheless, according to Janvier (1981), this is probably because of the considerable forward shifting of the gill compartments relative to the brain. Consequently the homology with the condition in gnathostomes is difficult to test.

De Beer (1937) and Young (1986) suggested that the glossopharyngeus nerve in gnathostomes is primitively enclosed in a canal beneath the otic capsule. Nevertheless, this view is probably the consequence of the assumption that the modern shark condition was primitive, and the passage of the glossopharyngeus nerve through the otic capsule as in arthrodires, acanthodians, osteichthyans, extant chimaeroids, and now iniopterygians may in fact represents a primitive feature. According to Young (1986), the presence of a hypotic lamina may be a plesiomorphic condition for gnathostomes. Conversely, Schaeffer (1981) suggested that the hypotic lamina is a derived structure of elasmobranchs and this implies that its embryonic fusion to the floor of the otic capsule is a derived feature of neoselachians and hybodonts.

Presence of a crus commune between the anterior and posterior semicircular canal

In extant lampreys, osteichthyans and holocephalans, the anterior and posterior canals meet dorsally to form a crus commune (Retzius 1881). By contrast, in modern elasmobranchs, the anterior and horizontal semicircular canals are connected together. The posterior semicircular canal appears thus separated to form a complete circuit, and is connected only to the vestibular region.

The former condition seems to be plesiomorphic for chondrichthyans, since osteostracans, galeaspids (Janvier 1996), *Mimia* Gardiner & Bartram, 1977 (Gardiner 1984), *Acanthodes* (Miles 1973) and many Paleozoic chondrichthyans, such as *Pucapampella* (Maisey 2001a, 2004a), *Cladodoides*, *Orthacanthus*, *Tamiobatis* sp. (Maisey 2004a; 2005), "*Cobelodus*" (Maisey 2007) and sibyrhynchidss (see above) display much the same arrangement, while only *Egertonodus*, and apparently *Dicksonosteus* possess the latter arrangement (Goujet 1984; Maisey 2004b). Stensiö (1963) and Goujet (1984) suggested that there is a crus commune between the anterior and horizontal semicircular canal in *Kujdanowiaspis* Brotzen, 1934 and *Dicksonosteus*, as in modern elasmobranchs. Nevertheless, other placoderms (e.g., *Jagorina* Jaekel, 1921, *Brindabellaspis* Young, 1980 [Young 1980]) show the dorsal part of the anterior and posterior semicircular canals close together. In addition, the posterior semicircular canal of *Kujdanowiaspis* is apparently connected to the horizontal semicircular canal, so that the former is not isolated as in neoselachians (Maisey 2005). This suggests that, even though some placoderms share with the neoselachians a crus commune between the anterior and horizontal semicircular canals, the arrangement of the skeletal labyrinth is not entirely the same in the two taxa, and some placoderms may show an autapomorphic condition.

Absence of a chondrified medial capsular wall

In Recent elasmobranchs, the endocranial and labyrinth cavities are almost completely separated from each other by a medial capsular wall, which is well chondrified, apart from the foramina for the octaval and glossopharyngeus nerves and the perilymphatic fenestra (De Beer 1931; Holmgren 1940; Jollie 1971; Maisey 2001b, 2004a, 2005). The medial capsular wall forms mainly in the taenia medialis, which also floors the endolymphatic fossa.

Such a condition is also present in *Egertonodus* (Maisey 2004a) and probably in *Tristychius*, according to Maisey (2005).

The medial capsular wall is fully ossified in *Dicksonosteus* (Goujet 1984) and osteostracans (Janvier 1996).

By contrast, the medial capsular wall is unchondrified in many Paleozoic chondrichthyans (e.g., *Pucapampella*, *Cladodoides*, "*Cobelodus*", *Orthacanthus*, *Tamiobatis* sp., Sibyrhynchidae; Maisey 2001a, 2005, 2007; Schaeffer 1981, see above), as well as in osteichthyans and extant chimaeroids. According to Maisey (2005), this is probably the consequence of an absence of chondrification in the taenia medialis. This is supported by the fact that taxa which do not possess a chondrified medial capsular wall, do not also display a floor of the endolymphatic fossa.

The condition in *Acanthodes*, *Tamiobatis vetustus*, *Cladoselache*, *Akmonistion*, and *Helodus* is unknown, since there are no data about their internal anatomy. Consequently, the phylogenetic status of this character is doubtful and needs more data to be as certaines.

Absence of a lagenar chamber

A lagenar chamber is a division of the saccular chamber, in which is housed the lagenar macula. It is present in neoselachians, but not in extant chimaeroids (Retzius 1881) and the Paleozoic chondrichthyans in which the saccular chamber is known. It is also absent in osteostracans (e.g., *Norselaspis*; Janvier 1981), actinopterygians (e.g., *Mimia*; Gardiner 1984) and *Dicksonosteus*, and in *Acanthodes*, most of the vestibular region is unknown. This suggests that absence of a lagenar chamber may be a plesiomorphic state for chondrichthyans.

Same pattern of arterial supply to the brain

In crown-holocephalans, the internal carotid arteries are aborted in the adult and do not enter the braincase (Allis 1912; De Beer & Moy-Thomas 1935), except *Rhinochimaera* Garman, 1901, in which the internal carotid arteries enter the skull through an unpaired foramen, but do not supply the blood to the brain. In Recent chimaeroids, the efferent pseudobranchial artery passed through the basicranium to ensure the only blood supply to the brain via the orbits (Holmgren 1942). The internal carotid arteries never meet the efferent pseudobranchial arteries, contrary to what happens in neoselachians and other Paleozoic chondrichthyans. Nevertheless, the efferent pseudobranchial artery ran dorsal to the inferred embryonic trabecula before entering the cranial cavity, as in other chondrichthyans.

Such a condition is present in the sibyrhynchids studied here (see above). Except for an ambiguous case (the Bolivian neurocranium of *Pucapumpella*; Maisey & Anderson 2001), this condition is only seen in extant chimaeroids and the sibyrhynchids among gnathostomes. This suggests that it represents a synapomorphy of a putative clade gathering these two taxa.

In *Helodus*, a possible stem-holocephalan, there is a "ventral short aortic canal, which is continued forward as a shallow groove almost to the hypophysial foramen" (Moy-Thomas 1936). This groove is assumed to have housed the dorsal aorta. Nevertheless, there is no evidence of grooves for internal carotid arteries. Consequently, the dorsal aorta may have divided into lateral dorsal aortae, but not internal carotid arteries. Therefore, the bucco-hypophysial foramen may not have housed the internal carotid arteries, as in extant chimaeroids. In addition, anterior to the basicranial fenestra, there are paired distinct foramina for the efferent pseudobranchial arteries, which pierce the basicranium, probably as in extant chimaeroids, either at the lateral margin of inferred embryonic trabeculae, or between them and the palatoquadrate, which is fused to the neurocranium (Moy-Thomas 1936; Patterson 1965).

Absence of a hyomandibular attachment on the braincase

Since the rise of segmentalist theories about early head evolution (see review in Janvier 1996; Kimmel & Eberhart 2008), a possible visceral contribution to the braincase is still under discussion. Extant chimaeroids are the only gnathostomes that possess a presumed "complete" hyoid arch with basi-, cerato-, epi- and pharyngohyal elements, like the branchial arches. Their hyoid arch is not involved in jaw suspension, since the palatoquadrate of chimaeroids is fused to the neurocranium (holostylic jaw suspension). It is assumed that the palatoquadrate of *Helodus* and the Sibyrhynchidae is also fused to the neurocranium (Patterson 1965; see above). There is no evidence of either a fossa, or a process, for an articulation with the hyomandibula on either the otic capsule, or the postorbital process. This suggests that their jaw suspension also does not involve an articulation with the hyomandibula.

De Beer & Moy-Thomas (1935) suggested that the "unmodified" hyoid arch of modern holocephalans is a plesiomorphic condition for gnathostomes.

However, Maisey (1984) argued that the hyoid arch of extant holocephalans is not an unmodified plesiomorphic hyoid arch on the basis of five anatomical characteristics: 1) the pharyngohyal of holocephalans lies lateral to the efferent hyoidean artery, while their pharyngobranchials lie medial to their efferent arteries (an observation made by Watson [1937: 141] and later reiterated by Patterson [1965: 103, footnote]); 2) the embryonic spiracle is small and does not represent a complete hyoidean gill slit. The pseudobranch fails to develop, as in relatively derived members of other taxa, which suggests that holocephalans are specialized in this respect; 3) the epihyal does not bear endoskeletal gill rays, contrary to epibranchials; 4) the hyoid arch possesses no equivalent of the branchial adductor muscles that connect the epibranchials and ceratobranchials; 5) the interpharyngobranchial muscles do not insert into the pharyngohyal. In addition, the "efferent pseudobranchial artery" of extent chimaeroids has a "reversed" blood flow. Nevertheless, as suggested by Didier (1995), the supposed pharyngohyal element of the hyoid arch of extant chimaeroids may be a real pharyngohyal, and the development of a complete hyoid arch may be a secondarily derived condition associated with the evolution of holostyly. This hypothesis may be acceptable if one follows Maisey's (1980, 2001a) conclusion that the hyomandibula primitively lends some support to the jaw. However, Lund & Grogan (1997b), Grogan & Lund (2000) and Wilga (2002) concluded that the hyoid arch is not primitively involved in jaw suspension in chondrichthyans (the "autodiastylic" condition) and De Beer & Moy-Thomas (1935), and Patterson (1965) proposed that the holostylic condition is primitive for holocephalans.

Consequently, it is still uncertain whether the presence of a hyomandibular articulation is an apomorphic condition, or evolved more than once.

Presence of a telencephalon medium?

In Recent chimaeroids, the telencephalon is separated from the diencephalon/mesencephalon by a specialized, elongated "telencephalon medium" (*sensu* Northcutt 1978), which possesses a membranous roof and lies along the floor of the braincase beneath the entire length of the membranous interorbital septum (Jollie 1962: fig. 13-13; Kuhlenbeck & Niimi 1969: figs 5, 6, 8; Northcutt 1978: fig. 8). In addition, the extant chimaeroids lack a specialization of the telencephalic roof, termed central nucleus, which is characteristic of all elasmobranch (Northcutt 1978), so that a membranous tissue (telencephalon medium) arises immediately anterior to the optic tectum.

As mentioned above, the telencephalon of the sibyrhynchids described here was probably long. Same condition as in extant holocephalans is possible in sibyrhynchids, even though there is no interorbital septum. It is also possible that the olfactory tracts, which arise from a central nucleus, very long and extend forward through the endocranial cavity. Nevertheless, the region situated dorsal to the optic chiasm and immediately anterior to the optic tectum is missing, whereas the ventral optic chiasm and optic nerves (diencephalon) are preserved. Consequently, one may suppose that membranous tissues, which are not preserved in the fossil, were present at this level, as in extant chimaeroids, rather than a central nucleus, as in extant elasmobranchs. If this hypothesis is confirmed by further investigations, and if the Sibyrhynchidae are close to extant chimaeroids, then a specialized membranous telencephalon medium is not necessarily correlated with the presence of an interorbital septum and may have occurred before the appearance of this structure in chimaeroids.

Absence of a lateral commissure?

According to Holmgren (1940), the lateral commissure of neoselachians connects the ventral (formed from the otic capsule) and dorsal (the primary postorbital process, which is formed from a blastemic element) parts of the postorbital process. It covers laterally the main trunk of the facial nerve and the lateral head vein (which later becomes the jugular vein). A lateral commissure, when present, usually covers laterally the ganglia for facial and trigeminal nerves (geniculate and Gasser's ganglia). It forms the trigemino-facial chamber, whose medial wall is the prefacial commissure, and which is apparently homologous to that of osteichthyans (Gardiner 1984: 236; Maisey 2005).

Nevertheless, the lateral commissure is rarely fully chondrified, forming a complete postorbital wall that encloses the jugular canal, and is connected both dorsally and ventrally to the braincase. Among neoselachians, only *Squatina* and *Scymnodon* Barbosa du Bocage & Brito Capello, 1864 possess a well-chondrified lateral commissure, thereby forming a complete postorbital wall (Holmgren 1941). In *Squalus*, the lateral commissure is present, but not totally chondrified, so that there is no complete postorbital wall (Holmgren 1940). According to Holmgren (1940, 1941), the lateral commissure does not persist in hexanchiforms.

There is a general consensus that the lateral commissure of chondrichthyans is homologous to that of actinopterygians (De Beer 1937; Holmgren 1940; Schaeffer 1981; Gardiner 1984). The embryonic origin of the lateral commissure is still debated in both taxa (see discussion in Gardiner 1984), and the hyomandibular does not usually articulate with or near it in chondrichthyans, contrary to what is observed in osteichthyans and placoderms (Schaeffer 1981; Gardiner 1984; Goujet 1984). In *Mimia*, the lateral commissure is a massive endochondral structure, which is penetrated by a long jugular canal (Gardiner 1984). Nevertheless, contrary to elasmobranchs, the orbital artery ran into the jugular canal. In addition, according to De Beer (1937: 391), the embryonic derivation of the dorsal and ventral processes of the postorbital wall differs in osteichthyans. The dorsal process (i.e. the prootic process) is formed by a lateral projection from the wall of the otic capsule, rather than from an independent blastemic element. The ventral process (i.e. the basitrabecular or basipterygoid and postpalatine processes) is derived from the margins of the trabeculae and parachordal plate, rather than from the ventral part of the otic capsule. Nevertheless, as in neoselachians, it lies lateral to the jugular vein and forms the side wall of the trigeminal chamber, laterally to the prefacial commissure. In addition, the inferred lateral commissure of Paleozoic sharks seems to be attached ventrally to the inferred embryonic polar cartilage in "*Cobelodus*" (Maisey 2007), or to the trabecular-polar plate in *Pucapampella* (Maisey 2001a), suggesting that the ventral attachment of the lateral commissure is more variable in elasmobranchs than previously supposed. This arrangement may be correlated with the relative location of the otic capsule and the postorbital process, since in these two taxa, the otic capsules lie entirely posterior to the postorbital process, contrary to the condition in neoselachians, in which the otic capsules usually extend anterioly between the postorbital processes.

In sum, in extant actinopterygians and neoselachians, the lateral commissure is present and probably primary homologous, but its dorsal and ventral attachments differ. In fossils, it is difficult to decide the presumed embryonic origin of the dorsal attachment (prootic process or primary postorbital process). In addition, the nature of the ventral attachment appears variable in Paleozoic chondrichthyans, and is difficult to infer in most cases. The nature of ventral attachment is probably a consequence of the position of the otic capsule relative to the postorbital process and/or the presence of a basitrabecular process continuous with the postorbital wall, as in some Paleozoic forms. Consequently, no distinction between the elasmobranch and actinopterygian pattern is made in the present work.

A lateral commissure is assumed to be present in fossils when a complete postorbital wall, which extends from the posterior part of the supraorbital shelf to the basicranium, encloses the jugular vein in a canal. Such a condition is present in the chondrichthyans *Akmonistion* (Coates & Sequeira 1998), *Egertonodus* (Maisey 1983), *Pucapampella* (Maisey 2001a), *Cladodoides* (Maisey 2005), "*Cobelodus*", *Cladoselache* (Maisey 2007), *Tristychius* (Maisey 2007), *Orthacanthus*, *Tamiobatis* (Schaeffer 1981).

In the placoderm *Dicksonosteus*, the anterior postorbital process forms a complete dorsoventral wall (Goujet 1984). Moreover, it encloses the jugular canal, so that it was probably also derived from the embryonic lateral commissure. Miles (1973) and Maisey (2005) assumed that there is a lateral commissure in *Acanthodes*.

In extant chimaeroids, there is apparently no lateral commissure, since this feature is correlated with the presence of a spiracular canal in the adult elasmobranchs (Holmgren 1942: 195). Yet a spiracle is present in the chimaeroids embryos. The embryonic cranioquadrate passage through which pass the orbital artery, palatine and mandibular-hyoidean rami of the facial nerve and the jugular vein is reduced to three foramina in the suborbital shelf, containing (from front to rear) the efferent pseudobranchial artery, the palatine ramus and orbital artery, and the mandibular-hyoidean ramus and the jugular vein (Schauinsland 1903; Goodrich 1930; De Beer 1937; Holmgren 1942; Grogan *et al.* 1999).This cranioquadrate passage is supposed to be formed from the junction of the basitrabecular process, parachordal and hypochordal cartilages, and the otic process (De Beer & Moy-Thomas 1935; Grogan *et al.* 1999). The lateral wall of the jugular canal is therefore formed from the otic process, which is apparently not a lateral commissure, but an extension of the otic capsule. In addition, in Recent holocephalans there is no evidence of a trigemino-facial chamber, also suggesting the absence of a lateral commissure.

In the sibyrhynchids described here, a complete postorbital wall, which extends from the posterior part of the supraorbital shelf to the basicranium, encloses the jugular vein in a canal. In addition, a prefacial commissure is probably present (see above). Moreover, the division of the palatine ramus of the facial nerve occurs intracranially, and its anterior and posterior ramules probably ran through the canal for the orbital artery. This condition is similar to that of "*Cobelodus*" and *Cladodoides*, in which the division of the palatine ramus arises within the lateral commissure (postorbital process), and its anterior and posterior ramules reach the braincases in the groove housing the orbital artery (Maisey 2005, 2007).

This suggests the presence of a lateral commissure in sibyrhynchids. The otic capsules appear in dorsal position relative to the ventral end of the postorbital wall. The dorsal part of the postorbital wall may therefore represent a lateral projection from the wall of the otic capsule, rather than the primary postorbital process. The ventral part of the postorbital wall cannot be a ventral projection of the otic capsule, because of the dorsal position of the otic capsule. It may rather be a lateral projection of the trabecular/polar cartilages, i.e. the basitrabecular process. This is also suggested by the fact that the palatoquadrate probably fused posteriorly with a basitrabecular process, so that the posterior part of the suborbital shelf of the iniopterygians described here may have been formed from a basitrabecular process. In actinopterygians, the ventral part of the postorbital wall corresponds to the basitrabecular process. Consequently, the condition in iniopterygians may be similar to that of actinopterygians. The dorsal part of the postorbital wall is formed from a prootic process, while its ventral part is formed from the basitrabecular process, which is fused anteriorly with the palatoquadrate, and a lateral commissure joins these two parts to form a complete postorbital wall. The lateral commissure may have covered laterally the ganglia for the facial and trigeminal nerves and forms the trigemino-facial chamber, whose medial wall is the prefacial commissure.

Nevertheless, the postorbital wall of iniopterygian slightly merges ventroanteriorly with the palatoquadrate that is fused to the neurocranium, as in extant chimaeroids. Consequently, it has a different relation to surrounding structures of the neurocranium and mandibular arch than that of the Paleozoic sharks, the crown-elasmobranchs and the actinopterygians. Considering these observations and the pattern of the formation of the suborbital shelf in extant chimaeroids, the postorbital wall of iniopterygians may have been formed without a lateral commissure. In fact, the process, which forms the dorsal part of the postorbital wall of iniopterygians, may correspond to the otic process of extant chimaeroids in a markedly dorsal position, because of the shallow and dorsally place of the otic capsule in the former. As previously mentioned, the extent of the inferred embryonic polar cartilage in iniopterygians may be either very limited in a "shark model", or more important in a "chimaeroid model", depending on the embryonic landmarks used for delimiting it. In a "chimaeroid model", the embryonic polar cartilages may have formed a prominent lateral basitrabecular process between the dorsal otic process and the ventral palatoquadrate. The fusion of these structures may have formed a complete suborbital shelf/postorbital wall, since these structures form together a complete suborbital shelf in extant chimaeroids. The extension of the suborbital shelf to a postorbital wall in sibyrhynchids may be explained by the fact that the otic process developed in a dorsal position rather than in a ventral position, as in extant chimaeroids. In addition, in *Callorhinchus*, the dorsal postorbital process does not merge with the suborbital shelf (De Beer 1937), but in *Chimaera monstrosa*, the postorbital process extends ventrally to reach the suborbital shelf slightly anterior to the otic process (pers. obs.).

Therefore, in such a case, there is no chondrified lateral commissure similar to that of neoselachians, Paleozoic sharks or actinopterygians. The lateral wall of the jugular canal is rather formed from the otic process, as in extant chimaeroids.

The presence of a lateral commissure is nevertheless probably a plesiomorphic condition for chondrichthyans, and there are more data suggesting the presence of a lateral commissure in sibyrhynchids, than data suggesting its absence. In addition, the data on the development of the skull of extant chimaeroids are very scarce, so that an absence of a lateral commissure in this taxon is not strongly supported. A cranioquadrate passage is present in *Helodus* (Moy-Thomas 1936; Patterson 1965). As in extant chimaeroids and sibyrhynchids, the palatoquadrate of *Helodus* is fused to the neurocranium, and the suborbital shelf, which merges with the postorbital wall, may be formed from the palatoquadrate. As in iniopterygians, the otic capsule appears particularly flat and dorsal in position. The postorbital wall of *Helodus* extends from the otic capsule to the suborbital shelf. It is possible that a lateral commissure was present in stem-holocephalans at least.

It appears that, among the cranial characters discussed here, only the characters relative to the blood supply to the brain can be undoubtedly regarded as synapomorphies for the clade gathering extant holocephalans and the Sibyrhynchidae. The Sibyrhynchidae also possess some crown-elasmobranch-like cranial characters (e.g., presence of an endolymphatic fossa, absence of interorbital septum, presence of foramina for the ascending branches of the superficial ophthalmic complex instead of an ethmoid canal). However, these characters are certainly plesiomorphic for chondrichthyans (see Schaeffer 1981; Maisey 1984, 2005, 2007; Maisey & Anderson 2001 for a review of potential elasmobranch synapomorphies).

CONCLUSIONS AND PROSPECTS

These new braincases, which are studied by means of new imaging techniques, belong to sibyrhynchid iniopterygians. They are very closed to that in all three genera previously described by Zangerl & Case (1973), and it is difficult to assign the new specimens to known genera with accuracy. They confirm the characteristics of the Subterbranchialia, i.e. the shoulder girdle located directly posterior to the head (Pradel *et al.* 2009), and the branchial basket situated beneath the neurocranium.

Moreover, the new specimens described here provide more information about the cranial anatomy of this taxon. Indeed, besides the previous observations of the fusion of the palatoquadrate to the neurocranium, sibyrhynchids and extant holocephalans share the same cranial arterial pattern. The internal carotid arteries probably not entered the braincase, and the efferent pseudobranchial arteries probably supplied blood to the brain. These characters may represent synapomorphies of a taxon gathering the Sibyrhynchidae and the Recent holocephalans. The Sibyrhynchidae also possess several cranial characters that are probably plesiomorphic for chondrichthyans (e.g., a continuous dental arcade with "vomerine" teeth, a massive postorbital wall, a crus commune between anterior and posterior semicircular canals). This description of a neurocranium of a possible stem-holocephalan provides some new characters and informations for further phylogenetic studies.

The new techniques allowed the observation of an exceptional case of a fossilized brain. It shows the same axial configuration as the modern chondrichthyan brain. There is no general match between the morphology of the brain and that of the endocranial cavity, and the cast of the endocranial cavity for inferring the morphology of the brain must be considered with caution. The discovery of a fossilized brain shows that the finding of exceptional preservation of an authigenetically phosphatized brain in key fossil vertebrates may occur, and that SR-µCT and holotomography may reveal it in a larger number of taxa, including in key taxa, such as stem gnathostomes or piscine stem tetrapods. Further studies of the mode of formation of the Carboniferous phosphatic concretions from North America will probably provide new hints at such findings.

New holotomographic scans have been recently performed in order to explore the entire endocranial cavity of KUNHM 22060, and may provide further information about the brain. In addition to the neurocranium, some postcranial elements are also preserved inside the nodules. A description based on these new data will be provided later.

We are constrained by the available data on the ontogeny of the neurocranium of extant holocephalans, in order to compare its morphology to that of elasmobranchs, especially as to their important differences that are probably due to the fusion of the palatoquadrate to the neurocranium. Some features may be actually homologous, but in a highly modified state (e.g., the lateral commissure).

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