General palaeontology

Study of the pectoral girdle and fins of the Late Carboniferous sibyrhynchid iniopterygians (Vertebrata, Chondrichthyes, Iniopterygia) from Kansas and Oklahoma (USA) by means of microtomography, with comments on iniopterygian relationships

Étude de la ceinture et des nageoires pectorales des inioptérygiens Sibyrhynchidae (Vertebrata, Chondrichthyes, Iniopterygia) du Carbonifère supérieur du Kansas et de l'Oklahoma (USA) à l'aide de la microtomographie, avec des commentaires sur les relations de parenté des inioptérygiens

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ABSTRACT

The latest works on iniopterygians question their monophyly when considering only the neurocranium of the two families (*Sibyrhynchidae* and *Iniopterygidae*), which have different conditions of preservation. Some of the synapomorphies of the Iniopterygia concern the pectoral girdle and fins. However, the anatomy of these different elements is still poorly known in this taxon. Here we describe in details three dimensionally preserved cartilages of the pectoral girdle and fins of the sibyrhynchid *Iniopera* sp. These structures have been extracted virtually from phosphatised nodules thanks to conventional and synchrotron microtomography, using absorption and phase contrast based techniques in the later case. The pectoral girdle of *Iniopera* sp. consists of three elements, which are, from dorsal to ventral, a paired suprascapular cartilage, a pair of robust scapulocoracoids and an unpaired intercoracoid cartilage. The scapular part of the scapulocoracoids is extremely reduced and the suprascapular cartilages link the scapulocoracoids to the rear of the neurocranium. These characters may be iniopterygian synapomorphies. Iniopterygians, stem and crown-holocephalans share a basipterygium that articulates with the pectoral girdle and bears an enlarged first pectoral fin radial. Posteriorly, the basipterygium articulates with either a well-defined metapterygium (in crown-holocephalans) or a metapterygial axis (in stem-holocephalans).

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RÉSUMÉ

Les travaux récents sur les inioptérygiens posent la question de leur monophylie, unique-ment sur la base du neurocrâne des deux familles du groupe (*Sibyrhynchidae* et *Inioptery-gidae*) et avec des états de préservation différents. Quelques-unes des synapomorphies

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des Iniopterygia portent sur la ceinture et les nageoires pectorales. Cependant, l'anatomie de ces différents éléments est encore peu connue chez ce groupe. Nous décrivons ici en détail les cartilages de la ceinture et des nageoires pectorales, conservés en trois dimensions, du sibyrhynchide *Iniopera* sp. Ces structures ont été extraites virtuellement de nodules phosphatés grâce à la microtomographie conventionnelle et synchrotron, en contraste d'absorption et de phase pour cette dernière. La nageoire pectorale de *Iniopera* sp. comprend trois éléments qui sont, de haut en bas, une paire de cartilages suprascapulaires, une paire de scapulocoracoïdes et un cartilage intercoracoïdien impair. La partie scapulaire des scapulocoracoïdes est extrêmement réduite et les suprascapulaires relient les scapulocoracoïdes au neurocrâne. Ces caractères peuvent représenter des synapomorphies des inioptérygiens. Les inioptérygiens, les holocéphales souches et apicaux partagent la présence d'un basiptérygium qui s'articule avec la ceinture pectorale et qui porte le premier radial, élargi, des nageoires. Postérieurement, le basiptérygium s'articule avec, soit un métaptérygium bien défini (chez les holocéphales apicaux), soit un axe métaptérygial (chez les holocéphales souches).

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1. Introduction

The Iniopterygia are a Late Carboniferous order of chondrichthyans, first described by Zangerl and Case (1973) on the basis of flattened specimens from the Pennsylvanian of Indiana (USA). Other iniopterygians have been described later from the Late Carboniferous of USA, namely from the Pennsylvanian of Indiana (Zangerl, 1997), the Mississippian of Montana (Grogan and Lund, 2009) and the Pennsylvanian of Kansas and Oklahoma (Pradel et al., 2009; Pradel, 2010). In addition, some skeletal elements of an iniopterygian have been recently discovered in the Lower Carboniferous of Beardsen (Scotland) (M.I. Coates pers. com., 2010). Iniopterygians currently include two families: the Sibyrhynchidae, which possess a holostylic jaw suspension, like in extant and fossil holocephalans, and the Iniopterygidae, which retain a free palatoquadrate (Stahl, 1980). Even though the neurocranium of the two iniopterygian families displays different kinds of jaw suspension, Stahl (1980) and Zangerl (1981) considered iniopterygians as a clade among stem holocephalan. The neurocranium of the Sibyrhynchidae is now well known, thanks to new specimens, which are the only three dimensionally preserved iniopterygians ever described (Pradel et al., 2009; Pradel, 2010). These were studied by means of CT X-ray imaging using both conventional machines and synchrotron radiation scanning (Tafforeau et al. 2006). Comparative anatomy studies on the neurocranium of the Sibyrhynchidae suggest that these iniopterygians can be resolved as stem holocephalans (Pradel et al., 2009; Pradel, 2010), as previously considered by Stahl (1980), Zangerl (1981) and Zangerl and Case (1973). However, a recent cladistic analysis on the neurocranium of new, but flattened specimens referred to the other iniopterygian family, the Iniopterygidae, brings them in a more stemward position, before the divergence between the elasmobranchs and holocephalans (Grogan and Lund, 2009). The phylogenetic position of these new Iniopterygidae, *Rainerichthys* and *Papilionichthys*, is mainly due to the fact that they have been interpreted as possessing neurocranial fissures and an intracranial joint (Grogan and Lund, 2009). Nevertheless, these features are lacking in the other Iniopterigydae (i.e. *Iniopteryx* and *Promexyele*), as well as in all known Sibyrhynchidae. Consequently, the

phylogenetic status of iniopterygians based only on neurocranial characters of the two families, and on specimens with different states of preservation (three dimensionally preserved or flattened), is still debated. Additional data, especially on the postcranial anatomy, are therefore necessary to test these different hypotheses of relationships.

Actually the previous studies of pectoral girdle and fins of iniopterygians had already provided some unambiguous synapomorphies of iniopterygians, such as enlarged pectoral fins, which articulate dorsolateraly to the shoulder girdle (Zangerl and Case, 1973). Nevertheless, the anatomy of the different elements of the pectoral girdle and fins was still poorly known, because the previously described specimens are preserved in a single plane (Grogan and Lund, 2009; Stahl, 1980; Zangerl 1997; Zangerl and Case, 1973). Here we describe in detail three dimensionally preserved cartilages of the pectoral girdle and fins of the Sibyrhynchidae and provide a detail description of pectoral girdle characters that are only shared by the two iniopterygian families.

In addition, we discuss the potential phylogenetic signal of some other pectoral girdle and fin characters that are present in iniopterygians, some other chondrichthyans and other gnathostomes. These include the suprascapular cartilages, which were already described in *Rainerichthys* and *Papilionichthys* (Grogan and Lund, 2009), but not yet in the Sibyrhynchidae, the intercoracoid element(s) and the basal cartilages of the pectoral fin.

The pectoral girdle and fins studied here are preserved in the same nodules as the previously described neurocrania from the Pennsylvanian of Kansas and Oklahoma (Pradel et al. 2009; Pradel, 2010) and articulated to the latter. According to the previous description of the neurocranium, mandible, teeth and dermal denticles of the specimens studied here, it was assumed that the latter belong to closely related species (probably of the same genus) of the Sibyrhynchidae (Pradel et al. 2009; Pradel, 2010). Nevertheless, the description of the neurocranium and teeth provided by Pradel (2010) did not allow him to decide whether the specimens should be referred to either *Iniopera* or *Sibyrhynchus*. The new data on the pectoral girdle and fin provided here allows the attribution of these specimens to *Iniopera*.

2. Material and methods

2.1. Material

The material from Kansas studied here comprises two specimens belonging to the Kansas University Natural History Museum, Lawrence, Kansas, USA (KUNHM 22060, KUNHM 21894). A map showing the sources of this material is provided in Hamel and Poplin (2008). One specimen, OKM 38, comes from Oklahoma, belongs to the American Museum of Natural History, New York, and was loaned by Dr John Maisey (AMNH, New York). Images of the original nodules are provided in Pradel et al. (2009) and Pradel (2010).

The Kansas nodules crop out approximately 150 km southeast of Kansas City, between Lawrence and Baldwin, in about thirty different localities. 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 (see Pradel, 2010, for details on the paleoenvironment and the taphonomy). This sequence is part of the Douglas Group, dated as Late Virgilian, Upper Pennsylvanian (Ca 305–299 Myr).

The Oklahoma specimen was collected by Dr. Royal Mapes (Geology Department, Ohio University, Athens, Ohio, USA) from the Coffeyville Formation (dated as Pennsylvanian, Missourian, Ca 307 Myr), at a roadcut in Tulsa County, Oklahoma (Center of NW sec. 2., T. 18 N, R. 12 E, Sapulpa North 7½ Quadrangle).

KUNHM 22060 and OKM 38 display scattered elements of the pectoral girdle and fins, whereas the pectoral girdle and fin of KUNHM 21894 are well preserved, almost in natural position. Most of the illustrations are therefore based on the latter specimen.

2.2. Methods

OKM 38 has been scanned by μCT scan at the University of Texas High-Resolution X-ray CT Facility, Austin, USA. 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. The scan is acquired with 19 slices per rotation and 15 slices per set. Flash and ring-removal processing are based on correction of raw sinogram data by Alison Mote using IDL routines "RK_SinoDeSpike" and "RK_SinoRingProcSimul," both with default parameters. There was no gantry tilt. The first four duplicate slices of each rotation are deleted, except for slices 1–4 and the rotation correction processing has made using the IDL routine "DoRotationCorrection." Total no of final slices = 649.

KUNHM 21894 was imaged using X-ray based synchrotron microtomography in absorption contrast (SR-μCT) (Tafforeau et al., 2006) on beamline ID19 of the European Synchrotron Radiation Facility (ESRF, Grenoble, France). 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). Reconstructed slices were converted from 32 bits to 8 bits in order to reduce the data size for 3D processing.

Because KUNHM 22060 is much more mineralized than other specimens, absorption contrast was not sufficient to observe all the features present inside the nodules. Consequently, a more powerful technique based on propagation phase contrast was used on that specimen on the beamline ID19 of the ESRF (Tafforeau et al., 2006). That scan was done with a voxel size of 7.46 μm at an energy of 60 keV, with a propagation distance of 900 mm. In order to obtain 2.9 cm of lateral field of view, the scan was made in half-acquisition geometry, with the centre of rotation on one side of the field of view and a 360 degrees rotation. That technique allows one to nearly double the lateral field of view. We used 5000 projections over 360 degrees with an exposure time of 0.7 s for each of the 9 scans performed, each of them covering 5.8 mm vertically. Reconstruction was performed using an adapted filtered backprojection algorithm, allowing reconstruction with half-acquisition and local tomography (PyHST software, ESRF). After reconstruction, all the scans were concatenated in order to generate a single slices stack in tif 16 bits mode. A second version of that dataset with a $2 \times 2 \times 2$ binning in 8 bits was then computed in order to reduce the data size for the general anatomy investigations.

Segmentation and 3D rendering were performed with MIMICS® 13.1 software (Materialise Inc. NV, Leuven, Belgium) and with Volume Graphics VG Studio MAX© 2.0×64.

Many of the illustrations in this work are images captured from MIMICS and VG Studio MAX, respectively in isosurface and volume renderings. Adobe Photoshop CS3 extended v.10.0.1 was used to optimize the contrast of the MIMICS and VG Studio MAX 3D renderings and make the final illustration.

2.3. Systematics

Systematic paleontology
Class CHONDRICHTHYES Huxley, 1880
Order INIOPTERYGIA Zangerl and Case, 1973
Family SIBYRHYNCHIDAE Zangerl and Case, 1973
Genus INIOPERA Zangerl and Case, 1973
Type species: *Iniopera richardsoni* Zangerl and Case, 1973.
Etymology: from the Greek inion (= nape) and pera (= leathery pouch).
Iniopera sp. indet.
Examined material: KUNHM 22060, KUNHM 21894 and OKM 38 (deposited in the AMNH).

2.3.1. Characters

Iniopera sp. shares with the other species of the order Iniopterygia the following features: enlarged pectoral fins, which articulate dorsolaterly to the shoulder girdle; a single, massive proximal pectoral radial (basipterygium); enlarged anteriormost distal pectoral fin radial; scapuloco-

racoids articulated with the branchial skeleton; branchial skeleton entirely situated ventral to the neurocranium; terminal mouth; the dentition is heterodont and consists of linguo-labially oriented tooth families.

Holostylic jaw suspension, linguo-labially oriented tooth families that fuse to form tooth whorls of different size and shape, and Meckel's cartilages that are fused at the symphysis are shared uniquely with the Sibyrhynchidae.

The following characteristics are autapomorphic for *Iniopera*: the anteriormost distal pectoral fin radial is much larger than the other fin radials; the symphysial region of the mandible is more rectangular in shape than that of *Sibyrhynchus*; the skull bears a pavement of dermal denticles on its posterodorsal surface.

Iniopera sp. differs from *Iniopera richardsoni* by the absence of symphysial tooth whorl in the upper jaw, the number of tooth whorls in the upper jaw (15 in *I. richardsoni*, 10 in *Iniopera* sp.), the number of "canine" whorls in the upper jaw (2 pairs in position 3 and 4 in *I. richardsoni*, one pair in position 4 in *Iniopera* sp.), the absence of plates that cover the floor or the roof of the mouth cavity in *Iniopera* sp., and the apparent absence of pectoral pouch in the pectoral fin of *Iniopera* sp.

2.3.2. Remarks

Despite the absence of a consensus about the phylogenetic relationships of some Iniopterygidae on the one hand (stemward position, before the divergence between the elasmobranchs and holocephalans; Grogan and Lund, 2009) and of the other Iniopterygidae and the Sibyrhynchidae on the other hand (stem holocephalans; Pradel et al., 2009; Pradel, 2010; Stahl, 1980; Zangerl, 1981; Zangerl and Case, 1973), the taxon Iniopterygia is treated here as a clade in the present systematic context.

3. Description

3.1. Pectoral girdle

The pectoral girdle of sibyrhynchids consists of a pair of prominent, elongated and robust scapulocoracoids, a pair of small and thin triangular suprascapular cartilages and an unpaired intercoracoid basal plate (sc, supsc, intc, Fig. 1). The pectoral girdle and left pectoral fin of KUNHM 21894 are preserved, almost articulated, in a natural position (Fig. 1A). The scapular region of the scapulocoracoids lies immediately posterior to the neurocranium, or braincase (br, Fig. 1A), whereas the rest of the element is preserved almost horizontal, beneath the ventral surface of the braincase, with its anteroventral end reaching the mid-length of the braincase. Nevertheless, the scapulocoracoids may have been slightly displaced during fossilisation and were in fact more vertical in life (Fig. 1B). The general outline of the scapulocoracoid is L-shaped, with its ventral half bending forward, so that its anteroventral end was probably situated ventral to the otico-occipital region of the braincase, and its anteriormost and dorsalmost parts stood approximately at a right angle to one another. The anteroventral end of the scapulocoracoids are not fused together at the ventral midline, contrary to what is observed in most extant chondrichthyans (Compagno,

1999; Didier, 1995). In contrast, the ventral end of the scapulocoracoids articulates with the intercoracoid cartilage (see below), along the posterolateral sides of the latter.

The suprascapular elements (see below) are situated dorsal to the scapular region of the scapulocoracoids.

3.1.1. Scapulocoracoids

The dorsal part of the scapulocoracoids is much larger and more robust than their ventral part, which becomes progressively sharper anteriorly. The anterior margin of the lateral surface of the scapulocoracoids is not continuously concave: a triangular process, the 'anterior shoulder' (as, Fig. 2A1–A3, A5), located about midway along the height of the scapulocoracoid, forms a slightly dorsal projection on the anterior margin of the scapulocoracoid, ventral to the fin articulation (see below). This 'anterior shoulder' shows a flattened surface on the lateral side of the cartilage. Such a feature is present in stem Paleozoic chondrichthyans (e.g., *Akmonistion*; Coates and Sequeira, 2001) and in some stem elasmobranchs, such as *Orthacanthus* (Lane and Maisey, 2009).

A process located on the posterodorsolateral surface of the scapulocoracoid is directed anterolaterally, slanting obliquely and ventrally, and its anterodorsalmost end is enlarged, forming an articular glenoid condyle for the pectoral fin (glc, Figs. 1B4 and 2A1, A3, A4). It is received by a corresponding glenoid fossa in the basal element of the pectoral fin (see below) (glf, Fig. 2D1, D3, D4). Foramina for the diazonal nerves and blood vessels of the fin are present on three surfaces of the dorsal part of the scapulocoracoid around the glenoid condyle. The main diazonal canal originates on the anterior surface of the scapulocoracoid (amdf, Fig. 2A3), and then bifurcates, terminating in the paired dorsal and posterolateral foramina, which are respectively located on the dorsal and posterolateral surface of the cartilage (dmdf, Figs. 1B4, 2A3, A4; plmdf, Figs. 1B4, 2A1). A diazonal canal with three openings is also found in the Iniopterygidae *Cervifurca nasuta* (Zangerl, 1997), some hybodontiformes (e.g., *Tribodus*), *Orthacanthus* and many neoselachians (e.g., *Carcharhinus*) (Lane and Maisey, 2009). Only one diazonal foramen anterior and dorsal to the fin articulation is considered as general for early chondrichthyans (Coates and Gess, 2007). Two additional, smaller canals pass through the scapulocoracoid and do not connect the main diazonal canal (df, Fig. 2A3–A5). The dorsalmost one opens on the anteromedial and posteromedial surface of the cartilage at about the same horizontal level as the anterior and posterolateral foramina of the main diazonal canal. The ventralmost one is situated midway along the length of the scapulocoracoid, ventral to the 'anterior shoulder'.

The dorsal position of the glenoid condyle and diazonal canals suggests that the scapular process is reduced to the enlarged portion of the scapulocoracoid, which is thus mainly composed by an unusually long coracoid portion.

The dorsal surface of the scapular region is flat and may have accommodated the suprascapular cartilage. This flat area forms with the rest of the scapulocoracoid a posterolateral angle (pla, Fig. 2A1, A4). This angle at the dorsal apex of the scapular region generally indicates the
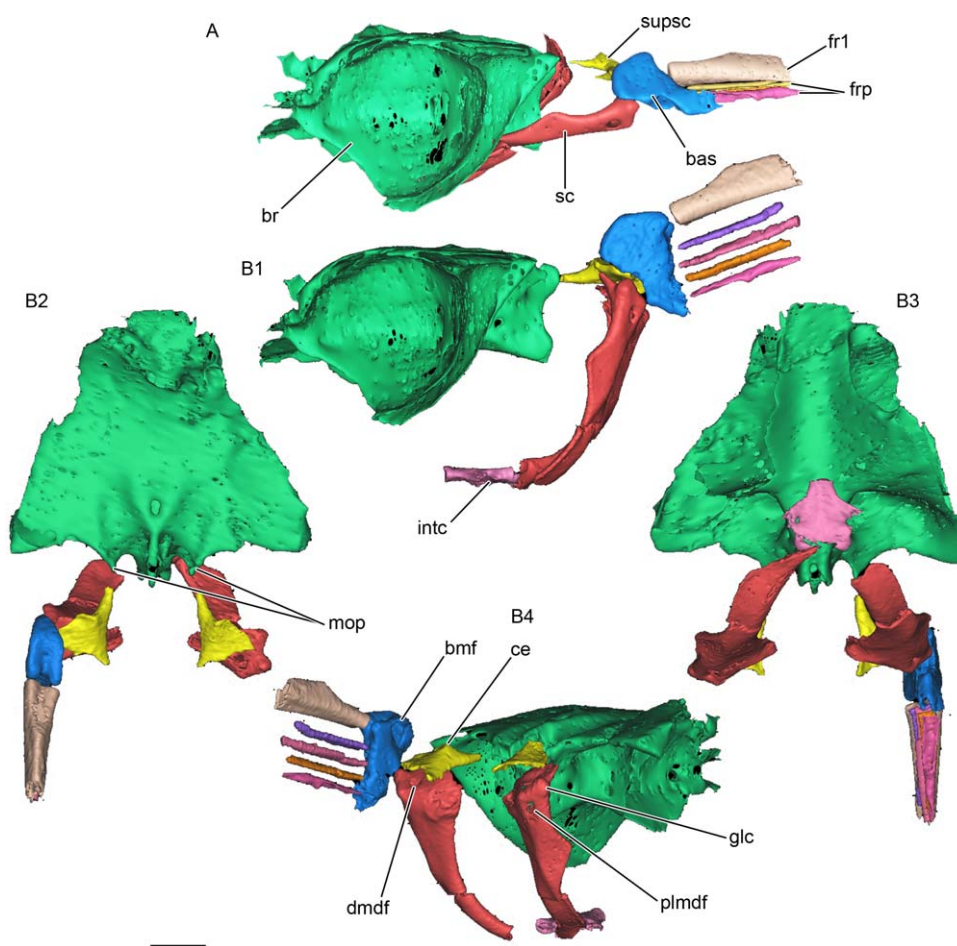
Fig. 1. Surface rendering generated from Synchrotron Radiation microtomographic slices of the braincase, pectoral girdle and left fin of KUNHM 21894. A. Relative position of the braincase, pectoral girdle and left pectoral fin as preserved inside the nodule, in left lateral view. B. Braincase, pectoral girdle and left fin restored virtually in their supposed natural position, in lateral (B1), dorsal (B2), ventral (B3) and posterolateral (B4) views. The elements (notably the distal radials) illustrated in Fig. 1B have been slightly separated from each other for the clarity of the figure. **br:** braincase (neurocranium); **bas:** basipterygium; **bmf:** basipterygium medial fossa; **ce:** central elevation of the suprascapular cartilage; **dmdf:** dorsal opening of the main diazonal canal; **fr1:** first (anterior) distal radial; **frp:** posterior distal radials; **glc:** glenoid condyle; **intc:** intercoracoid cartilage; **mop:** medial otic process of the braincase; **plmdf:** posterolateral opening of the main diazonal canal; **sc:** scapulocoracoid; **supsc**: suprascapular cartilage. Scale bar = 0.5 cm.

Fig. 1. Reconstitution de surface réalisée à partir d'images microtomographiques Synchrotron du crâne, de la ceinture pectorale et de la nageoire pectorale gauche du spécimen KUNHM 21894. A. Position relative du crâne, de la ceinture pectorale et de la nageoire pectorale gauche, tels que conservés à l'intérieur du nodule, en vue latérale gauche. B. Crâne, ceinture pectorale et nageoire pectorale gauche virtuellement replacés en position naturelle supposée, en vues latérale (B1), dorsale (B2), ventrale (B3) et postérolaterale (B4). Les éléments (notamment les radiaux distaux) illustrés sur la Fig. 1B ont été légèrement séparés les uns des autres, dans un souci de clarté de la figure. **br :** crâne (neurocranium) ; **bas :** basiptérygium ; **bmf :** fosse médiale du basiptérygium ; **ce :** élévation centrale du cartilage suprascapulaire ; **dmdf :** ouverture dorsale du principal canal diazonal ; **fr1 :** premier (antérieur) radial distal ; **frp :** radiaux postérieurs distaux ; **glc :** condyle glénoïde ; **intc :** cartilage intercoracoïdien ; **mop :** processus otique médial du crâne ; **plmdf :** ouverture postérolaterale du principal canal diazonal ; **sc :** scapulocoracoïde ; **supsc** : cartilage suprascapulaire. Barre d'échelle = 0,5 cm.

insertion area for the dorsal pectoral retractor muscle in chondrichthyans (Coates and Gess, 2007; Didier, 1995). Although the peculiar arrangement of the pectoral girdle of the Sibyrhynchidae, the posterolateral angle of the latter, along with the lateral surface of the lateral 'anterior shoulder', may have provided insertion areas for the dorsoventral series of pectoral retractor muscles. A marked posterolateral angle of the scapulocoracoid is considered as a primitive chondrichthyan feature (Coates and Gess, 2007).

The anterior shoulder separates dorsal and ventral embayments of the anterior margin of the coracoid region. The dorsal one may have accommodated the cucullaris

superficialis and dorsal pectoral protractor muscles, while the ventral one may have been the insertion area of the coracobranchial muscles. In modern holocephalans, which possess a holostylic jaw suspension, like sibyrhynchids, the coracohyoideus and coracomandibularis muscles also originate from the anterior surface of the coracoid region (Didier, 1995). A similar arrangement may have been present in *Iniopera* sp.

The ventral end of the coracoid region ends with a slender, rounded and anteromedially directed process (corp, Fig. 2A). The proximal end of the latter shows medially a pronounced, rounded concave facet, which corresponds to the area of articulation between the scapu-
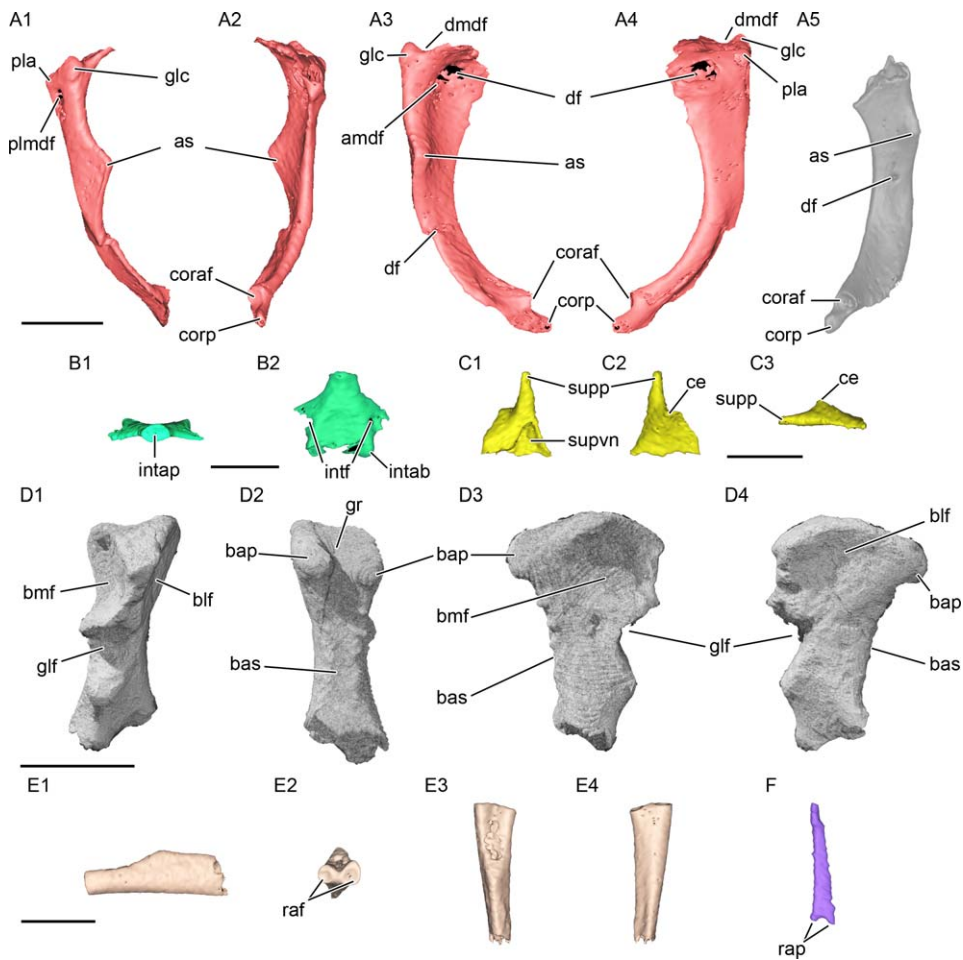
Fig. 2. Surface rendering generated from Synchrotron Radiation microtomographic slices of the pectoral girdle and left fin of KUNHM 21894 (A1–A4, B, C, E, F), KUNHM 22060 (D) and OKM 38 (A5). A. Right scapulocoracoid in lateral (A1), medial (A2), anterior (A3) and posterior (A4) views. A5. Left scapulocoracoid in anterior view. B. Intercoracoid cartilage in anterior (B1) and dorsal (B2) views. C. Right suprascapular cartilage in ventral (C1), dorsal (C2) and medial (C3) views. D. Left basipterygium in ventral (proximal) (D1), dorsal (distal) (D2), medial (D3) and lateral (D4) views. E. Left first (anterior) distal radial in lateral (E1), anterior (proximal) (E2), dorsal (E3) and ventral (E4) views. F. Posterior distal radial in dorsal views. **amdf:** anterior opening of the main diazonal canal; **as:** 'anterior shoulder'; **bap:** basipterygium articular process for the first (anterior) distal radial; **bas:** basipterygium articular surface for posterior distal radials; **blf:** basipterygium lateral fossa; **bmf:** basipterygium medial fossa; **ce:** central elevation of the suprascapular cartilage; **coraf:** coracoid articular fossa for the intercoracoid cartilage; **corp:** coracoid process; **df:** other diazonal foramina; **dmdf:** dorsal opening of the main diazonal canal; **glc:** glenoid condyle; **glf:** glenoid fossa; **gr:** basipterygial groove; **mdf:** main diazonal foramen; **pla:** posterolateral angle; **intab:** intercoracoid articular bulge; **intap:** intercoracoid anterior process; **intf:** intercoracoid foramina; **plmdf:** posterolateral opening of the main diazonal canal; **raf:** articular fossa of the first (anterior) distal radial; **rap:** articular process of the posterior distal radial; **supp:** suprascapular process; **supvn:** suprascapular ventral notch. Scale bar = 0.5 cm.

Fig. 2. Reconstitution de surface réalisée à partir d'images microtomographiques Synchrotron de la ceinture pectorale et de la nageoire pectorale gauche des spécimens KUNHM 21894 (A1-A4, B, C, E, F), KUNHM 22060 (D) et OKM 38 (A5). A. Scapulocoracoïde droit en vues latérale (A1), médiale (A2), antérieure (A3) et postérieure (A4). A5. Scapulocoracoïde gauche en vue antérieure. B. Cartilage intercoracoïdien en vues antérieure (B1) et dorsale (B2). C. Cartilage suprascapulaire en vues ventrale (C1), dorsale (C2) et médiale (C3). D. Basiptérygium gauche en vues ventrale (proximale) (D1), dorsale (distale) (D2), médiale (D3) et latérale (D4). E. Premier (antérieur) radial distal gauche en vues latérale (E1), antérieure (proximale) (E2), dorsale (E3) et ventrale (E4). F. Radial distal postérieur en vue dorsale. **amdf:** ouverture antérieure du principal canal diazonal; **as:** « épaule antérieure »; **bap:** processus articulaire du basiptérygium pour le premier (antérieur) radial distal; **bas:** surface articulaire du basiptérygium pour les radiaux distaux postérieurs; **blf:** fosse latérale du basiptérygium; **bmf:** fosse médiale du basiptérygium; **ce:** élévation centrale du cartilage suprascapulaire; **coraf:** fosse articulaire du coracoïde pour le cartilage intercoracoïdien; **corp:** processus coracoïdien; **df:** autres foramens diazonaux; **dmdf:** ouverture dorsale pour le principal canal diazonal; **glc:** condyle glénoïde; **glf:** fosse glénoïde; **gr:** sillon basiptérygial; **mdf:** principal foramen diazonal; **pla:** angle postérolatéral; **intab:** renflement articulaire du cartilage intercoracoïdien; **intap:** processus antérieur du cartilage intercoracoïdien; **intf:** foramen du cartilage intercoracoïdien; **plmdf:** ouverture postérolatérale du principal canal diazonal; **raf:** fosse articulaire du premier (antérieur) radial distal; **rap:** processus articulaire du radial distal postérieur; **supp:** processus suprascapulaire; **supvn:** encoche ventrale du cartilage suprascapulaire. Barre d'échelle = 0,5 cm.

locoracoid and the intercoracoid cartilage (coraf, Fig. 2A). Consequently, the anteroventral process of the coracoid part of the scapulocoracoid probably extends ventrally to the posteroventrolateral edge of the intercoracoid cartilage.

3.1.2. Intercoracoid cartilage

The intercoracoid cartilage is a rather narrow, hexagonal, unpaired and symmetrical cartilage, which articulates posterolaterally with the ventral end of the two scapulocoracoids. This articulation is situated on the two bulges

located on the posterolateral corner of the cartilage (intab, Fig. 2B2). On the dorsal surface of the cartilage, these bulges merge with anteriorly convergent, low ridges that meet together at the level of an anterior, deeper process. Between the two ridges is a slightly concave area posteriorly, which may have housed the heart, since the heart of extant chondrichthyans is usually located dorsal to the pectoral girdle symphysis. The anterior process of the intercoracoid cartilage is oval in section and forms a smooth surface anteriorly (intap, Fig. 2B1), which may be an articular surface for a basibranchial cartilage situated immediately anterior to it. At the base of the anterior process, the lateral edges of the cartilage flare posterolaterally until about the mid-length of the intercoracoid basal plate. Then, the lateral edges mark a right angle and merge posteromedially to meet the anteriorly convergent ridges. Between the latter and the lateralmost part of the cartilage are paired and symmetrical foramina (intf, Fig. 2B2), which may have accommodated blood vessels. The ventral surface of the cartilage is flat, or slightly concave.

3.1.3. Suprascapular cartilages

The suprascapular cartilages are relatively small, narrow, triangular and paired cartilages (Fig. 2C) whose posterior margin is larger than the anterior one. Their ventral surface is flat and extends anteriorly by a prominent, forwardly tapering medial suprascapular process (supp, Fig. 2C). The anterior end of this process probably articulates with the rear of the neurocranium at the level of the medial otic process (mop, Fig. 1B2), whereas the ventral surface of the suprascapular rests on the flattened dorsal surface of the scapulocoracoid (Figs. 1B2, B4). At the base of the scapular process, the ventral surface displays a broad notch, which originates from the rear of the cartilage and tapers anteriorly along with the scapular process (supvn, Fig. 2C1). The dorsal surface of the suprascapular cartilage displays a central elevation (ce, Figs. 1B4, 2C3).

3.2. Pectoral fin

The pectoral fin consists of a single robust proximal basal element (basipterygium), which articulates with the dorsolateral part of the scapulocoracoid, and bears a series of distal pectoral radials along its dorsal edge (bas, fr1, frp, Fig. 1A). The anteriormost pectoral fin distal radial is much larger than the posteriorly following ones, as in *Iniopera richardsoni* (Zangerl and Case, 1973: fig. 78).

3.2.1. Basipterygium

The basipterygium is a robust and elongated element (Fig. 2D). Its outline recalls that of the basipterygium of *Iniopera richardsoni* (Zangerl and Case, 1973: figs. 59, 61). Its anterior part, which articulates with the anteriormost distal radial, is broader and more complex than the posterior one. Its anterolateral surface is slightly concave and may have housed pectoral fin muscles (blf, Fig. 2D1, D4). The anteroventral margin of the cartilage is sharp but flares posterodorsolaterally to form a broad anterodorsal part. The medial surface of the anterior part of the basipterygium displays a large concavity (bmf, Figs. 1B4, 2D1, D3),

which may have accommodated the central elevation of the suprascapular cartilage (ce, Fig. 1B4) during the vertical flexor fin movement. It may also have accommodated pectoral fin muscles. The anteriormost part of the anterodorsal surface of the basipterygium is rounded and smooth, but merges posterodorsally with prominent parallel and elongated bulges, which are separated from one another by a rather deep groove (gr, Fig. 2E2). These bulges form two rounded, anterodorsal processes (bap, Fig. 2D2-D4), which articulate with the first distal pectoral radial (see below). Posterior to these articular processes, the posterodorsal surface of the cartilage display a smooth and elongated area (bas, Fig. 2D2-D4) where the other distal pectoral radials were inserted (Fig. 1B1, B4). The glenoid fossa is situated on the ventral surface of the basipterygium, about at its mid-length (glf, Fig. 2D1, D3, D4). It consists of an elongated concavity, which is deeper anteriorly, for the glenoid condyle of the scapulocoracoid.

3.2.2. Distal radials

Only five distal pectoral radials are preserved, almost in natural position in KUNHM 21894, whereas *Iniopera richardsoni* possesses at least eight distal radials (Zangerl and Case, 1973).

The first distal radial is stouter than the others (Fig. 2E), and its proximal end displays two pronounced concavities (raf, Fig. 2E2) that match the articular area of the two rounded anterodorsal processes of the basipterygium (bap, Fig. 2D2). The outline of its proximal part recalls the shape of two elongated, closely set pipes placed side by side. The radial becomes deeper but narrower posteriorly, with dorsal and ventral processes. Unfortunately, the radial is incomplete posteriorly, so that it is impossible to know whether or not it is segmented, as Zangerl and Case (1973) suggested for *Iniopera richardsoni*. The posteriorly following distal radials have a different shape (Fig. 2F); i.e. they form a distally tapered rod, in which the proximal part is narrow in section. They end with two small processes, which are well apart, proximally (rap, Fig. 2F). All these fin distal radials, except the first one, are almost identical in length.

4. Discussion

The latest studies on the neurocranium of the two iniopterygian families provided no consensus as to the phylogenetic status of the Iniopterygia (Grogan and Lund, 2009; Pradel et al., 2009; Pradel, 2010). Moreover, the neurocranial characters used by Grogan and Lund (2009) do not support the clade including the Iniopterygidae and Sibyrhynchidae (Appendices 1, 2, 3). This may be explained by the very different conditions of preservation of the neurocranium in the Iniopterygidae and Sibyrhynchidae, respectively may be one. More, and better preserved (preferably in three dimensions) specimens of Iniopterygidae are needed for obtaining a more balanced quality of the data.

It is therefore necessary to explore the postcranial characters, which may gather the two families into a monophyletic group. Some of the classical iniopterygian synapomorphies concern the pectoral girdle and fin; i.e.

enlarged pectoral fins, dorsolaterally attached to the shoulder girdle via a single basipterygium. The description of the pectoral girdle and fin of the Sibyrhynchidae provides more characters, which are also present in Iniopterygidae, such as the presence of suprascapular and intercoracoid cartilages. Here we discuss some of these characters that may be useful for further phylogenetic analysis.

4.1. Intercoracoid element(s)

In none of the Paleozoic chondrichthyans are the coracoids fused ventrally (Zangerl, 1981), and this condition is commonly supposed to be plesiomorphic for chondrichthyans (Stahl, 1999). An unpaired cartilage situated between the ventral extremities of the two coracoids is present in some modern hexanchiforms, such as *Notorynchus* (Haswell, 1884; Kälin, 1931, Parker, 1891), which are considered as primitive neoselachians (Maisey et al., 2004). In all modern holocephalans (Chimaeroidei), the scapulocoracoids are fused ventrally. Nevertheless, a possible Jurassic Chimaeroidei (Didier, 1995), *Ischyodus schuebleri*, possesses an intercoracoid cartilage that articulates with the two scapulocoracoids ventrally (Heimberg, 1947: fig. 6a). The latter displays exactly the same outline as the intercoracoid cartilage of the Sibyrhynchidae *Iniopera* sp., which can be resolved as a stem holocephalan (see above; Janvier, 1996; Pradel et al. 2009; Pradel, 2010; Zangerl, 1981). The Sibyrhynchidae *Sibyrhynchus* also shows an unpaired intercoracoid cartilage, as also does the Iniopterygidae *Promexyele* (Zangerl and Case, 1973). Another putative stem-holocephan, the eugeneodontid *Ornithoprion* (Grogan and Lund, 2004; Janvier, 1996), also possesses an intercoracoid cartilage (Zangerl, 1966, 1981).

Among the other Paleozoic chondrichthyans, some taxa, such as stethacanthids, symmoriids and primitive caseodontid, (Coates and Sequeira, 2001; Zangerl, 1981), display large, paired and ventral procoracoid cartilages at the ventral end of the scapulocoracoids. According to Coates and Gess (2007), these procoracoid cartilages are homologous with the separate coracoid cartilages of xenacanths (Heidtke and Schwinde, 2004). In the Iniopterygidae *Papilionichthys* and *Rainerichthys*, the ventral surface of each pectoral girdle is linked to the branchial apparatus through paired, elongate cartilages, although Grogan and Lund (2009) interpreted these elements as hypobranchials. It was also suggested that the unpaired intercoracoid plate of the other iniopterygians is connected to the branchial apparatus (see above; Zangerl, 1981).

In acanthodians, a pair of procoracoids is present in the endoskeletal pectoral girdle (Miles, 1973). In acanthodian taxa in which the dermal skeleton of the pectoral girdle is more developed, such as the Climatiidae and Diplacanthidae, there is one or two median, unpaired dermal lorical plate (Gardiner, 1984; Miles, 1973).

In osteichthyans and placoderms, there is neither evidence of an endoskeletal intercoracoid, except in the lungfish *Ceratodus* (Goodrich, 1930), nor evidence of endoskeletal procoracoids. Nevertheless, the endoskeletal scapulocoracoid is generally reduced, and a dermal interclavicle is present between the two clavicles in osteichthyans (Janvier, 1996), whereas the anterior and posterior median ventral plates are wedged between the anterior ventrolateral plates in placoderms (Goujet, 1984). Gardiner (1984) homologized the ventral median dermal plates of osteichthyans, placoderms and acanthodians.

The interclavicle is obviously not homologous to an endoskeletal intercoracoid element. Nevertheless, in some taxa, the interclavicle lies ventral to, or fuses with unpaired, median endoskeletal element. In some tetrapods, a dermal interclavicle extends along the ventral surface of the endoskeletal sternum (Goodrich, 1930). In addition, according to Patterson (1977), the urohyal of teleosteans is actually derived from the fusion of the dermal interclavicle and the endochondral urohyal.

These observations suggest that the endoskeletal and dermal pectoral shoulder of gnathostomes are primitively separated ventrally by either unpaired or paired endoskeletal intercoracoid elements, or dermal bones, respectively. The median endoskeletal intercoracoid cartilages may have been lost in most derived chondrichthyans, so that the coracoid part of the two scapulocoracoids meets ventrally. Moreover, Parker (1891) interpreted the intercoracoid element of *Notorynchus* as a sternal element, which is divided into two parts, a pre-omosternum and a post-omosternum. Zangerl and Case (1976), suggested that the "sternum" of chondrichthyan was primitively paired (the condition seen in some Iniopterygidae, stethacanthids, symmoriids, caseodontids and xenacanths), and that the unpaired "sternum" of *Notorynchus* is the result of a secondary fusion of the originally paired elements. The intercoracoid cartilage of *Iniopera* sp. may provide support for this interpretation, as it is perfectly symmetrical and displays a pair of symmetrical foramina. One may suppose that this cartilage results from the fusion of two embryonic structures, ventral to the embryonic coracoids.

4.2. Suprascapular cartilages

The sibyrhynchid *Iniopera* sp. possesses a pair of suprascapular cartilages dorsal to the scapulocoracoids. Suprascapular cartilages were already reported in two Iniopterygidae, *Rainerichthys* and *Papilionichthys*, although in larger numbers (Grogan and Lund, 2009). The presence of suprascapular cartilages in other fossil chondrichthyans is poorly documented, but they are present in xenacanths (Zangerl, 1981), and in the hybodont *Lissodus cassangensis* (Maisey, 1982). Among extant chondrichthyans, only batomorphs possess suprascapular cartilages, which articulate with the neural arches of the vertebrae, or directly with the synarcual (Capetta, 1987).

The endoskeletal shoulder girdle of some acanthodians, such as *Acanthodes*, displays a pair of suprascapular elements. Nevertheless, these bones are absent in other forms, such as climatiiforms (Janvier, 1996).

In osteichthyans, the endoskeletal pectoral girdle is tripartite. It ossifies, however, as a single element, except in primitive living teleosts, in which a dorsal mesocoracoid is separated from a medial scapula that is also distinct from the ventral coracoid (Gardiner, 1984). Gardiner (1984) supposed that the primitive number of ossifications in the endoskeletal shoulder girdle is three in osteichthyans. Pla-

coderms never display any endoskeletal element dorsal to the scapular blade.

The phylogenetic signal of endoskeletal suprascapular elements is thus unclear in gnathostomes.

It was suggested that the suprascapular cartilages of iniopterygians link the pectoral girdle to the rear of the neurocranium (see above; Grogan and Lund, 2009). This condition is unique among chondrichthyans, since the pectoral girdle is always separated from the rear of the neurocranium in other chondrichthyans, even in batomorphs, xenacanths and *Lissodus cassangensis*, which possess suprascapular cartilages, and this could represent a synapomorphy of iniopterygians.

A series of dermal bones links the dermal pectoral girdle to the dermal bones of the head in osteichthyans and placoderms, suggesting that a dorsal connection between the pectoral girdle and the head could be plesiomorphic for gnathostomes.

4.3. Size of the scapular region

All iniopterygians known to date possess a pectoral fin that articulates with the dorsal part of the scapulocoracoid, and their scapular region is thus extremely reduced. Among extant and fossil chondrichthyans, this feature is unique and could be a non-ambiguous autapomorphy of iniopterygians. The position of the attachment of the pectoral fin is located at the level of about one-third to mid-length of the scapulocoracoid in most of the Paleozoic chondrichthyans, such as symmoriiforms, xenacanths, ctenacanths, eugeneodontiforms, as well as in hybodontiforms and neoselachians (Lane and Maisey, 2009; Zangerl, 1981). The position of this fin attachment is much more variable among the holocephalans. The condition in many stem-holocephalans, such as *Debeerius* (Grogan and Lund, 2000), is almost similar to that in, e.g., hybodontiforms and neoselachians. However, the pectoral fin articulation is situated slightly more dorsally in *Harpagofututor* (Lund, 1982), and much farther ventrally in, e.g., *Squaloraja*, *Ischyodus* and modern chimaeroids (Stahl, 1999). The dorsal position of the pectoral fin attachment relative to the scapulocoracoid may thus be considered as a derived condition for chondrichthyans.

4.4. Pectoral fin

All iniopterygians possess a monobasal pectoral fin with a single, proximal, enlarged basal element (basipterygium), which articulates with the scapulocoracoid, and which is variously sized according to the genus (see above; Grogan and Lund, 2009; Zangerl and Case, 1973). The distal radials of the pectoral fin are attached all along the distal edge of this basal element.

A monobasal pectoral fin may represent a plesiomorphic condition for gnathostomes, since various stem gnathostomes display a single basal element, as in, e.g., the osteostracan *Escuminaspis*, and some placoderms (Goujet, 2001; Goujet and Young, 2004; Janvier et al., 2004). Nevertheless, the presence of three or more proximal basals supporting distal radials is supposed to be a feature of crown-gnathostomes (Coates, 2003; Goujet, 2001; Goujet and Young, 2004; Janvier et al., 2004; Mabee and Noordsy, 2004). Proximal premetapterygial and metapterygial radials, either or not forming a basal plate, are present in most Paleozoic chondrichthyans (e.g., symmoriiforms, primitive xenacanths, hybodonts, eugeneodontids), and a monobasal pectoral fin, like that of iniopterygians, may therefore represent a derived condition among chondrichthyans.

In the Iniopterygidae, the pectoral basipterygium also supports an axis made up by small cartilages at its posterodistal corner, which bears distal radials (Grogan and Lund, 2009; Zangerl and Case, 1973), whereas this feature is absent in the Sibyrhynchidae (see above; Zangerl and Case, 1973). An axis of small cartilages, which articulates with a proximal basal cartilage of the pectoral fin distally, and which bears, in some genera, distal radials, is a widespread feature among Paleozoic chondrichthyans (e.g., the symmoriiform *Cobelodus*; Zangerl and Case, 1976; the xenacanth *Orthacanthus*; Hampe and Heidtke, 1997; the eugeneodontid *Fadenia*; Bendix-Almgreen, 1975; the stem holocephalans *Traquairus*; Lund and Grogan, 1997). Consequently, the presence of this pectoral axis (as in the Iniopterygidae) may be considered as a plesiomorphic condition for chondrichthyans.

Zangerl (1981) suggested that the single basal element of the iniopterygian pectoral fin may actually be a compound element. The shape of the basipterygium of the specimens studied here, along with its topographic relation to the distal radials compared to extant chimaeroids, may provide support for this assumption. The pectoral fin of crown holocephalans displays a distinctive endoskeletal pattern; i.e. the pectoral fin is dibasal, with a propterygium and a metapterygium that bear all the distal radials. This condition is supposed to be derived for chondrichthyans (Coates and Sequeira, 2001). In addition, in extant species, such as *Callorhinchus milii* and *Harriotta releighana*, only the small propterygium articulates with the scapulocoracoid. Moreover, the anteriormost distal radials of extant chimaeroids fuse to form a more robust element, which articulates with the propterygium, whereas the posteriorly following distal radials articulate with the metapterygium (Didier, 1995). The anteriormost distal radial of sibyrhynchids and iniopterygids (see above; Zangerl and Case, 1973), as well as that of many other stem holocephalans (Stahl, 1999), is also more robust than the following posterior ones. In addition, the shape of the enlarged anteriormost distal radial of iniopterygians suggests a fusion of two adjacent distal radials. This robust distal radial articulates with the anterior part of the single basipterygium, which is larger and more complex than its posterior part, at any rate in sibyrhynchids (the morphology of the basipterygium of iniopterygids is poorly known). The following posterior distal radials are supported by the posterodistal edge of the basipterygium. One may therefore infer that the single basipterygium is in fact derived from the fusion of the pro- and metapterygium, and that only the propterygial part of the basipterygium bears the anteriormost fused distal radials, as in extant chimaeroids. The condition in other stem holocephalans is unclear. For instance, it was suggested that *Traquairus*

(Lund and Grogan, 1997) and *Debeerius* (Grogan and Lund, 2000) possess a dibasal pectoral fin, as in extant chimaeroids, plus a more or less segmented metapterygial axis posteriorly. The metapterygium and the metapterygial axis support distal radials. Nevertheless, in both cases, the cartilage that Lund and Grogan (1997) and Grogan and Lund (2000) have interpreted as the propoterygium, and its position relative to the scapulocoracoid and the proximal basal cartilage of the pectoral fin, are not clearly visible in the specimens (Grogan and Lund, 2000: p. 228, fig. 12A; Lund and Grogan, 1997: p. 482, fig. 3.4). It is possible that it rather represents an enlarged anteriormost distal radial supported by a single basal cartilage, which articulates with the pectoral girdle anteriorly, and is followed by a metapterygial axis posteriorly. In such a case, the condition in these two taxa is the same as that described above for iniopterygians. Consequently, one may suppose that the plesiomorphic condition for holocephalans is the presence of a single basipterygium, which articulates with the scapulocoracoid. The basipterygium articulates posteriorly with a well-defined metapterygium in extant holocephalans, and a metapterygial axis in some stem holocephalans.

5. Conclusions

The pectoral girdle and fin of the specimens, in which the neurocranium was previously described, allows their attribution to an already known sibyrhynchid genus, *Iniopera*.

The pectoral girdle of *Iniopera* sp. consists of three elements, which are, from dorsal to ventral, a paired suprascapular cartilage, a pair of robust scapulocoracoids and an unpaired intercoracoid cartilage.

It is assumed that the suprascapular element articulates with the rear of the neurocranium of *Iniopera* sp., as they also do in the Iniopterygidae *Rainerichthys* and *Papilionichthys*. This may represent a synapomorphy of the two iniopterygian families.

The scapular part of iniopterygians is extremely reduced, since the articular glenoid condyle of the scapulocoracoid is situated on the dorsolateral surface of the cartilage. This may be a autapomorphy of iniopterygians.

The two scapulocoracoids of iniopterygians are separated ventrally; a plesiomorphic condition of gnathostomes. The presence of paired intercoracoid cartilages may be plesiomorphic for chondrichthyans, and a single, median intercoracoid cartilage may be regarded as derived from the fusion of these paired elements. The latter condition is present in some iniopterygians, and in some Jurassic crown holocephalans (e.g., *Ischyodus*).

A single basipterygium (monobasal pectoral fin) may be a derived condition within chondrichthyans. Stem and crown holocephalans may share the presence of a propterygium, which articulates with the scapulocoracoid and bears an enlarged first distal pectoral fin radial, as in iniopterygians. Farther posteriorly, the basipterygium articulates with either a well-defined metapterygium (crown-holocephalans) or a metapterygial axis (stem-holocephalans).

Although many characters suggest that iniopterygians are a clade, more data are needed for resolving their detail relationships. The neurocranium does not clearly allow gathering of the two iniopterygian families into clade. Some postcranial characters, such as the pectoral fin structure, may provide uniquely derived characters shared by iniopterygians and holocephalans. Notably, the presence of an unpaired intercoracoid cartilage in sibyrhynchid iniopterygians and some Jurassic crown holocephalans, and the similar arrangement of the pectoral girdle and fin in stem holocephalans and iniopterygians, which prefigures that of extant holocephalans, may support a close relationship between iniopterygians and holocephalans.

It is noteworthy that the endoskeletal elements and dermal bones have primitively, and in parallel, generated the same arrangement of the pectoral girdle. Scapulocoracoids are primitively separated ventrally by either endoskeletal elements (e.g., intercoracoid cartilage of sibyrhynchids), or dermal bones (e.g., interclavicle of osteichthyans, median ventral plate of placoderms). One may suppose that similar developmental patterning processes have induced both endoskeletal and dermal elements of the pectoral girdle in primitive gnathostomes.

This work confirms the rapidly growing potential of X-ray synchrotron radiation techniques in paleontology, and especially the phase contrast imaging when dealing with highly mineralized specimens. It imposes synchrotron radiation as a powerful tool for non-destructive imaging of fossils.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.crpv.2010.07.015. Goloboff et al., 2000; Nixon, 2002.

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