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Neurocranial development of the coelacanth and the evolution of the sarcopterygian head

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Supplementary Information for

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I. Additional results and discussion

I.1 Morphometric measurements and effect of the fixatives

To further compare the growth of the brain, the notochord, and the endocranial cavity we measured the volume of these structures (Extended Data Table 1). Brain volume was measured from the portion laying just posteriorly to the foramen for the vagus nerve to the tip of the telencephalon. Regarding the juvenile brain, the portion of the rhombencephalon cut during the dissection was restored with a cylinder spanning up to the back of the vagus nerve, which allowed us to estimate the volume of the juvenile brain within the endocranial cavity. The same posterior limit was taken for measuring the volume of the endocranial cavity. These measurements show that the brain reaches almost a quarter of its final size at the end of the prenatal development (Extended Data Table 1). The volume of the notochord was measured from the edge of basioccipital (i.e. the posteriomost point of the neurocranium) to its anterior tip in contact with the basisphenoid. The absolute size of the brain is higher than that of the notochord only in the fetus.

Fixation prevents tissues decay, but also inevitably alters the shape and size of the tissues to different degrees. Therefore, a key question concerning our observations is whether the formalin fixation could have induced the important discrepancy observed between the volume of the brain and that of the endocranial cavity in the different development stages. The change in volume and shape depends on the type of fixative used. Formalin and

glutaraldehyde can induce a slight swelling of the tissues, followed by a shrinkage phase before stabilization in the volume (Vickerton et al. 2013). By contrast, ethanol produces a more important and continuous shrinkage of the tissues (Vickerton et al. 2013). Based on the affine registration of MRI acquisitions, Schulz et al. (2011) reported that *in situ* formalin (10%) fixation causes an anisotropic shrinkage of 8.1% in the volume of human brains over a period of 70 days. The different regions of the brain do not deform in the same manner, and maximal strain fields were quantified in the peripheral layers of the brain (Schulz et al. 2011). When dissected and immersed in 10% formaldehyde in PBS during 28 days, the average shrinkage rate for skeletal muscle, cardiac muscles and cerebellum is slightly higher (around 12%, fig. 3 in (Vickerton et al. 2013) that what would expected when fixed *in situ* (Vickerton et al. 2013). However, there is a close correspondence between the measurements in brain volume and cortical thickness made with MRI on formalin fixed (10%) and live rhesus macaques (*Macaca mulatta*) (Calabrese et al. 2015). Taking the volume of the endocranial cavity as a reference, the shrinkage rate would have been of 87% in P2, and 99% in the adult for the brain to obtain its measured volume. The experimental studies published hence indicate that, despite having an effect on the tissues, the formalin fixation cannot result in a sufficient shrinkage for the brain to have the condition observed in the coelacanth specimens. Moreover, all specimens underwent fixation likely causing a similar degree of shrinkage in all specimens.

The limited impact of the fixation on the tissues is also supported by the comparison of the formalin fixed pups and the juvenile. The latter was frozen at -18°C about two hours after death and sent to Paris for study in 1974 (Anthony & Robineau 1976; Nulens et al. 2011). The specimen was still frozen upon arrival at the MNHN (Anthony & Robineau 1976; Nulens et al. 2011), and the skull roof was removed to observe the brain *in situ* (Extended Data Fig. 5) the day following the defrosting of the specimen. We observed a close correspondence in the position and relative size of the brain between this specimen and the pups fixed in formalin, which further supports that the fixation had little effect on the tissues and allows for a gross anatomical study of these specimens.

Regarding the adults, our calculation of the ratio between the volume of the brain and that of the endocranial cavity is very similar to the estimates that were made fifty three years ago by Millot and Anthony (1965) on specimens recently fixed in formalin. This suggests that formalin has little long-term effects on the tissues, or if there are any, they might be balanced by the intraspecific variability and/or the method employed to perform the measurements. In addition, the measurements of brain volumes, and the ratio between the brain and endocranial volume are similar in adult specimens, despite the fact that the adult was stained with a solution of 5% phosphomolybdic acid in 70% ethanol (Dutel et al. 2013). Finally, reports indicate that

the specimens were rapidly (within a few hours) formalin fixed or frozen after being captured in Comoro islands (Millot & Anthony 1965; Nulens et al. 2011), thus indicating that the decay and alteration of the tissues after death was limited.

The fixation with ethanol has been reported to cause more shrinkage in tissues than formalin (Vickerton et al. 2013). Indeed, ethanol fixes the tissues by causing its dehydration, and the degree of shrinkage of the tissues is proportional to the concentration in ethanol of the solution (Boyde & Maconnachie 1980). Therefore, the brain volume we measured in the fetus, which was fixed in ethanol, likely represents a greater underestimation than that for the other developmental stages. Yet, the topographic relationship between the brain and the endocranial cavity, as exemplified by the position of the foramina of the cranial nerves is consistent with what can be observed in other taxa. Thus, this suggest that the shrinkage that could have been caused by the fixation did not alter dramatically the position of the brain within the endocranial cavity. As such, we think that the potential bias in the brain volume measured in the fetus does not change our results pertaining to the understanding of the relationships between the brain and the braincase during coelacanth development.

In the juvenile specimen, the extraction of the brain from the endocranial cavity has altered its shape and volume. When compared with the photograph showing the brain *in situ* within the endocranial cavity (Extended Data Fig. 5), the brain reconstructed appears to have the auriculae cerebelli and the telencephalon squashed along the body of the brain (Fig. 3, Extended Data Fig. 3). In addition, the digital reconstruction of the regions of the braincase destroyed during the dissection might also introduce biases in the measurements made on this developmental stage. Although probably underestimated, the ratio between the brain and endocranial volume matches the values found for P1 and P2 and provide insight into the position and relative volume of the brain in free-swimming juveniles.

As a conclusion, the fixative used to preserve the specimens represents a potential source of error in the measurements of the brain volume. However, experimental studies and comparison with unfixed specimens show that the important discrepancy between the brain and endocranial volumes is not artefactual, and rather results from the negative allometric growth of the brain relative to the endocranial cavity. In addition, the correspondence between measurements made on formalin-fixed specimen more than 50 years ago and ours indicates that such natural history collections are suitable for being used in gross-anatomical studies.

I.3 Additional anatomical observations and comparisons

External morphology of the neurocranium

Until now, the development of the extant coelacanth *Latimeria* was known only through the description of the head morphology of a juvenile (Anthony & Robineau 1976), and the description of the cranial nerves of a prepartum specimen (Northcutt & Bemis 1993). Our study hence represents the first comprehensive description of the development of the brain and neurocranium in one of the two species of living coelacanth.

The overall dimensions of the neurocranium vary during the ontogeny of *Latimeria* (Figs. 2,3, Extended Data Figs. 1-3). The ethmosphenoid portion is markedly longer and narrower than the otoccipital portion in the adult than in the fetus (Fig. 3, Extended Data Fig. 3). The ethmosphenoid portion of the braincase is much broader in the fetus than in adult *Latimeria*, and the ethmoid region markedly shorter in length. During the development, the short and broad ethmoid region observed in the fetus narrows and expands posteriorly and anteriorly, so that the overall proportions of the ethmosphenoid portion in adult *Latimeria* is similar to what is observed in *Eusthenopteron* (Downs et al. 2008; Jarvik 1980) (Fig 3, Extended Data Fig. 3). The neurocranial dimensions of these taxa differ from those of more basal tetrapodomorph and sarcopterygian fishes, but more closely matches the elpistostegalian *Panderichthys* (Ahlberg et al. 1996). The trends towards a longer ethmosphenoid division of the neurocranium is also observed in the coelacanth lineage: the neurocranium of early coelacanths *Miguashaia* (Cloutier 1996), *Diplocercides* (Forey 1998; Stensiö 1937), *Gavinia* (Long 1999), and *Euporosteus* (Stensiö 1937; Zhu et al. 2012), and *Styloichthys* (which was interpreted as either a basal actinistian [Friedman 2007] or stem sarcopterygian [King et al. 2017; Qiao et al. 2016]) shares similar neurocranial dimensions with the fetus of *Latimeria*, as well as a short ethmoid region, large orbits, the presence of a metotic fissure, and a buccohypophyseal canal opening on the parasphenoid. The fetus of *Latimeria* (Figs. 1, 2) is strikingly similar to the fossil embryo of the Triassic coelacanth *Rhaboderma* (Schultze 1972), and later prenatal stages show similar proportions of their neurocranium with the juvenile specimens of the Devonian coelacanth *Serenichthys* (Gess & Coates 2015). Unfortunately, the preservation of these specimens does not allow a detailed observation of the external and internal neurocranial anatomy. With the exception of the recently described genus *Foreyia* (Cavin et al. 2017), Mesozoic coelacanths (Carnier Fragoso et al. 2018; Cavin et al. 2016; Dutel et al. 2012, 2015; Forey 1998; Maisey 1986) are similar to adult specimens of *Latimeria*, and share with it a longer and narrower ethmosphenoid portion, and the absence of the an opening for the buccohypophyseal canal on the parasphenoid. The variation in

neurocranial form is exemplified in Mawsoniidae, in which the relative length ethmosphenoid portion is longer than in *Latimeria* (Carnier Fragoso et al. 2018; Dutel et al. 2015; Maisey 1986). The trend towards a slender and elongate snout appears to be associated with an increase of the overall body size in fossil coelacanth (Dutel et al. 2012, 2015; Maisey 1986) and during the ontogeny of *Latimeria*. The congruence between this evolutionary trend and the developmental pattern observed in *Latimeria* suggests that allometry likely represents a strong driver of variation of skull shape during coelacanth evolution.

The broad ethmoid region of the fetus also differs from the adult in the position of the articulation with the palate. In the fetus of *Latimeria*, as well as in stem-sarcopterygians (Yu 1998) and onychodonts (Andrews et al. 2006), the ethmoid articulation lies posterior to the postnasal wall. By contrast, this articulation is located in a fossa ventrolateral to the nostrils and formed by the lateral ethmoid and the ascending wing of the parasphenoid in the pups, juvenile, and adult *Latimeria* (Millot and Anthony 1958), as well as in fossil coelacanths (Friedman 2007). Our observation of the developmental stages of *Latimeria* shows that the displacement of the ethmoid articulation is related to the shallowing and anteroposterior extension of the ethmoid region, which might be constrained by the expansion of the rostral organ and its lateral canals (Fig. 3, Extended Data Fig. 3).

The otoccipital portion is shorter and broader in the fetus than in the adult. In ventral view, the otoccipital region of the fetus shows a short otic shelf, and much narrower basicranial fenestra where the notochord passes through. With respect to other neurocranial structures, the notochord is much smaller in the fetus than in the other stages. The commissura prefacialis is open in the fetus, and that the cartilaginous rods that forms the descending process for the postparietal in adults is still separated from the otic shelf (Extended Data Fig. 1). The posterior wall of the otic region narrows markedly, and is perforated by the large metotic fontanelle, which spans ventrally to the foramen for the glossopharyngeal and vagus nerves (Extended Data Fig. 1). The otic process that carries the articulatory facets for the hyomandibula, which position is lower in the fetus than in the adult. The walls of the endocranial cavity are pierced by two large openings, through which the acoustic and glossopharyngeal nerves are passing.

The fetus and adult *Latimeria* specimens show marked differences in the position of the foramen for the cranial nerves and blood vessels. In the fetus, the foramen for the internal carotid artery and the foramen for the pituitary vein are located ventrally and posteroventrally to the foramen for the oculomotor nerve, respectively (Fig. 2, Extended Data Figs. 1, 3). In the adult, the foramen for the pituitary vein and the foramen for the internal carotid artery are displaced anteroventrally to the foramen for the oculomotor nerve (Extended Data Fig. 3). Because of the reduction of the optic foramen and its dorsal displacement during ontogeny,

the foramen for the internal carotid artery lies ventrally to the optic foramen in the adult (Extended Data Fig. 3). The foramen for the trochlear nerve opens more anteriorly with respect to the foramen for the maxillary branch of the trigeminal nerve in the fetus. The relative position of the foramina on the ethmosphenoid portion of the skull in the fetus is hence similar to what can be observed in *Psarolepis* (Yu 1998), as well as in the Devonian coelacanths *Diplocercides* (Stensiö 1937, 1963) and *Euporosteus* (Forey 1998; Stensiö 1937), and in the stem-tetrapodomorph *Tungsenia* (Lu et al. 2012). With respect to the otoccipital portion of the neurocranium, the foramen for the facial nerve and the jugular canal are located more anteriorly to the foramen for the vagus nerve in the fetus. During *Latimeria* development, the position of the foramen for the vagus nerve, the jugular canal and the foramen for the glossopharyngeal nerve appear to be displaced posteriorly closer to each other. Comparison with fossil coelacanths is however difficult, as the otoccipital portion is largely made of cartilage in Mesozoic coelacanths (Forey 1998) and poorly or not preserved in Devonian coelacanths.

The *Latimeria* fetus shares with stem sarcopterygians the presence of a foramen in the middle of the notochordal pit, through which an extension of the notochord passes to reach to hypophyseal fossa (Fig. 2, Extended Data Fig. 1). Such a foramen is also observed in the stem-sarcopterygian *Psarolepis* (Yu 1998) and in *Onychodus* (Andrews et al. 2006). This condition is not observed in later development stages of *Latimeria*, and might reflects the anteriormost position occupied by the notochord during the embryonic development.

Endocast

The *Latimeria* fetus presents short olfactory tract canals and olfactory capsules that are widely separated relative to the midline, and are positioned close to the hypophyseal fossa (Fig. 3, Extended Data Fig. 3). By contrast, other developmental stages show longer olfactory tract canals and closed olfactory capsules that are positioned further away from the hypophyseal fossa (Fig. 3, Extended Data Fig. 3). The morphology of the nasal capsules in *Latimeria* fetus is also observed in placoderms (Stensiö 1963; Young 1979), in the chondrichthyan *Cladodoides* (Maisey 2005), in the stem-osteichthyan *Ligulalepis* (Clement et al. 2018), in early actinopterygians, in the stem-sarcopterygians *Psarolepis* (Qiao et al. 2011), *Quigmenodus* (Lu et al. 2016) and in the tetrapodomorph *Tungsenia* (Lu et al. 2012). The endocast of the pups, juvenile, and adult markedly differ from that of the fetus in having a deep depression in its anterior aspect, which was called “ensellure rostrale” by Millot and Anthony (1965). This depression goes along the ventral margin of the cavity for the rostral organ, which is more developed in these stages than in the fetus. As such, the development of a coelacanth-

specific neurosensory organ likely constrains the shape of the ethmoid region of the neurocranium.

The ethmosphenoid region of the endocast is much boarder in the fetus than in other developmental stages (Fig. 3, Extended Data Fig. 3). The ethmosphenoid region of the endocast is about the same width than the otoccipital portion, with the broader point located at the level of the foramen for the trochlear nerve (Fig. 3, Extended Data Figs. 1, 3). Ventrally, the endocranial cavity extends to the floor of the braincase with a very short hypophyseal fossa which expands posterodorsally as a well-developed swelling perforated by the foramen for the pituitary vein (Fig. 2, Extended Data Figs. 1, 2). This recess in the endocast houses the hypothalamus and the pars intermedia of the hypophysis, that are positioned ventral to the mesencephalon in the fetus (Fig. 3, Extended Data Fig. 3). The configuration of the hypophyseal region in the fetus recalls that of *Ligulalepis* (Clement et al. 2018), and *Tungsenia* (Lu et al. 2012). By contrast, the hypophyseal region in the pups resemble more to what is observed in onychodonts (Lu et al. 2016).

Contrary to what is observed in other living taxa, the otoccipital division of *Latimeria* endocranium is positioned very dorsally by respect to its anterior counterpart. Accordingly, the mesencephalon and rhombencephalon are positioned dorsally to the forebrain, which is packed within the ethmosphenoid division of the braincase in the fetus. The endocranium of *Latimeria* fetus is flexed ventrally at the level of the cephalic flexure, which is positioned above the hypophyseal fossa. The configuration of the brain observed in *Latimeria* fetus is markedly different from what is observed in living chondrichthyans, actinopterygians, lungfishes and amphibians (Nieuwenhuys et al. 1998). In these taxa, the brain straightens as it extensively folds during the early ontogeny, so that the rhombencephalon, the mesencephalon and the forebrain develop merely in line, and encapsulated within the endocranium. In addition, the hypothalamus and the hypophysis are displaced posteroventrally to the diencephalon and span horizontally below the mesencephalon as a deep cephalic flexure develops in these taxa (Nieuwenhuys et al. 1998). This developmental pattern is associated with the reduction of the notochord, and its displacement towards the otic capsule (de Beer 1938; Goodrich 1930) (Fig. 4). By contrast, the notochord is enlarged and ends close to the hypophyseal fossa in the fetus of *Latimeria* (Figs. 2, 3, Extended Data Figs. 1, 3) and later developmental stages. As such, the neurocranial floor in the otoccipital portion is displaced dorsally to the neurocranial floor in the ethmosphenoid portion because of the volume occupied by the underlying notochord. We suggest that the alteration of the developmental trajectory of the notochord in *Latimeria* results in the unusual configuration of the brain and neurocranium observed in the fetus.

In dorsal view, the endocast of the pups, the juvenile and the adult is much narrower at the level of the ethmosphenoid region than in the otoccipital region (Fig. 3, Extended Data Fig. 3). The endocranial cavity shows a marked notch at the level of the intracranial joint, but widens laterally at the level of the foramen for the trochlear nerve, just dorsal to the level of the hypophyseal fossa. This widening of the endocranial cavity is more marked in P1, P2 and the juvenile than in the adults, as this portion of the braincase houses the telencephalic hemispheres and the narrower diencephalon spans the intracranial joint (Fig. 3, Extended Data Fig. 3). Such a swelling of the endocast is also observed the early actinopterygian *Mimipiscis* (Giles & Friedman 2014) and in the stem-osteichthyan *Ligulalepis* (Clement et al. 2018). In the latter, the short hypophyseal fossa is tilted posteriorly, ventral to the widest region of the endocranium which is interpreted as housing the mesencephalon and the cerebellum. Our observations support this interpretation and show that the marked swellings of the endocranial wall in *Latimeria* accommodate larger brain regions, despite the fact that the brain form does not closely matches that of the endocranial cavity. The width of the endocast is more regular in the ethmosphenoid portion of the adult *Latimeria* (Extended Data Fig. 3), and reminiscent of the condition observed in *Eusthenopteron* (Jarvik 1980; Stensiö 1963). In this taxa, the brain was reconstructed as filling the entire endocranial cavity, with the forebrain reaching the olfactory canals (Jarvik 1980; Stensiö 1963). Yet, we think that the previous neuroanatomical reconstructions in *Eusthenopteron* will ought to be re-evaluated based on the new developmental data available for *Latimeria*.

The otoccipital portion of the endocast presents less variation across the developmental stages of *Latimeria* than the ethmosphenoid portion. In dorsal view, the otoccipital portion of the endocast is slightly wider than the ethmosphenoid in the fetus, the widest point being located at mid-length, at the level of the auricula cerebelli and anteriorly to the emergence of the facial nerve (Fig. 3, Extended Data Fig. 1). The foetal endocast narrows and reduces in height progressively in its posterior half, before broadening at the level of the foramen for the vagus nerve. The upper half of the inner ear is positioned in the recess made by the braincase. The endocast of the otoccipital portion is deeper than the notochord, and the ventral aspect of the sacculus lies at the level of the ventral side of the notochord (Extended Data Fig. 3). In the fetus, the otoccipital portion of the endocast only houses the posterior portion of the mesencephalon and the rhombencephalon (Fig. 3, Extended Data Figs. 1, 3). In P1, P2, and the juvenile, the endocast of the otoccipital portion is slenderer and shallower (Fig. 3, Extended Data Fig. 3). In the pups, the roof the endocast is markedly flexed to accommodate the cerebellum, whereas it is slightly curved in the adult.

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