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Ontogenetical changes in the quadrate of basal tetanurans

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Although nonavian theropod have received considerable interest in the last years, their ontogeny still remains poorly understood, especially the ontogenetical changes affecting their skull (Rauhut and Fechner, 2005). The quadrate, for instance, is preserved in several embryos and juvenile specimens belonging to many clades of theropods such as the Tyrannosauridae (Carr, 1999), Compsognathidae (Dal Sasso and Maganuco, 2011), Therizinosauroidea (Kúndrat et al., 2007), Oviraptoridae (Norell et al., 1994; Norell et al., 2001; Weishampel et al., 2008) and Troodontidae (Varrichio et al., 2002) but very little is usually said about the anatomy of this bone and no one has ever investigated ontogenetical variation in the nonavian theropod quadrate. The discovery of two quadrates belonging to embryos of the sinraptorid *Lourinhanosaurus antunesi* from Portugal and five isolated quadrates pertaining to juvenile, subadult and adult specimens of Spinosauridae from Morocco fills this gap and allows some ontogenetic information to be drawn for this bone in these two specific clades of Theropoda.

Institutional abbreviations

BMNH	The Natural History Museum, London, United Kingdom.
IVPP	Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China.
MCNA	Museo de Ciencias Naturales y Antropológicas (J. C. Moyano) de Mendoza, Mendoza, Argentina.
ML	Museu da Lourinhã, Lourinhã, Portugal.
MNN	Musée National du Niger, Niamey, Niger.
MSNM	Museo di Storia Naturale di Milano, Milan, Italy.
SMA	Sauriermuseum of Aathal, Aathal, Switzerland.

Quadrate ontogeny in Sinraptoridae

Two isolated quadrates (ML565-10; ML565-150; fig. 1 and 2) were discovered among the skeletal remains of several embryos ascribed to the sinraptorid (Allosauroidea) *Lourinhanosaurus antunesi* (Mateus et al., 1998; Ricqlès et al., 2001; Mateus, 2005) from the Lourinhã Formation (Kimmeridgian – Tithonian, Upper Jurassic) of Portugal. Formerly regarded as a basal Allosauroidea (Mateus, 1998) and a eustreptospondylid (Mateus, 2005; Mateus et al., 2006), *Lourinhanosaurus antunesi* is currently classified among Sinraptoridae (Benson, 2009). Absence of cranial material in the holotype of *Lourinhanosaurus autunesi*, a mature specimen, does not allow direct comparison between the embryos and adult, thereby the two quadrates have been compared to the well-preserved quadrates of the most closely related taxon *Sinraptor dongi* (Currie, 2006).

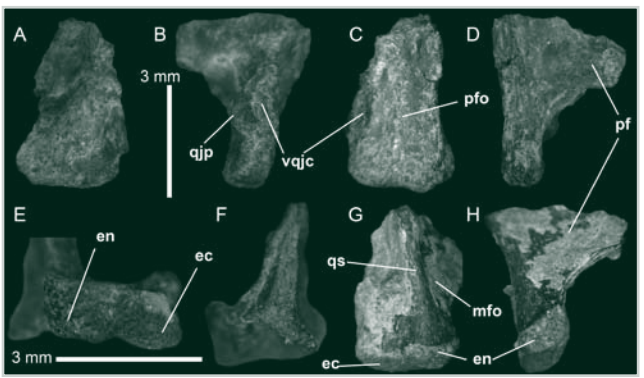

Figure 1. Incomplete left quadrate of *Lourinhanosaurus antunesi* embryo (ML565-150) in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) ventral, (F) dorsal, (G) posteromedial and (H) ventromedial views (the quadrate in G and H was photographed before preparation). Abbreviations: dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; mfo, medial fossa; pf, pterygoid flange; pfo, posterior fossa; qjp, quadratojugal process; qs, quadrate shaft; vqjc, ventral quadratojugal contact.

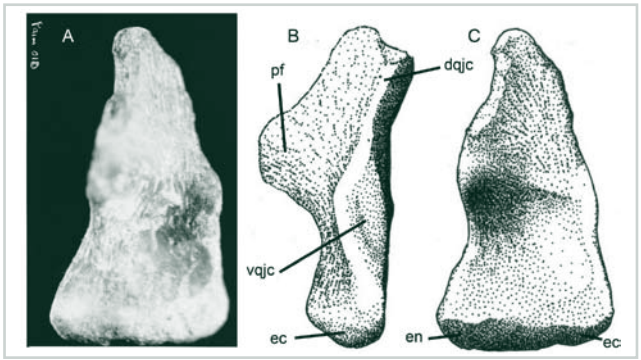

Figure 2. Incomplete left quadrate of *Lourinhanosaurus antunesi* embryo (ML565-10; lost) in (A, C) anterior and (B) lateral views. Abbreviations: dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; pf, pterygoid flange; vqjc, ventral quadratojugal contact (drawings by Simão Mateus).

ML565-150 (Fig. 1) and ML565-10 (Fig. 2) are two incomplete left quadrates missing the dorsal part of the quadrate body, the cotylus, and part of the pterygoid flange. ML565-10 is the best preserved one but the bone was lost in the 1990s and only one photograph and two drawings of it remain (Fig. 2). The bone surface of the second remaining quadrate ML565-150 has been damaged during preparation but the general morphology is still preserved.

Although incomplete, the two quadrates share numerous features with the quadrate of allosauroids, and especially *Sinraptor dongi*. Such as basal allosauroids, the pterygoid flange is slightly medially curved and gets attached to the quadrate body well-above the mandibular articulation, the ventral quadratojugal contact shows a well-developed quadratojugal process projecting anteriorly and the posterior fossa is deep, strongly ventro-dorsally elongated and positioned on the quadrate body in between the quadrate shaft and the quadratojugal contact. The quadrate shaft is rod-shaped and well-delimited at one half of the quadrate body and the shaft gets flared dorsal to the entocondyle without reaching the later, like in *Allosaurus* sp. (SMA 127) but different from *Sinraptor dongi* (IVPP 10600). As seen in the neovenatorid *Aerosteon riocoloradensis* (MCNA-PV 3137) but not in allosaurids and sinraptorids, the ventral quadratojugal contact is straight instead of convex and the ventral margin of the pterygoid flange is not folded medially or medio-dorsally. Finally, ML565-10 and ML565-150 share with *Sinraptor dongi* a piriform ventral quadratojugal contact facing postero-laterally, a dorsal quadratojugal contact forming an elongated line and laterally positioned, and a very shallow medial fossa.

When directly compared to other allosauroid taxa, the two quadrates show a few differences that can most likely be linked to the embryonic stage of the individuals. Unlike all allosauroids, the quadrate foramen is absent so that both ventral and dorsal quadratojugal contact are connected. In addition, rather than displaying the typical allosauroid mandibular articulation displaying two elliptical, globular and prominent condyles separated by a deep intercondylar sulcus, the mandibular articulation of the two embryonic quadrates is made of two shallow and not well-delimited ento- and ectocondyle barely separated by a broad and very shallow intercondylar sulcus. The latter seems to run perpendicular to the long axis passing through the mandibular articulation on the contrary of the diagonally oriented intercondylar sulcus of allosauroids. Whether the absence of a medially-folded ventral margin of the pterygoid flange and a short parabolic flange projecting laterally just above the ventral quadratojugal contact, two features present in *Sinraptor dongi*, is an intertaxic variation among sinraptorids or an ontogenetic feature cannot be determined.

Quadrate ontogeny in Spinosauridae

Five isolated quadrates from the Kem Kem beds (lower Cenomanian, Upper Cretaceous) of South-eastern Morocco (MSNM V6896; Eldonia Coll.) are determined to be from a same taxon of Spinosauridae based on the presence of a thick and prominent quadrate shaft, a quadrate foramen ventro-dorsally elongated, an elongated tear-drop shaped dorsal quadratojugal contact, a subquadrangular pterygoid ala reaching the entocondyle on its ventral part, an elongated and helicoidal ectocondyle, and a concavity on the anterior side of the entocondyle, a combination of features only visible in the quadrates of the spinosaurids *Baryonyx walkeri* (BMNH R.9951) and *Suchomimus tenerensis* (MNN GAD 502). Spinosaurid materials are common in

the Kem Kem beds of Morocco and this clade is only represented by the genus *Spinosaurus* so far (e.g. Buffetaut, 1989; Russel, 1996; Dal Sasso et al., 2005). Therefore, and although no quadrate have been preserved in this taxon hitherto, the five quadrates most likely belong to *Spinosaurus* sp.

Based on size and the presence and absence of features linked to ontogenetical variations, the smallest quadrate is interpreted to belong to a juvenile (Fig. 3) whereas three medium-sized quadrates most likely belong to subadult specimens and the largest one pertains to a fully grown adult. Sequence lists of ontogenetic character transformations (maturity dependant characters) are the following:

- Juvenile state (Fig. 3): Ventral and dorsal quadratojugal contact smooth (contact with the quadratojugal weak and perhaps mobile) and ectocondyle poorly delimited.
- Subadult state 1: Intercondylar sulcus shallow and poorly delimited, entocondyle poorly delimited, cotyle poorly developed, and absence of a ventral projection of the dorsal quadratojugal suture.
- Subadult state 2 (Fig. 4): Dorsal quadratojugal suture with two longitudinal grooves.
- Adult state: Dorsal quadratojugal contact deeply excavated (strong contact in between the quadrate and quadratojugal) and ectocondyle, entocondyle and cotyle well-delimited.

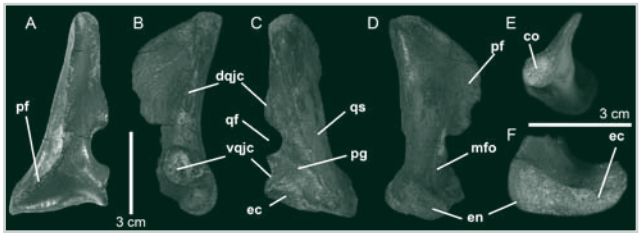

Figure 3. Left quadrate of a juvenile cf. *Spinosaurus* sp. in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) dorsal, and (F) ventral views. Abbreviations: co, cotyle; dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; mfo, medial fossa; pg, posterior groove; qf, quadrate foramen; qs, quadrate shaft; pf, pterygoid flange; vqjc, ventral quadratojugal contact.

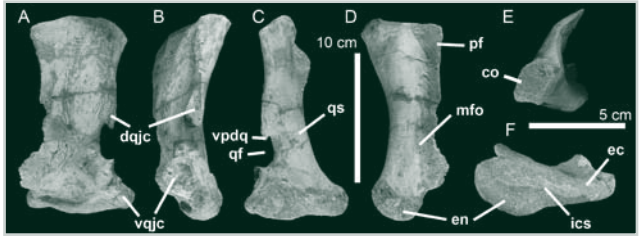

Figure 4. Left quadrate of a subadult cf. *Spinosaurus* sp. (MSNM V6896) in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) dorsal, and (F) ventral views. Abbreviations: co, cotyle; dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; mfo, medial fossa; qf, quadrate foramen; qs, quadrate shaft; pf, pterygoid flange; vpdq, ventral projection of the dorsal quadratojugal contact; vqjc, ventral quadratojugal contact.

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