The nonavian theropod quadrate I: standardized terminology and overview of the anatomy, function and ontogeny

By allowing the articulation of the mandible with the cranium, the quadrate of diapsids and most other tetrapods plays an important role morphofunctionally. In Theropoda, its morphology is particularly complex and varies importantly among different clades of nonavian theropods so that the quadrate possesses a strong taxonomic potential. Inconsistencies in the notation and terminology used in discussions of the theropod quadrate anatomy have been noticed, a number of no less than height different terms being sometimes given to a same structure. A standardization list of terms and notation for each quadrate anatomical entity is here proposed, with the goal of facilitating future descriptions of this important cranial bone. An overview of the quadrate function, pneumaticity and ontogeny in nonavian theropods is also given. The quadrate of the large majority of nonavian theropod is akinetic and the diagonally oriented sulcus of the mandibular articulation allowed both rami of the mandible to move laterally when opening the mouth in many of them. Pneumaticity of the quadrate is also present in most of tetanuran clades and the pneumatic chamber, invaded by the quadrate diverticulum of the mandibular arch pneumatic system, was connected to one or several pneumatopores on the medial, lateral, posterior, anterior or ventral sides of the quadrate. Absence of a quadrate foramen in allosauroid embryos and a poor delimitation of mandibular condyles in both embryonic and juveniles tetanurans seems to be ontogenetic features of some theropods. Finally, the numerous morphological differences existing in the quadrates of the two specimens of *Shuvuuia deserti*, interpreted by some as juvenile and adult individuals, are considered as ontogenetic, taphonomic, and perhaps also taxonomic variations.

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ABSTRACT

By allowing the articulation of the mandible with the cranium, the quadrate of diapsids and most other tetrapods plays an important role morphofunctionally. In Theropoda, its morphology is particularly complex and varies importantly among different clades of nonavian theropods so that the quadrate possesses a strong taxonomic potential. Inconsistencies in the notation and terminology used in discussions of the theropod quadrate anatomy have been noticed, a number of no less than height different terms being sometimes given to a same structure. A standardization list of terms and notation for each quadrate anatomical entity is here proposed, with the goal of facilitating future descriptions of this important cranial bone.

An overview of the quadrate function, pneumaticity and ontogeny in nonavian theropods is also given. The quadrate of the large majority of nonavian theropod is akinetic and the diagonally oriented sulcus of the mandibular articulation allowed both rami of the mandible to move laterally when opening the mouth in many of them. Pneumaticity of the quadrate is also present in most of tetanuran clades and the pneumatic chamber, invaded by the quadrate diverticulum of the mandibular arch pneumatic system, was connected to one or several pneumatopores on the medial, lateral, posterior, anterior or ventral sides of the quadrate. Absence of a quadrate foramen in allosauroid embryos and a poor delimitation of mandibular condyles in both embryonic and juveniles tetanurans seems to be ontogenetic features of some theropods. Finally, the numerous morphological differences existing in the quadrates of the two specimens of *Shuvuuia deserti*, interpreted by some as juvenile and adult individuals, are considered as ontogenetic, taphonomic, and perhaps also taxonomic variations.

INTRODUCTION

The quadrate (in Latin *quadratum*, meaning ‘square’) is a cranial bone of endochondral origin that articulates with the mandible in all gnathostomes except mammals, in which it evolved into the incus (Carroll 1988; Benton 2005; Brusatte 2012). In theropods, this bone plays many important functions such as a structural support for the basicranium, articulatory element with the lower jaws, attachment for several muscles, audition and hosting important nerves and vascular passages (e.g., Witmer 1990, 1997; Bakker 1998; Sedlmayr 2002; Kundrát and Janáček 2007; Holliday and Witmer 2008; Tahara and Larsson 2011; Appendix 1).

Its rather simple architecture, an elongated body bearing an anteriorly projected blade, therefore tends to vary significantly in the structure of its head, mandibular articulation, quadratojugal contact and the presence of pneumatic openings, quadrate foramen and lateral processes, among theropods with a large variability of feeding strategies (e.g., Holtz 2003; Therrien et al. 2005; Hone and Rauhut 2010; Zanno and Makovicky 2011). Such morphological variation has been recognized in avian theropods in particular, revealing the great taxonomical utility of the quadrate in this clade (e.g., Lowe 1926; Samejima and Otsuka 1987; Barbosa 1990; Elzanowski et al. 2001; Elzanowski and Stidham 2010). Likewis[illegible]t to a lesser degree, the systematic potential of the quadrate bone has also been noted for nonavian theropods (Maryańska and Osmólska 1997; Currie 2006), witnessing the particular importance that should be accorded to the description of this bone in the literature on nonavian theropod anatomy. Nevertheless, the terminology and abbreviations of the quadrate anatomy has been inconsistent in nonavian theropods, several different anatomical terms for the same quadrate sub-entity being often used (Appendix 2). Although a thorough list of anatomical terms has been given by Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for the avian quadrate, the terminology proposed by these authors has never been followed in the description of the nonavian theropod quadrate hitherto. Indeed, the quadrate of birds has greatly changed in its morphology throughout the evolution of this clade and therefore displays many features absent in more primitive theropods, so that many anatomical terms coined by Elzanowski et al. (2001) and Elzanowski and Stidham (2010) cannot be applied for the nonavian theropod quadrate. Likewise, some quadrate entities such as the quadrate foramen and the lateral process observable in nonavian theropods are absent in their avian ~~descents~~, and do not appear in the list of these authors.

The present paper has two major aims. The first is to propose a standardization of the anatomical terms for the quadrate sub-units, each associated with a two to four letters abbreviation and followed by a definition, in order to facilitate future description of this bone in the literature. The second is to give a general overview of the function, pneumaticity and ontogeny of this important bone in nonavian theropods.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, U.S.A.; **BMNH,** The Natural History Museum, London, U.K.; **BYUVP,** Brigham Young University Vertebrate Paleontology, Provo, Utah, U.S.A.; **CMNH,** Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.; **FMNH,** Field Museum of Natural History, Chicago, Illinois, U.S.A.; **IGM,** Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **IVPP,** Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN,** Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MCF PVPH,** Museo Municipal Carmen Funes, Paleontologia de Vertebrados, Plaza Huincul, Argentina; **MCNA,** Museo de Ciencias Naturales y Antropológicas de Mendoza, Mendoza, Argentina; **MIWG,** Dinosaur Isle, Isle of Wight Museum Services, Sandown, U.K.; **ML,** Museu da Lourinhã, Lourinhã, Portugal; **MNHN,** Muséum national d'Histoire Naturelle, Paris, France; **MNN,** Musée National du Niger, Niamey, Niger; **MSNM,** Museo di Storia Naturale di Milano, Milan, Italy; **MUCPv,** Museo de Ciencias Naturales de la Universidad Nacional de Comahue, Neuquén, Argentina; **NH,** Horniman Museum & Gardens, London, U.K.; **OUMNH,** Oxford University Museum, Oxford, U.K.; **PVSJ,** Instituto y Museo de Ciencias Naturales, San Juan, Argentina; **SMA,** Sauriermuseum Aathal, Aathal, Switzerland; **SMNS,** Staatliches Museum für Naturkunde, Stuttgart, Germany; **RTMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UCMP,** University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UC,** University of Chicago Paleontological Collection, Chicago, U.S.A.; **UMNH,** Utah Museum of Natural History, Salt Lake City, Utah, U.S.A.; **USNM,** United State National Museum Vertebrate Paleontology, Washington, D. C., U.S.A.; **WDIS,** Wyoming Dinamation International Society, Casper, Wyoming, U.S.A.

PROPOSED TERMINOLOGY OF THE QUADRATE ANATOMY

Figure 1

Table 1

Quadrate body (qb). Part of the quadrate that includes the mandibular articulation, the quadrate shaft, the quadrate ridge, the quadrate head, the lateral contact (quadratojugal and/or squamosal contact), and the lateral process, and excludes the pterygoid flange. In posterior view, the quadrate body is delimited by the lateral margin of the lateral contact and sometimes the medial margin of the quadrate foramen, the ventral margin of the mandibular articulation, the dorsal margin of the quadrate head, and a medial margin mostly formed by the quadrate shaft and the medial fossa of the pterygoid flange. The quadrate body corresponds to the corpus ossis quadrati of Baumel and Witmer (1993), and the corpus quadrati of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Quadrate shaft (qs). Part of the quadrate body that excludes the lateral process and all articulating surfaces (i.e., quadrate head, quadratojugal/squamosal/pterygoid contacts, and mandibular articulation). The quadrate shaft, as called by Welles (1984), Sereno and Novas (1994), Norell et al. (2006), Sampson and Witmer (2007), Sereno et al. (2008), Carrano et al. (2011), and Brusatte et al. (2012), is also referred as the quadrate pillar by Madsen and Welles (2000), and the ascending process by Colbert (1989).

Quadrate ridge (qr). Dorsoventrally elongated column, ridge or crest located on the quadrate body and visible in posterior view. Although the quadrate ridge is present in the large majority of nonavian theropods, a description of the structure is often omitted in the literature. The quadrate ridge is referred as 'a column' ~~for~~ Welles (1984), a 'ridge-like mediodorsal edge' ~~for~~ Carr (1996), 'a prominent rounded ridge' ~~for~~ Smith et al. (2007), a 'columnar ridge' ~~for~~ Rauhut et al. 2010) and a 'robust ridge' ~~for~~ Brusatte et al. (2012).

Quadrate ridge groove (qrg). Groove dividing the quadrate ridge in two different units at two-thirds, or more dorsally, of the quadrate body height. A quadrate ridge groove exists in some allosauroid theropods.

Quadrate head (qh). Dorsal articulation of the quadrate abutting to the cotyle of the squamosal and touching other bones of the braincase in some theropod taxa. The quadrate head, as it is called by Britt (1991), Charig and Milner (1997), Madsen and Welles (2000), Sampson and Witmer (2007), Sereno et al. (2008), Norell et al. (2009) and Brusatte et al. (2012) among others, has also been termed quadrate cotylus (Currie 2003; Coria and Currie 2006) quadrate cotyle (Currie 2003; Coria and Currie 2006), squamosal condyle (Coria and Salgado 1998), squamosal articulation (Turner et al. 2011), otic process (Maryańska and Osmólska 1997; Burnham 2004; Holliday and Witmer 2008), squamosal capitulum (Zanno 2010) ~~and~~, processus oticus (Baumel and Witmer 1993; Figure 2), and caput quadrati (Elzanowski et al. 2001; Elzanowski and Stidham 2010). When the quadrate head is double, it divides into otic and squamosal capitula.

Otic capitulum (otc). Medial capitulum of the quadrate head articulating with the braincase. The otic capitulum corresponds to the capitulum (condylus) oticum of Baumel and Witmer (1993; Figure 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Squamosal capitulum (sqc). Lateral capitulum of the quadrate head articulating with the squamosal. The squamosal capitulum corresponds to the capitulum (condylus) squamosum of Baumel and Witmer (1993; Figure 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Intercapitular sulcus (icas). Groove separating the ~~o~~otic capitulum from the squamosal capitulum on the dorsal surface of the quadrate head. The intercapitular sulcus (sensu Witmer 1990) corresponds to the incisura intercapitularis of Baumel and Witmer (1993; Figure 2), and the vallecula intercapitularis of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Quadrate foramen (qf). Aperture in the quadrate body or concavity on the lateral margin of the quadrate body and delimited ventrally by the ventral quadratojugal contact and dorsally by the dorsal quadratojugal contact and its ventral projection in some theropod taxa. Most authors usually refer to this perforation as the quadrate foramen (e.g., Welles 1984; Sereno and Novas 1994; Charig and Milner 1997; Maryańska and Osmólska 1997; Currie and Carpenter 2000; Coria and Currie 2006; Currie 2006; Norell et al. 2006; Zanno 2010; Choiniere et al. 2010; Foth and Rauhut 2012; Brusatte et al. 2012) but it can be also called the paraquadratic foramen (e.g., Barsbold and Osmólska 1999; Kobayashi and Lü 2003; Kobayashi and Barsbold 2005), the paraquadrate foramen (Sampson and Witmer 2007; Dal Sasso and Maganuco 2011), the paraquadrate fenestra (Smith et al. 2007) or the quadrate fenestra (e.g., Carr 1996; Sereno et al. 1998; Currie 2003; Eddy and Clarke 2011). A quadrate foramen exists in all nonavian theropods but Ceratosauria and Megalosauridae.

Mandibular articulation (mar). Ventral surface of the quadrate, articulating with the mandible and fitting in the glenoid fossa of the lower jaw. It includes the ectocondyle, entocondyles, sometimes a mediocondyle, and an intercondylar sulcus. Corresponds to the pars or processus mandibularis of Baumel and Witmer (1993; Figure 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods. Although most authors (e.g., Currie 2006; Sampson and Witmer 2007; Rauhut et al. 2010; Brusatte et al. 2012) referred the ectocondyle and entocondyles as the lateral and medial condyles (or hemicondyles) respectively, the terms 'ectocondyle' and 'entocondyle' have been used by Welles (1984), and Madsen and Welles (2000). The condyle present in between the ecto- and entocondyles in some theropods is here coined mediocondyle.

Ectocondyle (ecc). Lateral condyle of the mandibular articulation. The ectocondyle corresponds to the condylus (mandibularis) lateralis of Baumel and Witmer (1993; Figure 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Entocondyle (enc). Medial condyle of the mandibular articulation. The entocondyle corresponds to the condylus (mandibularis) medialis of Baumel and Witmer (1993; Figure 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Mediocondyle (mdc). Median condyle of the mandibular articulation. The mediocondyle is referred as the third condyle by Clark et al. (1994) and Xu and Wu (2001), the accessory condyle by Kobayashi and Lü (2003), and the condyle~~s~~ caudalis of Baumel and Witmer (1993) and Elzanowski et al. (2001) for avian theropods.

Intercondylar sulcus (ics). Groove separating the ectocondyle from the entocondyle and sliding along the interglenoid ridge of the articular. The intercondylar sulcus, a term also used by Carrano et al. (2011), can be referred as a groove (e.g., Madsen 1976; Britt 1991; Madsen and Welles 2000; Currie 2006), swelling (Charig and Milner 1997), sulcus (e.g., Kobayashi and Lü 2003; Norell et al. 2006; Sadleir et al. 2008), trochlea (Brochu 2003; Brusatte et al. 2010), trochlear surface (Brusatte et al. 2010, 2012), and intercondylar bridge (Zanno 2010). The intercondylar sulcus corresponds to the sulcus intercondylaris (Baumel and Witmer 1993) and the vallecula intercondylaris (Elzanowski et al. 2001; Elzanowski and Stidham 2010) of the quadrate of avian theropods.

Intercondylar notch (icn). Notch located in between the ectocondyle and entocondyle, either on the anterior or posterior margin of the mandibular articulation, and corresponding to the depressio praecondylaris of Elzanowski et al. (2001) for avian theropods.

Lateral process (lpq). Lateral or anterolateral projection of the lateral margin of the quadrate body. Also known as the dorsal wing (Welles 1984; Currie 2006), the anterolateral wing (Madsen and Welles 2000), the lateral lamina (Coria and Salgado 1998) and the lateral ramus (Sampson and Witmer 2007), this process can contact the quadratojugal and/or the squamosal and therefore either be referred to the quadratojugal ramus by Sampson and Witmer (2007) or the squamosal ramus Norell et al. (2006).

Quadratojugal contact (qjc). Contact of the quadrate with the quadratojugal on the lateral, anterolateral or, posterolateral margin of the quadrate body. The quadratojugal contact, which corresponds to the cotyla quadratojugalis of Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods, can be divided into a ventral and a dorsal quadratojugal contact when the quadrate foramen is present and delimited by both quadrate and quadratojugal.

Ventral quadratojugal contact (vqjc). ventral contact of the quadrate with the quadratojugal. The ventral quadratojugal contact of the quadrate always receives the quadratojugal bone.

Dorsal quadratojugal contact (dqjc). dorsal contact of the quadrate with the quadratojugal. The ventral quadratojugal contact of the quadrate can either receive the quadratojugal or both quadratojugal and squamosal in some theropod taxa.

Ventral projection of the dorsal quadratojugal contact (vpdq). Small projection of the dorsal quadratojugal contact delimiting the dorsolateral margin of the quadrate foramen.

Quadratojugal process (qjp). Anterior projection of the ventral quadratojugal contact of the quadrate.

Squamosal contact (sqc). Contact on the lateral margin of the quadrate with the squamosal.

Posterior fossa (pfq). Depression or concavity situated on the posterior side of the quadrate body and dorsal to the mandibular articulation, ventral to the quadrate head and lateral to the quadrate ridge. The posterior fossa can include or exclude the quadrate foramen.

Quadrate diverticulum (qdi). Air sac invading the pneumatic chamber inside the quadrate body and communicating with other diverticula by the quadrate pneumatopores.

Dorsal pneumatopore (dpne). Pneumatic foramen or recess located on the dorsal part of the quadrate, beneath the quadrate head. The dorsal pneumatopore corresponds to the foramen pneumaticum caudomediale of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Medial pneumatopore (mpne). Pneumatic foramen or recess situated on the medial side of the quadrate, typically in the ventromedial part of the pterygoid flange. The medial pneumatopore corresponds to the foramen pneumaticum basiorbitale of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Posterior pneumatopore (ppne). Pneumatic foramen or recess on the posterior side of the quadrate body, typically at one-height of the quadrate. The posterior pneumatopore corresponds to the ‘foramen pneumaticum rostromediale’ of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Ventral pneumatopore (vpne). Pneumatic foramen or recess on the ventral side of the quadrate. The ventral pneumatopore corresponds to the foramen pneumaticum adventitium of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Pterygoid flange (pfl). Sheet-like projection attached to the quadrate body and extending anteriorly or anteromedially to contact the pterygoid bone. The pterygoid flange, a term also used by Charig and Milner (1997), Brochu (2003), Currie (2006), Coria and Currie (2006) and (Rauhut et al. 2010), is also known as the quadrate/anterior flange (e.g., Colbert 1989; Norell et al. 2006; Brusatte et al. 2010, 2012), the pterygoid ramus (e.g., Sereno and Novas 1994; Sampson and Witmer 2007; Choiniere et al. 2010), the pterygoid wing (e.g., Welles 1984; Madsen and Welles 2000; Eddy and Clarke 2011), the pterygoid ala (e.g., Currie 2003, 2006; Sadleir et al. 2008; Dal Sasso and Maganuco 2011), the pterygoid process (Molnar 1991; Carr 1996; Sereno et al. 2008), the optic wing (Balanoff and Norell 2012), the orbital process (Clark et al. 1994; Chiappe et al. 2002), and the processus orbitalis (Baumel and Witmer 1993; Elzanowski et al. 2001; Elzanowski and Stidham 2010; Figure 2) for avian theropods.

Pterygoid contact (ptc). Contact on the medial margin of the pterygoid flange, or the quadrate body, with the pterygoid. The pterygoid contact corresponds, for avian theropods, to the facies pterygoidea in Elzanowski et al. (2001) and the facies articularis pterygoidea in Elzanowski and Stidham (2010), as well as the condylus pterygoideus, located on the quadrate body, in Baumel and Witmer (1993; Figure 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010).

Medial fossa (mfq). Depression or concavity situated ventroposteriorly on the pterygoid flange. It is delimited by the quadrate shaft and the ventral shelf in some theropod taxa. The medial fossa corresponds to the fossa corporis quadrati of Fuchs (1954) and the fossa basiorbitalis of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Ventral shelf (vsh). ~~a~~ medial or medioposterior fold of the ventral margin of the pterygoid flange. The term ‘shelf’ was employed by Sereno and Novas (1994) and ‘ventral shelf’ was used by Sampson and Witmer (2007), Eddy and Clarke (2011) and Carrano et al. (2011).

Figure 2

Inter-taxic Topological Homologies

To establish comparisons between taxa with widely disparate quadrate morphology, a homology concept of the feature in question is required. Here, we will give a general account of the variability within different anatomical sub-units of the quadrate and by following the criteria summarized in Rieppel (2006).

The quadrate ridge (Figure 1, qr) is easily distinguishable in many theropod taxa such as *Aerosteon riocoloradensis* (MCNA-PV 3137) and *Proceratosaurus bradleyi* (NHM R.4860) but the limits of this structure on the quadrate body can be subtle like in *Noasaurus leali* (PVL 4061), *Majungasaurus crenatissimus* (FMNH PR 2100), and *Eustreptospondylus oxoniensis* (OUMNH J.13558). The quadrate ridge corresponds to a columnar ridge in many theropod clades like in *Dilophosaurus wetherilli* (Welles 1984), *Allosaurus* (SMA 005/02) and *Eotyrannus lengi* (MIWG, 1997.550) but can also corresponds to a thin crest as in Tyrannosauridae (AMNH 5027; Carr 1996; Brusatte et al. 2012). Although the ventral portion of the quadrate ridge is usually demarcated just above the medial condyle of the mandibular articulation, its dorsal termination is more variable. The dorsal termination can reach the quadrate head like in *Acrocanthosaurus atokensis* (NCSM 14345) or flatten at the mid-height of the quadrate such as in *Albertosaurus sarcophagus* (Currie 2003, figure 10B). Despite being the same structure, the quadrate ridge can be separated by a deep groove like in *Allosaurus fragilis* (AMNH 600) and *Allosaurus europaeus* (ML 415) or flare and reappear more dorsally at the second third of the quadrate such as in some derived Spinosauridae (pers. observ.). Likewise, the ventral portion can also be divided in two parts separated by a concavity such as in the tyrannosaurids *Albertosaurus sarcophagus*, *Daspletosaurus* sp. (Currie 2003, figure 10 and 28) and *Tyrannosaurus rex* (AMNH 5027).

The pterygoid flange (Figure 1, pfl) contacts the quadrate process of the pterygoid anteriorly or anteromedially, and sometimes other bones such as the epipterygoid in *Herrerasaurus ischigualastensis* (PVSJ 407), the basipshenoid and prootic in *Erlikosaurus andrewsi* (Clark et al. 1994), and the squamosal in *Khaan mckennai* (Balanoff and Norell 2012).

Although the pterygoid flange can be easily homologized between taxa, it may acquire subtrapezoidal, subtriangular, subrectangular and M-shaped outlines or form a large semi-oval structure. The ventral limit of the flange can reach the mandibular condyles (e.g., *Baryonyx walkeri*, *Tyrannosaurus rex*) or get attached to the quadrate body well-above the mandibular articulation (e.g., *Majungasaurus crenatissimus*). This single structure can in some instances be divided into two ridges delimited by a deep pneumatic fossa facing ventrally (e.g., *Alioramus altai*, Brusatte et al. (2012), figure 23c; *Tyrannosaurus rex* FMNH PR2081). In anterior view, the pterygoid flange can be straight and only directed anteriorly like in the carcharodontosaurid *Shaochilong maortuensis* (Brusatte et al. 2010, figure 7a), or completely recurved anteromedially and its anteroventral margin can be either straight, or fold medially and dorsally, forming the ventral shelf, such as in *Majungasaurus crenatissimus* (FMNH PR 2100), *Carnotaurus sastrei* (MACN-CH 894) and *Allosaurus fragilis* (Madsen 1976:plate 3d).

The medial fossa of the quadrate (Figure 1, mfq) can be easily recognizable between taxa as it is always situated on the pterygoid flange, usually on the ventral part of it. This fossa is posteriorly delimited by the quadrate body in nonavian theropods and sometimes by the ventral shelf of the pterygoid flange. The medial fossa can be of variable depth (deep in *Cryolophosaurus* and shallow in *Eustreptospondylus*), pneumatized (e.g., *Falcarius*), and situated in the ventralmost part of the pterygoid flange (e.g., *Tsaagan*) or at mid-height of it and just above a large pneumatic recess like in *Mapusaurus roseae* (MCF PVPH-108.102).

The posterior fossa of the quadrate (Figure 1, pfq) can be located either in between the quadrate and the quadratojugal, being centred on the lateral margin of the quadrate (e.g., *Ceratosaurus*); or in the middle of the quadrate shaft and between the quadrate ridge and the lateral margin of the quadrate (e.g., ‘*Syntarsus*’; *Majungasaurus*; *Tsaagan*). Difficulties to recognize this structure between taxa may arise because it is not always well-delimited (e.g., *Shaochilong*). The posterior fossa can either be strongly ventrodorsally elongated like in the megalosaurid *Torvosaurus tanneri*, or form an oval concavity lateromedially wide (e.g., *Majungasaurus*). Similarly to the medial fossa, the posterior fossa can have a large pneumatic recess positioned dorsally (e.g., *Sinornithomimus*) or ventrally (e.g., *Garudimimus*) inside the fossa.

Due to the highly variable morphology of the quadrate foramen (Figure 1, qf), this structure deserves special attention. It can be completely absent (e.g., *Carnotaurus*, *Torvosaurus*), or form a very small aperture (e.g., '*Syntarsus*') to a large opening (e.g., *Tsaagan*). In most nonavian theropods, the quadrate foramen is mostly delimited by the quadrate and only its lateral margin is bounded by the quadratojugal (e.g., *Sinraptor*). In some nonavian theropods, however, the medial margin of the quadrate foramen and part of the ventral and dorsal margins are formed by the quadrate, the other lateral half being delimited by the quadratojugal (e.g., *Dromaeosaurus*). Finally, in a few theropods, the foramen can be completely enclosed in the quadrate (e.g., *Aerosteon*).

The quadratojugal contact of the quadrate (Figure 1, qjc) can either be a single extensive contact or made of two contacts separated by the quadrate foramen. In the latter case, the ventral quadratojugal contact and the dorsal quadratojugal contact of the quadrate are not always clearly separated and their dorsal and ventral margins, respectively, can overlap like in the sinraptorid *Sinraptor dongi* (IVPP 10600). If the quadrate foramen is absent or located inside the quadrate, the lateral quadratojugal contact is an elongated line of variable width along the lateral margin of the quadrate. If separated by the quadrate foramen, the ventral and dorsal contacts can display a wide variety of shapes that, nevertheless, are easily recognizable inter-taxically. Both quadratojugal contacts may face laterally, anteriorly or posteriorly and their articulating surface can be smooth, irregular or deeply grooved by several radiating ridges as in *Allosaurus fragilis* (Madsen 1976). The ventral quadratojugal contact is usually D-shaped or ovoid and its anterior margin can extend far anteriorly, forming the quadratojugal process occasionally forming a large subtriangular projection (Norell et al. 2006). The dorsal quadratojugal contact can vary from a very thin line to a broad surface and its dorsal extension can reach the dorsal condyle or terminate well beneath it. A ventral projection of this contact may be present, and such projection delimiting part of the lateral border of the quadrate can either be short, like in *Daspletosaurus* sp. (Currie 2003, figure 28A), or formed an elongated ramus, like in the therizinosaurid *Falcarius utahensis* (Zanno 2010, figure 1H) and the coelurosaur *Zuolong salleei* (Choiniere et al. 2010, figure 3B).

In some basal theropods, ceratosaurs and dromaeosaurids, the lateral process of the quadrate (Figure 1, lpq) forms a wing-like projection similar to the pterygoid flange. This process is an extension of the quadrate body laterally so that it can be difficult to delimitate and one can see the presence of such process in *Allosaurus* '*jimmadseni'* (SMA 005/02), *Sinraptor dongi* (Currie 2006, figure 1D), and *Erlikosaurus andrewsi* (Clark et al. 1994, figure 7). The lateral process can also vary in shape and size, as it can be short and parabolic (e.g., *Carnotaurus*) or elongated and subtriangular (e.g., *Tsaagan*). Its ventral border can also extend to the quadrate foramen (e.g., *Bambiraptor*) or more ventrally, sometimes reaching the medial condyle of the mandibular articulation (e.g., *Ilokelesia*).

The quadrate head (Figure 1, qh) always articulates with the deep cotylus of the squamosal and contacts more rarely other bones of the braincase such as the opisthotic in oviraptorids (Maryańska and Osmólska 1997), the prootic in *Mononykus olecranus* (Perle et al. 1994; Chiappe et al. 2002) and the postorbital in *Shuvuuia deserti* (Chiappe et al. 1998, 2002). The contact of the braincase between the dorsal part of the quadrate and the opistothic-exoccipital or the paroccipital process is also present in *Herrerasaurus ischigualastensis* (Sereno and Novas 1994), *Dilophosaurus wetherilli* (Welles 1984), *Ceratosaurus magnicornis* (Madsen and Welles 2000; Sanders and Smith 2005), tyrannosaurids (Currie 2003), *Heyuannia huangi* (Lü 2005), and perhaps *Erlikosaurus andrewsi* (Clark et al. 1994), but this contact occurs on a small medial surface just below the quadrate head and not with the quadrate head itself. The large majority of nonavian theropods have a single headed quadrate head (Rauhut 2003; pers. observ.); however, oviraptorids (Maryańska and Osmólska 1997, figure 3B) and the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998) have a unique double head. A bistylic quadrate head has also been observed in the dromaeosaurid *Mahakala omnogovae* (Turner et al. 2007) but Turner et al. (2011, figure 4) later reconsidered the head of the quadrate as not being double headed. The morphology of the quadrate head is variable; it may be subtriangular in most basal theropods (Sereno and Novas 1994; UCMP 37302), oval or subcircular in megalosaurids (UC OBA1; BYUVP 9246) and allosauroids (MCNA-PV-3137; IVPP 10600; IVPP V2885.3), subquadrangular in Spinosaurinae (SMNS 58022; MSNM V6896) or conical in Oviraptoridae (Maryańska and Osmólska 1997, figure 1B). Whilst most nonavian theropods have either a convex or a flattened quadrate head, the quadrate of some allosaurids (Bakker 1998, figure 5C) and derived tyrannosaurids (FMNH PR208) can also possess a well-marked concavity on the dorsal margin of the quadrate head. Despite this variability, the quadrate head can be easily homologized inter-taxically due to the obvious location of this structure.

With the exception of the therizinosaur *Erlikosaurus andrewsi* and the ornithomimosaur *Sinornithomimus dongi* which both seem to have a unique tricondylar condition on the mandibular articulation (Clark et al. 1994; Kobayashi and Lü 2003), all other nonavian theropods have two mandibular condyles. The presence of three mandibular condyles was also noted in the alvarezsaurid *Avimimus portentosus* (Chatterjee 1995) and the dromaeosaurid *Sinornithosaurus millenii* (Xu and Wu 2001). However, Vickers-Rich et al. (2002) only found two condyles in the former and our observations confirm that the third condyle of the latter seems to be part of the much broader lateral condyle (Xu and Wu 2001, figure 4D).

The intercondylar sulcus (Figure 1, ics) varies in orientation, size and depth. It can be large, shallow and sub-perpendicular to the long axis passing through the mandibular articulation as in *Tyrannosaurus rex* (FMNH PR2081); or narrow, deep and strongly lateromedially-oriented as in some derived spinosaurids (pers. observ.).

The shape of the mandibular articulation (Figure 1, mar) in posterior view can vary from the biconvex condition known in most theropods, to the W-shaped articulation typical of *Citipati osmolskae* (Clark et al. 2002, figure 6) or a unique convex articulation seen in some dromaeosaurids such as *Tsaagan ~~manga~~* (GM 100/1015). The intercondylar notch (Figure 1, icn) is present in *Allosaurus* '*jimmadseni*' (Bakker 1998, figure 5B, C; SMA 005/02) and *Suchomimus tenerensis* (MNN GAD 502) on the posterior side of the mandibular articulation, and in *Majungasaurus crenatissimus* (FMNH PR 2100) and *Carnotaurus sastrei* (MACN-CH 894) on its anterior margin. The ectocondyle (Figure 1, ecc) and entocondyle (Figure 1, ent) are highly variable among each clade of nonavian theropods in terms of shape, size and orientation.

Pneumaticity of the quadrate can either be internal or, obviously expressed externally by pneumatopores. The establishment of inter-taxic homologies is difficult to assess, because these structures have very diverse interspecific variability. Nevertheless, as in other saurischian taxa (Schwarz et al. 2007), these pneumatic structures have phylogenetic signal. These openings can appear on different views and portions of the quadrate. The medial and posterior pneumatopores (Figure 1, ppne) usually occur in the medial and posterior fossa respectively, and their position inside the fossae is again quite variable. Pneumatopores can also be located in a pneumatic recess outside the medial fossa and just beneath it such as in the carcharodontosaurids *Mapusaurus roseae* (Coria and Currie 2006) and *Acrocanthosaurus atokensis* (Eddy and Clarke 2011). In the latter, the pneumatic aperture is divided by a septum.

OVERVIEW OF THE FUNCTION, PNEUMATICITY AND ONTOGENY

Figure 3

Function of the Quadrate

Although in all archosaurs, and all amniotes except mammals, the main function of the quadrate is the articulation of the cranium with the mandible, this bone can also play an important role in the mobility of the skull in many extant theropods. Quadrate movement inside the skull, known as streptostyly, is a fundamental property of all avian theropods, and cranial kinesis in birds, known already in the beginning of the, 19th century (Nitzsch 1816), has been extensively studied in the past sixty years (e.g., Fisher 1955; Bock 1964, 1999, 2000; Bühler 1981; Zusi 1984, 1993; Bühler et al. 1985, 1988; Chatterjee 1991, 1997; Hoese and Westneat 1996; Zweers et al. 1997; Zweers and Vanden Berge 1998; Bout and Zweers 2001; Gussekloo and Bout 2005; Meekangvan et al. 2006). Streptostyly consists of the rotation of the quadrate at its dorsal articulation against the squamosal and/or supratemporal and usually corresponds to a transversal movement, although a lateral movement of the quadrate around an anteroposteriorly directed axis occurs in some lepidosaurs taxa (Metzger 2002). Cranial kinesis in avian theropods with a streptostylic quadrate includes upward (protraction) and downward (retraction) rotation of the upper jaw relative to the braincase and three main types of kinesis are recognized relative to the position of the dorsal flexion zone of the cranium and the nature of the nasal opening in modern theropods (Bock 1964; Bühler 1981; Zusi 1984; Meekangvan et al. 2006). There are the prokinesis where the flexion occurs at the nasofrontal joint and the upper jaw thereby moves as one unit, the amphikinesis where the flexion occurs in two zones of flexibility and the upper jaw and its tip are bent upward, and finally the rhynchokinesis where the flexion happens forward from the nasofrontal joint, allowing its rostral part to be moved.

Inference of the cranial kinesis and quadrate mobility in nonavian theropods has been recently investigated by Holliday and Witmer (2008) which regard the cranium of this group of dinosaurs as partially kinetically competent, since synovial joints and protractor muscles are present, but not fully kinetic like in birds. The strong suture of the quadrate to the quadratojugal and the immobile contact of the quadrate and the pterygoid on the medial side of the pterygoid flange in most nonavian theropods seem to indicate a very limited movement, and perhaps even the total absence of movement of this bone within the cranium. Although the synovial quadrate head joint existing in theropods, and all other archosaurs, is necessary to infer cranial kinesis, its presence in akinetic taxa such as crocodiles and thyreophorans demonstrates that the synovial joint cannot be considerate alone as an argument for cranial kinesis. Synovial joints have actually been interpreted as growth zones rather than articular surfaces of mobile joints based on the presence of very thin articular cartilage covering the end of this joint (Holliday and Witmer 2008). According to Holliday and Witmer (2008) “articular cartilage persists in loading environments that exert hydrostatic pressures (which result in a change in volume but not shape) but exert low shear stresses”. Indeed, one of the key centres of deformation during normal biting is the quadrate-squamosal contact, which would have experienced large shear stresses associated with torque and asymmetrical loading during biting (Rayfield 2005), and the presence of a minimal amount of cartilage between the quadrate and squamosal would therefore suggest that the synovial zone was rather a growth zone than a mobile one. A streptostylic quadrate in *Tyrannosaurus rex* (Molnar 1991, 1998), *Oviraptor philoceratops* (Smith 1992), *Heyuannia huangi* (Lü 2005) and *Dromiceiomimus brevitertius* (Russell 1972) based on the saddle joint between the quadrate and squamosal only is thereby unlikely.

Nevertheless, and more convincingly, a streptostylic quadrate has also been proposed in the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998) in which the quadratojugal/jugal (Dufeau (2003) suggested that the quadratojugal may be absent in *Shuvuuia deserti*), rather than being firmly sutured to the quadrate, like in other nonavian theropods, would have contacted the quadrate though a movable joint (Chiappe et al. 1998, 2002; Figure 3). According to Chiappe et al. (1998), the absence of a latero-dorsal contact of the quadrate with the quadratojugal/jugal, as well as a ventro-lateral process of the squamosal, would have permitted to the quadrate of this mononykine to pivot antero-posteriorly, and the upper jaw to rotate ventro-dorsally thanks to this transversal movement. Although these authors have implied the existence of a bending zone between the frontals and the nasal–preorbital bones in *S. deserti*, allowing the flexion of the snout as a single unit when the quadrate displaced forward, like in prokinetic birds, the complex contacts between the nasal, frontal and prefrontal illustrated by Sereno (2001, figure 12B) makes assessment of Chiappe et al. (1998) hypothesis quite dubious (Holliday and Witmer 2008). In addition, Holliday and Witmer (2008) noted that a maxillojugal and palatal flexion zones authorizing a true prokinesis to be present in alvarezsaurids is still not clear. Likewise, the contact between the pterygoid flange of the quadrate and the pterygoid needs also to be better documented in order to imply any specific movement of the quadrate inside the cranium of *S. deserti*.

A movable articulation between the quadrate and quadratojugal may also have been present in the oviraptorids *Heyuannia huangi* (Lü 2003) and *Nemegtia huangi* (Lü et al. 2004) in which the quadrate and quadratojugal articulation of the former corresponds to a trochlea-like structure (Lü 2003, 2005), while the quadratojugal contact of the latter is convex and fit into a quadratojugal cotyle (Lü et al. 2004).

Quadrate articulation with the mandible and orientation of the intercondylar sulcus are highly variable among nonavian theropods, therefore suggesting some variation in the movement of the rami when the jaw opened. The helical intercondylar sulcus present in many nonavian theropods, but not all of them (pers. observ.), was noticed by Bakker (1998) in primitive theropod dinosaurs, Hendrickx and Buffetaut (2008) in spinosaurids, and Molnar (1991) and (Larson 2008) in *Tyrannosaurus rex*. These authors suggested that such spiral groove of the mandibular articulation constrained the diagonal ridge of the articular glenoid fossa, which fitted into the intercondylar sulcus, to slide laterally, therefore forcing the rami of the mandible to displace laterally when the lower jaw was depressed, enlarging the width of the larynx in order to swallow food of large size (Hendrickx and Buffetaut 2008).

In allosaurid quadrates, the marked constriction of the intercondylar sulcus, associated with the enlargement of the mandibular condyles, the backward bent of the ventral part of the quadrate, and the intercondylar notch, were interpreted by Bakker (1998) as joint-stabilization zones. According to this author, the enlargement of the articulating surface would improve the stability of the joint when the mouth was widely opened, while the posterior depression would correspond to the area for attachment of one or several ligaments within the quadrate-mandibular articulation ((Bakker 1998). An intercondylar notch has also been noticed in the abelisaurids *Carnotaurus sastrei* (MACN-CH 894) and *Majungasaurus crenatissimus* (FMNH PR 2100), and the spinosaurid *Suchomimus tenerensis* (MNN GAD 502), implying a similar mechanic of the mandibular articulation than *Allosaurus*.

Figure 4

Pneumaticity in the Quadrate

Pneumatization of the quadrate bone has long been recognized for its phylogenetic value (e.g., Gauthier 1986; Holtz 1998; Chiappe 2001; Rauhut 2003; Holtz et al. 2004; Smith et al. 2007; Benson 2010; Carrano et al. 2012; Turner et al. 2012; Novas et al. 2013; Choiniere et al. 2014). Pneumatopores within the quadrate are widespread among avetheropod clades (Gold et al. 2013; Figure 4). The presence of one or several pneumatopores has indeed been recorded in carcharodontosaurids (e.g., Coria and Currie 2006; Eddy and Clarke 2011), neovenatorids (Sereno et al. 2008), tyrannosauroids (e.g., Molnar 1991; Brochu 2003; Currie 2003; Xu et al. 2004; Brusatte et al. 2012; Gold et al. 2013), compsognathids (Currie and Chen 2001), therizinosauroids (Clark et al. 1994; Zanno 2010), oviraptorids (e.g., Maryańska and Osmólska 1997; Lü 2003; Kundrát and Janáček 2007; Balanoff and Norell 2012), ornithomimoids (Witmer

1997; Tahara and Larsson 2011), dromaeosaurids (Makovicky et al. 2005) and troodontids (Barsbold et al. 1987; Currie and Zhao 1993; Varricchio 1997; Xu et al. 2002; Xu and Norell 2004). An incipient development of a pneumatic recess also exists in the basal allosauroid *Sinraptor dongi* (Currie 2006), and quadrate pneumaticity therefore seems to be an avetheropod synapomorphy (Figure 4). Among nonavian avetheropods, there is however no evidence of a pneumatic quadrate in Alvarezsauroidea hitherto.

The pneumatic foramen is particularly large in some allosauroids such as *Aerosteon riocoloradensis* (Sereno et al. 2008) and *Acrocanthosaurus atokensis* (Eddy and Clarke 2011), and the therizinosaur *Falcarius utahensis* (Zanno 2010; Figure 5). It however corresponds to a small rounded or oval aperture lodged in the posterior fossa of the quadrate body in most avetheropods (Figure 5). Indeed, a posterior pneumatopore exists in the tyrannosauroid *Dilong paradoxus* (Xu et al. 2004), the compsognathid *Sinosauropteryx prima* (Currie and Chen 2001, figure 3f), the ornithomimids *Garudimimus brevipes* (the 'paraquadrate foramen' or 'paraquadratic foramen' of Kobayashi and Barsbold 2005), *Sinornithomimus dongi* (the 'paraquadratic foramen' of Kobayashi and Lü 2003) and *Ornithomimus edmontonicus* (Tahara and Larsson 2011), the dromaeosaurid *Buitreraptor gonzalezorum* (Makovicky et al. 2005), and the troodontids *Mei long* (Xu and Norell 2004), and *Sinovenator changii* (Xu et al. 2002). A pneumatopore can also be located in the ventral corner of the pterygoid flange, as observed in the carcharodontosaurids *Acrocanthosaurus atokensis* (Eddy and Clarke 2011), *Mapusaurus roseae* (Coria and Currie 2006), *Giganotosaurus carolinii* (MUCPv-CH-1), and the tyrannosaurid *Albertosaurus sarcophagus* (Currie 2003, figure 10B). A pneumatic opening is also present anteroventrally, within a recess on the posteroventral part of the pterygoid flange ('funnellike external opening on the rostral surface of the quadrate, above the condyles' of Gold et al., 2013, p. 37) like in the therizinosauroid *Falcarius utahensis* (Zanno 2010) and the tyrannosaurids *Alioramus altai* ((Brusatte et al. 2012; Gold et al. 2013), *Daspletosaurus* sp. (Currie 2003, figure

28C) and *Tyrannosaurus rex* (Brochu 2003). This ventral pneumatopore has also been reported in the basal tyrannosauroid *Dilong paradoxus* (Gold et al. 2013) but was not observed in the closely related taxa *Guanlong wucaii*, *Proceratosaurus lengi*, and *Xiongguanlong baimoensis* (Gold et al. 2013), and its presence cannot be established in *Eotyrannus lengi* (contra Gold et al. 2013; pers. obs.). More rarely, a pneumatic opening can be situated on the lateral surface of the quadrate body, as in *Aerosteon riocoloradensis* (MCNA-PV 3137), and in the anterior part of the quadrate, as in *Mapusaurus roseae* (Coria and Currie 2006), *Troodon formosus* (Currie and Zhao 1993), *Heyuannia huangi* (Lü 2005), and perhaps *Tyrannosaurus rex* (Molnar 1991).

Figure 5

Carcharodontosauridae (Coria and Currie 2006; Eddy and Clarke 2011) and Tyrannosauridae (Molnar 1991; Brochu 2003) possess several pneumatic openings which perforate different sides of the quadrate and sometimes intercommunicate (Brochu 2003). The pneumatic foramina usually enter a large pneumatic chamber within the quadrate bone such as in *Tyrannosaurus rex* (Molnar 1991; Brochu 2003), *Alioramus altai* (Gold et al. 2013), *Conchoraptor gracilis* (Kundrát and Janáček 2007) or *Ornithomimus edmontonicus* (Tahara and Larsson 2011). The neovenatorid *Aerosteon riocoloradensis* also possess a large posterior pneumatopore leading to a pneumatic chamber, as well as a shallow pneumatic recess on the lateral surface of the quadrate shaft (pers. obs.).

These pneumatopores and the pneumatic chamber associated with them are invaded by the quadrate diverticulum of the mandibular arch pneumatic system which, together with the periotic pneumatic system, forms the tympanic sinus of archosaurs (Tahara and Larsson 2011). The mandibular arch pneumatic system includes the quadrate and/or the articular diverticulum which both have their embryological origins as parts of the first pharyngeal (= mandibular) arch, like the middle ear sac itself (Witmer 1997). As nonavian theropods, the quadrate diverticulum of modern birds exhibits a large variety of morphologies, and can either pneumatize the quadrate by entering through a single medial or anteromedial foramen or not (Witmer 1990; Tahara and Larsson 2011). In the basal theropods that do not have a pneumatic quadrate, both medial and posterior fossae of the quadrate correspond to the osteological trace of the quadrate diverticulum. In nonavian theropods with a pneumatic quadrate, the position of the quadrate diverticulum is variable such as in ornithomimids (Tahara and Larsson 2011), carcharodontosaurids and oviraptorids (pers. observ.). The quadrate diverticulum of nonavian theropods may also have communicated with other diverticula such as the squamosal diverticulum as in *Conchoraptor gracilis* (Kundrát and Janáček 2007), and the siphoneal diverticulum of the articular as in *Dilong paradoxus*, *Aerosteon riocoloradensis* and perhaps other nonavian maniraptorans (Sereno et al. 2008; Tahara and Larsson 2011). In *Tyrannosaurus rex*, however, the siphoneal diverticulum does not pass through the quadrate and the quadrate diverticulum only enters the ventral opening of the pterygoid flange, and then passes with or without the siphoneal diverticulum along the medial fossa of the pterygoid flange. Likewise, the quadrate diverticulum only pneumatizes two distinct regions of the quadrate in *Acrocanthosaurus atokensis* and *Mapusaurus roseae* (Tahara and Larsson 2011).

Figure 6

Quadrate Ontogeny

Skull ontogeny has been generally poorly studied in nonavian theropod, especially in their early stage of development (Rauhut and Fechner 2005), but the ontogeny of the quadrate bone has particularly received very little attention when compared to other cranial bones (see Carr 1999; Loewen 2010). Although the quadrate of embryonic and juvenile specimens has been reported in many nonavian theropod clades such as basal Megalosauroidea (Rauhut et al. 2012), Spinosauridae (Hendrickx and Mateus 2012), basal Avetheropoda (Hendrickx and Mateus 2012), Tyrannosauridae (e.g. Bakker et al. 1988; Carr and Williamson 2010; Tsuihiji et al. 2011), Compsognathidae (Dal Sasso and Maganuco 2011), alvarezsaurid (Dufeau 2003), Oviraptoridae (Norell et al. 1994, 2001; Weishampel et al. 2008) and Troodontidae (Varricchio et al. 2002), the ontogenic variations of the nonavian theropod quadrate has only been investigated by Hendrickx and Mateus (2012) hitherto. These authors reported two incomplete quadrates belonging to embryos of *Lourinhanosaurus autunesi* (Figure 6) from the Upper Jurassic of Portugal (Mateus et al. 1998; de Ricqlès et al. 2001; Mateus 2005). Comparison of these two bones with the quadrates of the closest relative of *Lourinhanosaurus*, *Sinraptor dongi* (Benson 2010; Benson et al. 2010) allowed Hendrickx and Mateus (2012) to suggest that the absence of a quadrate foramen and the poor delimitation of the two mandibular condyles and the intercondylar sulcus were most likely ontogenetical features present in the allosauroid quadrate. Hendrickx and Mateus (2012) also examined the ontogenic changes of the quadrate in spinosaurids from the Cenomanian of Eastern Morocco. Based on five quadrates belonging to juvenile, subadult and adult specimens of *Spinosaurus* sp., they were able to propose a list of ontogenetical steps that they divided into juvenile, subadult and adult stages. The ontogenetical transformation occurring in the *Spinosaurus* quadrate are the clear delimitation of the ento- and ectocondyle, the intercondylar sulcus and the quadrate head, as well as the development of a ventral projection of the dorsal quadratojugal contact and the excavation of both ventral and dorsal quadratojugal contacts, allowing a firm contact between the quadrate and quadratojugal to be present in sub-adult~~s~~ and adult~~s~~ specimens.

Well-preserved quadrates are present in a small and large specimens of the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998; Dufeau 2003). Dufeau (2003), who interprets the small skull (IGM 100-1001) and the larger one (IGM 100-977) as belonging to a juvenile and adult specimens of *Shuvuuia deserti*, respectively, comprehensively described the quadrate bone but did not investigate the ontogenetic variation occurring in the skull of *Shuvuuia deserti*. Personal examination of the two specimens allowed to observe major differences in the quadrate morphology (Figure 3.3-3.6) that could be interpreted as ontogenetic variations. The quadrate body of IGM 100-1001 is extremely ventro-dorsally elongated, with a prominent and narrow quadrate ridge along the dorsal half of the quadrate bone. On the other hand, the quadrate body of the larger specimen IGM 100-977 is shorter, with a relatively shallow quadrate ridge. The mandibular articulation of IGM 100-1001 is lateromedially expanded and the lateral part of the articulation is subtriangular in outline and strongly projects laterally. The mandibular articulation of IGM 100-977 is particularly short, subrectangular in outline in posterior view, and lacks a lateral projection (Figure 3.3, 3.5). This projection may however be broken and present as an isolated piece of bone displaced on the ventrolateral surface of the pterygoid flange (pers. obs.). In IGM 100-1001, the lateral process is ventro-dorsally long, subtriangular in lateral view, almost subrectangular in posterior view, and reaches the quadrate head dorsally. The most lateral corner projects anteriorly to contact the postorbital, and the postorbital contact of the quadrate extends along the anterodorsal surface of the lateral process. The ventral most part of the lateral process forms a small corner dorsal to the parabolic outline of the ventral part of the quadrate body. On the contrary, the lateral process of IGM 100-977 only projects laterally and does not extend to the quadrate head dorsally. The lateral margin of the lateral process is parabolic in outline, and neither includes a small corner ventrally, nor an important projection anteriorly. The quadrate foramen of IGM 100-1001, forms a large fenestra delimited by the quadrate, jugal and, postorbital. If an articulation between the postorbital and the lateral corner of the lateral process was present in IGM 100-977 as well, the quadrate foramen of this specimen would have been much smaller, and delimited by the ventral half of the quadrate only. The quadrate head of the small specimen (IGM 100-1001) is incipiently bistylic and oriented posteromedially to contact the squamosal dorsally, and the braincase posteromedially (Figure 3.3). The quadrate head of IGM 100-977 is strongly inclined laterally and seems to include a single condyle only, although

Dufeau (2003) noted that the quadrate head was also divided by a very weak intercondylar sulcus in the adult specimen.

Dufeau (2003) interpreted these differences in the two specimens of *Shuvuuia deserti* as ontogenetic and taphonomic variations (Dufeau pers. comm.). According to Dufeau (2003), the contact between the quadrate head and the junction of the squamosal and postorbital, which is unique in IGM 100-1001 among nonavian theropods, is, for instance, interpreted as a taphonomic condition where the quadrate head would be taphonomically displaced laterally. Nevertheless, both left and right quadrate of IGM 100-1001 occupy the same position and share similar contact with the postorbital and squamosal, and the skull suffered neither compressional nor shear distortions (Dufeau 2003; pers. obs.). A taphonomic displacement of the quadrate of IGM 100-1001 seems therefore unlikely, and the postorbital contact of the quadrate is an autapomorphy of *Shuvuuia deserti*. Despite the fact that the right quadrate of the larger specimen IGM 100-977 may have been subject to important postmortem compression (as the rest of the skull which is ventro-dorsally flattened), the numerous differences existing between IGM 100-1001 and IGM 100-977 suggests that these variations may be taphonomic, ontogenetic, but also perhaps taxonomic. The ontogenetic variations occurring in the spinosaurid quadrates are subtle and only concern the delimitation of the condyles and quadrate head, and the reinforcement of the quadrate and quadratojugal suture, so that the general morphology of the quadrate bone does not change at all. If the features differentiating IGM 100-1001 and IGM 100-977 are mostly ontogenetic, the quadrate of *Shuvuuia deserti* would therefore undergo a major metamorphosis during its development, including a dorsoventral shortening of the quadrate bone, rotation of the quadrate head from a medial to a lateral orientation, posterior displacement of the lateral process, and morphological transformation of the lateral process from a subtriangular to a parabolic process. Although plausible, these ontogenetic transformations seem a bit extreme, and it is reasonable to suggest that IGM 100-977 and IGM 100-977 may belong to two taxa, perhaps two species of *Shuvuuia*.

Quadrate pneumaticity appears early in ontogeny as it has been reported in the embryo of *Troodon formosus* (Varricchio et al. 2002) and the juvenile *Tarbosaurus baatar* (Tsuihiji et al. 2011). Although absent in the embryonic specimen of *Lourinhanosaurus autunesi*, a quadrate foramen exists in many juvenile specimens of theropods such as the hatchling *Scipionyx samniticus* (Dal Sasso and Maganuco 2011) and the early posthatchling *Sciurumimus albersdoerferi* (Rauhut et al. 2012). Although the quadrate and quadratojugal are weakly articulated to each other in immature tetanurans (Hendrickx and Mateus 2012), a fusion between the quadrate and pterygoid was already present in oviraptorid embryos (Norell et al. 2001).

CONCLUSIONS

A revised nomenclature of the quadrate bone, along with a corresponding set of abbreviations, is here proposed and provides a standard set of terms for describing this cranial bone in nonavian theropod dinosaurs. The quadrate can be divided into two regional categories, the quadrate body and the pterygoid flange, and twelve anatomical sub-units, the quadrate shaft, quadrate head, quadrate ridge, quadrate foramen, lateral process, quadratojugal contact, squamosal contact, pterygoid contact, mandibular articulation, medial fossa, and posterior fossa. Although being highly variable in shape, all of these quadrate entities, with perhaps the exception of the posterior fossa, are easily recognisable inter-taxa and a description of their morphology should be provided in the literature.

A summary of the current knowledge on the quadrate function, pneumaticity and ontogeny in nonavian theropods allows some evidence about this bone to be highlighted. The quadrate of large majority of nonavian theropods is akinetic and a streptostylic quadrate may have been present in some derived coelurosaurs such as the alvarezsaurid *Shuvuuia deserti* and the oviraptorid *Nemegtia huangi*. A lateral movement of the rami while the mandible was depressed was permitted in many theropods such as spinosaurids thanks to a helicoidal and diagonally oriented intercondylar sulcus of the mandibular articulation. Likewise, the presence of an intercondylar notch constricting the intercondylar sulcus in allosaurids was interpreted to be a joint-stabilization zone that would improve the stability of the mandibular articulation when the mouth was widely opened.

A pneumatic quadrate was present in members of most nonavian avetheropod clades such as allosauroids, tyrannosaurids, compsognathids, therizinosauroids, ornithomimoids, oviraptorids, troodontids and dromaeosaurids, in which pneumatopores typically open in the ventral part of the pterygoid flange and in the medial and lateral fossae. Although the pneumatic recess invaded by the quadrate diverticulum of the mandibular arch pneumatic system was linked to only one pneumatopore in most avetheropods, the presence of several pneumatic openings perforating different sides of the quadrate have been recorded in Neovenatoridae, Carcharodontosauridae and Tyrannosauridae.

A poorly delimited mandibular condyles, intercondylar sulcus and quadrate head, and a quadratojugal contact with a smooth surface have been interpreted as ontogenetical features in the quadrate of embryonic and juvenile basal tetanurans. The development of a quadrate foramen and a ventral projection of the dorsal quadratojugal contact seem also to happen during ontogeny in allosauroids and spinosaurids, respectively. On the other hand, pneumaticity and a strong suture between the quadrate and quadratojugal appear early in ontogeny, in the embryonic stage of coelurosaurs. Finally, based on the quadrate morphology, the two specimens assigned to *Shuvuuia deserti*, considered by some as juvenile and adult specimens, may belong to two distinct taxa.

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FIGURE CAPTIONS AND TABLES

FIGURE 1. Anatomy of nonavian theropod quadrates. Right (**1–5**) quadrate of *Tsaagan mangas* (IGM 100-1015; courtesy shared by Mick Ellison © AMNH) in (**1**) anterior, (**2**) lateral, (**3**) posterior, (**4**) medial and (**5**) ventral views; left (**6–10**) and right (**11**) quadrates of (**6**) *Baryonyx walkeri* (BMNH R9951), (**7**) *Aerosteon riocoloradensis* (MCNA-PV-3137; courtesy shared by Martín Ezcurra), (**8**) an indeterminate Oviraptoridae (GIN A; Maryańska and Osmólska 1997, figure 1), (**9**) *Tyrannosaurus rex* (BHI 3333, cast; Larson and Carpenter, 2008), (**10**) *Allosaurus* '*jimmadseni*' (SMA 005/02), and (**11**) *Majungasaurus crenatissimus* (FMNH PR 2100, cast; courtesy shared by Lawrence Witmer) in (**6–9**) posterior and (**10–11**) ventral views. Abbreviations: **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process of the quadrate; **mar**, mandibular articulation; **mfq**, medial fossa of the quadrate; **pfl**, pterygoid flange (in green); **pfq**, posterior fossa of the quadrate; **ppne**, posterior pneumatopore; **qb**, quadrate body (in blue); **qf**, quadrate foramen (delimited by a broader line); **qh**, quadrate head; **qj**, quadratojugal; **qjp**, quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge groove; **qs**, quadrate shaft (in light blue); **sqc**, squamosal contact; **vqjc**, ventral quadratojugal contact; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vsh**, ventral shelf.

FIGURE 2. Avian and non-avian theropod terminology of the quadrate bone. Left quadrate of *Fregata minor* (Great Frigatebird) in medial view annotated with (**1**) Baumel and Witmer (1993) terminology, and (**2**) the here proposed terminology for the nonavian theropod quadrate (image from Witmer 1990 and Baumel and Witmer (1993; modified).

FIGURE 3. Skull comparison between (**1**) the bird *Corythaeola cristata* (Great Blue Turaco; NH.34.26; courtesy of the Horniman Museum & Gardens), and (**2**) the alvarezsaurid *Shuvuuia deserti* (IGM 100-1001; reversed) in lateral view. Comparison between the left quadrate of the juvenile? specimen of *Shuvuuia deserti* (IGM 100-1001) in (**3**) posterior, and (**4**) lateral view, and the right quadrate of the adult specimen of *Shuvuuia deserti* (IGM) in (**5**) posterior, and (**6**) posterolateral views. Abbreviations: **j**, jugal; **jc**, jugal contact; **lpq**, lateral process; **otc**, otic capitulum; **pfl**, pterygoid flange; **po**, postorbital; **poc**, postorbital contact; **qf**, quadrate foramen; **sq**, squamosal; **sqc**, squamosal capitulum. Scale bars = 2 cm (1-2), 1 cm (5-6), and 5 mm (3-4).

FIGURE 4. Morphology and position of pneumatic openings in the quadrate of nonavian Theropoda. Pneumatic fossa (**1**) of the right quadrate of the metriacanthosaurid *Sinraptor dongi* (IVPP 10600) in posterior view (courtesy of Philip Currie). Medial pneumatopore (**2**) of the right quadrate of the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345) in medial view. Medial pneumatopore (**3**) of the left quadrate of the carcharodontosaurid *Giganotosaurus carolinii* (MUCPv CH 1) in medial view. Posterior pneumatopore (**4**) of the left quadrate of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in posterior view (courtesy of Martín Ezcurra). Ventral pneumatopore (**5**) of the right quadrate of the tyrannosaurid *Alioramus altai* (IGM 100−844) in ventral view (courtesy of Mick Ellison). Ventral pneumatopore (**6**) of the left quadrate of the tyrannosaurid *Tyrannosaurus rex* (FMNH PR2081; cast) in ventral view. Medial pneumatopore (**7**) on the right quadrate of the therizinosauroid *Falcarius utahensis* (UMNH VP 14559) in medial view (courtesy of Lindsay Zanno). Posterior pneumatopore (**8**) of the left quadrate of the ornithomimid *Garudimimus brevipes* (IGM 100−13) in posterior view (courtesy of Yoshitsugu Kobayashi). Posterior pneumatopore (**9**) of the right quadrate of the dromaeosaurid *Buitreraptor gonzalezorum* (MPCA 245) in posterior view. Scale bars = 5 cm (1−3,6), 2 cm (4,8), 1 cm (5,7), 5 mm (9).

FIGURE 5. Distribution of quadrate pneumaticity in Theropoda. Simplified cladogram of theropod dinosaurs showing the phylogenetic distribution of a pneumatic quadrate denoted in red (from Bhullar et al., 2012; Modified). Pneumaticity is present in the quadrate of Allosauroidea (*Acrocanthosaurus*, *Mapusaurus*, *Giganotosaurus*), Tyrannosauroidea (*Alioramus*, *Albertosaurus*, *Tyrannosaurus*), Compsognathidae (*Sinosauropteryx*), Ornithomimosauria (*Ornithomimus*), Therizinosauria (*Falcarius*), Oviraptorosauria (*Conchoraptor*), Troodontidae (*Sinovenator*), Dromaeosauridae (*Buitreraptor*) and many birds. There is no evidence of a pneumatic quadrate in Alvarezsauroidea hitherto. When optimized onto this simplified tree, a pneumatic quadrate is a synapomorphy of Avetheropoda.

FIGURE 6. Quadrate of *Lourinhanosaurus antunesi* embryo. Incomplete left (**1–8**) quadrate (ML565-150) in (**1**) anterior, (**2**) lateral, (**3**) posterior, (**4**) medial, (**5**) ventral, (**6**) dorsal, (**7**) posteromedial, and (**8**) ventromedial views (the quadrate in (**7**) and (**8**) was photographed before preparation). Abbreviations: **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **mfq**, medial fossa; **pfl**, pterygoid flange; **pfq**, posterior fossa; **qjp**, quadratojugal process; **qr**, quadrate ridge; **vqjc**, ventral quadratojugal contact.

TABLE 1. Standardized terminology and abbreviation of the nonavian theropod quadrate and comparison with the terminology of the avian quadrate based on Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010).

Nonavian theropod quadrate (q)		**Avian theropod quadrate**
Quadrate body	qb	Corpus quadrati
Quadrate shaft	qs	/
Quadrate ridge	qr	/
Quadrate ridge groove	qrg	/
Quadrate head	qh	Processus oticus/Pars otica/Caput quadrati
Otic capitulum	otc	Capitulum oticum
Squamosal capitulum	sqc	Capitulum squamosum
Intercapitular sulcus	icas	Incisura/Vallecula intercapitularis
Quadrate foramen	qf	/
Mandibular articulation	mar	Pars/Processus mandibularis
Ectocondyle	ecc	Condylus (mandibularis) lateralis
Entocondyle	enc	Condylus (mandibularis) medialis
Mediocondyle	mec	Condylus caudalis
Intercondylar sulcus	ics	Vallecula intercondylaris
Intercondylar notch	icn	Depressio praecondylaris
Lateral process	lpq	/
Quadratojugal contact	qjc	Cotyla quadratojugalis
Ventral quadratojugal contact	vqjc	/
Dorsal quadratojugal contact	dqjc	/
Quadratojugal process	qjp	/
Ventral projection of the dorsal quadratojugal contact	vpdq	/
Squamosal contact	sqc	/
Posterior fossa	pfq	/
Quadrate diverticulum	qdi	/
Dorsal pneumatopore	dpne	Foramen pneumaticum caudomediale
Medial pneumatopore	mpne	Foramen pneumaticum basiorbitale
Posterior pneumatopore	ppne	Foramen pneumaticum rostromediale
Ventral pneumatopore	vpne	Foramen pneumaticum adventitium
Pterygoid flange	pfl	Processus orbitalis
Pterygoid contact	ptc	Condylus pterygoideus/Facies articularis pterygoidea
Medial fossa	mfq	Fossa basiorbitalis
Ventral shelf	vsh	/

Figure 1

Anatomy of nonavian theropod quadrates

Right (**1–5**) quadrate of *Tsaagan mangas* (IGM 100-1015; courtesy shared by Mick Ellison © AMNH) in (**1**) anterior, (**2**) lateral, (**3**) posterior, (**4**) medial and (**5**) ventral views; left (**6–10**) and right (**11**) quadrates of (**6**) *Baryonyx walkeri* (BMNH R9951), (**7**) *Aerosteon riocoloradensis* (MCNA-PV-3137; courtesy shared by Martín Ezcurra), (**8**) an indeterminate Oviraptoridae (GIN A; Maryańska and Osmólska 1997 :fig. 1), (**9**) *Tyrannosaurus rex* (BHI 3333, cast; Larson and Carpenter, 2008), (**10**) *Allosaurus* '*jimmadseni*' (SMA 005/02), and (**11**) *Majungasaurus crenatissimus* (FMNH PR 2100, cast; courtesy shared by Lawrence Witmer) in (**6–9**) posterior and (**10–11**) ventral views. Abbreviations: **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process of the quadrate; **mar**, mandibular articulation; **mfq**, medial fossa of the quadrate; **pfl**, pterygoid flange (in green); **pfq**, posterior fossa of the quadrate; **ppne**, posterior pneumatopore; **qb**, quadrate body (in blue); **qf**, quadrate foramen (delimited by a broader line); **qh**, quadrate head; **qj**, quadratojugal; **qjp**, quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge groove; **qs**, quadrate shaft (in light blue); **sqc**, squamosal contact; **vqjc**, ventral quadratojugal contact; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vsh**, ventral shelf.

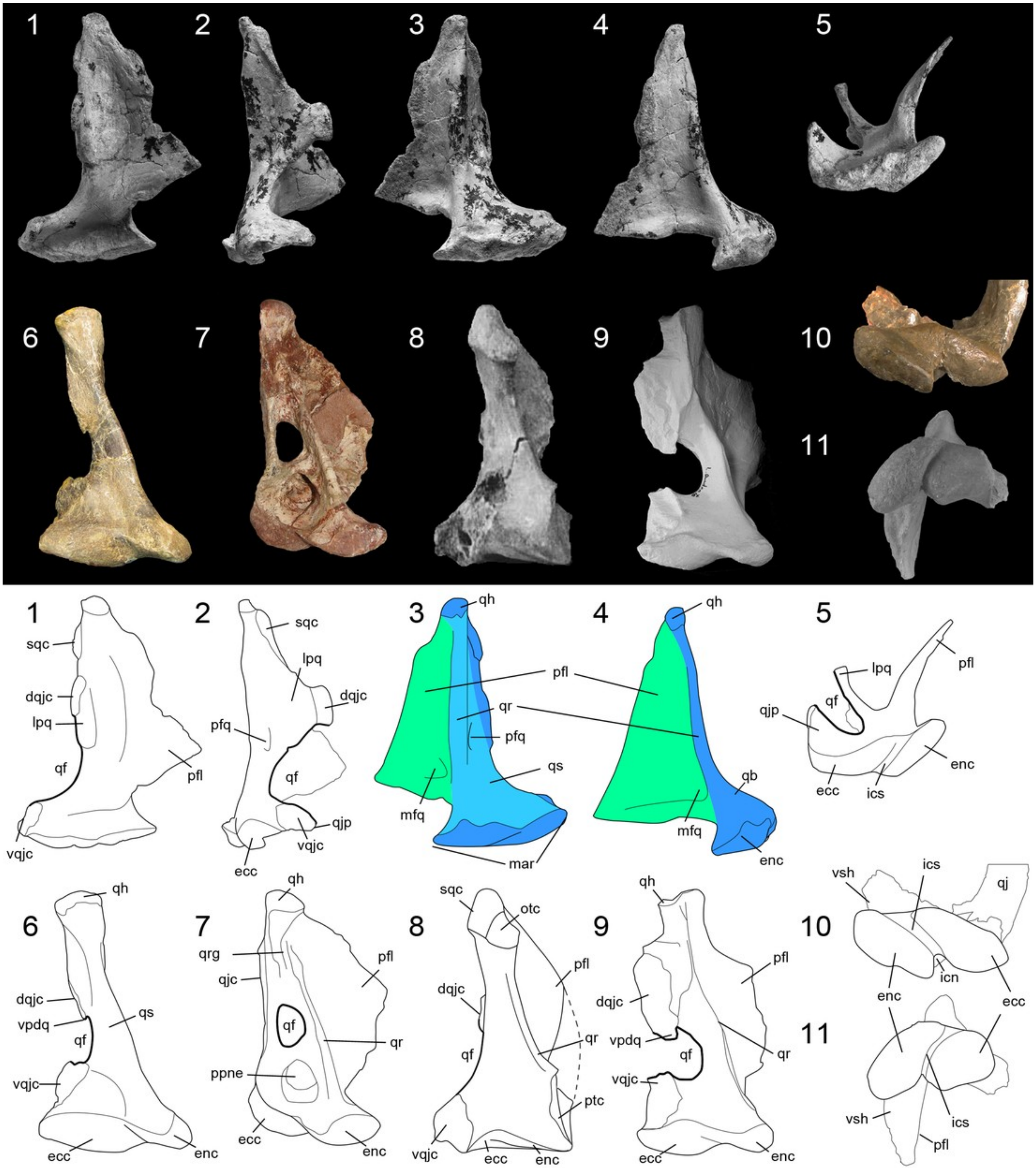
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Figure 2

Avian and non-avian theropod terminology of the quadrate bone

Left quadrate of *Fregata minor* (Great Frigatebird) in medial view annotated with (**1**) Baumel and Witmer (1993) terminology, and (**2**) the here proposed terminology for the nonavian theropod quadrate (image from Witmer 1990 and Baumel and Witmer (1993) ; modified).

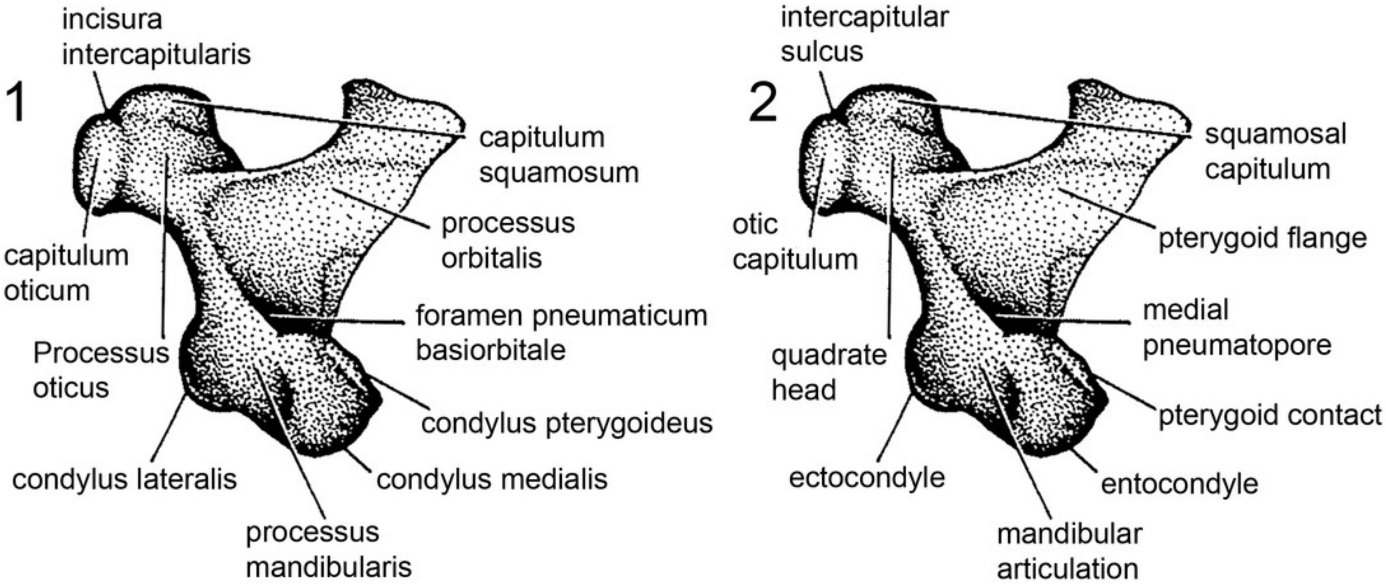

Figure 3

Skull comparison between *Corythaeola* and *Shuvuuia*

Skull comparison between (**1**) the bird *Corythaeola cristata* (Great Blue Turaco; NH.34.26; courtesy of the Horniman Museum & Gardens), and (**2**) the alvarezsaurid *Shuvuuia deserti* (IGM 100-1001; reversed) in lateral view. Comparison between the left quadrate of the juvenile? specimen of *Shuvuuia deserti* (IGM 100-1001) in (**3**) posterior, and (**4**) lateral view, and the right quadrate of the adult specimen of *Shuvuuia deserti* (IGM) in (**5**) posterior, and (**6**) posterolateral views. Abbreviations: **j**, jugal; **jc**, jugal contact; **lpq**, lateral process; **otc**, otic capitulum; **pfl**, pterygoid flange; **po**, postorbital; **poc**, postorbital contact; **qf**, quadrate foramen; **sq**, squamosal; **sqc**, squamosal capitulum. Scale bars = 2 cm (1-2), 1 cm (5-6), and 5 mm (3-4).

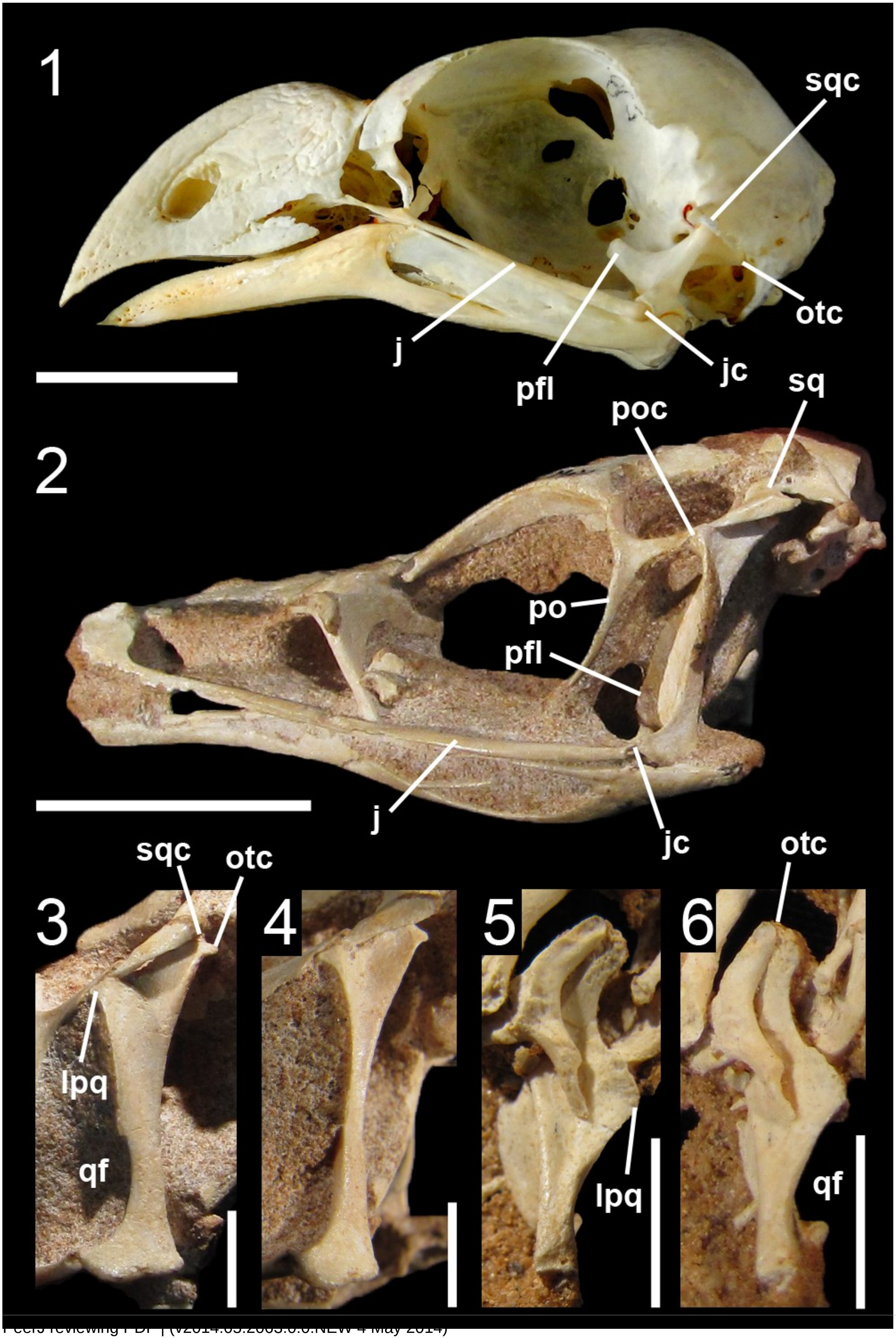
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Figure 4

Morphology and position of pneumatic openings in the quadrate of nonavian Theropoda

Pneumatic fossa (**1**) of the right quadrate of the metriacanthosaurid *Sinraptor dongi* (IVPP 10600) in posterior view (courtesy of Philip Currie). Medial pneumatopore (**2**) of the right quadrate of the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345) in medial view. Medial pneumatopore (**3**) of the left quadrate of the carcharodontosaurid *Giganotosaurus carolinii* (MUCPv CH 1) in medial view. Posterior pneumatopore (**4**) of the left quadrate of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in posterior view (courtesy of Martín Ezcurra). Ventral pneumatopore (**5**) of the right quadrate of the tyrannosaurid *Alioramus altai* (IGM 100−844) in ventral view (courtesy of Mick Ellison). Ventral pneumatopore (**6**) of the left quadrate of the tyrannosaurid *Tyrannosaurus rex* (FMNH PR2081; cast) in ventral view. Medial pneumatopore (**7**) on the right quadrate of the therizinosauroid *Falcarius utahensis* (UMNH VP 14559) in medial view (courtesy of Lindsay Zanno). Posterior pneumatopore (**8**) of the left quadrate of the ornithomimid *Garudimimus brevipes* (IGM 100−13) in posterior view (courtesy of Yoshitsugu Kobayashi). Posterior pneumatopore (**9**) of the right quadrate of the dromaeosaurid *Buitreraptor gonzalezorum* (MPCA 245) in posterior view. Scale bars = 5 cm (1–3,6), 2 cm (4,8), 1 cm (5,7), 5 mm (9).

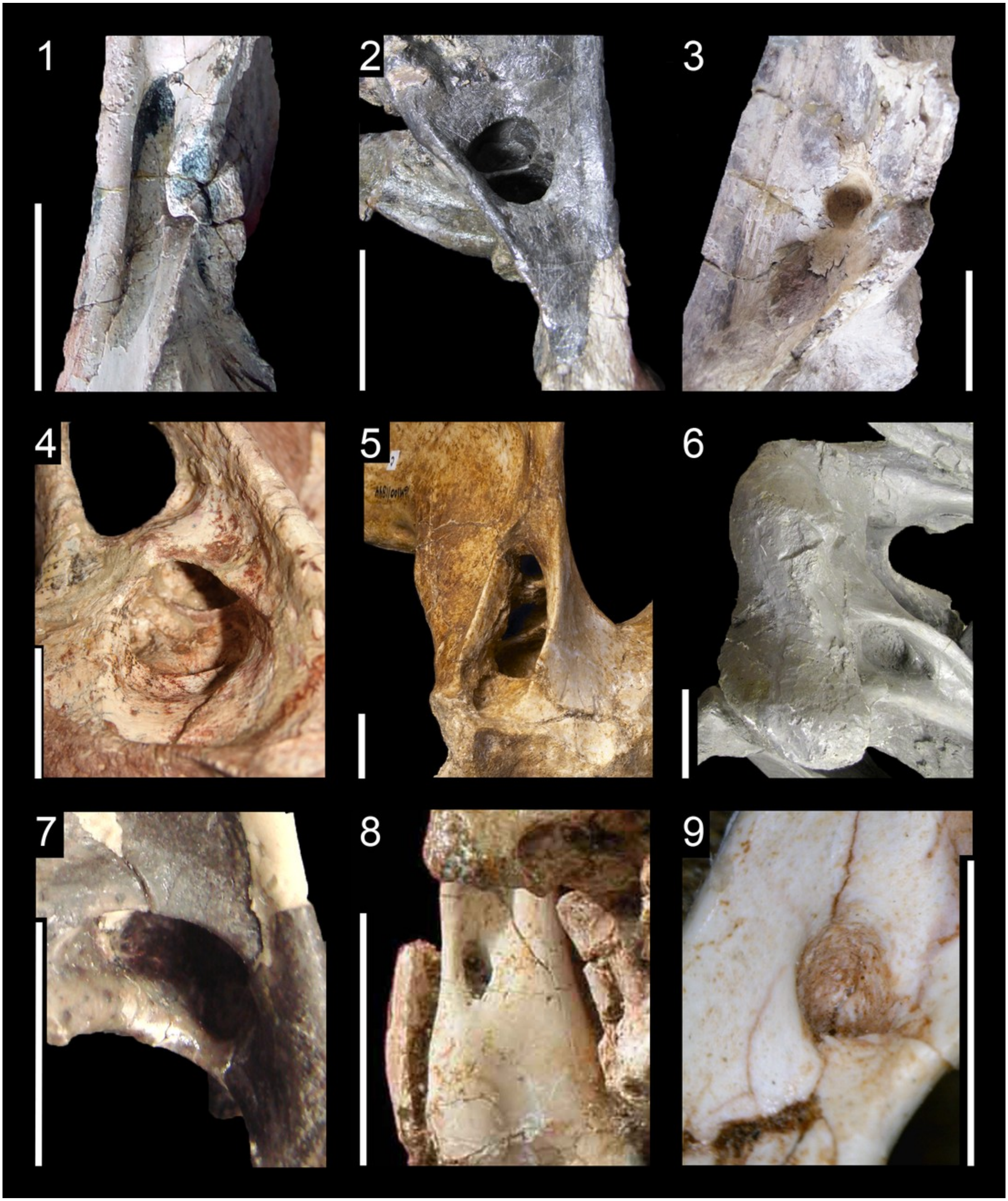
1
2
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Figure 5

Distribution of quadrate pneumaticity in Theropoda

Simplified cladogram of theropod dinosaurs showing the phylogenetic distribution of a pneumatic quadrate denoted in red (from Bhullar et al., 2012; Modified). Pneumaticity is present in the quadrate of Allosauroidea (*Acrocanthosaurus*, *Mapusaurus*, *Giganotosaurus*), Tyrannosauroidea (*Alioramus*, *Albertosaurus*, *Tyrannosaurus*), Compsognathidae (*Sinosauropteryx*), Ornithomimosauria (*Ornithomimus*), Therizinosauria (*Falcarius*), Oviraptorosauria (*Conchoraptor*), Troodontidae (*Sinovenator*), Dromaeosauridae (*Buitreraptor*) and many birds. There is no evidence of a pneumatic quadrate in Alvarezsauroidea hitherto. When optimized onto this simplified tree, a pneumatic quadrate is a synapomorphy of Avetheropoda.

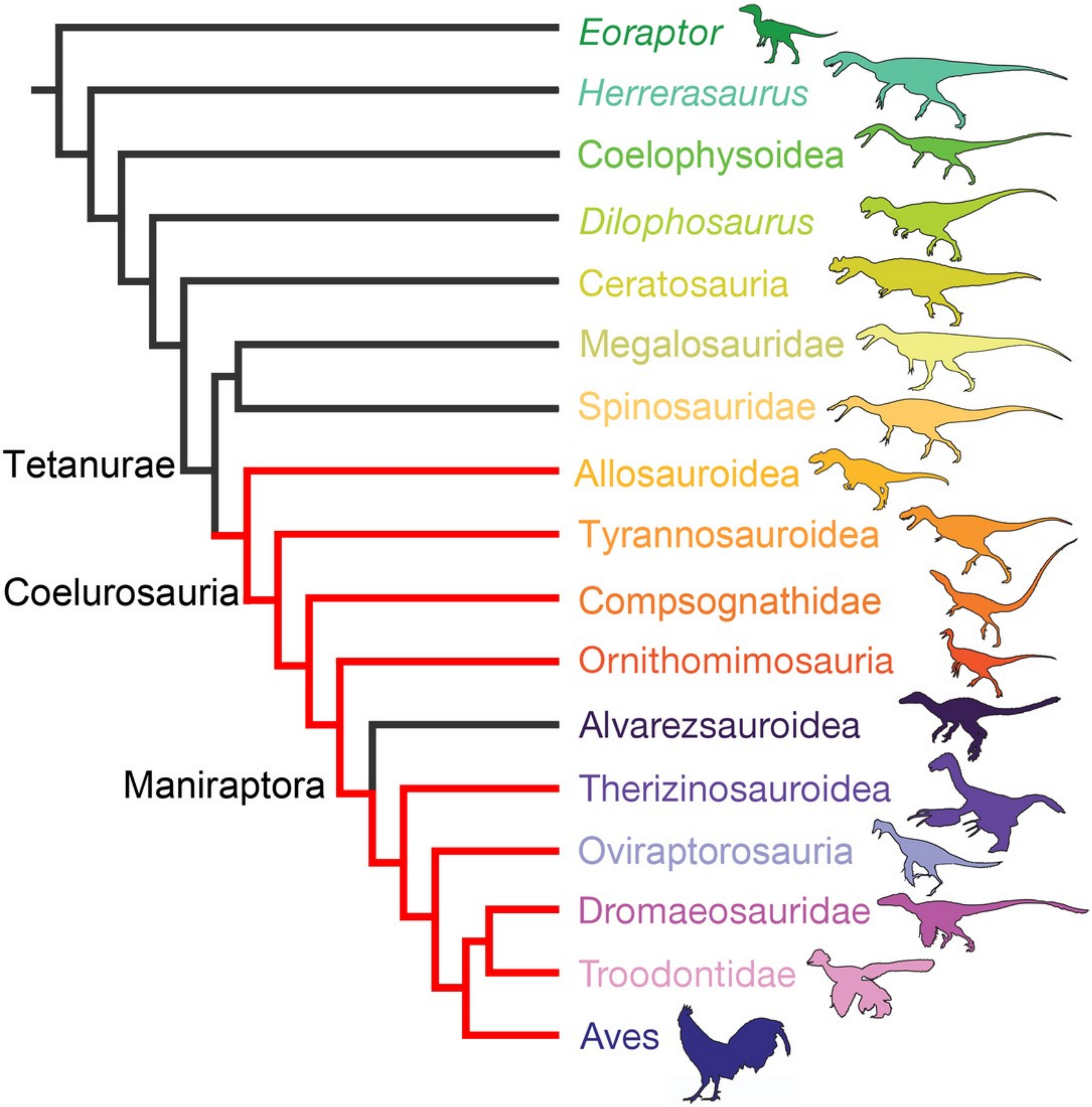
Eoraptor
Herrerasaurus
Coelophysoidea
Dilophosaurus
Ceratosauria
Megalosauridae
Spinosauridae
Tetanurae
Allosauroidea
Tyrannosauroidea
Coelurosauria
Compsognathidae
Ornithomimosauria
Alvarezsauroidea
Maniraptora
Therizinosauroidea
Oviraptorosauria
Dromaeosauridae
Troodontidae
Aves

Figure 6

Quadrate of *Lourinhanosaurus antunesi* embryo

Incomplete left (**1–8**) quadrate (ML565-150) in (**1**) anterior, (**2**) lateral, (**3**) posterior, (**4**) medial, (**5**) ventral, (**6**) dorsal, (**7**) posteromedial, and (**8**) ventromedial views (the quadrate in (**7**) and (**8**) was photographed before preparation). Abbreviations: **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **mfq**, medial fossa; **pfl**, pterygoid flange; **pfq**, posterior fossa; **qjp**, quadratojugal process; **qr**, quadrate ridge; **vqjc**, ventral quadratojugal contact.