

The non-avian theropod quadrate I: standardized terminology and overview of the anatomy, function and ontogeny

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The quadrate of reptiles and most other tetrapods plays an important morphofunctional role by allowing the articulation of the mandible with the cranium. In Theropoda, the morphology of the quadrate is particularly complex and varies importantly among different clades of non-avian theropods, therefore conferring it a strong taxonomic potential. Inconsistencies in the notation and terminology used in discussions of the theropod quadrate anatomy have been noticed, namely a number of no less than eight different terms being sometimes given to the same structure. A standardized list of terms and notations for each quadrate anatomical entity is proposed here, with the goal of facilitating future descriptions of this important cranial bone. In addition, an overview of the literature on the quadrate function, pneumaticity and ontogeny in non-avian theropods is also presented, along with the inferences that could be made from this research. Specifically, the quadrate of the large majority of non-avian theropods is akinetic but the diagonally oriented intercondylar sulcus of the mandibular articulation allowed both rami of the mandible to move laterally when opening the mouth in many of theropods. Pneumaticity of the quadrate is also present in most tetanuran clades and the pneumatic chamber—invaded by the quadrate diverticulum of the mandibular arch pneumatic system—was connected to one or several pneumatic foramina on the medial, lateral, posterior, anterior or ventral sides of the quadrate. Absence of a quadrate foramen and a poor delimitation of mandibular condyles seem to be ontogenetic features of some tetanurans.

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ABSTRACT

The quadrate of reptiles and most other tetrapods plays an important morphofunctional role by allowing the articulation of the mandible with the cranium. In Theropoda, the morphology of the quadrate is particularly complex and varies importantly among different clades of non-avian theropods, therefore conferring it a strong taxonomic potential. Inconsistencies in the notation and terminology used in discussions of the theropod quadrate anatomy have been noticed, namely a number of no less than eight different terms being sometimes given to the same structure. A standardized list of terms and notations for each quadrate anatomical entity is proposed here, with the goal of facilitating future descriptions of this important cranial bone.

In addition, an overview of the literature on the quadrate function, pneumaticity and ontogeny in non-avian theropods is also presented, along with the inferences that could be made from this research. Specifically, the quadrate of the large majority of non-avian theropods is akinetic but the diagonally oriented intercondylar sulcus of the mandibular articulation allowed both rami of the mandible to move laterally when opening the mouth in many of theropods. Pneumaticity of the quadrate is also present in most tetanuran clades and the pneumatic chamber—invaded by the quadrate diverticulum of the mandibular arch pneumatic system—was connected to one or several pneumatic foramina on the medial, lateral, posterior, anterior or ventral sides of the quadrate. Absence of a quadrate foramen and a poor delimitation of mandibular condyles seem to be ontogenetic features of some tetanurans.

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, which have had the quadrate evolved into the incus (Carroll 1988; Brusatte 2012; Benton 2015). 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, hearing, and hosting important nerves, pneumatic sinuses, and vascular passages (e.g., Witmer 1990, 1997; Bakker 1998; Sedlmayr 2002; Kundrát and Janáček 2007; Holliday and Witmer 2008; Tahara and Larsson 2011; see Supplemental Information Appendix 1).

Although the outward morphology of the quadrate is relatively simple, it varies significantly among theropods with variable feeding strategies in the structure of its head, mandibular articulation, quadratojugal contact and the presence of pneumatic openings, quadrate foramen, and lateral processes (e.g., Holtz 2003; Therrien et al. 2005; Hone and Rauhut 2010; Zanno and Makovicky 2011). Variation in the quadrate morphology in the derived theropod group Aves has long been used as a means of systematic significance (e.g., Lowe 1926; Samejima and Otsuka 1987; Barbosa 1990; Elzanowski et al. 2001; Elzanowski and Stidham 2010). Similarly, but to a lesser degree, the systematic potential of the quadrate bone has also been noted for non-avian theropods (Maryańska and Osmólska 1997; Currie 2006), highlighting the importance that should be given to the description of this bone in the literature on non-avian theropod anatomy. Nevertheless, the terminology and abbreviations of the quadrate anatomy has been inconsistent in non-avian theropods, and several different anatomical terms for the same quadrate sub-entity are often used (see Supplemental Information Appendix 2). Although a list of anatomical terms has been given by Baumel and Witmer (1993), Elzanowski et al. (2001) and

Elzanowski and Stidham (2010) for the avian quadrate, the terminology proposed by these authors has not been applied to the description of the non-avian theropod quadrate hitherto. Indeed, the quadrate of birds has greatly changed in its morphology throughout the evolution of this clade and hence displays many features absent in more primitive theropods. Thus, many anatomical terms coined by Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) cannot be applied to the non-avian theropod quadrate. Moreover, some quadrate entities such as the quadrate foramen and the lateral process observable in non-avian theropods are absent in their avian descendants and do not appear in the list made by these authors.

The work presented here has two major aims. First, we 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 descriptions of this bone in the literature. Second, we present and discuss the current knowledge on the function, pneumaticity and ontogeny of this important bone in non-avian theropods. A comprehensive study on the anatomy and phylogenetic potential of the non-avian theropod quadrate through cladistic and phylogenetic morphometric analyses will be provided in a companion article that will be published latter.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, U.S.A.; **BHI**, Black Hills Institute, Hill City, South Dakota, USA; **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

89 Geology, Ulaan Bataar, Mongolia; **IVPP**, Institute for Vertebrate Paleontology and
 90 Paleanthropology, Beijing, China; **MACN**, Museo Argentino de Ciencias Naturales, Buenos
 91 Aires, Argentina; **MCF PVPH**, Museo Municipal Carmen Funes, Paleontología de Vertebrados,
 92 Plaza Huinul, Argentina; **MCNA**, Museo de Ciencias Naturales y Antropológicas de Mendoza,
 93 Mendoza, Argentina; **MIWG**, Dinosaur Isle, Isle of Wight Museum Services, Sandown, U.K.;
 94 **ML**, Museu da Lourinhã, Lourinhã, Portugal; **NCSM**, North Carolina Museum of Natural
 95 Sciences, Raleigh, North Carolina, USA; **MNHN**, Muséum national d'Histoire Naturelle, Paris,
 96 France; **MNN**, Musée National du Niger, Niamey, Niger; **MPCA**, Museo Provincial Carlos
 97 Ameghino, Cipolletti, Río Negro, Argentina; **MSNM**, Museo di Storia Naturale di Milano,
 98 Milan, Italy; **MUCPv**, Museo de Ciencias Naturales de la Universidad Nacional de Comahue,
 99 Neuquén, Argentina; **NH**, Horniman Museum & Gardens, London, U.K.; **NHM**, The Natural
 100 History Museum, London, U.K.; **OUMNH**, Oxford University Museum, Oxford, U.K.; **PVL**,
 101 Fundación 'Miguel Lillo,' San Miguel de Tucumán, Argentina; **PVSJ**, Instituto y Museo de
 102 Ciencias Naturales, San Juan, Argentina; **SMA**, Sauriermuseum Aathal, Aathal, Switzerland;
 103 **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **RTMP**, Royal Tyrrell
 104 Museum of Palaeontology, Drumheller, Alberta, Canada; **UCMP**, University of California
 105 Museum of Paleontology, Berkeley, California, U.S.A.; **UC**, University of Chicago
 106 Paleontological Collection, Chicago, U.S.A.; **UMNH**, Utah Museum of Natural History, Salt
 107 Lake City, Utah, U.S.A.

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Theropod classification

110 The theropod phylogeny adopted here follows the classification summarized by Hendrickx et al.
 111 (in pressa) for non-avian theropods. Megaraptoran theropods are here considered as belonging to

the clade Allosauroidae, as proposed by Benson et al. (2010) and Carrano et al. (2012). The phylogenetic definitions of each non-avian theropod clade also follow those compiled and given by Hendrickx et al. (in pressa: table 1).

PROPOSED TERMINOLOGY OF THE QUADRATE ANATOMY

Favored terminology

The anatomical terms of the theropod quadrate were grouped in five main sections: quadrate body, quadrate head, mandibular articulation, pterygoid flange, and pneumatic openings. The terms for each quadrate sub-units were selected by their relevance, significance and importance in the non-avian theropod literature. The non-standardized traditional Romerian directional and anatomical terms (Romer 1956; Wilson 2006) were, therefore, favored over the terminology of the *Nomina Anatomica Veterinaria* (NAV) defined by the ICVGAN (2012) and the *Nomina Anatomica Avium* (NAA) provided by Baumel (1993) as Romerian terms are the most commonly used in the non-avian theropod literature (e.g., Eddy and Clarke 2011; pers. obs.). Consequently, ‘anterior’ and ‘posterior’ are used as directional terms in lieu of the veterinarian alternatives ‘cranial’ and ‘caudal’, respectively. Because non-avian archosaurs are the direct ancestors of birds, Harris (2004) recommended to adopt the NAA as the standardized nomenclature to describe all archosaurs (and even diapsids), yet we favor Wilson (2006) opinion to retain Romerian terms for non-avian dinosaurs. As noted by Wilson (2006), the Romerian nomenclature is the lingua franca for most of the dinosaur/archosaur literature. In addition, standard terminologies using Romerian terms are often proposed to describe the saurischian anatomy (e.g., Hendrickx et al. in pressb; Wilson 1999; Wilson et al. 2011; Hendrickx and

Mateus 2014). Comparison between the NAA nomenclature and the Romerian terminology here proposed for the quadrate anatomy is provided in Figure and Table 1.

Romer (1956)'s terminology of the quadrate is, in fact, very limited. Indeed, this author only expanded the vocabulary to describe this bone in reptiles to six terms, namely: the main body, quadrate shaft, quadrate foramen, quadrate head, quadrate flange and articular termination. Three terms were kept as such in the proposed terminology of the quadrate (i.e., quadrate shaft, quadrate foramen, and quadrate head) and the three others were slightly modified. The quadrate body (instead of "main body of [the] quadrate" sensu Romer 1956: p. 640), mandibular articulation (instead of "articular termination" sensu Romer 1956: p. 632) and pterygoid flange (instead of "quadrate flange" sensu Romer 1956: p. 146) were chosen not only because they are more commonly used in the theropod literature currently describing the quadrate (pers. obs.), but are also more specific of the loci of the anatomical sub-entity described. It should be noted that the pterygoid flange of Romer (1956) describes a wing-like process of the pterygoid and not the anteriorly projected ramus of the quadrate.

Figure 1

Table 1

Quadrate body

Quadrate body (qb). Part of the quadrate that includes the quadrate shaft, the quadrate ridge, the lateral contact (quadratojugal and/or squamosal contact), and the lateral process, and excludes the quadrate head, mandibular articulation, and pterygoid flange (Figs. 1G, 2C). In posterior view, the quadrate body is delimited by the lateral margin of the lateral contact and sometimes by the medial margin of the quadrate foramen, the dorsal margin of the mandibular articulation, the ventral 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 is equivalent 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 (Fig. 1A).

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; Fig. 2C). 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), Brusatte et al. (2012), and Choiniere et al. (2014a, b) 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 (Fig. 2C). Although the quadrate ridge is present in the large majority of non-avian theropods, a description of the structure is often omitted in the literature. The quadrate ridge is referred as ‘a column’ by Welles (1984), a ‘ridge-like mediodorsal edge’ by Carr (1996), ‘a prominent rounded ridge’ by Smith et al. (2007), a ‘columnar ridge’ by Rauhut et al. (2010), a ‘robust ridge’ by Brusatte et al. (2012), a ‘ridge’ or ‘pillar’ by Choiniere et al. (2014a), and a ‘bulging ridge’ by Lautenschlager et al. (2014).

Quadrate ridge groove (qrg). Groove dividing the quadrate ridge in two different units at two-thirds, or more dorsally, of the quadrate body height (Fig. 2G). A quadrate ridge groove exists in some allosauroid 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 (Fig. 2A, E–G, I). 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; Choiniere et al. 2010, 2014a, b; Zanno 2010; Brusatte et al. 2012; Foth and Rauhut 2012). Yet, 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; Lautenschlager et al. 2014), 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 non-avian theropods but Ceratosauria and Megalosauridae.

Lateral process (lpq). Lateral or anterolateral projection of the lateral margin of the quadrate body (Fig. 2B). 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’ (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 (Fig. 2G). The quadratojugal contact, which is similar to the ‘cotyla quadratojugal’ of Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1B), 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 (Fig. 2B, F, H). The ventral quadratojugal contact of the quadrate always receives the quadratojugal bone.

Dorsal quadratojugal contact (dqjc). Dorsal contact of the quadrate with the quadratojugal (Fig. 2B, F). 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 (Fig. 2I).

Dorsal projection of the ventral quadratojugal contact (dpvq). Small projection of the ventral quadratojugal contact delimiting the ventrolateral margin of the quadrate foramen.

Quadratojugal process (qjp). Anterior projection of the ventral quadratojugal contact of the quadrate (Fig. 2B). Also known as the 'quadratojugal lamina' (Lautenschlager et al. 2014).

Lateroventral process (lvp)—Lateromedially oriented ventral projection of the ventral quadratojugal contact of the quadrate that bounds the quadratojugal ventrally (Fig. 2H). The lateroventral process is similar to the 'lateral process' of Maryńska and Osmólska (1997).

Squamosal contact (sqc). Contact on the lateral margin of the quadrate with the squamosal (Fig. 2B).

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 (Fig. 2B). The posterior fossa can include or exclude the quadrate foramen.

Quadrate head

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 (Fig. 2D). 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), Brusatte et al. (2012), Choiniere et al.

(2014*a, b*) and Lautenschlager et al. (2014) 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), ‘dorsal articular surface’ (Larson 2013), and ‘otic process’ (Maryańska and Osmólska 1997; Burnham 2004; Holliday and Witmer 2008). In avian theropods, the quadrate head is homologous to the ‘Caput quadrati’ of Elzanowski et al. (2001) and Elzanowski and Stidham (2010), and roughly equivalent to the ‘Processus oticus’ (Baumel and Witmer 1993). In birds, the ‘Processus oticus’ (Baumel and Witmer 1993), and the ‘Pars oticus’ of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) also includes several sub-units that are either absent in non-avian theropods (e.g., Crista Tympanica, Tuberculum subcapitulare), or here included in the quadrate body (e.g., Sulcus pneumaticus, Foramen pneumaticum rostromediale). The bistylic quadrate head present in some tyrannosaurids, alvarezsauroids, oviraptorids and avian theropods is divided into otic and squamosal capitula.

Otic capitulum (oca). Medial capitulum of the quadrate head articulating with the braincase (Fig. 2H). The otic capitulum is referred as the ‘capitulum (condylus) oticum’ by Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1A).

Squamosal capitulum (sca). Lateral capitulum of the quadrate head articulating with the squamosal (Fig. 2H). The squamosal capitulum is similar to the ‘capitulum (condylus) squamosum’ of Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1C).

Intercapitular sulcus (icas). Groove separating the otic capitulum from the squamosal capitulum on the dorsal surface of the quadrate head (Fig. 2H). The intercapitular sulcus (Witmer

1990) is equivalent to the ‘incisura intercapitularis’ of Baumel and Witmer (1993), and the ‘vallecula intercapitularis’ of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1E).

Mandibular articulation

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 (Fig. 2C). The mandibular articulation, also known as the ‘mandibular capitulum’ (Lautenschlager et al. 2014), is equivalent to the ‘Processus mandibularis’ of Baumel and Witmer (1993), and ‘Pars mandibularis’ of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1A). Although most authors (e.g., Currie 2006; Sampson and Witmer 2007; Rauhut et al. 2010; Brusatte et al. 2012; Lautenschlager et al. 2014) 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 (Fig. 6.2). The ectocondyle is equivalent to the ‘condylus (mandibularis) lateralis’ of Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1F).

Entocondyle (enc). Medial condyle of the mandibular articulation. The entocondyle has been referred as the ‘condylus (mandibularis) medialis’ by Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1F).

Mediocondyle (mdc). Posterior condyle of the mandibular articulation located between the ecto- and entocondyles. 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 Lautenschlager et al. (2014), and the ‘condylus 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 articulated with the interglenoid ridge of the articular (Fig. 2E, K). 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 is similar 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 (Fig. 1F).

Intercondylar notch (icn). Notch located in between the ectocondyle and entocondyle, either on the anterior or posterior margin of the mandibular articulation, and being referred as the ‘pit’ by Bakker (1998) (Fig. 2J).

Figure 2

Pterygoid flange

Pterygoid flange (pfl). Ventrodorsally elongated sheet-like process projecting anteriorly or anteromedially from the anterior surface of the quadrate body to contact the pterygoid bone (Fig. 2A, D). The pterygoid flange, a term also used by Charig and Milner (1997), Brochu (2003),

Currie (2006), Coria and Currie (2006), Rauhut et al. (2010) and Lautenschlager et al. (2014), 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, 2014a, b), 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) for avian theropods (Fig. 1B).

Pterygoid contact (ptc). Contact with the pterygoid on the medial margin of the pterygoid flange or the quadrate body (Fig. 2D). In avian theropods, the pterygoid contact is homologous 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), Elzanowski et al. (2001), and Elzanowski and Stidham (2010; Fig. 1D).

Medial fossa (mfq). Depression or concavity located on the medial surface of the pterygoid flange, typically in the posteroventral end of the pterygoid flange (Fig. 2D). The medial fossa is delimited by the quadrate shaft and the ventral shelf in some theropod taxa. The medial fossa is similar 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 (Fig. 1D).

Ventral shelf (vsh). A medial or medioposterior fold of the ventral margin of the pterygoid flange (Fig. 3A, G, M). 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).

Pneumatic openings

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

Dorsal pneumatic foramen (dpf). Aperture located on the anterodorsal surface of the quadrate, just ventral to the quadrate head.

Medial pneumatic foramen (mpf). Aperture or recess situated on the medial side of the quadrate, typically in the ventromedial part of the pterygoid flange (Fig. 5A-D). The medial pneumatic foramen is homologous to the ‘foramen pneumaticum’ of Baumel and Witmer (1993), and the ‘foramen pneumaticum basiorbitale’ of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

Posterior pneumatic foramen (ppf). Aperture or recess on the posterior surface of the quadrate body, typically at mid-height of the quadrate (Figs. 2G, 5). The posterior pneumatic foramen is similar to the ‘foramen pneumaticum caudomediale’ of Elzanowski and Stidham (2010) for avian theropods (Fig. 1C).

Anterior pneumatic foramen (apf). Aperture or recess on the anterior surface of the quadrate body, typically at mid-height of the quadrate (Fig. 5K). The anterior pneumatic foramen is likely homologous to the ‘foramen pneumaticum medial’ of Elzanowski et al. (2001), and the ‘foramen pneumaticum rostromediale’ of Elzanowski and Stidham (2010).

Ventral pneumatic foramen (vpf). Aperture or recess on the ventral surface of the quadrate.

The ventral pneumatic foramen is equivalent to the ‘foramen pneumaticum adventitium’ (or ectopic pneumatic foramen) of Elzanowski and Stidham (2010) for avian theropods (Fig. 5I, J).

Lateral pneumatic foramen (lpf). Aperture or recess on the lateral surface of the quadrate (Fig. 5L).

Figure 3 & 4

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 by following the criteria summarized in Rieppel (2006) to establish inter-taxic topological homologies.

The quadrate ridge is easily distinguishable in many theropod taxa such as *Dilophosaurus wetherilli* (Welles 1984; Fig. 3C), *Aerosteon riocoloradensis* (MCNA-PV 3137; Fig. 4C) and *Proceratosaurus bradleyi* (NHM R.4860) but the demarcation of this structure may be only subtly developed, as in *Noasaurus leali* (PVL 4061), *Majungasaurus crenatissimus* (FMNH PR 2100; Fig. 3I), and *Eustreptospondylus oxoniensis* (OUMNH J.13558; Fig. 3U). The quadrate ridge is developed as a ‘columnar ridge’ in many theropod clades like in *Dilophosaurus wetherilli* (Welles 1984), *Allosaurus ‘jimmadseni’* (SMA 0005; *Allosaurus ‘jimmadseni’* sensu Chure 2000; Loewen 2010) and *Eotyrannus lengi* (MIWG 1997.550) but also forms 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 entocondyle 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: fig. 10B). The quadrate ridge can be divided into two ridges by a deep groove as in *Allosaurus fragilis* (AMNH 600) and *Allosaurus europaeus* (ML 415). The quadrate ridge can also flare at the second dorsal third of the quadrate, and reappears slightly more dorsally, as observed in some derived Spinosauridae (Hendrickx et al. 2014). Likewise, the ventral portion of the quadrate ridge can also dichotomize into two crests separated by a concavity such as in the tyrannosaurids *Albertosaurus sarcophagus*, *Daspletosaurus* sp. (Currie 2003: figs. 10 and 28) and *Tyrannosaurus rex* (AMNH 5027).

The pterygoid flange (Fig. 2D, pfl) contacts the quadrate process of the pterygoid anteriorly or anteromedially, and sometimes other bones such as the epipterygoid in *Herrerasaurus ischigualastensis* (Sereno and Novas 1994), the basisphenoid and prootic in *Erlikosaurus andrewsi* (Clark et al. 1994; Lautenschlager et al. 2014), 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 ~~as well~~. The ventral limit of the flange can reach the mandibular condyles (e.g., *Tyrannosaurus rex*, *Baryonyx walkeri*; Fig. 3P) or get attached to the quadrate body ~~well~~ above the mandibular articulation (e.g., *Majungasaurus crenatissimus*; Fig. 3J). This structure can in some instances be divided into two ridges delimited by a deep pneumatic foramen facing ventrally (e.g., *Alioramus altai*; Fig. 6.4J; *Tyrannosaurus rex* FMNH PR2081). In anterior view, the pterygoid flange can be straight and only projected anteriorly, as in the carcharodontosaurid *Shaochilong maortuensis* (Brusatte et al. 2010: fig. 7a), or anteromedially recurved. The anteroventral margin of the pterygoid flange can either be

straight, or medially and/or dorsally deflected, forming an horizontally oriented or dorsally inclined shelf-like structure here referred as the ventral shelf, as in *Majungasaurus crenatissimus* (FMNH PR 2100; Fig. 3G), *Carnotaurus sastrei* (MACN-CH 894) and *Allosaurus fragilis* (Madsen 1976: plate 3d).

The medial fossa of the quadrate (Fig. 2D, mfq) is easily homologized between taxa as it is always situated on the pterygoid flange, typically on its dorsoventral surface. This fossa is posteriorly delimited by the quadrate body in non-avian 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*; Fig. 4P), 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 (Fig. 2B, pfq) can be located either in between the quadrate and the quadratojugal, being confluent with the quadrate foramen (e.g., *Mapusaurus*), or in the middle of the quadrate shaft and between the quadrate ridge and the lateral limit of the quadrate shaft (e.g., ‘*Syntarsus*’, *Tsaagan*, *Majungasaurus*; Fig. 3I). The posterior fossa can either be strongly ventrodorsally elongated like in the carcharodontosaurid *Acrocanthosaurus*, 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, this structure deserves special attention. It can be completely absent (e.g., *Carnotaurus*, *Torvosaurus*, *Eustreptospondylus*; Fig. 3U), or form a very small aperture (e.g., *Megapnosaurus*) to a large opening (e.g., *Bambiraptor*; Fig. 4T). In most non-avian theropods, the quadrate foramen is

406 mostly delimited by the quadrate and only its lateral margin is bounded by the quadratojugal
407 (e.g., *Sinraptor*). In some non-avian theropods, however, the medial margin of the quadrate
408 foramen and part of the ventral and dorsal margins are formed by the quadrate, the other lateral
409 half being delimited by the quadratojugal (e.g., *Dromaeosaurus*). Finally, in a few theropods, the
410 foramen can be completely enclosed in the quadrate (e.g., *Aerosteon*; Fig. 4C).

411 The quadratojugal contact of the quadrate (Fig. 2G, qjc) can either be a ~~unique~~ extensive
412 contact or made of two contacts separated by the quadrate foramen. In the latter case, the ventral
413 quadratojugal contact and the dorsal quadratojugal contact of the quadrate are not always clearly
414 separated and their dorsal and ventral margins, respectively, can overlap like in the ~~sinraptorid~~
415 *Sinraptor dongi* (IVPP 10600). If the quadrate foramen is absent or located ~~inside~~ the quadrate,
416 the lateral quadratojugal contact typically **corresponds to** an elongated line of variable width
417 along the lateral margin of the quadrate. Where separated by the quadrate foramen, the ventral
418 and dorsal contacts can display a wide variety of surface and outlines. Both quadratojugal
419 contacts may face laterally, anteriorly or posteriorly, and their articulating surface can be smooth,
420 irregular or deeply grooved by several radiating ridges, as in *Allosaurus fragilis* (Madsen 1976).
421 The ventral quadratojugal contact is typically D-shaped or ovoid in lateral view. Its anterior
422 margin can extend far anteriorly, forming the quadratojugal process (Norell et al. 2006), and its
423 ventral margin can project far laterally, as in Oviraptoridae (Maryńska and Osmólska 1997).
424 The dorsal quadratojugal contact can vary from a very thin line to a broad surface in lateral or
425 posterior views and its dorsal extension can reach the dorsal condyle or terminate well beneath it.
426 A ventral projection of this contact may be present, and such projection delimiting part of the
427 lateral border of the quadrate can either be short, like in *Daspletosaurus* sp. (Currie 2003: fig.
428 28A) and *Baryonyx walkeri* (Fig. 3O), or form an elongated ramus, like in the therizinosaurid

429 *Falcarius utahensis* (Zanno 2010: fig. 1H) and the coelurosaur *Zuolong salleei* (Choiniere et al.
430 2010: fig. 3B).

431 In some basal theropods, ceratosaurs and dromaeosaurids, the lateral process of the
432 quadrate (Fig. 2B, lpq) forms a wing-like projection similar to the pterygoid flange. This process
433 is an extension of the quadrate body laterally so it is difficult to **delimitate**. Such process is
434 present in *Allosaurus 'jimmadseni'* (SMA 0005), *Sinraptor dongi* (Currie 2006: fig. 1D), and
435 *Erlikosaurus andrewsi* (Clark et al. 1994: fig. 7). The lateral process can also vary in shape and
436 size, as it is **lateromedially** short and parabolic in posterior view (e.g., *Carnotaurus*), or
437 **lateromedially elongated and subtriangular in posterolateral view (e.g., *Dilophosaurus*; Fig. 3B).**
438 **Its ventral border can also extend to the quadrate foramen (e.g., *Bambiraptor*; Fig. 4T) or more**
439 **ventrally, sometimes reaching the medial condyle of the mandibular articulation (e.g., *Ilokelesia*,**
440 ***Majungasaurus*; Fig. 3I).**

441 The quadrate head always articulates with the **deep cotylus** of the squamosal and contacts
442 ~~more rarely~~ other bones of the braincase such as the opisthotic in oviraptorids (Maryńska and
443 Osmólska 1997), the prootic in *Mononykus olecranus* (Perle et al. 1994; Chiappe et al. 2002) and
444 the postorbital in *Shuvuuia deserti* (Chiappe et al. 1998, 2002). **The contact of the braincase**
445 **between the dorsal part of the quadrate and the opisthotic-exoccipital or the paroccipital process**
446 **is also present in *Herrerasaurus ischigualastensis* (Serenó and Novas 1994), *Dilophosaurus***
447 ***wetherilli* (Welles 1984), *Ceratops magnicornis* (Madsen and Welles 2000; Sanders and**
448 **Smith 2005), tyrannosaurids (Currie 2003), *Heyuannia huangi* (Lü 2005), and *Erlikosaurus***
449 ***andrewsi* (Lautenschlager et al. 2014), yet this contact occurs on a small medial surface just**
450 **below the quadrate head and not with the quadrate head itself. The large majority of non-avian**
451 **theropods have a monostylic quadrate head (Rauhut 2003; pers. obs.); however, oviraptorids**

(Maryńska and Osmólska 1997: fig. 3B), the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998), and some tyrannosaurids such as *Tyrannosaurus* and *Gorgosaurus* (Larson 2013) have the apomorphic condition of possessing a bistylic quadrate head. This condition has also been observed in the dromaeosaurid *Mahakala omnogovae* (Turner et al. 2007) but Turner et al. (2011: fig. 4) later reconsidered the head of the quadrate as not being bistylic. The morphology of the quadrate head is variable; it may be **subtriangular** in most basal theropods (Sereno and Novas 1994) like *Dilophosaurus* (UCMP 37302; Fig. 3E), *Erlikosaurus* (Lautenschlager et al. 2014) and *Bambiraptor* (AMNH 30556; Fig. 4V), **oval or subcircular** in megalosaurids like *Afrovenator* (UC OBA1) and *Torvosaurus* (BYUVP 9246), and allosauroids such as *Aerosteon* (MCNA-PV-3137; Fig. 4E), *Sinraptor* (IVPP 10600) and *Shaochilong* (IVPP V2885.3), subquadrangular in Spinosaurinae like *Irritator* (SMNS 58022), or **conical** in Oviraptoridae (Maryńska and Osmólska 1997: fig. 1B). ~~Whilst~~ most non-avian theropods have either a **convex** **or a flattened quadrate head**, the quadrate of some allosaurids (Bakker 1998: fig. 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 intertaxically 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; Lautenschlager et al. 2014), all other non-avian 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: fig. 4D).

The intercondylar sulcus (Fig. 2E, 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. obs.).

The shape of the mandibular articulation (Fig. 2C, 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: fig. 6) or a unique convex articulation seen in some dromaeosaurids such as *Tsaagan mangas* (IGM 100/1015). The intercondylar notch (Fig. 2J, icn) is present in *Allosaurus* (Bakker 1998: fig. 5B, C; SMA 0005) 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 (Fig. 2E, ecc) and entocondyle (Fig. 2E, ent) are highly variable among each clade of non-avian theropods in terms of shape, size and orientation.

Pneumaticity of the quadrate can either be internal or, externally expressed by pneumatic foramina. 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 sides and portions of the quadrate. The medial and posterior pneumatic foramina (Fig. 2G, ppf) usually occur in the medial and posterior fossa respectively, and their position inside the fossae is again quite variable. Pneumatic foramina 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.

REVIEW OF THE QUADRATE FUNCTION, PNEUMATICITY AND ONTOGENY IN NON-AVIAN THEROPODS

Function of the Quadrate

In all archosaurs, and all amniotes except Mammaliaformes, the main function of the quadrate is the articulation of the cranium with the mandible, yet this bone also play an important role in the mobility of the skull in many extant theropods. Streptostyly is a fundamental property of all avian theropods, and quadrate kinesis in birds, known already in the beginning of the 19th century (Nitzsch 1816), has been extensively studied over 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 which typically lead to a transverse movement, although a lateral movement of the quadrate around an anteroposteriorly directed axis occurs in some lepidosaur 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). In prokinesis, flexion occurs at the nasofrontal joint and the upper jaw thereby moves as

521 one unit; in amphikinesis, flexion occurs in two zones of flexibility and the upper jaw and its tip
522 are bent upward in rhynchokinesis, flexion occurs forward from the nasofrontal joint, allowing
523 its anterior part to be moved (Zusi 1984).

524 Inference of the cranial kinesis and quadrate mobility in non-avian theropods has been
525 investigated by Holliday and Witmer (2008) which regard the cranium of this group of dinosaurs
526 as partially kinetically competent, because synovial joints and protractor muscles are present, but
527 not fully kinetic like in birds. The strong suture of the quadrate to the quadratojugal and the
528 immobile contact of the quadrate and the pterygoid on the medial side of the pterygoid flange in
529 most non-avian theropods seem to indicate a very limited movement, and perhaps even the total
530 absence of movement of this bone within the cranium. Although the synovial quadrate head joint
531 existing in theropods, and all other archosaurs, is necessary to infer cranial kinesis, its presence
532 in akinetic taxa such as crocodiles demonstrates that the synovial joint cannot be considered
533 alone as an argument for cranial kinesis. Synovial joints have actually been interpreted as growth
534 zones rather than articular surfaces of mobile joints based on the presence of very thin articular
535 cartilage covering the end of this joint (Holliday and Witmer 2008). According to Holliday and
536 Witmer (2008) “articular cartilage persists in loading environments that exert hydrostatic
537 pressures (which result in a change in volume but not shape) but exert low shear stresses”.
538 Indeed, one of the key centers of deformation during normal biting is the quadrate-squamosal
539 contact, which would have experienced large shear stresses associated with torque and
540 asymmetrical loading during biting (Rayfield 2005), and the presence of a minimal amount of
541 cartilage between the quadrate and squamosal would therefore suggest that the synovial zone
542 was rather a growth zone than a mobile one. A streptostylic quadrate in *Tyrannosaurus rex*
543 (Molnar 1991, 1998), *Nanotyrannus lancensis* (Larson 2013), *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 there by unlikely.

Nevertheless, and more convincingly, a streptostylic quadrate was also proposed in the alvarezsaurid *Shuvuuia deserti* by Chiappe et al. (1998). In this taxon, the quadratojugal/jugal? (n.b., it has been suggested that the quadratojugal is absent in *Shuvuuia deserti*; see Dufeau 2003), instead of being firmly sutured to the quadrate as in other non-avian theropods, would have contacted the lateral surface of the quadrate through a movable joint (Chiappe et al. 1998, 2002; see Supplemental Information Fig. S3). 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 the quadrate to pivot anteroposteriorly, and the upper jaw to rotate ventrodorsally thanks to this transversal movement. 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. Nevertheless, the complex contacts between the nasal, frontal and prefrontal illustrated by Sereno (2001: fig. 12B) makes assessment of Chiappe et al. (1998) hypothesis quite dubious (Holliday and Witmer 2008). Holliday and Witmer (2008) also note that a maxillojugal and palatal flexion zones allowing 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 was proposed in the oviraptorosaurids *Heyuannia huangi* (Lü 2003) and *Nemegtomaia huangi* (Lü et al. 2004, 2005). In *Heyuannia*, the quadrate and quadratojugal articulation corresponds to a trochlea-like structure

(Lü 2003, 2005), while the quadratojugal contact of *Nemegtomaia* is diagnostically convex and was described as a lateral cotyle by Lü et al. (2004). Although such articulation suggests some mobility between the quadrate and quadratojugal, it is unlikely that the skull of these two oviraptorids could display ~~some~~ kinesis. As in other non-avian theropods, the oviraptorid quadrate was an immovable bone (Barsbold 1977; Maryńska and Osmólska 1997) so that the quadratojugal, if kinetic, could only pivot either ventrodorsally or mediolaterally from the quadratojugal contact of the quadrate. Yet, the quadratojugal of at least *Nemegtomaia* does not seem to have a loose articulation with the jugal given that the articulating surface between the two bones is anteroposteriorly extensive (Lü et al. 2004: fig. 2), disallowing mobility between the jugal and quadratojugal. Consequently, we consider unlikely that movement was possible between the quadrate and quadratojugal in *Heyuannia* and *Nemegtomaia* and, unlike Barsbold (1977), see the oviraptorosaur skull as akinetic.

Quadrate articulation with the mandible and orientation of the intercondylar sulcus are highly variable among non-avian theropods, therefore suggesting some variation in the movement of the **rami** when the jaw opened. The helical intercondylar sulcus present in many non-avian theropods (pers. obs.) was noticed by Bakker (1998) in basal theropod dinosaurs, Hendrickx and Buffetaut (2008) in spinosaurids, and Molnar (1991) and Larson (2008) in *Tyrannosaurus rex*. These authors suggested that the spiral groove of the mandibular articulation constrained the diagonal ridge of the articular glenoid fossa, which ~~fitted~~ into the intercondylar sulcus, to slide laterally. This would force the rami of the mandible to displace laterally when the lower jaw was depressed, enlarging the width of the larynx in order to swallow large-size prey items (Hendrickx and Buffetaut 2008).

In *Allosaurus*, the enlargement of the mandibular condyles associated with the posteroventral inclination of the ventral part of the quadrate, and the intercondylar notch, were interpreted by Bakker (1998) as joint-stabilization zones. According to Bakker (1998), the anteroposterior enlargement of the articulating surface would improve the stability of the mandibular articulation when the mouth was widely opened, whereas the intercondylar notch, morphologically convergent to the depression of knee joints in crocodiles and birds, would be hosting one or several ligaments within the quadrate-mandibular articulation (Bakker 1998). An intercondylar notch is present in the abelisaurids *Carnotaurus sastrei* (MACN-CH 894) and *Majungasaurus crenatissimus* (FMNH PR 2100), and the spinosaurid *Suchomimus tenerensis* (MNN GAD 502), perhaps implying similar jaw mechanics of the mandibular articulation as in *Allosaurus*. Yet, Bakker (1998)'s jaw mechanics hypotheses based on the shape of the mandibular articulation and the presence of an intercondylar notch require further investigation with modern functional analysis methods such as FEA to be tested.

Figure 5 & 6

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. 2014b). Pneumatic foramina of the quadrate are widespread among avetheropod clades (Gold et al. 2013; Fig. 4). The presence of one or several pneumatic foramina has indeed been recorded in carcharodontosaurids (e.g., Coria and Currie 2006; Eddy and Clarke 2011), megaraptorans (Serenio et al. 2008), tyrannosauroids (e.g., Molnar 1991; Brochu 2003; Currie 2003; Xu et al.

2004; Witmer and Ridgely 2010; Brusatte et al. 2012; Gold et al. 2013), compsognathids (Currie and Chen 2001), alvarezsauroids (Choiniere pers. comm.), therizinosauroids (Clark et al. 1994; Zanno 2010), oviraptorids (e.g., Maryńska and Osmólska 1997; Lü 2003; Kundrát and Janáček 2007; Balanoff and Norell 2012), ornithomimosaurs (e.g., 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), suggesting that quadrate pneumaticity may be an avetheropod synapomorphy. Yet, external manifestation of quadrate pneumaticity only occurs in derived members of Allosauroidae, Tyrannosauroidae, and Ornithomimosauria and an apneumatic quadrate exists in the basal members of each of these clades (i.e., *Sinraptor* and *Allosaurus* for Allosauroidae (Currie 2006); pers. obs., *Tanycolagreus* and *Proceratosaurus* for Tyrannosauroidae (Carpenter et al. 2005; Rauhut et al. 2010), and *Nqwebasaurus* for Ornithomimosauria; see Choiniere et al. (2012) codings of their datamatrix). Pneumatic foramina have not been reported for any alvarezsauroid taxa, but is present in basalmost members of Therizinosauria, Oviraptorosauria and Paraves. This suggests that external quadrate pneumaticity occurred independently in several basal avetheropod clades and is a possibly synapomorphy of the clade Therizinosauria + Pennaraptora (Fig. 6).

The pneumatic opening is particularly large in some allosauroids such as *Aerosteon riocoloradensis* (Serenó et al. 2008; Fig. 5F) and *Acrocanthosaurus atokensis* (Eddy and Clarke 2011; Fig. 5A), and the therizinosaur *Falcarius utahensis* (Zanno 2010; Fig. 5D). It however corresponds to a small rounded or oval aperture lodged in the posterior fossa of the quadrate body in most avetheropods (Fig. 5). The posterior pneumatic foramen is the most common quadrate pneumatic aperture in non-avian theropods and can be observed in many coelurosaur

clades. For instance, it is present in the tyrannosauroid *Dilong paradoxus* (Xu et al. 2004), the compsognathid *Sinosauroptryx prima* (Currie and Chen 2001: fig. 3f), the ornithomimids *Hexing qingyi* (the ‘quadratic foramen’ of Liyong et al. 2012), *Garudimimus brevipes* (the ‘foramen’ of Kobayashi and Barsbold 2005; Fig. 5G), *Sinornithomimus dongi* (the ‘quadratic foramen’ of Kobayashi and Lü 2003) and *Struthiomimus altus* (AMNH 5339), the basal oviraptorosaur *Incisivirosa gauthieri* (Balanoff et al. 2009), the dromaeosaurid *Buitreraptor gonzalezorum* (Makovicky et al. 2005; Fig. 5H), and the troodontids *Mei long* (Xu and Norell 2004), *Sinovenator changii* (Xu et al. 2002) and possibly *Gobivenator mongoliensis* (Tsuihiji et al. 2014). The posterior pneumatic foramen is, in fact, incorrectly interpreted by several authors as the quadrate foramen in ornithomimosaur (e.g., Kobayashi and Lü 2003; Kobayashi and Barsbold 2005; Choiniere et al. 2012). A genuine quadrate foramen between the quadrate and quadratojugal, as seen in the large majority of other theropods, is found in most (possibly all) ornithomimosaur possessing a posterior pneumatic foramen (e.g., *Garudimimus*, *Struthiomimus*; Kobayashi and Barsbold 2005; pers. obs.). Tahara and Larsson (2011) wrote that “no obvious foramen or fossa was identified on the posterior surface of the quadrate” in *Ornithomimus edmontonicus*. Yet, a deep posterior fossa seems to be present on the right side of the specimen they studied (TMP 95-110-1; n.b., the fossa seems to be filled with sediment on the left side), in the homologous position of that of the posterior fossa of other ornithomimosaur (pers. obs.). It is, therefore, surprising that this fossa was apneumatic, as implied by Tahara and Larsson (2011). Consequently, we consider likely that a posterior pneumatic foramen was also leading to the pneumatic chamber hosting the quadrate diverticulum in this taxon. An incipient development of a posterior pneumatic foramen is seen in *Sinraptor dongi* in which the quadrate, though apneumatic, includes a well-delimited pneumatic fossa between the quadrate foramen and

658 quadrate ridge (Currie 2006; Fig. 5E). The presence of a posterior pneumatic foramen is a
 659 possible synapomorphy of the clade Pennaraptora, which encompasses Oviraptorosauria and
 660 Paraves (Foth et al. 2014; Fig. 6). The medial pneumatic foramen, located in the ventral corner of
 661 the pterygoid flange, has also been reported in several theropod clades. It is present in the
 662 carcharodontosaurids *Acrocanthosaurus atokensis* (Eddy and Clarke 2011; Fig. 5A),
 663 *Mapusaurus roseae* (Coria and Currie 2006; Fig. 5B), and *Giganotosaurus carolinii* (MUCPv-
 664 CH-1; Fig. 5C), the tyrannosaurids *Albertosaurus sarcophagus* (Currie 2003: fig. 10B) and
 665 *Tyrannosaurus rex* (Molnar 1991; Brochu 2003), the therizinosauroid *Falcarius utahensis*
 666 (Zanno 2010; Fig. 5D), the oviraptorosaurids *Conchoraptor gracilis* and possibly *Ajancingenia*
 667 *yanshini* (Maryńska and Osmólska 1997; Kunderát and Janáček 2007), and the basal avialan
 668 *Archaeopteryx lithographica* (Domínguez Alonso et al. 2004). A pneumatic foramen has also
 669 been noticed in the dorsomedial part of the quadrate in the ornithomimosaur *Ornithomimus*
 670 *edmontonicus* (Tahara and Larsson 2011). A pneumatic foramen piercing the quadrate medially
 671 is a probable synapomorphic feature of Carcharodontosauridae or carcharodontosaurids more
 672 derived than *Concavenator corcovatus* and/or *Eocarcharia dinops*, pending on the results of the
 673 latest phylogenetic analyses on carcharodontosaurids (i.e., Ortega et al. 2010; Carrano et al.
 674 2012). In non-avian theropods, the ventral pneumatic foramen that occurs within a recess on the
 675 posteroventral part of the pterygoid flange ('funnel-like external opening on the rostral surface of
 676 the quadrate, above the condyles' of Gold et al., 2013: p. 37) is only present in
 677 Tyrannosauroidae. It is observed in the tyrannosaurids *Alioramus altai* (Brusatte et al. 2012;
 678 Gold et al. 2013; Fig. 5I), *Daspletosaurus* sp. (Currie 2003: fig. 28C) and *Tyrannosaurus rex*
 679 (Brochu 2003; Witmer and Ridgely 2010; Fig. 5J). In non-tyrannosaurid tyrannosauroid, such
 680 ventral pneumatic foramen is present in *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). Yet, it is not clearly present in *Eotyrannus lengi* (contra Gold et al. 2013; pers. obs.). A ventral pneumatic foramen of the quadrate is most likely synapomorphic of non-proceratosaurid Tyrannosauroida (Fig. 6). More rarely, a pneumatic opening can be situated on the lateral surface of the quadrate body, as in *Aerosteon riocoloradensis* (MCNA-PV 3137; Fig. 5L), and on the anterior surface of the quadrate, as in *Mapusaurus roseae* (Coria and Currie 2006; Fig. 5K), *Heyuannia huangi* (Lü 2005), *Erlikosaurus andrewsi* (Lautenschlager et al. 2014), *Troodon formosus* (Currie and Zhao 1993), and perhaps *Tyrannosaurus rex* (Molnar 1991). The presence of an anterior or lateral pneumatic foramen is an ambiguous autapomorphy in each of these taxa.

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 as in *Tyrannosaurus rex* (Molnar 1991; Brochu 2003; Witmer and Ridgely 2010), *Alioramus altai* (Gold et al. 2013), *Conchoraptor gracilis* (Kundrát and Janáček 2007) or *Ornithomimus edmontonicus* (Tahara and Larsson 2011). The neovenatorid *Aerosteon riocoloradensis* also possesses a large posterior pneumatic foramen leading to a pneumatic chamber, as well as a shallow pneumatic recess on the lateral surface of the quadrate shaft (pers. obs.).

These pneumatic foramina 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 (Dufeu 2011; 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 in non-avian theropods, the quadrate diverticulum of modern birds exhibits a large variety of morphologies, and can pneumatize the quadrate by entering through a single medial or anteromedial foramen (Witmer 1990; Tahara and Larsson 2011). In basal theropods with an apneumatic quadrate, both medial and posterior fossae of the quadrate possibly correspond to the osteological trace of the quadrate diverticulum. In non-avian theropods having a pneumatic quadrate, the position of the quadrate diverticulum is variable as in ornithomimids (Tahara and Larsson 2011), carcharodontosaurids and oviraptorids (pers. obs.). The quadrate diverticulum of non-avian 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 non-avian maniraptorans (Serenó 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 7

Quadrate Ontogeny

Skull ontogeny has been generally poorly studied in non-avian theropods, especially in their early stage of development (Rauhut and Fechner 2005; Araújo et al. 2013), but the ontogeny of the

quadrate bone has particularly received little attention when compared to other cranial bones (see Carr 1999; Loewen 2010; Foth et al. 2015). Although the quadrate of embryonic and juvenile specimens has been reported in several non-avian theropod clades such as basal Megalosauroida (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), Alvarezsauroida (Dufeau 2003; see Supplemental Information Fi. 3), Oviraptoridae (Norell et al. 1994, 2001; Weishampel et al. 2008) and Troodontidae (Varricchio et al. 2002), the ontogenetic variation of the non-avian theropod quadrate has only been investigated by Hendrickx and Mateus (2012). These authors reported two incomplete quadrates tentatively belonging to embryos of *Lourinhanosaurus autunesi* (see Supplemental Information Figs. S1-S2) 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 ontogenetic features present in the allosauroid quadrate (see Supplemental Information Appendix 3 for a more detail discussion on the quadrate ontogeny in *Lourinhanosaurus autunesi* and *Shuvuuia deserti*). Hendrickx and Mateus (2012) also examined the ontogenetic 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*, they were able to propose a list of ontogenetic steps ~~divided into juvenile, subadult and adult stages~~. The ontogenetic 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. This allows a firm contact between the quadrate and quadratojugal to be present in sub-adult and adult specimens.

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 reported as *Lourinhanosaurus autunesi*, a quadrate foramen exists in several theropod juvenile specimens 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

Here we propose a revised nomenclature of the quadrate bone and a corresponding set of abbreviations that provide a standard set of terms for describing this cranial bone in non-avian 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 they are highly variable in shape, all quadrate entities, with perhaps the exception of the posterior fossa, are easy to homologize across taxa, and a description of their morphology should be provided in the literature.

772 ~~A review of the current literature on the quadrate function, pneumaticity and~~
773 ~~ontogeny in non-avian theropods allowed us to draw some conclusions.~~ The quadrate of the large
774 majority of non-avian theropods is akinetic, and it is unlikely that the streptostylic quadrate is
775 present in the derived alvarezsauroids *Shuvuuia deserti*, as it was previously thought. A lateral
776 movement of the rami while the mandible was depressed occurred in various theropods (e.g.
777 spinosaurids). This lateral movement of the rami was due to a helicoidal and diagonally oriented
778 intercondylar sulcus of the mandibular articulation. The presence of an intercondylar notch in
779 allosaurids was interpreted as a joint-stabilization zone that would improve the stability of the
780 mandibular articulation when the mouth was widely opened. However, this assumption needs
781 further investigation from modern functional morphology techniques.

782 A pneumatic quadrate was present in members of most non-avian avetheropod clades, in
783 which a pneumatic foramen is present in the ventral part of the pterygoid flange and in the
784 medial and lateral fossae. Pneumatic foramina invading the quadrate seem to be independently
785 acquired by allosauroids, tyrannosaurids, compsognathids, and ornithomimosaurs throughout
786 their evolution. The presence of pneumatic foramina in the quadrate of basalmost members of
787 therizinosauroids, oviraptorids, troodontids and dromaeosaurids suggests that quadrate
788 pneumaticity is a synapomorphy of the clade Therizinosauria + Pennaraptora. Although the
789 pneumatic recess invaded by the quadrate diverticulum of the mandibular arch pneumatic system
790 was linked to a single pneumatic foramen in most avetheropods, the presence of several
791 pneumatic openings perforating different sides of the quadrate has been recorded in
792 Megaraptora, Carcharodontosauridae and Tyrannosauridae.

793 Poorly delimited mandibular condyles, intercondylar sulcus and quadrate head, as well as
794 a quadratojugal contact with a smooth surface were interpreted as ontogenetic 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 at the embryonic stage of coelurosaurs.

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FIGURE CAPTIONS AND TABLES

FIGURE 1. Avian and non-avian theropod terminology of the quadrate bone. Left quadrate of the common ostrich *Struthio camelus* (NH.11.75; courtesy of Paolo Viscardi) in (A, G) anterior, (B, H) lateral, (C, I) posterior, (D, J) medial, (E, K) dorsal, and (F, L) ventral views. The ostrich quadrate is annotated with (A-F) Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) terminologies, and (G-L) the here proposed terminology for the non-avian theropod quadrate.

FIGURE 2. Anatomy of non-avian theropod quadrates. Line drawings of the right (A-E) quadrate of *Tsaagan mangas* (IGM 100-1015) in (A) anterior, (B) lateral, (C) posterior, (D) medial and (E) ventral views; left (F-I) and right (J-K) quadrates (F) of *Baryonyx walkeri* (NHM R9951), (G) *Aerosteon riocoloradensis* (MCNA-PV-3137), (H) an indeterminate Oviraptoridae (GIN A; Maryńska and Osmólska 1997), (I) *Tyrannosaurus rex* (BHI 3333; Larson and Carpenter, 2008), (J) *Allosaurus 'jimmadseni'* (SMA 0005), and (K) *Majungasaurus crenatissimus* (FMNH PR 2100) in (F-I) posterior and (J-K) 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 (in red); **mfq**, medial fossa of the quadrate; **oca**, otic capitulum; **pfl**, pterygoid flange (in green); **pfq**, posterior fossa of the quadrate; **ppf**, posterior pneumatic foramen; **qb**, quadrate body (in light and dark blue); **qf**, quadrate foramen (delimited by a broader line); **qh**, quadrate head (in yellow); **qj**, quadratojugal; **qjp**, quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge groove; **qs**, quadrate shaft (in light blue); **sqc**, squamosal contact; **sca**, squamosal capitulum;

vqjc, ventral quadratojugal contact; **vpdq**, ventral projection of the dorsal quadratojugal contact;
vsh, ventral shelf.

FIGURE 3. Topological homologies in the non-averostran theropod quadrate. Left (**A**, **C**, **F**) and right (**B**, **D**, **E**; reversed) quadrates of *Dilophosaurus wetherilli* (UCMP 37302) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**) medial, (**E**) dorsal and (**F**) ventral views (courtesy of Randall Irmis and Matthew Carrano). Right quadrate (**G–L**; reversed) of *Majungasaurus crenatissimus* (FMNH PR 2100) in (**G**) anterior, (**H**) lateral, (**I**) posterior, (**J**) medial, (**K**) dorsal, and (**L**) ventral views. Left quadrate (**M–R**) of *Baryonyx walkeri* (NHM R9951) in (**M**) anterior, (**N**) lateral, (**O**) posterior, (**P**) medial, (**Q**) dorsal, and (**R**) ventral views. Right quadrate (**S–W**) of *Eustreptospondylus oxoniensis* (OUMNH J.13558; reversed) in (**S**) anterior, (**T**) lateral, (**U**) posterior, (**V**) medial and (**W**) ventral views (courtesy of Paul Barrett). Abbreviations: **afq**, anterior fossa; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process; **mfq**, medial fossa; **pfq**, posterior fossa; **pfl**, pterygoid flange; **qf**, quadrate foramen; **qh**, quadrate head; **qip**, quadratojugal process; **qr**, quadrate ridge; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vqjc**, ventral quadratojugal contact; **vsh**, ventral shelf of the pterygoid flange.

FIGURE 4. Topological homologies in the non-avian averostran quadrate. Left quadrate (**A–F**) of *Aerosteon riocoloradensis* (MCNA-PV-3137) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**) medial, (**E**) dorsal, and (**F**) ventral views (courtesy of Martin Ezcurra). Left quadrate (**G–K**) of *Alioramus altai* (IGM 100-1844) in (**G**) anterior, (**H**) lateral, (**I**) posterior, (**J**) medial, and (**K**) dorsal, (courtesy of Mike Ellison © AMNH). Right quadrate (**L**) of *Qianzhousaurus sinensis*

(GM F10004-1; reversed) in ventral views (courtesy of Stephen Brusatte). Right quadrate (**M–Q**) of *Falcarius utahensis* (UMNH VP 14559; reversed) in (**M**) anterior, (**N**) lateral, (**O**) posterior, (**P**) medial, and (**Q**) ventral views (courtesy of Lindsay Zanno). Left quadrate (**R–W**) of *Bambiraptor feinbergi* (AMNH 30556) in (**R**) anterior, (**S**) lateral, (**T**) posterior, (**U**) medial, (**V**) dorsal, and (**W**) ventral views. Abbreviations: **afq**, anterior fossa; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process; **mfq**, medial fossa; **mpf**, medial pneumatic foramen; **pfq**, posterior fossa; **ppf**, posterior pneumatic foramen; **pfl**, pterygoid flange; **qf**, quadrate foramen; **qh**, quadrate head; **qjp**, quadratojugal process; **qr**, quadrate ridge; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vpf**, ventral pneumatic foramen; **vqjc**, ventral quadratojugal contact; **vsh**, ventral shelf of the pterygoid flange.

FIGURE 5. Morphology and position of pneumatic openings in the quadrate of non-avian Theropoda. Right quadrate (**A**) of the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345; reversed) in medial view. Left quadrate (**B**) of the carcharodontosaurid *Mapusaurus roseae* (MCF-PVPH-108) in medial view. Left quadrate (**C**) of the carcharodontosaurid *Giganotosaurus carolinii* (MUCPv CH 1) in medial view. Right quadrate (**D**) of the therizinosauroid *Falcarius utahensis* (UMNH VP 14559; reversed) in medial view (courtesy of Lindsay Zanno). Right quadrate (**E**) of the metriacanthosaurid *Sinraptor dongi* (IVPP 10600; reversed) in posterior view (courtesy of Philip Currie). Left quadrate (**F**) of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in posterior view (courtesy of Martín Ezcurra). Left quadrate (**G**) of the ornithomimid *Garudimimus brevipes* (IGM 100–13) in posterior view (courtesy of Yoshitsugu Kobayashi). Right quadrate (**H**) of the dromaeosaurid *Buitreraptor*

1338 *gonzalezorum* (MPCA 245; reversed) in posterior view. Right quadrate (**I**) of the tyrannosaurid
 1339 *Alioramus altai* (IGM 100–844) in ventral view (courtesy of Mick Ellison). Left quadrate (**J**) of
 1340 the tyrannosaurid *Tyrannosaurus rex* (FMNH PR2081; cast, reversed) in ventral view. Left
 1341 quadrate (**K**) of the carcharodontosaurid *Mapusaurus roseae* (MCF-PVPH-108) in anterior view.
 1342 Left quadrate (**L**) of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in lateral
 1343 view (courtesy of Martín Ezcurra). Abbreviations: **apf**, anterior pneumatic foramen; **lpq**, lateral
 1344 process; **lpf**, lateral pneumatic foramen; **mpf**, medial pneumatic foramen; **ppf**, posterior
 1345 pneumatic foramen; **ppfo**, posterior pneumatic fossa; **qf**, quadrate foramen; **vpf**, ventral
 1346 pneumatic foramen. Scale bars = 10 cm (A–C, J, K), 5 cm (E–G,L), 1 cm (D,H, I).

1347

1348 **FIGURE 6.** Distribution of quadrate pneumaticity in Theropoda. Cladogram of non-avian
 1349 theropods based on the theropod classification summarized by Hendrickx et al. (in press*a*) and
 1350 showing the phylogenetic distribution of quadrate pneumaticity and the different quadrate
 1351 pneumatic foramina in theropod dinosaurs. Silhouettes by Funkmonk (*Dilophosaurus*, *Shuvuuia*
 1352 and *Dromaeosauroides*), M. Martyniuk (*Ornitholestes* and *Similicaudipteryx*), T. Michael
 1353 Keesey (*Deinocheirus* and *Suzhousaurus*), Choiniere et al. (2010; *Zuolong*; modified) and S.
 1354 Hartman (all others).

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1356 **TABLE 1.** Standardized terminology and abbreviation of the non-avian theropod quadrate and
 1357 comparison with the terminology of the avian quadrate based on Baumel and Witmer (1993),
 1358 Elzanowski et al. (2001) and Elzanowski and (Stidham 2010).

Non-avian theropod quadrate		Avian theropod quadrate
Quadrate	q	Os quadratum (Quadratum)
Quadrate body	qb	Corpus quadrati
Quadrate shaft	qs	/
Quadrate ridge	qr	/
Quadrate ridge groove	qrg	/
Quadrate foramen	qf	/
Lateral process	lpq	/
Quadratojugal contact	qjc	Cotyla quadratojugal
Ventral quadratojugal contact	vqjc	/
Dorsal quadratojugal contact	dqjc	/
Quadratojugal process	qjp	/
Ventral projection of the dorsal quadratojugal contact	vpdq	/
Dorsal projection of the ventral quadratojugal contact	dpvq	/
Squamosal contact	sqc	/
Posterior fossa	pfq	/
Quadrate head	qh	Caput quadrati
Otic capitulum	oca	Capitulum oticum

Squamosal capitulum	sca	Capitulum squamosum
Intercapitular sulcus	icas	Incisura/Vallecula intercapitularis
Mandibular articulation	mar	Pars/Processus mandibularis
Ectocondyle	ecc	Condylus (mandibularis) lateralis
Entocondyle	enc	Condylus (mandibularis) medialis
Mediocondyle	mec	Condylus caudalis
Intercondylar sulcus	ics	Sulcus/Vallecula intercondylaris
Intercondylar notch	icn	/
Pterygoid flange	pfl	Processus orbitalis
Pterygoid contact	ptc	Condylus pterygoideus/Facies articularis pterygoidea
Medial fossa	mfq	Fossa basiorbitalis
Ventral shelf	vsh	/
Quadrato diverticulum	qdi	/
Dorsal pneumatic foramen	dpf	/
Medial pneumatic foramen	mpf	Foramen pneumaticum basiorbitale
Posterior pneumatic foramen	ppf	Foramen pneumaticum caudomediale
Anterior pneumatic foramen	apf	Foramen pneumaticum rostromedial
Ventral pneumatic foramen	vpf	Foramen pneumaticum adventitium
Lateral pneumatic foramen	lpf	/

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SUPPLEMENTAL INFORMATION

1361

1362 - Text S1: Function of quadrate sub-entities, quadrate sub-units terminology, and quadrate
1363 ontogeny in *Lourinhanosaurus antunesi* and *Shuvuuia deserti*.

1364 - Fig. S1: Quadrate of embryonic specimen of *Lourinhanosaurus antunesi* (ML565-150).

1365 - Fig. S2: Incomplete left quadrate of *Lourinhanosaurus antunesi* embryo (ML565-10; lost).

1366 - Fig. S3: Quadrates of juvenile and adult specimens of *Shuvuuia deserti*.

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Figure 1. Avian and non-avian theropod terminology of the quadrate bone.

Left quadrate of the common ostrich *Struthio camelus* (NH.11.75; courtesy of Paolo Viscardi) in **(A, G)** anterior, **(B, H)** lateral, **(C, I)** posterior, **(D, J)** medial, **(E, K)** dorsal, and **(F, L)** ventral views. The ostrich quadrate is annotated with **(A-F)** Baumel and Witmer (1993) , Elzanowski et al. (2001) and Elzanowski and Stidham (2010) terminologies, and **(G-L)** the here proposed terminology for the non-avian theropod quadrate.

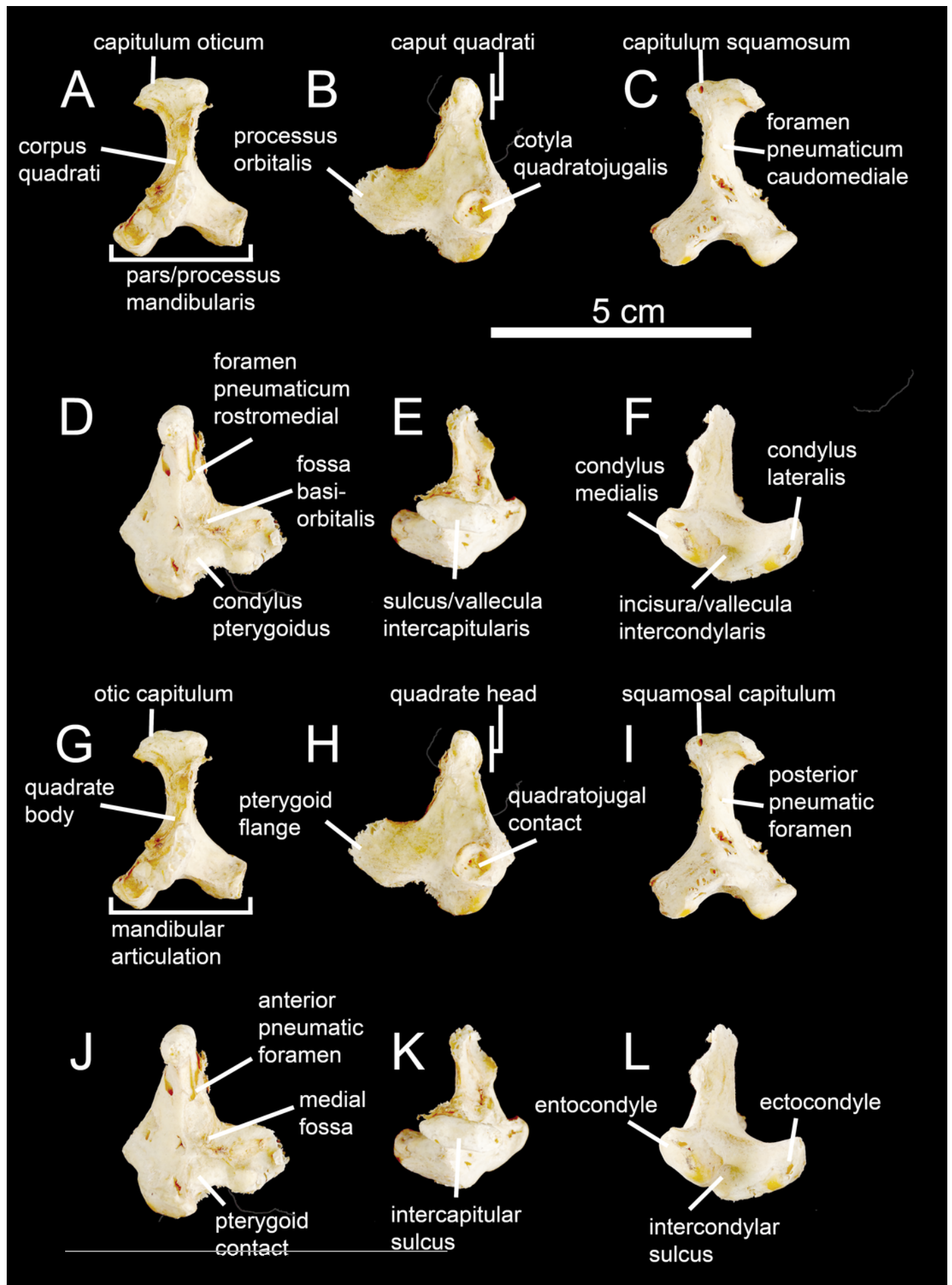
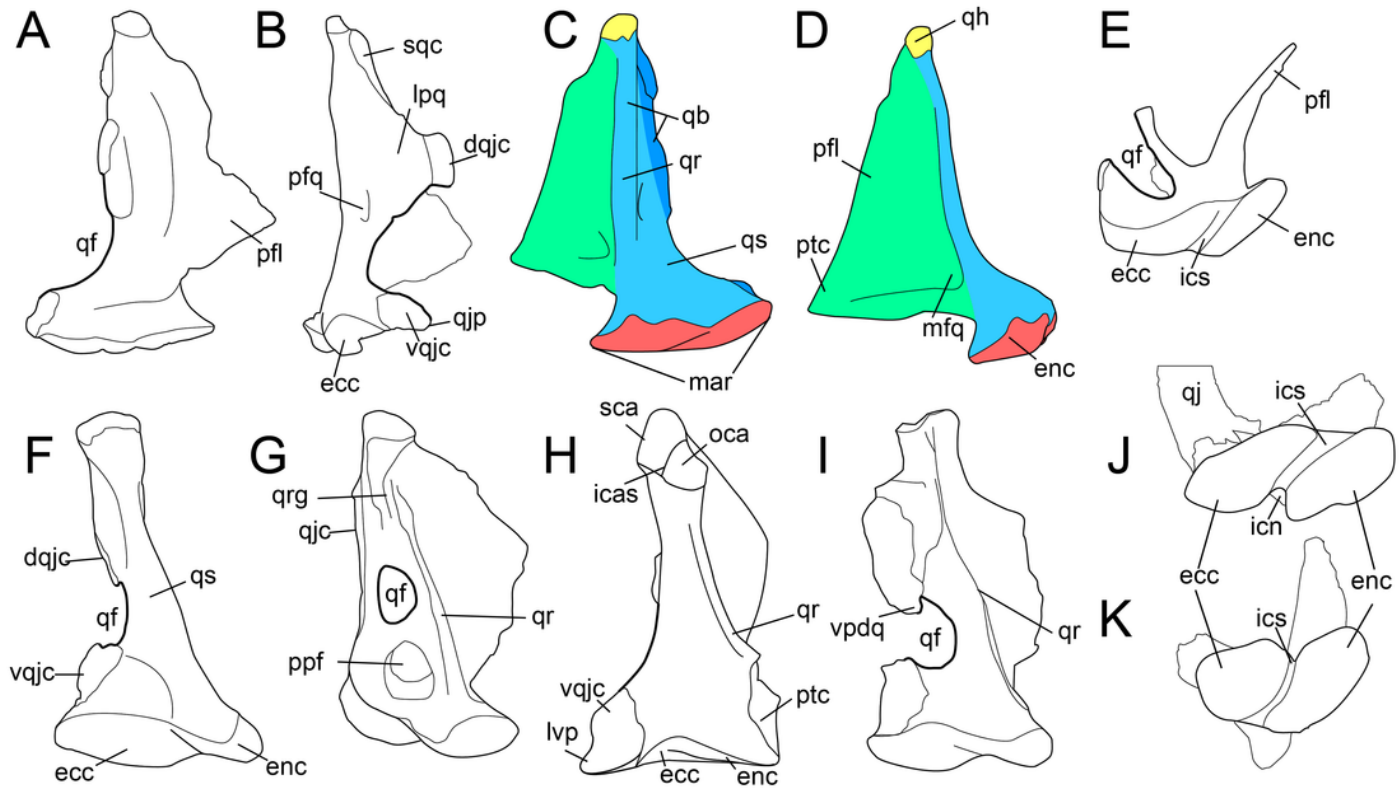


Figure 2. Anatomy of non-avian theropod quadrates.

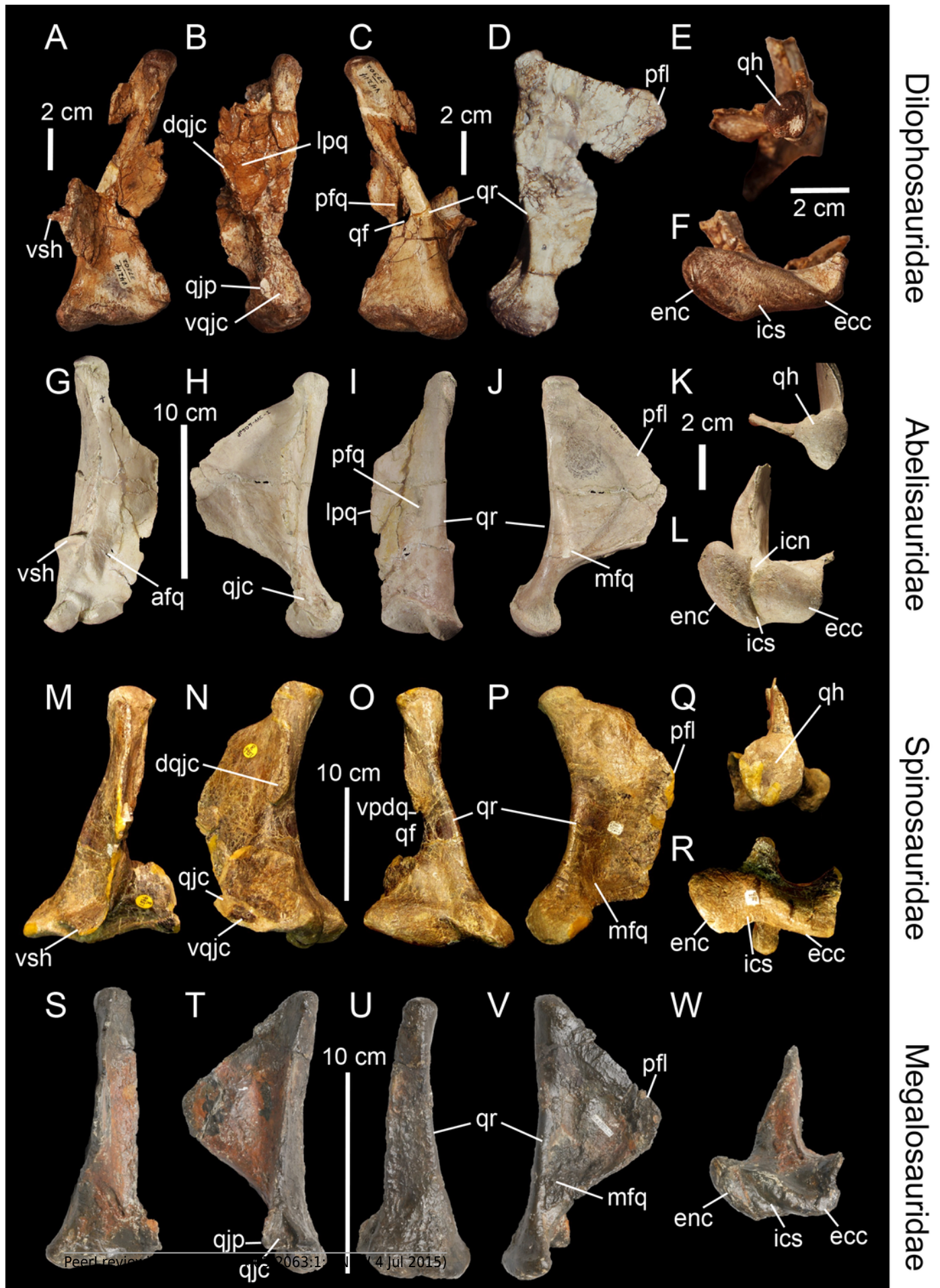
Line drawings of the right (**A–E**) quadrate of *Tsaagan mangas* (IGM 100-1015) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**) medial and (**E**) ventral views; left (**F–I**) and right (**J–K**) quadrates (**F**) of *Baryonyx walkeri* (NHM R9951), (**G**) *Aerosteon riocoloradensis* (MCNA-PV-3137), (**H**) an indeterminate Oviraptoridae (GIN A; Maryńska and Osmólska 1997) , (**I**) *Tyrannosaurus rex* (BHI 3333; Larson and Carpenter, 2008), (**J**) *Allosaurus 'jimmadseni'* (SMA 0005), and (**K**) *Majungasaurus crenatissimus* (FMNH PR 2100) in (**F–I**) posterior and (**J–K**) 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 (in red); **mfq**, medial fossa of the quadrate; **oca**, otic capitulum; **pfl**, pterygoid flange (in green); **pfq**, posterior fossa of the quadrate; **ppf**, posterior pneumatic foramen; **qb**, quadrate body (in light and dark blue); **qf**, quadrate foramen (delimited by a broader line); **qh**, quadrate head (in yellow); **qj**, quadratojugal; **qjp**, quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge groove; **qs**, quadrate shaft (in light blue); **sqc**, squamosal contact; **sca**, squamosal capitulum; **vqjc**, ventral quadratojugal contact; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vsh**, ventral shelf.



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Figure 3. Topological homologies in the non-averostran theropod quadrate.

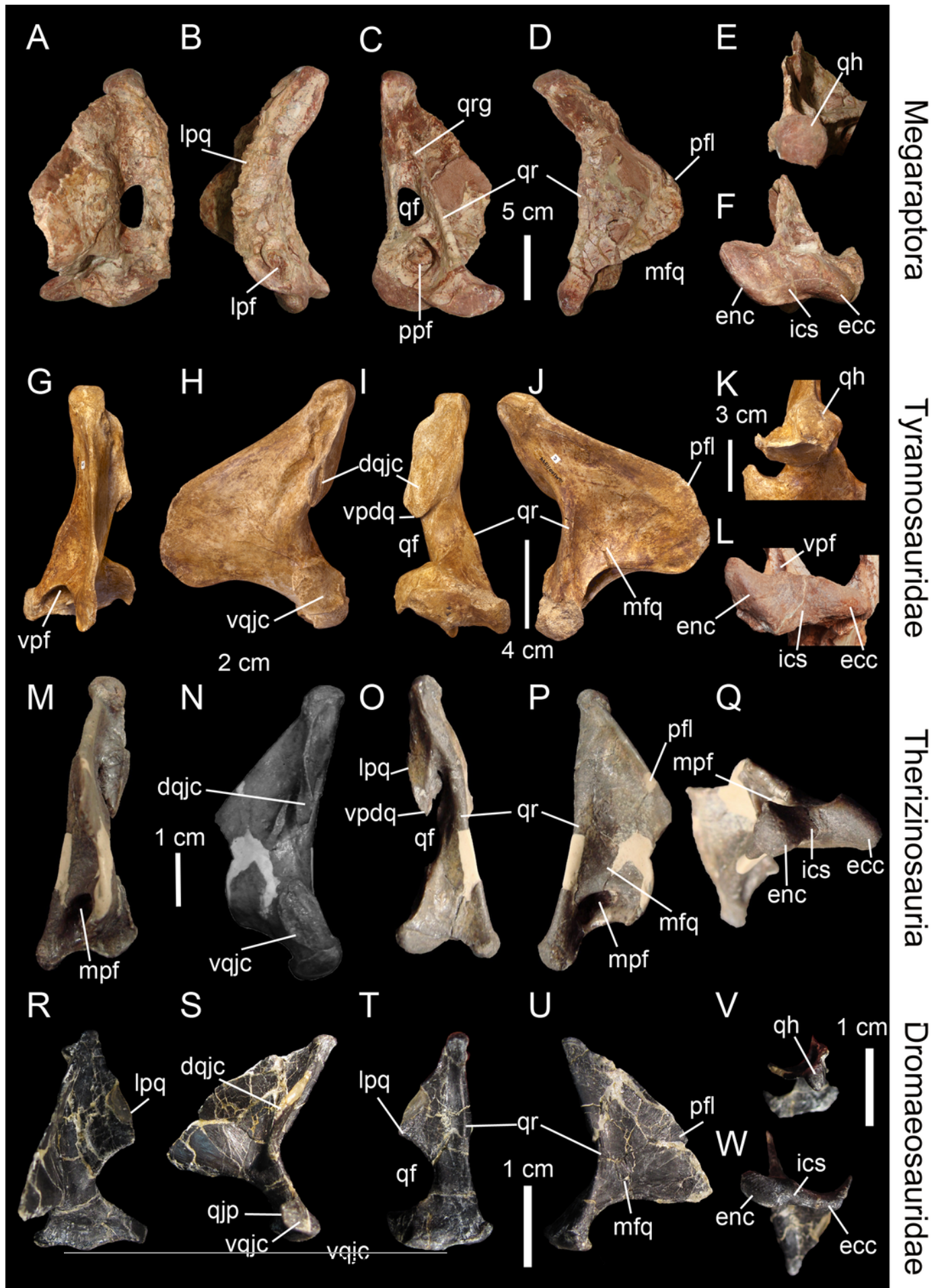
Left (**A, C, F**) and right (**B, D, E**; reversed) quadrates of *Dilophosaurus wetherilli* (UCMP 37302) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**) medial, (**E**) dorsal and (**F**) ventral views (courtesy of Randall Irmis and Matthew Carrano). Right quadrate (**G-L**; reversed) of *Majungasaurus crenatissimus* (FMNH PR 2100) in (**G**) anterior, (**H**) lateral, (**I**) posterior, (**J**) medial, (**K**) dorsal, and (**L**) ventral views. Left quadrate (**M-R**) of *Baryonyx walkeri* (NHM R9951) in (**M**) anterior, (**N**) lateral, (**O**) posterior, (**P**) medial, (**Q**) dorsal, and (**R**) ventral views. Right quadrate (**S-W**) of *Eustreptospondylus oxoniensis* (OUMNH J.13558; reversed) in (**S**) anterior, (**T**) lateral, (**U**) posterior, (**V**) medial and (**W**) ventral views (courtesy of Paul Barrett). Abbreviations: **afq**, anterior fossa; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process; **mfq**, medial fossa; **pfq**, posterior fossa; **pfl**, pterygoid flange; **qf**, quadrate foramen; **qh**, quadrate head; **qjp**, quadratojugal process; **qr**, quadrate ridge; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vqjc**, ventral quadratojugal contact; **vsh**, ventral shelf of the pterygoid flange.



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Figure 4. Topological homologies in the non-avian averostran quadrate.

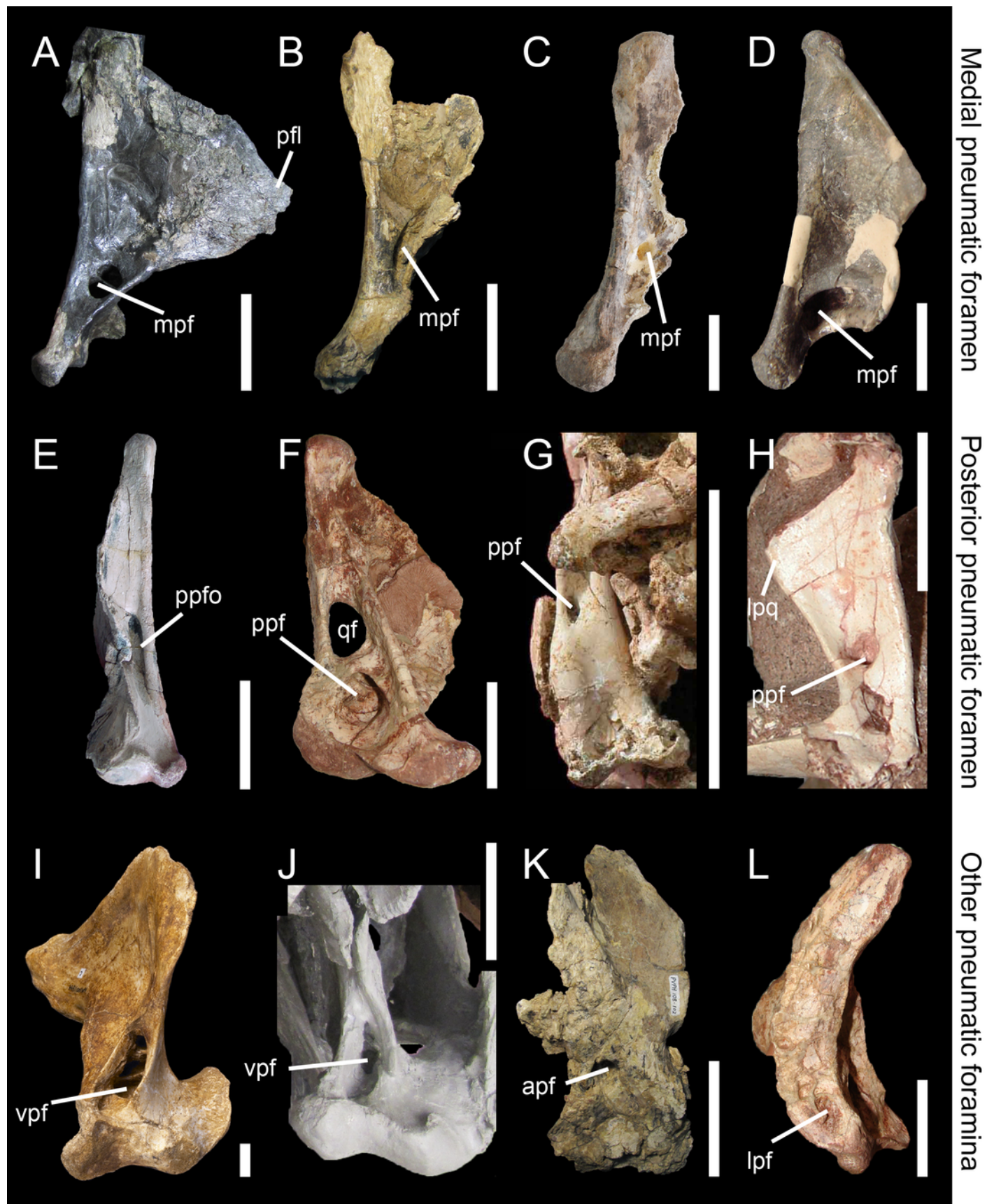
Left quadrate (**A-F**) of *Aerosteon riocoloradensis* (MCNA-PV-3137) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**) medial, (**E**) dorsal, and (**F**) ventral views (courtesy of Martin Ezcurra). Left quadrate (**G-K**) of *Alioramus altai* (IGM 100-1844) in (**G**) anterior, (**H**) lateral, (**I**) posterior, (**J**) medial, and (**K**) dorsal, (courtesy of Mike Ellison © AMNH). Right quadrate (**L**) of *Qianzhousaurus sinensis* (GM F10004-1; reversed) in ventral views (courtesy of Stephen Brusatte). Right quadrate (**M-Q**) of *Falcarius utahensis* (UMNH VP 14559; reversed) in (**M**) anterior, (**N**) lateral, (**O**) posterior, (**P**) medial, and (**Q**) ventral views (courtesy of Lindsay Zanno). Left quadrate (**R-W**) of *Bambiraptor feinbergi* (AMNH 30556) in (**R**) anterior, (**S**) lateral, (**T**) posterior, (**U**) medial, (**V**) dorsal, and (**W**) ventral views. Abbreviations: **afq**, anterior fossa; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process; **mfq**, medial fossa; **mpf**, medial pneumatic foramen; **pfq**, posterior fossa; **ppf**, posterior pneumatic foramen; **pfl**, pterygoid flange; **qf**, quadrate foramen; **qh**, quadrate head; **qjp**, quadratojugal process; **qr**, quadrate ridge; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vpf**, ventral pneumatic foramen; **vqjc**, ventral quadratojugal contact; **vsh**, ventral shelf of the pterygoid flange.



5

Figure 5. Morphology and position of pneumatic openings in the quadrate of non-avian Theropoda.

Right quadrate (**A**) of the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345; reversed) in medial view. Left quadrate (**B**) of the carcharodontosaurid *Mapusaurus roseae* (MCF-PVPH-108) in medial view. Left quadrate (**C**) of the carcharodontosaurid *Giganotosaurus carolinii* (MUCPv CH 1) in medial view. Right quadrate (**D**) of the therizinosauroid *Falcarius utahensis* (UMNH VP 14559; reversed) in medial view (courtesy of Lindsay Zanno). Right quadrate (**E**) of the metriacanthosaurid *Sinraptor dongi* (IVPP 10600; reversed) in posterior view (courtesy of Philip Currie). Left quadrate (**F**) of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in posterior view (courtesy of Martín Ezcurra). Left quadrate (**G**) of the ornithomimid *Garudimimus brevipes* (IGM 100–13) in posterior view (courtesy of Yoshitsugu Kobayashi). Right quadrate (**H**) of the dromaeosaurid *Buitreraptor gonzalezorum* (MPCA 245; reversed) in posterior view. Right quadrate (**I**) of the tyrannosaurid *Alioramus altai* (IGM 100–844) in ventral view (courtesy of Mick Ellison). Left quadrate (**J**) of the tyrannosaurid *Tyrannosaurus rex* (FMNH PR2081; cast, reversed) in ventral view. Left quadrate (**K**) of the carcharodontosaurid *Mapusaurus roseae* (MCF-PVPH-108) in anterior view. Left quadrate (**L**) of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in lateral view (courtesy of Martín Ezcurra). Abbreviations: **apf**, anterior pneumatic foramen; **lpq**, lateral process; **lpf**, lateral pneumatic foramen; **mpf**, medial pneumatic foramen; **ppf**, posterior pneumatic foramen; **ppfo**, posterior pneumatic fossa; **qf**, quadrate foramen; **vpf**, ventral pneumatic foramen. Scale bars = 10 cm (A–C, J, K), 5 cm (E–G,L), 1 cm (D,H, I).



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Figure 6. Distribution of quadrate pneumaticity in Theropoda.

Cladogram of non-avian theropods based on the theropod classification summarized by Hendrickx et al. (in pressa) and showing the phylogenetic distribution of quadrate pneumaticity and the different quadrate pneumatic foramina in theropod dinosaurs. Silhouettes by Funkmonk (*Dilophosaurus*, *Shuvuuia* and *Dromaeosauroides*), M. Martyniuk (*Ornitholestes* and *Similicaudipteryx*), T. Michael Keesey (*Deinocheirus* and *Suzhousaurus*), Choiniere et al. (2010 ; *Zuolong*; modified) and S. Hartman (all others).

