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

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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 a strong taxonomic potential. Inconsistencies in the notation and terminology used in discussions of the theropod quadrate anatomy have been noticed, including at least one instance when no less than eight different terms were 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 quadrate function and pneumaticity ontogeny in non-avian theropods is presented, along with a discussion of 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.

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an overview of the anatomy and function

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ABSTRACT

25   The quadrate of reptiles and most other tetrapods plays an important morphofunctional role by

26   allowing the articulation of the mandible with the cranium. In Theropoda, the morphology of the

27   quadrate is particularly complex and varies importantly among different clades of non-avian

28   theropods, therefore conferring a strong taxonomic potential. Inconsistencies in the notation and

29   terminology used in discussions of the theropod quadrate anatomy have been noticed, including

30   at least one instance when no less than eight different terms were given to the same structure. A

31   standardized list of terms and notations for each quadrate anatomical entity is proposed here,

32   with the goal of facilitating future descriptions of this important cranial bone.

33   In addition, an overview of the literature on quadrate function and pneumaticity ontogeny

34   in non-avian theropods is presented, along with a discussion of the inferences that could be made

35   from this research. Specifically, the quadrate of the large majority of non-avian theropods is

36   akinetic but the diagonally oriented intercondylar sulcus of the mandibular articulation allowed

37   both rami of the mandible to move laterally when opening the mouth in many of theropods.

38   Pneumaticity of the quadrate is also present in most tetanuran clades and the pneumatic

39   chamber—invaded by the quadrate diverticulum of the mandibular arch pneumatic system—was

40   connected to one or several pneumatic foramina on the medial, lateral, posterior, anterior or

41   ventral sides of the quadrate.

INTRODUCTION

43 The quadrate (in Latin *quadratum*, meaning 'square') is a cranial bone of endochondral origin

44 that articulates with the mandible in all gnathostomes except mammaliaforms, which have had

45 the quadrate evolved into the incus (Reichert 1837; Takechi and Kuratani 2010; Brusatte 2012;

46 Benton 2015). In theropods, this bone plays many important functions such as a structural

47 support for the basicranium, articulatory element with the lower jaws, attachment for several

48 muscles, hearing, and hosting important nerves, pneumatic sinuses, and vascular passages (e.g.,

49 Witmer 1990, 1997; Bakker 1998; Sedlmayr 2002; Kundrát and Janáček 2007; Holliday and

50 Witmer 2008; Tahara and Larsson 2011; see Supplemental Information Appendix 1).

51 Although the outward morphology of the quadrate is relatively simple, it varies

52 significantly among theropods in the structure of its head, mandibular articulation, quadratojugal

53 contact and the presence of pneumatic openings, quadrate foramen, and lateral processes (e.g.,

54 Holtz 2003; Therrien et al. 2005; Hone and Rauhut 2010; Zanno and Makovicky 2011).

55 Variation in the quadrate morphology in the derived theropod group Aves has long been used as

56 a means of systematic significance (e.g., Lowe 1926; Samejima and Otsuka 1987; Barbosa 1990;

57 Elzanowski et al. 2001; Elzanowski and Stidham 2010). Similarly, but to a lesser degree, the

58 systematic potential of the quadrate bone has also been noted for non-avian theropods

59 (Maryańska and Osmólska 1997; Currie 2006), highlighting the importance that should be given

60 to the description of this bone in the literature on non-avian theropod anatomy. Nevertheless, the

61 terminology and abbreviations of the quadrate anatomy has been inconsistent in non-avian

62 theropods, and several different anatomical terms for the same quadrate sub-entity are often used

63 (see Supplemental Information Appendix 2). Although a list of anatomical terms has been given

64 by Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for

65   the avian quadrate, the terminology proposed by these authors has not been applied to the

66   description of the non-avian theropod quadrate hitherto. Indeed, the quadrate of birds has greatly

67   changed in its morphology throughout the evolution of this clade and hence displays many

68   features absent in more primitive theropods. Thus, many anatomical terms coined by Baumel and

69   Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) cannot be applied

70   to the non-avian theropod quadrate. Moreover, some quadrate entities such as the quadrate

71   foramen and the lateral process observable in non-avian theropods are absent in their avian

72   descendants and do not appear in the list made by these authors.

73   The work presented here has two major aims. First, we propose a standardization of the

74   anatomical terms for the quadrate sub-units, each associated with a two to four letters

75   abbreviation and followed by a definition, in order to facilitate future descriptions of this bone in

76   the literature. Second, we present and discuss the current knowledge on the function and

77   pneumaticity of this important bone in non-avian theropods. A comprehensive study on the

78   anatomy and phylogenetic potential of the non-avian theropod quadrate through cladistic and

79   phylogenetic morphometric analyses will be provided in a companion article that will be

80   published later.

81

82   **Institutional Abbreviations**

83   **AMNH,** American Museum of Natural History, New York, U.S.A.; **BHI,** Black Hills Institute,

84   Hill City, South Dakota, USA; **BYUVP,** Brigham Young University Vertebrate Paleontology,

85   Provo, Utah, U.S.A.; **CMNH,** Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.; **FMNH,**

86   Field Museum of Natural History, Chicago, Illinois, U.S.A.; **IGM,** Mongolian Institute of

87   Geology, Ulaan Bataar, Mongolia; **IVPP,** Institute for Vertebrate Paleontology and

88   Paleoanthropology, Beijing, China; **MACN,** Museo Argentino de Ciencias Naturales, Buenos

89   Aires, Argentina; **MCF PVPH,** Museo Municipal Carmen Funes, Paleontologia de Vertebrados,

90   Plaza Huincul, Argentina; **MCNA,** Museo de Ciencias Naturales y Antropológicas de Mendoza,

91   Mendoza, Argentina; **MIWG,** Dinosaur Isle, Isle of Wight Museum Services, Sandown, U.K.;

92   **ML,** Museu da Lourinhã, Lourinhã, Portugal; **NCSM,** North Carolina Museum of Natural

93   Sciences, Raleigh, North Carolina, USA; **MNHN,** Muséum national d'Histoire Naturelle, Paris,

94   France; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MNN,** Musée National

95   du Niger, Niamey, Niger; **MPCA,** Museo Provincial Carlos Ameghino, Cipolletti, Río Negro,

96   Argentina; **MSNM,** Museo di Storia Naturale di Milano, Milan, Italy; **MUCPv,** Museo de

97   Ciencias Naturales de la Universidad Nacional de Comahue, Neuquén, Argentina; **NH,**

98   Horniman Museum & Gardens, London, U.K.; **NHM,** The Natural History Museum, London,

99   U.K.; **OUMNH,** Oxford University Museum, Oxford, U.K.; **PVL,** Fundación 'Miguel Lillo,'

100   San Miguel de Tucumán, Argentina; **PVSJ,** Instituto y Museo de Ciencias Naturales, San Juan,

101   Argentina; **SMA,** Sauriermuseum Aathal, Aathal, Switzerland; **SMNS,** Staatliches Museum für

102   Naturkunde, Stuttgart, Germany; **RTMP,** Royal Tyrrell Museum of Palaeontology, Drumheller,

103   Alberta, Canada; **UCMP,** University of California Museum of Paleontology, Berkeley,

104   California, U.S.A.; **UC,** University of Chicago Paleontological Collection, Chicago, U.S.A.;

105   **UMNH,** Utah Museum of Natural History, Salt Lake City, Utah, U.S.A.

106

107   **Theropod classification**

108   The theropod phylogeny adopted here follows the classification summarized by Hendrickx et al.

109   (2015) for non-avian theropods. Megaraptoran theropods are here considered as belonging to the

110   clade Allosauroidea, as proposed by Benson et al. (2010) and Carrano et al. (2012). The

111   phylogenetic definitions of each non-avian theropod clade also follow those compiled and given

112   by Hendrickx et al. (2015): table 1).

113

114   **PROPOSED TERMINOLOGY OF THE QUADRATE ANATOMY**

115   **Favored terminology**

116   The anatomical terms of the theropod quadrate were grouped in five main sections: quadrate

117   body, quadrate head, mandibular articulation, pterygoid flange, and pneumatic openings. The

118   terms for each quadrate sub-units were selected by their relevance, significance and importance

119   in the non-avian theropod literature. The non-standardized traditional Romerian directional and

120   anatomical terms (Romer 1956; Wilson 2006) were, therefore, favored over the terminology of

121   the *Nomina Anatomica Veterinaria* (NAV) defined by the ICVGAN (2012) and the *Nomina*

122   *Anatomica Avium* (NAA) provided by Baumel (1993) as Romerian terms are the most commonly

123   used in the non-avian theropod literature (e.g., Eddy and Clarke 2011; pers. obs.). Consequently,

124   'anterior' and 'posterior' are used as directional terms in lieu of the veterinarian alternatives

125   'cranial' and 'caudal', respectively. Because non-avian archosaurs are the direct ancestors of

126   birds, Harris (2004) recommended to adopt the NAA as the standardized nomenclature to

127   describe all archosaurs (and even diapsids), yet we favor Wilson's (2006) opinion to retain

128   Romerian terms for non-avian dinosaurs. As noted by Wilson (2006), the Romerian

129   nomenclature is the lingua franca for most of the dinosaur/archosaur literature. In addition,

130   standard terminologies using Romerian terms are often proposed to describe the saurischian

131   anatomy (e.g., Hendrickx et al. in press; Wilson 1999; Wilson et al. 2011; Hendrickx and Mateus

132   2014). Comparison between the NAA nomenclature and the Romerian terminology here

133   proposed for the quadrate anatomy is provided in Figure and Table 1.

134   Romer (1956)'s terminology of the quadrate is limited. He only expanded the vocabulary

135   to describe this bone in reptiles to six terms, namely: the main body, quadrate shaft, quadrate

136   foramen, quadrate head, quadrate flange and articular termination. Three terms were kept as such

137   in the proposed terminology of the quadrate (i.e., quadrate shaft, quadrate foramen, and quadrate

138   head) and the three others were slightly modified. The quadrate body (instead of "main body of

139   [the] quadrate" sensu Romer 1956: p. 640), mandibular articulation (instead of "articular

140   termination" sensu Romer 1956: p. 632) and pterygoid flange (instead of "quadrate flange" sensu

141   Romer 1956: p. 146) were chosen not only because they are more commonly used in the

142   theropod literature currently describing the quadrate (pers. obs.), but are also more specific of the

143   loci of the anatomical sub-entity described. It should be noted that the pterygoid flange of Romer

144   (1956) describes a wing-like process of the pterygoid and not the anteriorly projected ramus of

145   the quadrate.

146   Figure 1

147   Table 1

148   **Quadrate body**

149   **Quadrate body (qb).** Part of the quadrate that includes the quadrate shaft, the quadrate ridge, the

150   lateral contact (quadratojugal and/or squamosal contact), and the lateral process, and excludes

151   the quadrate head, mandibular articulation, and pterygoid flange (Figs. 1G, 2A). In posterior

152   view, the quadrate body is delimited by the lateral margin of the lateral contact and sometimes

153   by the medial margin of the quadrate foramen, the dorsal margin of the mandibular articulation,

154   the ventral margin of the quadrate head, and a medial margin mostly formed by the quadrate

155   shaft and the medial fossa of the pterygoid flange. The quadrate body is equivalent to the

156   'Corpus ossis quadrati' of Baumel and Witmer (1993), and the 'Corpus quadrati' of Elzanowski

157   et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1A).

158   **Quadrate shaft (qs).** Part of the quadrate body that excludes the lateral process and all

159   articulating surfaces (i.e., quadrate head, quadratojugal/squamosal/pterygoid contacts, and

160   mandibular articulation; Fig. 2C). The quadrate shaft, as called by Welles (1984), Sereno and

161   Novas (1994), Norell et al. (2006), Sampson and Witmer (2007), Sereno et al. (2008), Carrano et

162   al. (2011), Brusatte et al. (2012), and Choiniere et al. (2014*a*, *b*) is also referred as the 'quadrate

163   pillar' by Madsen and Welles (2000), and the 'ascending process' by Colbert (1989).

164   **Quadrate ridge (qr).** Ventrodorsally elongated column, ridge or crest located on the quadrate

165   body and visible in posterior view (Fig. 2C). Although the quadrate ridge is present in the large

166   majority of non-avian theropods, a description of the structure is often omitted in the literature.

167   The quadrate ridge is referred as 'a column' by Welles (1984), a 'ridge-like mediodorsal edge'

168   by Carr (1996), 'a prominent rounded ridge' by Smith et al. (2007), a 'columnar ridge' by

169   Rauhut et al. (2010), a 'robust ridge' by Brusatte et al. (2012), a 'ridge' or 'pillar' by Choiniere

170   et al. (2014*a*), and a 'bulging ridge' by Lautenschlager et al. (2014).

171   **Quadrate ridge groove (qrg).** Groove dividing the quadrate ridge in two different units at two-

172   thirds, or more dorsally, of the quadrate body height (Fig. 2G). A quadrate ridge groove exists in

173   some allosauroid theropods.

174   **Quadrate foramen (qf).** Aperture in the quadrate body or concavity on the lateral margin of the

175   quadrate body and delimited ventrally by the ventral quadratojugal contact and dorsally by the

176   dorsal quadratojugal contact and its ventral projection in some theropod taxa (Fig. 2A, E–G, I).

177   Most authors usually refer to this perforation as the quadrate foramen (e.g., Welles 1984; Sereno

178   and Novas 1994; Charig and Milner 1997; Maryańska and Osmólska 1997; Currie and Carpenter

179   2000; Coria and Currie 2006; Currie 2006; Norell et al. 2006; Choiniere et al. 2010, 2014*a*, *b*;

180   Zanno 2010; Brusatte et al. 2012). Yet, it can be also called the 'paraquadratic foramen' (e.g.,

181   Barsbold and Osmólska 1999; Kobayashi and Lü 2003; Kobayashi and Barsbold 2005), the

182   'paraquadrate foramen' (Sampson and Witmer 2007; Dal Sasso and Maganuco 2011;

183   Lautenschlager et al. 2014), the 'paraquadrate fenestra' (Smith et al. 2007) or the 'quadrate

184   fenestra' (e.g., Carr 1996; Sereno et al. 1998; Currie 2003; Eddy and Clarke 2011). A quadrate

185   foramen exists in all non-avian theropods but Ceratosauria and Megalosauridae.

186   **Lateral process (lpq).** Lateral or anterolateral projection of the lateral margin of the quadrate

187   body (Fig. 2B). Also known as the 'dorsal wing' (Welles 1984; Currie 2006), the 'anterolateral

188   wing' (Madsen and Welles 2000), the 'lateral lamina' (Coria and Salgado 1998) and the 'lateral

189   ramus' (Sampson and Witmer 2007), this process can contact the quadratojugal and/or the

190   squamosal and therefore either be referred to the 'quadratojugal ramus' (Sampson and Witmer

191   2007) or the 'squamosal ramus' (Norell et al. 2006).

192   **Quadratojugal contact (qjc)**. Area of contact of the quadrate with the quadratojugal on the

193   lateral, anterolateral or, posterolateral margin of the quadrate body (Fig. 2G). The quadratojugal

194   contact, which is similar to the 'cotyla quadratojugalis' of Baumel and Witmer (1993),

195   Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1B), can

196   be divided into a ventral and a dorsal quadratojugal contact when the quadrate foramen is present

197   and delimited by both quadrate and quadratojugal.

198   **Ventral quadratojugal contact (vqjc)**. Ventral area of contact of the quadrate with the

199   quadratojugal (Fig. 2B, F, H). The ventral quadratojugal contact of the quadrate always receives

200   the quadratojugal bone.

201   **Dorsal quadratojugal contact (dqjc)**. Dorsal area of contact of the quadrate with the

202   quadratojugal (Fig. 2B, F). The ventral quadratojugal contact of the quadrate can either receive

203   the quadratojugal or both quadratojugal and squamosal in some theropod taxa.

204   **Ventral projection of the dorsal quadratojugal contact (vpdq).** Small projection of the dorsal

205   quadratojugal contact delimiting the laterodorsal margin of the quadrate foramen (Fig. 2I).

206   **Dorsal projection of the ventral quadratojugal contact (dpvq).** Small projection of the ventral

207   quadratojugal contact delimiting the lateroventral margin of the quadrate foramen.

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

209   quadrate (Fig. 2B). Also known as the 'quadratojugal lamina' (Lautenschlager et al. 2014).

210   **Lateroventral process (lvp)**—Lateromedially oriented ventral projection of the ventral

211   quadratojugal contact of the quadrate that bounds the quadratojugal ventrally (Fig. 2H). The

212   lateroventral process is similar to the 'lateral process' of Maryańska and Osmólska (1997).

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

214   2B).

215   **Posterior fossa (pfq).** Depression or concavity situated on the posterior side of the quadrate

216   body and dorsal to the mandibular articulation, ventral to the quadrate head and lateral to the

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

218

219   **Quadrate head**

220   **Quadrate head (qh).** Dorsal articulation of the quadrate abutting to the cotyle of the squamosal

221   and touching other bones of the braincase in some theropod taxa (Fig. 2D). The quadrate head, as

222   it is called by Britt (1991), Charig and Milner (1997), Madsen and Welles (2000), Sampson and

223   Witmer (2007), Sereno et al. (2008), Norell et al. (2009), Brusatte et al. (2012), Choiniere et al.

224   (2014*a*, *b*) and Lautenschlager et al. (2014) among others, has also been termed 'quadrate

225   cotylus' (Currie 2003; Coria and Currie 2006), 'quadrate cotyle' (Currie 2003; Coria and Currie

226   2006), 'squamosal condyle' (Coria and Salgado 1998), 'squamosal articulation' (Turner et al.

227   2011), 'dorsal articular surface' (Larson 2013), and 'otic process' (Maryańska and Osmólska

228   1997; Burnham 2004; Holliday and Witmer 2008). In avian theropods, the quadrate head is

229   homologous to the 'Caput quadrati' of Elzanowski et al. (2001) and Elzanowski and Stidham

230   (2010), and roughly equivalent to the 'Processus oticus' (Baumel and Witmer 1993). In birds, the

231   'Processus oticus' (Baumel and Witmer 1993), and the 'Pars oticus' of Elzanowski et al. (2001)

232   and Elzanowski and Stidham (2010) also includes several sub-units that are either absent in non-

233   avian theropods (e.g., Crista Tympanica, Tuberculum subcapitulare), or here included in the

234   quadrate body (e.g., Sulcus pneumaticus, Foramen pneumaticum rostromediale). The bistylic

235   quadrate head present in some tyrannosaurids, alvarezsauroids, oviraptorids and avian theropods

236   is divided into otic and squamosal capitula.

237   **Otic capitulum (oca).** Medial capitulum of the quadrate head articulating with the braincase

238   (Fig. 2H). The otic capitulum is referred as the 'capitulum (condylus) oticum' by Baumel and

239   Witmer (1993), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian

240   theropods (Fig. 1A).

241   **Squamosal capitulum (sca).** Lateral capitulum of the quadrate head articulating with the

242   squamosal (Fig. 2H). The squamosal capitulum is similar to the 'capitulum (condylus)

243   squamosum' of Baumel and Witmer (1993), Elzanowski et al. (2001) and Elzanowski and

244   Stidham (2010) for avian theropods (Fig. 1C).

245   **Intercapitular sulcus (icas).** Groove separating the ootic capitulum from the squamosal

246   capitulum on the dorsal surface of the quadrate head (Fig. 2H). The intercapitular sulcus (Witmer

247 1990) is equivalent to the 'incisura intercapitularis' of Baumel and Witmer (1993), and the

248 'vallecula intercapitularis' of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for

249 avian theropods (Fig. 1E).

250

251 **Mandibular articulation**

252 **Mandibular articulation (mar).** Ventral surface of the quadrate, articulating with the mandible

253 and fitting into the glenoid fossa of the lower jaw. It includes the ectocondyle, entocondyles,

254 sometimes a mediocondyle, and a single intercondylar sulcus, even when three condyles are

255 present (Fig. 2C). The mandibular articulation, also known as the 'mandibular capitulum'

256 (Lautenschlager et al. 2014), is equivalent to the 'Processus mandibularis' of Baumel and

257 Witmer (1993), and 'Pars mandibularis' of Elzanowski et al. (2001) and Elzanowski and

258 Stidham (2010) for avian theropods (Fig. 1A). Although most authors (e.g., Currie 2006;

259 Sampson and Witmer 2007; Rauhut et al. 2010; Brusatte et al. 2012; Lautenschlager et al. 2014)

260 referred the ectocondyle and entocondyles as the lateral and medial condyles (or hemicondyles)

261 respectively, the terms ectocondyle and entocondyle have been used by Welles (1984), and

262 Madsen and Welles (2000). The condyle present in between the ecto- and entocondyles in some

263 theropods is here coined mediocondyle.

264 **Ectocondyle (ecc).** Lateral condyle of the mandibular articulation (Fig. 6.2). The ectocondyle is

265 equivalent to the 'condylus (mandibularis) lateralis' of Baumel and Witmer (1993), Elzanowski

266 et al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1F).

267 **Entocondyle (enc).** Medial condyle of the mandibular articulation. The entocondyle has been

268 referred as the 'condylus (mandibularis) medialis' by Baumel and Witmer (1993), Elzanowski et

269 al. (2001) and Elzanowski and Stidham (2010) for avian theropods (Fig. 1F).

270   **Mediocondyle (mdc)**. Posterior condyle of the mandibular articulation located between the ecto-

271   and entocondyles. The mediocondyle is referred as the 'third condyle' by Clark et al. (1994) and

272   Xu and Wu (2001), the 'accessory condyle' by Kobayashi and Lü (2003) and Lautenschlager et

273   al. (2014), and the 'condylus caudalis' of Baumel and Witmer (1993) and Elzanowski et al.

274   (2001) for avian theropods.

275   **Intercondylar sulcus (ics).** Groove separating the ectocondyle from the entocondyle and

276   articulated with the interglenoid ridge of the articular (Fig. 2E, K). The intercondylar sulcus, a

277   term also used by Carrano et al. (2011), can be referred as a 'groove' (e.g., Madsen 1976; Britt

278   1991; Madsen and Welles 2000; Currie 2006), 'swelling' (Charig and Milner 1997), 'sulcus'

279   (e.g., Kobayashi and Lü 2003; Norell et al. 2006; Sadleir et al. 2008), 'trochlea' (Brochu 2003;

280   Brusatte et al. 2010), 'trochlear surface' (Brusatte et al. 2010, 2012), and 'intercondylar bridge'

281   (Zanno 2010). The intercondylar sulcus is similar to the 'sulcus intercondylaris' (Baumel and

282   Witmer 1993) and the 'vallecula intercondylaris' (Elzanowski et al. 2001; Elzanowski and

283   Stidham 2010) of the quadrate of avian theropods (Fig. 1F).

284   **Anterior intercondylar notch (ain).** Notch located in between the ectocondyle and

285   entocondyle, on the anterior margin of the mandibular articulation (Fig. 2K).

286   **Posterior intercondylar notch (pin).** Notch located in between the ectocondyle and

287   entocondyle, on the posterior margin of the mandibular articulation, and being referred as the

288   'pit' by Bakker (1998) (Fig. 2J).

289   Figure 2

290

291   **Pterygoid flange**

292   **Pterygoid flange (pfl).** Ventrodorsally elongated sheet-like process projecting anteriorly or

293   anteromedially from the medial side of the anterior surface of the quadrate body to contact the

294   pterygoid bone (Fig. 2A, D). The pterygoid flange, a term also used by Charig and Milner

295   (1997), Brochu (2003), Currie (2006), Coria and Currie (2006), Rauhut et al. (2010) and

296   Lautenschlager et al. (2014), is also known as the 'quadrate/anterior flange' (e.g., Colbert 1989;

297   Norell et al. 2006; Brusatte et al. 2010, 2012), the 'pterygoid ramus' (e.g., Sereno and Novas

298   1994; Sampson and Witmer 2007; Choiniere et al. 2010, 2014*a*, *b*), the 'pterygoid wing' (e.g.,

299   Welles 1984; Madsen and Welles 2000; Eddy and Clarke 2011), the 'pterygoid ala' (e.g., Currie

300   2003, 2006; Sadleir et al. 2008; Dal Sasso and Maganuco 2011), the 'pterygoid process' (Molnar

301   1991; Carr 1996; Sereno et al. 2008), the 'optic wing' (Balanoff and Norell 2012), the 'orbital

302   process' (Clark et al. 1994; Chiappe et al. 2002), and the 'processus orbitalis' (Baumel and

303   Witmer 1993; Elzanowski et al. 2001; Elzanowski and Stidham 2010) for avian theropods (Fig.

304   1B).

305   **Pterygoid contact (ptc).** Area of contact with the pterygoid on the medial margin of the

306   pterygoid flange or the quadrate body (Fig. 2D). In avian theropods, the pterygoid contact is

307   homologous, to the 'facies pterygoidea' in Elzanowski et al. (2001) and the 'facies articularis

308   pterygoidea' in Elzanowski and Stidham (2010), as well as the 'condylus pterygoideus', located

309   on the quadrate body in Baumel and Witmer (1993), Elzanowski et al. (2001), and Elzanowski

310   and Stidham (2010; Fig. 1D).

311   **Medial fossa (mfq).** Depression or concavity located on the medial surface of the pterygoid

312   flange, typically on its posteroventral extremity (Fig. 2D). The medial fossa is delimited by the

313   quadrate shaft and the ventral shelf in some theropod taxa. The medial fossa is similar to the

314   'fossa corporis quadrati' of Fuchs (1954) and the 'fossa basiorbitalis' of Elzanowski et al. (2001)

315   and Elzanowski and Stidham (2010) for avian theropods (Fig. 1D).

316   **Ventral shelf (vsh).** A medial or posteromedial fold of the ventral margin of the pterygoid flange

317   (Fig. 3A, G, M). The term 'shelf' was employed by Sereno and Novas (1994) and ventral shelf

318   was used by Sampson and Witmer (2007), Eddy and Clarke (2011) and Carrano et al. (2011).

319

320   **Pneumatic foramina and fossae**

321   **Quadrate pneumatic chamber (qpc).** Internal chamber within the quadrate, either fully

322   contained within the bone or communicating externally by one or several pneumatic foramina.

323   The quadrate pneumatic chamber hosts the quadrate sinus/diverticulum and, in some cases,

324   includes several interconnected chambers separated by thin bony lamellae within the quadrate

325   body and pterygoid flange (Kundrát and Janáček 2007; Tahara and Larsson 2011; Gold et al.

326   2013)..

327   **Dorsal pneumatic foramen (dpf).** Aperture located on the anterodorsal surface of the quadrate,

328   just ventral to the quadrate head.

329   **Medial pneumatic foramen (mpf).** Aperture or recess situated on the medial side of the

330   quadrate, typically in the ventral portion of the medial surface of the pterygoid flange (Fig. 5A-

331   D). The medial pneumatic foramen is homologous to the 'foramen pneumaticum' of Baumel and

332   Witmer (1993), and the 'foramen pneumaticum basiorbitale' of Elzanowski et al. (2001) and

333   Elzanowski and Stidham (2010) for avian theropods.

334   **Posterior pneumatic foramen (ppf).** Aperture or recess on the posterior surface of the quadrate

335   body, typically at mid-height of the quadrate (Figs. 2G, 5). The posterior pneumatic foramen is

336   similar to and likely homologous to the 'foramen pneumaticum caudomediale' of Elzanowski

337   and Stidham (2010) for avian theropods (Fig. 1C).

338   **Anterior pneumatic foramen (apf).** Aperture or recess on the anterior surface of the quadrate

339   body, typically at mid-height of the quadrate (Fig. 5K). The anterior pneumatic foramen is likely

340   homologous to the 'foramen pneumaticum medial' of Elzanowski et al. (2001), and the 'foramen

341   pneumaticum rostromediale' of Elzanowski and Stidham (2010).

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

343   The ventral pneumatic foramen is equivalent to the 'foramen pneumaticum adventitium' (or

344   ectopic pneumatic foramen) of Elzanowski and Stidham (2010) for avian theropods (Fig. 5I, J).

345   **Posterior pneumatic fossa (ppfo).** Shallow and well-delimited pneumatic recess on the

346   posterior surface of the quadrate body, at mid-height of the bone and medial to the quadrate

347   foramen (Fig. 5E).

348   **Lateral pneumatic fossa (lpfo).** Shallow and poorly-delimited pneumatic recess on the ventral

349   portion of the lateral surface of the quadrate, shortly dorsal to the ectocondyle (Fig. 5L).

350

351   Figure 3 & 4

352   **MORPHOLOGICAL VARIATION IN QUADRATE SUB-UNITS**

353   To establish comparisons between taxa with widely disparate quadrate morphology, a homology

354   concept of the feature in question is required. Here, we will give a general account of the

355   variability within different anatomical sub-units of the quadrate by following the criteria

356   summarized in Rieppel (2006) to establish inter-taxic topological homologies.

357   The quadrate ridge is easily distinguishable in many theropod taxa such as *Dilophosaurus*

358   *wetherilli* (Welles 1984; Fig. 3C), *Aerosteon riocoloradensis* (MCNA-PV 3137; Fig. 4C) and

359   *Proceratosaurus bradleyi* (NHM R.4860) but the demarcation of this structure may be only

360   subtly developed, as in *Noasaurus leali* (PVL 4061), *Majungasaurus crenatissimus* (FMNH PR

361   2100; Fig. 3I), and *Eustreptospondylus oxoniensis* (OUMNH J.13558; Fig. 3U). The quadrate

362   ridge is developed as a 'columnar ridge' in many theropod taxa such as *Dilophosaurus wetherilli*

363   (Welles 1984), *Allosaurus 'jimmadseni'* (SMA 0005; *Allosaurus 'jimmadseni'* sensu Chure

364   2000; Loewen 2010) and *Eotyrannus lengi* (MIWG 1997.550) but also forms a thin crest as in

365   Tyrannosauridae (AMNH 5027; Carr 1996; Brusatte et al. 2012). Although the ventral portion of

366   the quadrate ridge is usually demarcated just above the entocondyle of the mandibular

367   articulation, its dorsal termination is more variable. The dorsal termination can reach the

368   quadrate head like in *Acrocanthosaurus atokensis* (NCSM 14345) or flatten at the mid-height of

369   the quadrate such as in *Albertosaurus sarcophagus* (Currie 2003: fig. 10B). The quadrate ridge

370   can be divided into two ridges by a deep groove as in *Allosaurus fragilis* (AMNH 600) and

371   *Allosaurus europaeus* (ML 415). The quadrate ridge can also flare at the second dorsal third of

372   the quadrate, and reappears slightly more dorsally, as observed in some derived Spinosauridae

373   (Hendrickx et al. 2014). Likewise, the ventral portion of the quadrate ridge can also dichotomize

374   into two crests separated by a concavity such as in the tyrannosaurids *Albertosaurus*

375   *sarcophagus*, *Daspletosaurus* sp. (Currie 2003: figs. 10 and 28) and *Tyrannosaurus rex* (AMNH

376   5027).

377   The pterygoid flange (Fig. 2D, pfl) contacts the quadrate process of the pterygoid

378   anteriorly or anteromedially, and sometimes other bones such as the epipterygoid in

379   *Herrerasaurus ischigualastensis* (Sereno and Novas 1994) and possibly *Incisivosaurus* (Balanoff

380   et al. 2009), the basisphenoid and prootic in *Erlikosaurus andrewsi* (Clark et al. 1994;

381   Lautenschlager et al. 2014), and the squamosal in *Khaan mckennai* (Balanoff and Norell 2012).

382   Although the pterygoid flange can be easily homologized between taxa, it may acquire

383   subtrapezoidal, subtriangular, subrectangular and M-shaped outlines, or form a large semi-oval

384   structure. The ventral limit of the flange can reach the mandibular condyles (e.g., *Tyrannosaurus*

385   *rex, Baryonyx walkeri*; Fig. 3P) or get attached to the quadrate body far above the mandibular

386   articulation (e.g., *Majungasaurus crenatissimus*; Fig. 3J). This structure can in some instances be

387   divided into two ridges delimited by a deep pneumatic foramen facing ventrally (e.g., *Alioramus*

388   *altai*; Fig. 6.4J; *Tyrannosaurus rex* FMNH PR2081). In anterior view, the pterygoid flange can

389   be straight and only projected anteriorly, as in the carcharodontosaurid *Shaochilong maortuensis*

390   (Brusatte et al. 2010: fig. 7a), or anteromedially recurved. The anteroventral margin of the

391   pterygoid flange can either be straight, or medially and/or dorsally deflected, forming a

392   horizontally oriented or dorsally inclined shelf-like structure here referred as the ventral shelf, as

393   in *Majungasaurus crenatissimus* (FMNH PR 2100; Fig. 3G), *Carnotaurus sastrei* (MACN-CH

394   894) and *Allosaurus fragilis* (Madsen 1976: plate 3d).

395   The medial fossa of the quadrate (Fig. 2D, mfq) is easily homologized between taxa as it

396   is always situated on the pterygoid flange, typically on its ventrodorsal surface. This fossa is

397   posteriorly delimited by the quadrate body in non-avian theropods and sometimes by the ventral

398   shelf of the pterygoid flange. The medial fossa can be of variable depth (deep in

399   *Cryolophosaurus*; FMNH PR1821; shallow in *Eustreptospondylus*; OUMNH J.13558),

400   pneumatized (e.g., *Falcarius*; UMNH VP 14559; Fig. 4P), and situated in the ventralmost part of

401   the pterygoid flange (e.g., *Tsaagan*; IGM 100-1015) or at mid-height of it and just above a large

402   pneumatic recess like in *Mapusaurus roseae* (MCF PVPH-108.102).

403   The posterior fossa of the quadrate (Fig. 2B, pfq) can be located either in between the

404   quadrate and the quadratojugal, being confluent with the quadrate foramen (e.g., *Mapusaurus*;

405 MCF PVPH-108.102), or in the middle of the quadrate shaft and between the quadrate ridge and

406 the lateral limit of the quadrate shaft (e.g., 'Syntarsus'; MNA V2623), Tsaagan (Norell et al.

407 2006), Majungasaurus (Sampson and Witmer 2007; Fig. 3I). The posterior fossa can either be

408 strongly ventrodorsally elongated like in the carcharodontosaurid Acrocanthosaurus (NCSM

409 14345), or form an oval concavity lateromedially wide (e.g., Majungasaurus; Sampson and

410 Witmer 2007). Similarly to the medial fossa, the posterior fossa can host a pneumatic foramen

411 positioned dorsally (e.g., Sinornithomimus; IVPP V11797−10) or ventrally (e.g., Garudimimus;

412 IGM 100-13) inside the fossa.

413   Due to the highly variable morphology of the quadrate foramen, this structure deserves

414 special attention. It can be completely absent (e.g., Carnotaurus, Torvosaurus,

415 Eustreptospondylus; Fig. 3U), or form a very small aperture (e.g., 'Syntarsus'; Tykoski 2005) to

416 a large opening (e.g., Bambiraptor; Fig. 4T). In most non-avian theropods, only a small portion

417 of the lateral margin of the quadrate foramen is delimited by the quadratojugal (e.g., Sinraptor;

418 Currie 2006) while in some non-avian theropods the majority of the lateral margin is formed by

419 the quadratojugal (e.g., Dromaeosaurus). Finally, in a few theropods, the foramen can be

420 completely enclosed in the quadrate (e.g., Aerosteon; Sereno et al. 2008; Fig. 4C).

421   The quadratojugal contact of the quadrate (Fig. 2G, qjc) can either be a single extensive

422 contact or made of two contacts separated by the quadrate foramen. In the latter case, the ventral

423 quadratojugal contact and the dorsal quadratojugal contact of the quadrate are not always clearly

424 separated and their dorsal and ventral margins, respectively, can overlap like in the sinraptorid

425 Sinraptor dongi (IVPP 10600). If the quadrate foramen is absent or fully enclosed by the

426 quadrate, the lateral quadratojugal contact typically forms an elongated line of variable width

427 along the lateral margin of the quadrate. Where separated by the quadrate foramen, the ventral

428   and dorsal contacts can display a wide variety of surface and outlines. Both quadratojugal

429   contacts may face laterally, anteriorly or posteriorly, and their articulating surface can be smooth,

430   irregular or deeply grooved by several radiating ridges, as in *Allosaurus fragilis* (Madsen 1976).

431   The ventral quadratojugal contact is typically D-shaped or ovoid in lateral view. Its anterior

432   margin can extend far anteriorly, forming the quadratojugal process (Norell et al. 2006), and its

433   ventral margin can project far laterally, as in Oviraptoridae (Maryańska and Osmólska 1997).

434   The dorsal quadratojugal contact can vary from a very thin line to a broad surface in lateral or

435   posterior views and its dorsal extension can reach the dorsal condyle or terminate well beneath it.

436   A ventral projection of this contact may be present, and such projection delimiting part of the

437   lateral border of the quadrate can either be short, like in *Daspletosaurus* sp. (Currie 2003: fig.

438   28A) and *Baryonyx walkeri* (Fig. 3O), or form an elongated ramus, like in the therizinosaurid

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

440   2010: fig. 3B).

441   In some basal theropods, ceratosaurs and dromaeosaurids, the lateral process of the

442   quadrate (Fig. 2B, lpq) forms a wing-like projection similar to the pterygoid flange. This process

443   is an extension of the quadrate body laterally so it is difficult to delimit. Such process is present

444   in *Allosaurus* '*jimmadseni*' (SMA 0005), *Sinraptor dongi* (Currie 2006: fig. 1D), and

445   *Erlikosaurus andrewsi* (Clark et al. 1994: fig. 7). The lateral process can also vary in shape and

446   size, as it is lateromedially short and parabolic in posterior view (e.g., *Carnotaurus*; MACN-CH

447   894), or lateromedially elongated and subtriangular in posterolateral view (e.g., *Dilophosaurus*;

448   UCMP 37302; Fig. 3B). Its ventral border can also extend to the quadrate foramen (e.g.,

449   *Bambiraptor*; AMNH 30556; Fig. 4T) or more ventrally, sometimes reaching the medial condyle

450   of the mandibular articulation (e.g., *Ilokelesia*, *Majungasaurus*; MCF PVPH 35, FMNH PR

451   2100; Fig. 3I).

452   The quadrate head always articulates with the cotylus of the squamosal and more rarely

453   with other bones of the braincase such as the opisthotic in oviraptorids (Maryańska and

454   Osmólska 1997), the prootic in *Mononykus olecranus* (Perle et al. 1994; Chiappe et al. 2002) and

455   the postorbital in *Shuvuuia deserti* (Chiappe et al. 1998, 2002). The contact between the quadrate

456   and the opistothic-exoccipital/paroccipital process is also present in *Herrerasaurus*

457   *ischigualastensis* (Sereno and Novas 1994), *Dilophosaurus wetherilli* (Welles 1984),

458   *Ceratosaurus magnicornis* (Madsen and Welles 2000; Sanders and Smith 2005), tyrannosaurids

459   (Currie 2003), *Heyuannia huangi* (Lü 2005), and *Erlikosaurus andrewsi* (Lautenschlager et al.

460   2014), yet this contact occurs on a small medial surface just immediately dorsal to the quadrate

461   head and not with the quadrate head itself. The large majority of non-avian theropods have a

462   monostylic quadrate head (Rauhut 2003; pers. obs.); yet, oviraptorids (Maryańska and Osmólska

463   1997: fig. 3B), the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998), and some

464   tyrannosaurids such as *Tyrannosaurus* and *Gorgosaurus* (Larson 2013) have the apomorphic

465   condition of possessing a bistylic quadrate head. In those theropods, the otic capitulum of the

466   quadrate head always contacts the braincase. This condition has also been observed in the

467   dromaeosaurid *Mahakala omnogovae* (Turner et al. 2007) but Turner et al. (2011: fig. 4) later

468   reconsidered the head of the quadrate as not being bistylic. The morphology of the quadrate head

469   is variable in dorsal view; it may be subtriangular in most basal theropods (Sereno and Novas

470   1994) like *Dilophosaurus* (UCMP 37302; Fig. 3E), *Erlikosaurus* (Lautenschlager et al. 2014)

471   and *Bambiraptor* (AMNH 30556; Fig. 4V), oval to subcircular in megalosaurids like *Afrovenator*

472   (UC OBA1) and *Torvosaurus* (BYUVP 9246), and allosauroids such as *Aerosteon* (MCNA-PV-

473 3137; Fig. 4E), *Sinraptor* (IVPP 10600) and *Shaochilong* (IVPP V2885.3) or subquadrangular in

474 some Spinosaurinae such as *Irritator* (SMNS 58022). While the dorsal surface of the quadrate

475 head is either convex or flattened in posterior view in most non-avian theropods , the quadrate

476 head of some allosaurids (Bakker 1998: fig. 5C) and derived tyrannosaurids (FMNH PR208)

477 shows a well-marked concavity on the dorsal margin. The quadrate head can also be conical in

478 posterior view, as in Oviraptoridae (Maryańska and Osmólska 1997: fig. 1B). Despite this

479 variability, the quadrate head can be easily homologized inter-taxically due to the obvious

480 location of this structure.

481 With the exception of the therizinosaur *Erlikosaurus andrewsi* and the ornithomimosaur

482 *Sinornithomimus dongi* which both seem to have an autapomorphical tricondylar condition on

483 the mandibular articulation (Clark et al. 1994; Kobayashi and Lü 2003; Lautenschlager et al.

484 2014), all other non-avian theropods have two mandibular condyles. The presence of three

485 mandibular condyles was also noted in the alvarezsaurid *Avimimus portentosus* (Chatterjee 1995)

486 and the dromaeosaurid *Sinornithosaurus millenii* (Xu and Wu 2001). However, Vickers-Rich et

487 al. (2002) only found two condyles in *Avimimus* and our observations confirm that the third

488 condyle of *Sinornithosaurus* seems to be part of the much broader lateral condyle (Xu and Wu

489 2001: fig. 4D).

490 The intercondylar sulcus (Fig. 2E, ics) varies in orientation, size and depth. It can be

491 large, shallow and sub-perpendicular to the long axis passing through the mandibular articulation

492 as in *Tyrannosaurus rex* (FMNH PR2081), or narrow, deep and strongly lateromedially-oriented

493 as in some derived spinosaurids (e.g., MHNM.KK376).

494 In posterior view, the shape of the mandibular articulation (Fig. 2C, mar) can vary from

495 the biconvex condition known in most theropods, to the W-shaped articulation typical of *Citipati*

496   *osmolskae* (Clark et al. 2002: fig. 6) or a single convex articulation seen in some dromaeosaurids

497   such as *Tsaagan mangas* (IGM 100/1015). In *Tsaagan*, the convex outline of the mandibular

498   articulation in posterior view results from a poor delimitation of the ecto- and entocondyle and

499   the separation of these two condyles by a shallow intercondylar sulcus; yet this morphology

500   might be due to poor preservation of the mandibular condyle. A posterior intercondylar notch

501   (Fig. 2J, pin) was observed in *Allosaurus* (Bakker 1998: fig. 5B, C; SMA 0005) and *Suchomimus*

502   *tenerensis* (MNN GAD 502) whereas an anterior intercondylar notch (Fig. 2K, ain) is present in

503   the abelisaurids *Majungasaurus crenatissimus* (FMNH PR 2100; Fig. 3L) and *Carnotaurus*

504   *sastrei* (MACN-CH 894). Pneumaticity of the quadrate can be externally expressed by

505   pneumatic foramina or restricted to an internal chamber within the quadrate bone. The

506   establishment of inter-taxic homologies is difficult to assess because these structures have very

507   diverse interspecific variability. Nevertheless, as in other saurischian taxa (Schwarz et al. 2007),

508   these pneumatic structures have phylogenetic signal (e.g., Gold et al. 2013; Hendrickx et al.

509   2014; see below). These openings can appear on different sides and portions of the quadrate. The

510   medial and posterior pneumatic foramina (Fig. 2G, ppf) usually occur in the medial and posterior

511   fossa respectively, and their position inside these fossae is quite variable. Pneumatic foramina

512   can also be located in a pneumatic recess outside the medial fossa and just beneath it such as in

513   the carcharodontosaurids *Mapusaurus roseae* (Coria and Currie 2006) and *Acrocanthosaurus*

514   *atokensis* (Eddy and Clarke 2011). In the latter, the pneumatic aperture is divided by a septum.

515

516   **REVIEW OF THE QUADRATE FUNCTION AND PNEUMATICITY IN**

517   **NON-AVIAN THEROPODS**

518

519 **Function of the Quadrate**

520 In all archosaurs, and all amniotes except Mammaliaformes, the main function of the quadrate is

521 the articulation of the cranium with the mandible, yet this bone also play an important role in the

522 mobility of the skull in many extant theropods. Streptostyly is a fundamental property of all

523 avian theropods, and quadrate kinesis in birds, known already in the beginning of the 19th

524 century (Nitzsch 1816), has been extensively studied over the past sixty years (e.g., Fisher 1955;

525 Bock 1964, 1999, 2000; Bühler 1981; Zusi 1984, 1993; Bühler et al. 1985, 1988; Chatterjee

526 1991, 1997; Hoese and Westneat 1996; Zweers et al. 1997; Zweers and Vanden Berge 1998;

527 Bout and Zweers 2001; Gussekloo and Bout 2005; Meekangvan et al. 2006). Streptostyly

528 consists of the rotation of the quadrate at its dorsal articulation against the squamosal which

529 typically lead to a transverse movement, although a lateral movement of the quadrate around an

530 anteroposteriorly directed axis occurs in some lepidosaur taxa (Metzger 2002). Cranial kinesis in

531 avian theropods with a streptostylic quadrate includes upward (protraction) and downward

532 (retraction) rotation of the rostrum relative to the braincase. Three main types of kinesis, in

533 which the role of the quadrate is relatively equivalent, are recognized relative to the position of

534 the dorsal flexion zone of the cranium and the nature of the nasal opening in modern theropods

535 (Bock 1964; Bühler 1981; Zusi 1984; Meekangvan et al. 2006). In prokinesis, flexion occurs at

536 the nasofrontal joint and the upper jaw thereby moves as one unit; in amphikinesis, flexion

537 occurs in two zones of flexibility and the upper jaw and its tip are bent upward in

538 rhynchokinesis, flexion occurs forward from the nasofrontal joint, allowing its anterior part to be

539 moved (Zusi 1984).

540   Inference of the cranial kinesis and quadrate mobility in non-avian theropods has been

541 investigated by Holliday and Witmer (2008) which regard the cranium of this group of dinosaurs

542   as partially kinetically competent, because synovial joints and protractor muscles are present, but

543   not fully kinetic like in birds. The strong suture of the quadrate to the quadratojugal and the

544   immobile contact of the quadrate and the pterygoid on the medial side of the pterygoid flange in

545   most non-avian theropods seem to indicate a limited movement, and perhaps even the total

546   absence of movement within the cranium. Although the synovial quadrate head joint existing in

547   theropods, and all other archosaurs, is necessary to infer cranial kinesis, its presence in akinetic

548   taxa such as crocodiles demonstrates that the synovial joint cannot be considered alone as an

549   argument for cranial kinesis. Synovial joints have actually been interpreted as growth zones

550   rather than articular surfaces of mobile joints based on the presence of very thin articular

551   cartilage covering the end of this joint (Holliday and Witmer 2008). According to Holliday and

552   Witmer (2008) "articular cartilage persists in loading environments that exert hydrostatic

553   pressures (which result in a change in volume but not shape) but exert low shear stresses".

554   Indeed, one of the key centers of deformation during normal biting is the quadrate-squamosal

555   contact, which would have experienced large shear stresses associated with torque and

556   asymmetrical loading during biting (Rayfield 2005), and the presence of a minimal amount of

557   cartilage between the quadrate and squamosal would therefore suggest that the synovial zone

558   was rather a growth zone than a mobile one. A streptostylic quadrate in *Tyrannosaurus rex*

559   (Molnar 1991, 1998), *Nanotyrannus lancensis* (Larson 2013), *Oviraptor philoceratops* (Smith

560   1992), *Heyuannia huangi* (Lü 2005) and *Dromiceiomimus brevitertius* (Russell 1972) based on the

561   saddle joint between the quadrate and squamosal only is therefore unlikely.

562   Nevertheless, and more convincingly, a streptostylic quadrate was also proposed in the

563   alvarezsaurid *Shuvuuia deserti* by Chiappe et al. (1998). In this taxon, the quadratojugal/jugal?

564   (n.b., Dufeau (2003) considers the quadratojugal to be absent in *Shuvuuia deserti*), instead of

565   being firmly sutured to the quadrate as in other non-avian theropods, would have contacted the

566   lateral surface of the quadrate through a movable joint (Chiappe et al. 1998, 2002; see

567   Supplemental Information Fig. S3). According to Chiappe et al. (1998), the absence of a

568   laterodorsal contact of the quadrate with the quadratojugal/jugal, as well as a lateroventral

569   process of the squamosal, would have permitted the quadrate to pivot anteroposteriorly, and the

570   upper jaw to rotate ventrodorsally due to this transversal movement. These authors have implied

571   the existence of a bending zone between the frontals and the nasal–preorbital bones in *S. deserti*,

572   allowing the flexion of the snout as a single unit when the quadrate displaced forward, like in

573   prokinetic birds. Nevertheless, the complex contacts between the nasal, frontal and prefrontal

574   illustrated by Sereno (2001: fig. 12B) makes assessment of Chiappe et al.'s (1998) hypothesis

575   dubious (Holliday and Witmer 2008). Holliday and Witmer (2008) also note that the

576   maxillojugal and palatal flexion zones necessary to allow a true prokinesis in alvarezsaurids are

577   still not clearly defined. Likewise, the contact between the pterygoid flange of the quadrate and

578   the pterygoid also needs to be better documented in order to imply any specific movement of the

579   quadrate inside the cranium of *S. deserti*.

580   A movable articulation between the quadrate and quadratojugal was proposed in the

581   oviraptosaurids *Heyuannia huangi* (Lü 2003) and *Nemegtomaia huangi* (Lü et al. 2004, 2005). In

582   *Heyuannia*, the quadrate and quadratojugal articulation forms a trochlea-like structure (Lü 2003,

583   2005), while the quadratojugal contact of *Nemegtomaia* is diagnostically convex and was

584   described as a lateral cotyle by Lü et al. (2004). Although such articulation suggests some

585   mobility between the quadrate and quadratojugal, it is unlikely that the skull of these two

586   oviraptorids could display avian-like kinesis. As in other non-avian theropods, the oviraptorid

587   quadrate was an immovable bone (Barsbold 1977; Maryańska and Osmólska 1997) so that the

588   quadratojugal, if kinetic, could only pivot either ventrodorsally or mediolaterally from the

589   quadratojugal contact of the quadrate. Yet, the quadratojugal of at least *Nemegtomaia* does not

590   seem to have a loose articulation with the jugal given that the articulating surface between the

591   two bones is anteroposteriorly extensive (Lü et al. 2004: fig. 2), disallowing mobility between

592   the jugal and quadratojugal. Consequently, we consider unlikely that movement was possible

593   between the quadrate and quadratojugal in *Heyuannia* and *Nemegtomaia* and, unlike Barsbold

594   (1977), see the oviraptorosaur skull as akinetic.

595   Quadrate articulation with the mandible and orientation of the intercondylar sulcus are

596   highly variable among non-avian theropods, therefore suggesting some variation in the

597   movement of the mandibular rami when the jaw opened. The helical intercondylar sulcus present

598   in many non-avian theropods (pers. obs.) was noticed by Bakker (1998) in basal theropod

599   dinosaurs, by Hendrickx and Buffetaut (2008) in spinosaurids, and by Molnar (1991) and Larson

600   (2008) in *Tyrannosaurus rex*. These authors suggested that the spiral groove of the mandibular

601   articulation constrained the diagonal ridge of the articular glenoid fossa, which fitted into the

602   intercondylar sulcus, to slide laterally. This would force the mandibular rami of the mandible to

603   displace laterally when the lower jaw was depressed, enlarging the width of the larynx in order to

604   swallow large-size prey items (Hendrickx and Buffetaut 2008).

605   In *Allosaurus*, the enlargement of the mandibular condyles associated with the

606   posteroventral inclination of the ventral part of the quadrate, and the intercondylar notch, were

607   interpreted by Bakker (1998) as joint-stabilization zones. According to Bakker (1998), the

608   anteroposterior enlargement of the articulating surface would improve the stability of the

609   mandibular articulation when the mouth was widely opened, whereas the intercondylar notch,

610   morphologically convergent to the depression of knee joints in crocodiles and birds, would be

611   hosting one or several ligaments within the quadrate-mandibular articulation (Bakker 1998). An

612   intercondylar notch is present in the abelisaurids *Carnotaurus sastrei* (MACN-CH 894) and

613   *Majungasaurus crenatissimus* (FMNH PR 2100), and the spinosaurid *Suchomimus tenerensis*

614   (MNN GAD 502), perhaps implying similar jaw mechanics of the mandibular articulation as in

615   *Allosaurus*. Yet, Bakker (1998)'s jaw mechanics hypotheses based on the shape of the

616   mandibular articulation and the presence of an intercondylar notch require further investigation

617   with modern functional analysis methods such as FEA to be tested.

618

619   Figure 5 & 6

620   **Pneumaticity in the Quadrate**

621   Pneumatization of the quadrate bone has long been recognized for its phylogenetic value (e.g.,

622   Gauthier 1986; Holtz 1998; Chiappe 2001; Rauhut 2003; Holtz et al. 2004; Smith et al. 2007;

623   Benson 2010; Carrano et al. 2012; Turner et al. 2012; Novas et al. 2013; Choiniere et al. 2014*b*).

624   Pneumatic foramina of the quadrate are widespread among avetheropod clades (Gold et al. 2013;

625   Fig. 4). The presence of one or several pneumatic foramina has indeed been recorded in

626   carcharodontosaurids (e.g., Coria and Currie 2006; Eddy and Clarke 2011), megaraptorans

627   (Sereno et al. 2008), tyrannosauroids (e.g., Molnar 1991; Brochu 2003; Currie 2003; Xu et al.

628   2004; Witmer and Ridgely 2010; Brusatte et al. 2012; Gold et al. 2013), compsognathids (Currie

629   and Chen 2001), alvarezsauroids (Choiniere pers. comm.), therizinosauroids (Clark et al. 1994;

630   Zanno 2010), oviraptorids (e.g., Maryańska and Osmólska 1997; Lü 2003; Kundrát and Janáček

631   2007; Balanoff and Norell 2012), ornithomimosaurs (e.g., Witmer 1997; Tahara and Larsson

632   2011), dromaeosaurids (Makovicky et al. 2005) and troodontids (Barsbold et al. 1987; Currie and

633   Zhao 1993; Varricchio 1997; Xu et al. 2002; Xu and Norell 2004). An incipient development of

634   a pneumatic recess, the posterior pneumatic fossa, also exists in the basal allosauroid *Sinraptor*

635   *dongi* (Currie 2006), suggesting that quadrate pneumaticity may be an avetheropod

636   synapomorphy. Yet, external manifestation of quadrate pneumaticity only occurs in derived

637   members of Allosauroidea, Tyrannosauroidea, and Ornithomimosauria and an apneumatic

638   quadrate exists in the basal members of each of these clades (i.e., *Sinraptor* and *Allosaurus* for

639   Allosauroidea (Currie 2006); pers. obs., *Tanycolagreus* and *Proceratosaurus* for

640   Tyrannosauroidea (Carpenter et al. 2005; Rauhut et al. 2010), and *Nqwebasaurus* for

641   Ornithomimosauria; see Choiniere et al. (2012) codings of their datamatrix). Pneumatic foramina

642   have not been reported for any alvarezsauroid taxa, but are present in basalmost members of

643   Therizinosauria, Oviraptorosauria and Paraves. This suggests that external quadrate pneumaticity

644   occurred independently in several basal avetheropod clades and is a possibly synapomorphy of

645   the clade Therizinosauria + Pennaraptora (Fig. 6).

646   The pneumatic opening is particularly large in some allosauroids such as *Aerosteon*

647   *riocoloradensis* (Sereno et al. 2008; Fig. 5F) and *Acrocanthosaurus atokensis* (Eddy and Clarke

648   2011; Fig. 5A), and the therizinosaur *Falcarius utahensis* (Zanno 2010; Fig. 5D). It, however,

649   forms a small rounded or oval aperture lodged in the posterior fossa of the quadrate body in most

650   avetheropods (Fig. 5). The posterior pneumatic foramen is the most common quadrate pneumatic

651   aperture in non-avian theropods and is seen in many coelurosaur clades. For instance, it is

652   present in the tyrannosauroid *Dilong paradoxus* (Xu et al. 2004), the compsognathid

653   *Sinosauropteryx prima* (Currie and Chen 2001: fig. 3f), the ornithomimids *Hexing qingyi* (the

654   'quadratic foramen' of Liyong et al. 2012), *Garudimimus brevipes* (the 'foramen' of Kobayashi

655   and Barsbold 2005; Fig. 5G), *Sinornithomimus dongi* (the 'quadratic foramen' of Kobayashi and

656   Lü 2003) and *Struthiomimus altus* (AMNH 5339), the basal oviraptorosaur *Incisivorosaurus*

657 *gauthieri* (Balanoff et al. 2009), the dromaeosaurid *Buitreraptor gonzalezorum* (Makovicky et al.

658 2005; Fig. 5H), and the troodontids *Mei long* (Xu and Norell 2004), *Sinovenator changii* (Xu et

659 al. 2002) and possibly *Gobivenator mongoliensis* (Tsuihiji et al. 2014). The posterior pneumatic

660 foramen is, in fact, incorrectly interpreted by several authors as the quadrate foramen in

661 ornithomimosaurs (e.g., Kobayashi and Lü 2003; Kobayashi and Barsbold 2005; Choiniere et al.

662 2012). A genuine quadrate foramen between the quadrate and quadratojugal, as seen in the large

663 majority of other theropods, is found in most (possibly all) ornithomimosaurs possessing a

664 posterior pneumatic foramen (e.g., *Garudimimus*, *Struthiomimus*; Kobayashi and Barsbold 2005;

665 pers. obs.). Tahara and Larsson (2011) wrote that "no obvious foramen or fossa was identified on

666 the posterior surface of the quadrate" in *Ornithomimus edmontonicus*. Yet, a deep posterior fossa

667 seems to be present on the right side of the specimen they studied (TMP 95-110-1; n.b., the fossa

668 seems to be filled with sediment on the left side), in the homologous position of that of the

669 posterior fossa of other ornithomimosaurs (pers. obs.). It is, therefore, surprising that this fossa

670 was apneumatic, as implied by Tahara and Larsson (2011). Consequently, we consider likely that

671 a posterior pneumatic foramen was also leading to the pneumatic chamber hosting the quadrate

672 diverticulum in this taxon. An incipient development of a posterior pneumatic foramen is seen in

673 *Sinraptor dongi* in which the quadrate, though apneumatic, includes a well-delimited pneumatic

674 fossa between the quadrate foramen and quadrate ridge (Currie 2006; Fig. 5E). The presence of a

675 posterior pneumatic foramen is a possible synapomorphy of the clade Pennaraptora, which

676 encompasses Oviraptorosauria and Paraves (Foth et al. 2014; Fig. 6). The medial pneumatic

677 foramen, located in the ventral corner of the pterygoid flange, has also been reported in several

678 theropod clades. It is present in the carcharodontosaurids *Acrocanthosaurus atokensis* (Eddy and

679 Clarke 2011; Fig. 5A), *Mapusaurus roseae* (Coria and Currie 2006; Fig. 5B), and

680   *Giganotosaurus carolinii* (MUCPv-CH-1; Fig. 5C), the tyrannosaurids *Albertosaurus*

681   *sarcophagus* (Currie 2003: fig. 10B) and *Tyrannosaurus rex* (Molnar 1991; Brochu 2003), the

682   therizinosauroid *Falcarius utahensis* (Zanno 2010; Fig. 5D), the oviraptosaurids *Conchoraptor*

683   *gracilis* and possibly *Ajancingenia yanshini* (Maryańska and Osmólska 1997; Kundrát and

684   Janáček 2007), and the basal avialan *Archaeopteryx lithographica* (Domínguez Alonso et al.

685   2004). A pneumatic foramen has also been noticed in the mediodorsal part of the quadrate in the

686   ornithomimosaur *Ornithomimus edmontonicus* (Tahara and Larsson 2011). A pneumatic foramen

687   piercing the quadrate medially is a probable synapomorphic feature of Carcharodontosauridae or

688   carcharodontosaurids more derived than *Concavenator corcovatus* and/or *Eocarcharia dinops*,

689   pending on the results of the latest phylogenetic analyses on carcharodontosaurids (i.e., Ortega et

690   al. 2010; Carrano et al. 2012). In non-avian theropods, the ventral pneumatic foramen that occurs

691   within a recess on the posteroventral part of the pterygoid flange ('funnel-like external opening

692   on the rostral surface of the quadrate, above the condyles' of Gold et al., 2013: p. 37) is only

693   present in Tyrannosauroidea. It is observed in the tyrannosaurids *Alioramus altai* (Brusatte et al.

694   2012; Gold et al. 2013; Fig. 5I), *Daspletosaurus* sp. (Currie 2003: fig. 28C) and *Tyrannosaurus*

695   *rex* (Brochu 2003; Witmer and Ridgely 2010; Fig. 5J). In non-tyrannosaurid tyrannosauroids,

696   such a ventral pneumatic foramen is present in *Dilong paradoxus* (Gold et al. 2013) but was not

697   observed in the closely related taxa *Guanlong wucaii*, *Proceratosaurus lengi*, and

698   *Xiongguanlong baimoensis* (Gold et al. 2013). Yet, it is not clearly present in *Eotyrannus lengi*

699   (contra Gold et al. 2013; pers. obs.). A ventral pneumatic foramen of the quadrate is most likely

700   synapomorphic of non-proceratosaurid Tyrannosauroidea (Fig. 6). A pneumatic foramen can also

701   be seen on the anterior surface of the quadrate, as in *Mapusaurus roseae* (Coria and Currie 2006;

702   Fig. 5K), *Heyuannia huangi* (Lü 2005), *Erlikosaurus andrewsi* (Lautenschlager et al. 2014),

703   *Troodon formosus* (Currie and Zhao 1993), and perhaps *Tyrannosaurus rex* (Molnar 1991). More

704   rarely, a pneumatic fossa can be situated on the lateral and posterior surface of the quadrate

705   body, as in *Aerosteon riocoloradensis* (MCNA-PV 3137; Fig. 5L) and *Sinraptor dongi* (Currie

706   2006; Fig. 5E), respectively. The presence of an anterior pneumatic foramen, a lateral pneumatic

707   fossa, or a posterior pneumatic fossa is an autapomorphy in each of these taxa.

708   Carcharodontosauridae (Coria and Currie 2006; Eddy and Clarke 2011) and

709   Tyrannosauridae (Molnar 1991; Brochu 2003) possess several pneumatic openings which

710   perforate different sides of the quadrate and sometimes intercommunicate (Brochu 2003). The

711   pneumatic foramina usually enter a large pneumatic chamber within the quadrate bone as in

712   *Tyrannosaurus rex* (Molnar 1991; Brochu 2003; Witmer and Ridgely 2010), *Alioramus altai*

713   (Gold et al. 2013), *Conchoraptor gracilis* (Kundrát and Janáček 2007) or *Ornithomimus*

714   *edmontonicus* (Tahara and Larsson 2011). The neovenatorid *Aerosteon riocoloradensis* also

715   possesses a large posterior pneumatic foramen leading to a pneumatic chamber, as well as a

716   shallow pneumatic recess on the lateral surface of the quadrate shaft (pers. obs.).

717   These pneumatic foramina and the pneumatic chamber associated with them are invaded

718   by the quadrate diverticulum of the mandibular arch pneumatic system which, together with the

719   periotic pneumatic system, forms the tympanic sinus of archosaurs (Dufeau 2011; Tahara and

720   Larsson 2011). The mandibular arch pneumatic system includes the quadrate and/or the articular

721   diverticulum which both have their embryological origins as parts of the first pharyngeal (=

722   mandibular) arch, like the middle ear sac itself (Witmer 1997). As in non-avian theropods, the

723   quadrate diverticulum of modern birds exhibits a large variety of morphologies, and can

724   pneumatize the quadrate by entering through a single medial or anteromedial foramen (Witmer

725   1990; Tahara and Larsson 2011). In basal theropods with an apneumatic quadrate, both medial

726 and posterior fossae of the quadrate possibly represent the osteological trace of the quadrate

727 diverticulum. In non-avian theropods having a pneumatic quadrate, the position of the quadrate

728 diverticulum is variable as in ornithomimids (Tahara and Larsson 2011), carcharodontosaurids

729 and oviraptorids (pers. obs.). The quadrate diverticulum of non-avian theropods may also have

730 communicated with other diverticula such as the squamosal diverticulum as in *Conchoraptor*

731 *gracilis* (Kundrát and Janáček 2007), and the siphoneal diverticulum of the articular as in *Dilong*

732 *paradoxus*, *Aerosteon riocoloradensis* and perhaps other non-avian maniraptorans (Sereno et al.

733 2008; Tahara and Larsson 2011). In *Tyrannosaurus rex*, however, the siphoneal diverticulum

734 does not pass through the quadrate and the quadrate diverticulum only enters the ventral opening

735 of the pterygoid flange, and then passes with or without the siphoneal diverticulum along the

736 medial fossa of the pterygoid flange. Likewise, the quadrate diverticulum only pneumatizes two

737 distinct regions of the quadrate in *Acrocanthosaurus atokensis* and *Mapusaurus roseae* (Tahara

738 and Larsson 2011).

739

740 Figure 7

741

742   **CONCLUSIONS**

743 Here we propose a revised nomenclature of the quadrate bone and a corresponding set of

744 abbreviations that provide a standard set of terms for describing this cranial bone in non-avian

745 theropod dinosaurs. The quadrate can be divided into two regional categories—the quadrate

746 body and the pterygoid flange—and twelve anatomical sub-units—the quadrate shaft, quadrate

747 head, quadrate ridge, quadrate foramen, lateral process, quadratojugal contact, squamosal

748 contact, pterygoid contact, mandibular articulation, medial fossa, and posterior fossa. Although

749 they are highly variable in shape, all quadrate entities, with perhaps the exception of the posterior

750 fossa, are easy to homologize across taxa, and a description of their morphology should be

751 provided in the literature.

752   The quadrate of the large majority of non-avian theropods is akinetic, and it is

753 unlikely that the streptostylic quadrate is present in the derived alvarezsauroids *Shuvuuia deserti*,

754 as was previously thought. A lateral movement of the rami while the mandible was depressed

755 occurred in various theropods (e.g. spinosaurids). This lateral movement of the rami was due to a

756 helicoidal and diagonally oriented intercondylar sulcus of the mandibular articulation. The

757 presence of an intercondylar notch in allosaurids is interpreted as a joint-stabilization zone that

758 would improve the stability of the mandibular articulation when the mouth was widely opened.

759 However, this assumption needs further investigation from modern functional morphology

760 techniques.

761   A pneumatic quadrate is present in members of most non-avian avetheropod clades, in

762 which a pneumatic foramen is seen in the ventral part of the pterygoid flange and in the medial

763 and lateral fossae. Pneumatic foramina invading the quadrate seem to be independently acquired

764 by allosauroids, tyrannosaurids, compsognathids, and ornithomimosaurs throughout their

765 evolution. The presence of pneumatic foramina in the quadrate of basalmost members of

766 therizinosauroids, oviraptorids, troodontids and dromaeosaurids suggests that quadrate

767 pneumaticity is a synapomorphy of the clade Therizinosauria + Pennaraptora. Although the

768 pneumatic recess invaded by the quadrate diverticulum of the mandibular arch pneumatic system

769 is linked to a single pneumatic foramen in most avetheropods, the presence of several pneumatic

770 openings perforating different sides of the quadrate has been recorded in Megaraptora,

771 Carcharodontosauridae and Tyrannosauridae.

772

773

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1197   trophic diversification. *Zoology* 100: 25–57.
1198

1199 **FIGURE CAPTIONS**

1200

1201 **FIGURE 1.** Avian and non-avian theropod terminology of the quadrate bone. Left quadrate of

1202 the common ostrich *Struthio camelus* (NH.11.75; courtesy of Paolo Viscardi) in (**A, G**) anterior,

1203 (**B, H**) lateral, (**C, I**) posterior, (**D, J**) medial, (**E, K**) dorsal, and (**F, L**) ventral views. The ostrich

1204 quadrate is annotated with (**A-F**) Baumel and Witmer (1993), Elzanowski et al. (2001) and

1205 Elzanowski and Stidham (2010) terminologies, and (**G-L**) the here proposed terminology for the

1206 non-avian theropod quadrate.

1207

1208 **FIGURE 2.** Anatomy of non-avian theropod quadrates. Line drawings of the right (**A–E**)

1209 quadrate of *Tsaagan mangas* (IGM 100-1015) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**)

1210 medial and (**E**) ventral views; left (**F–I**) and right (**J–K**) quadrates (**F**) of *Baryonyx walkeri*

1211 (NHM R9951), (**G**) *Aerosteon riocoloradensis* (MCNA-PV-3137), (**H**) an indeterminate

1212 Oviraptoridae (GIN A; Maryańska and Osmólska 1997), (**I**) *Tyrannosaurus rex* (BHI 3333;

1213 Larson and Carpenter, 2008), (**J**) *Allosaurus 'jimmadseni'* (SMA 0005), and (**K**) *Majungasaurus*

1214 *crenatissimus* (FMNH PR 2100) in (**F–I**) posterior and (**J–K**) ventral views. Abbreviations: **ain**,

1215 anterior intercondylar notch; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**,

1216 entocondyle; **ics**, intercondylar sulcus; **lpq**, lateral process of the quadrate; **mar**, mandibular

1217 articulation; **mfq**, medial fossa of the quadrate; **oca**, otic capitulum; **pfl**, pterygoid flange; **pfq**,

1218 posterior fossa of the quadrate; **pin**, posterior intercondylar notch; **ppf**, posterior pneumatic

1219   foramen; **qb**, quadrate body; **qf**, quadrate foramen; **qh**, quadrate head; **qj**, quadratojugal; **qjp**,

1220   quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge groove; **qs**, quadrate shaft; **sqc**,

1221   squamosal contact; **sca**, squamosal capitulum; **vqjc**, ventral quadratojugal contact; **vpdq**, ventral

1222   projection of the dorsal quadratojugal contact; **vsh**, ventral shelf.

1223

1224   **FIGURE 3.** Topological homologies in the non-averostran theropod quadrate. Left (**A, C, F**) and

1225   right (**B, D, E**; reversed) quadrates of *Dilophosaurus wetherilli* (UCMP 37302) in (**A**) anterior,

1226   (**B**) lateral, (**C**) posterior, (**D**) medial, (**E**) dorsal and (**F**) ventral views (courtesy of Randall Irmis

1227   and Matthew Carrano). Right quadrate (**G–L**; reversed) of *Majungasaurus crenatissimus*

1228   (FMNH PR 2100) in (**G**) anterior, (**H**) lateral, (**I**) posterior, (**J**) medial, (**K**) dorsal, and (**L**)

1229   ventral views. Left quadrate (**M–R**) of *Baryonyx walkeri* (NHM R9951) in (**M**) anterior, (**N**)

1230   lateral, (**O**) posterior, (**P**) medial, (**Q**) dorsal, and (**R**) ventral views. Right quadrate (**S–W**) of

1231   *Eustreptospondylus oxoniensis* (OUMNH J.13558; reversed) in (**S**) anterior, (**T**) lateral, (**U**)

1232   posterior, (**V**) medial and (**W**) ventral views (courtesy of Paul Barrett). Abbreviations: **afq**,

1233   anterior fossa; **ain**, anterior intercondylar notch; **dqjc**, dorsal quadratojugal contact; **ecc**,

1234   ectocondyle; **enc**, entocondyle; **ics**, intercondylar sulcus; **lpq**, lateral process; **mfq**, medial fossa;

1235   **pfq**, posterior fossa; **pfl**, pterygoid flange; **qf**, quadrate foramen; **qh**, quadrate head; **qjp**,

1236   quadratojugal process; **qr**, quadrate ridge; **vpdq**, ventral projection of the dorsal quadratojugal

1237   contact; **vqjc**, ventral quadratojugal contact; **vsh**, ventral shelf of the pterygoid flange.

1238

1239   **FIGURE 4.** Topological homologies in the non-avian averostran quadrate. Left quadrate (**A–F**)

1240   of *Aerosteon riocoloradensis* (MCNA-PV-3137) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**)

1241   medial, (**E**) dorsal, and (**F**) ventral views (courtesy of Martin Ezcurra). Left quadrate (**G–K**) of

1242   *Alioramus altai* (IGM 100-1844) in (**G**) anterior, (**H**) lateral, (**I**) posterior, (**J**) medial, and (**K**)

1243   dorsal, (courtesy of Mike Ellison © AMNH). Right quadrate (**L**) of *Qianzhousaurus sinensis*

1244   (GM F10004-1; reversed) in ventral views (courtesy of Stephen Brusatte). Right quadrate (**M–Q**)

1245   of *Falcarius utahensis* (UMNH VP 14559; reversed) in (**M**) anterior, (**N**) lateral, (**O**) posterior,

1246   (**P**) medial, and (**Q**) ventral views (courtesy of Lindsay Zanno). Left quadrate (**R–W**) of

1247   *Bambiraptor feinbergi* (AMNH 30556) in (**R**) anterior, (**S**) lateral, (**T**) posterior, (**U**) medial, (**V**)

1248   dorsal, and (**W**) ventral views. Abbreviations: **afq**, anterior fossa; **dqjc**, dorsal quadratojugal

1249   contact; **ecc**, ectocondyle; **enc**, entocondyle; **ics**, intercondylar sulcus; **lpq**, lateral process; **mfq**,

1250   medial fossa; **mpf**, medial pneumatic foramen; **pfq**, posterior fossa; **ppf**, posterior pneumatic

1251   foramen; **pfl**, pterygoid flange; **qf**, quadrate foramen; **qh**, quadrate head; **qjp**, quadratojugal

1252   process; **qr**, quadrate ridge; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vpf**,

1253   ventral pneumatic foramen; **vqjc**, ventral quadratojugal contact; **vsh**, ventral shelf of the

1254   pterygoid flange.

1255

1256   **FIGURE 5.** Morphology and position of pneumatic openings in the quadrate of non-avian

1257   Theropoda. Right quadrate (**A**) of the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM

1258   14345; reversed) in medial view. Left quadrate (**B**) of the carcharodontosaurid *Mapusaurus*

1259   *roseae* (MCF PVPH-108) in medial view. Left quadrate (**C**) of the carcharodontosaurid

1260   *Giganotosaurus carolinii* (MUCPv CH 1) in medial view. Right quadrate (**D**) of the

1261   therizinosauroid *Falcarius utahensis* (UMNH VP 14559; reversed) in medial view (courtesy of

1262   Lindsay Zanno). Right quadrate (**E**) of the metriacanthosaurid *Sinraptor dongi* (IVPP 10600;

1263   reversed) in posterior view (courtesy of Philip Currie). Left quadrate (**F**) of the neovenatorid

1264   *Aerosteon riocoloradensis* (MCNA-PV 3137) in posterior view (courtesy of Martín Ezcurra).

1265   Left quadrate (**G**) of the ornithomimid *Garudimimus brevipes* (IGM 100–13) in posterior view

1266   (courtesy of Yoshitsugu Kobayashi). Right quadrate (**H**) of the dromaeosaurid *Buitreraptor*

1267   *gonzalezorum* (MPCA 245; reversed) in posterior view. Right quadrate (**I**) of the tyrannosaurid

1268   *Alioramus altai* (IGM 100–844) in ventral view (courtesy of Mick Ellison). Left quadrate (**J**) of

1269   the tyrannosaurid *Tyrannosaurus rex* (FMNH PR2081; cast, reversed) in ventral view. Left

1270   quadrate (**K**) of the carcharodontosaurid *Mapusaurus roseae* (MCF PVPH-108) in anterior view.

1271   Left quadrate (**L**) of the neovenatorid *Aerosteon riocoloradensis* (MCNA-PV 3137) in lateral

1272   view (courtesy of Martín Ezcurra). Abbreviations: **apf**, anterior pneumatic foramen; **lpq**, lateral

1273   process; **lpfo**, lateral pneumatic fossa; **mpf**, medial pneumatic foramen; **ppf**, posterior pneumatic

1274   foramen; **ppfo**, posterior pneumatic fossa; **qf**, quadrate foramen; **vpf**, ventral pneumatic foramen.

1275   Scale bars = 10 cm (A–C, J, K), 5 cm (E–G,L), 1 cm (D,H, I).

1276

1277   **FIGURE 6.** Distribution of quadrate pneumaticity in Theropoda. Cladogram of non-avian

1278   theropods based on the theropod classification summarized by Hendrickx et al. (2015) and

1279   showing the phylogenetic distribution of quadrate pneumaticity and the different quadrate

1280   pneumatic foramina in theropod dinosaurs. Silhouettes by Funkmonk (*Dilophosaurus*, *Shuvuuia*

1281   and *Dromaeosauroides*), M. Martyniuk (*Ornitholestes* and *Similicaudipteryx*), T. Michael

1282   Keesey (*Deinocheirus* and *Suzhousaurus*), Choiniere et al. (2010; *Zuolong*; modified) and S.

1283   Hartman (all others).

1284

1285   **SUPPLEMENTAL INFORMATION**

1286   - Text S1: Function of quadrate sub-entities and quadrate sub-units terminology.

1

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.

A capitulum oticum
corpus quadrati
pars/processus mandibularis

B caput quadrati
processus orbitalis
cotyla quadratojugalis

5 cm

C capitulum squamosum
foramen pneumaticum caudomediale

D foramen pneumaticum rostromedial
fossa basi-orbitalis
condylus pterygoidus

E sulcus/vallecula intercapitularis

F condylus medialis
condylus lateralis
incisura/vallecula intercondylaris

G otic capitulum
quadrate body
mandibular articulation

H quadrate head
pterygoid flange
quadratojugal contact

I squamosal capitulum
posterior pneumatic foramen

J anterior pneumatic foramen
medial fossa
pterygoid contact

K intercapitular sulcus

L entocondyle
ectocondyle
intercondylar sulcus

2

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; Maryańska 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: **ain**, anterior intercondylar notch; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **ics**, intercondylar sulcus; **lpq**, lateral process of the quadrate; **mar**, mandibular articulation; **mfq**, medial fossa of the quadrate; **oca**, otic capitulum; **pfl**, pterygoid flange; **pfq**, posterior fossa of the quadrate; **pin**, posterior intercondylar notch; **ppf**, posterior pneumatic foramen; **qb**, quadrate body; **qf**, quadrate foramen; **qh**, quadrate head; **qj**, quadratojugal; **qjp**, quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge groove; **qs**, quadrate shaft; **sqc**, squamosal contact; **sca**, squamosal capitulum; **vqjc**, ventral quadratojugal contact; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vsh**, ventral shelf.

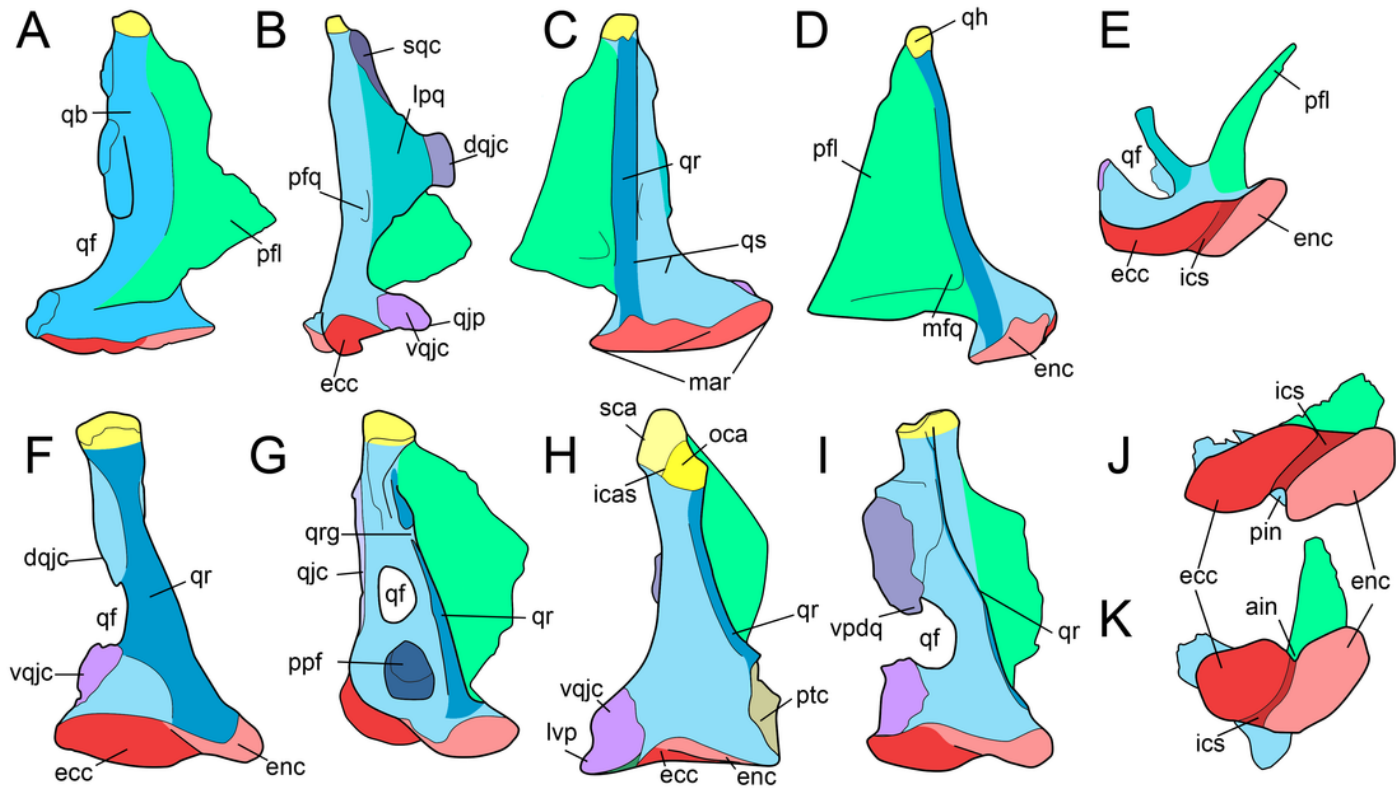



Figure 3. Topological homologies in the non-averostran theropod quadrate.

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; **ain**, anterior intercondylar notch; **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**, entocondyle; **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.

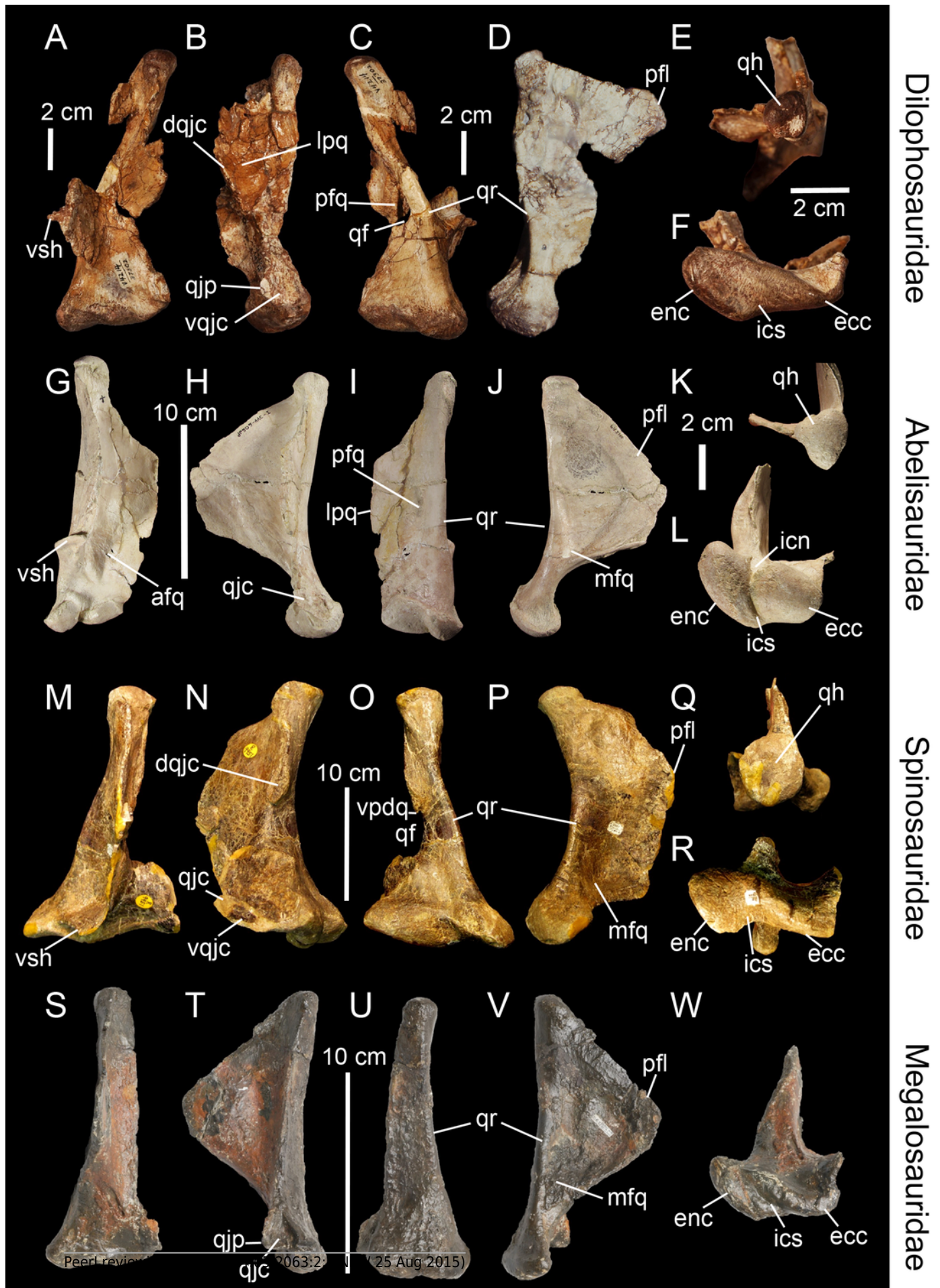



Figure 4. Topological homologies in the non-avian averostran quadrate.

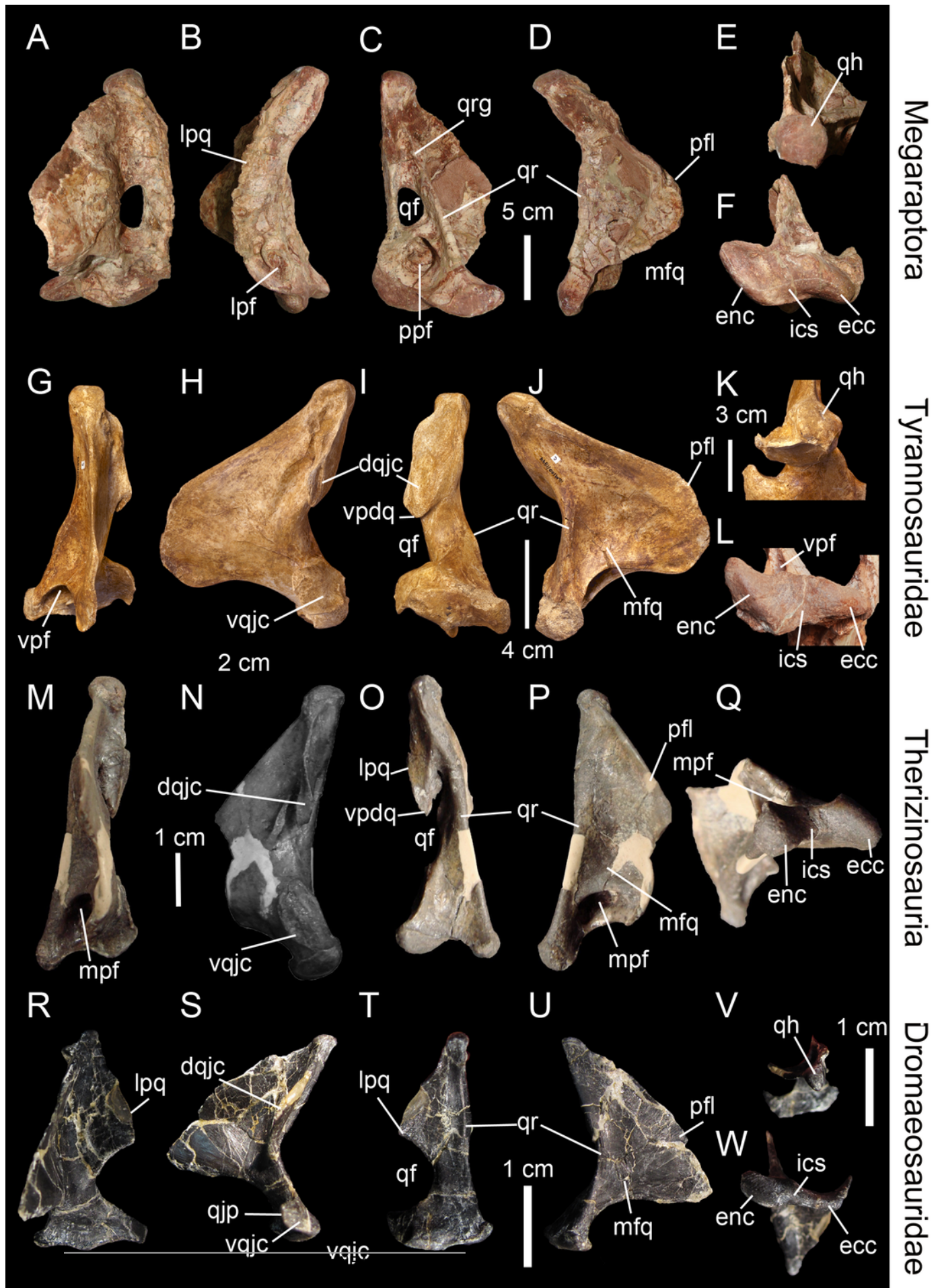
Left quadrate (**A–F**) of *Aerosteon riocoloradensis* (MCNA-PV-3137) in (**A**) anterior, (**B**) lateral, (**C**) posterior, (**D**) medial, (**E**) dorsal, and (**F**) ventral views (courtesy of Martin Ezcurra). Left quadrate (**G**–**K**) of *Alioramus altai* (IGM 100-1844) in (**G**) anterior, (**H**) 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).

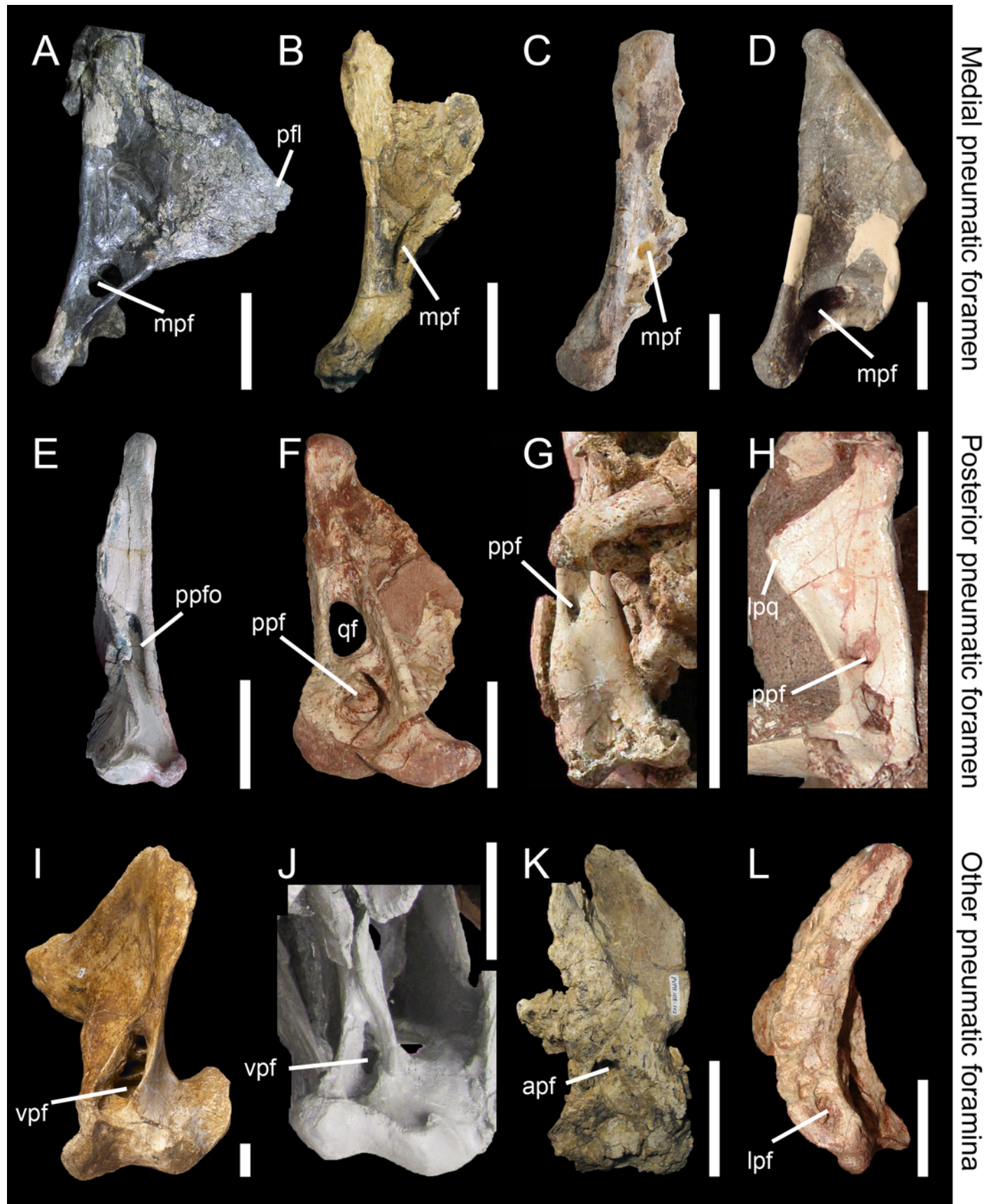



Figure 6. Distribution of quadrate pneumaticity in Theropoda.

Cladogram of non-avian theropods based on the theropod classification summarized by Hendrickx et al. (in press*a*) 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).

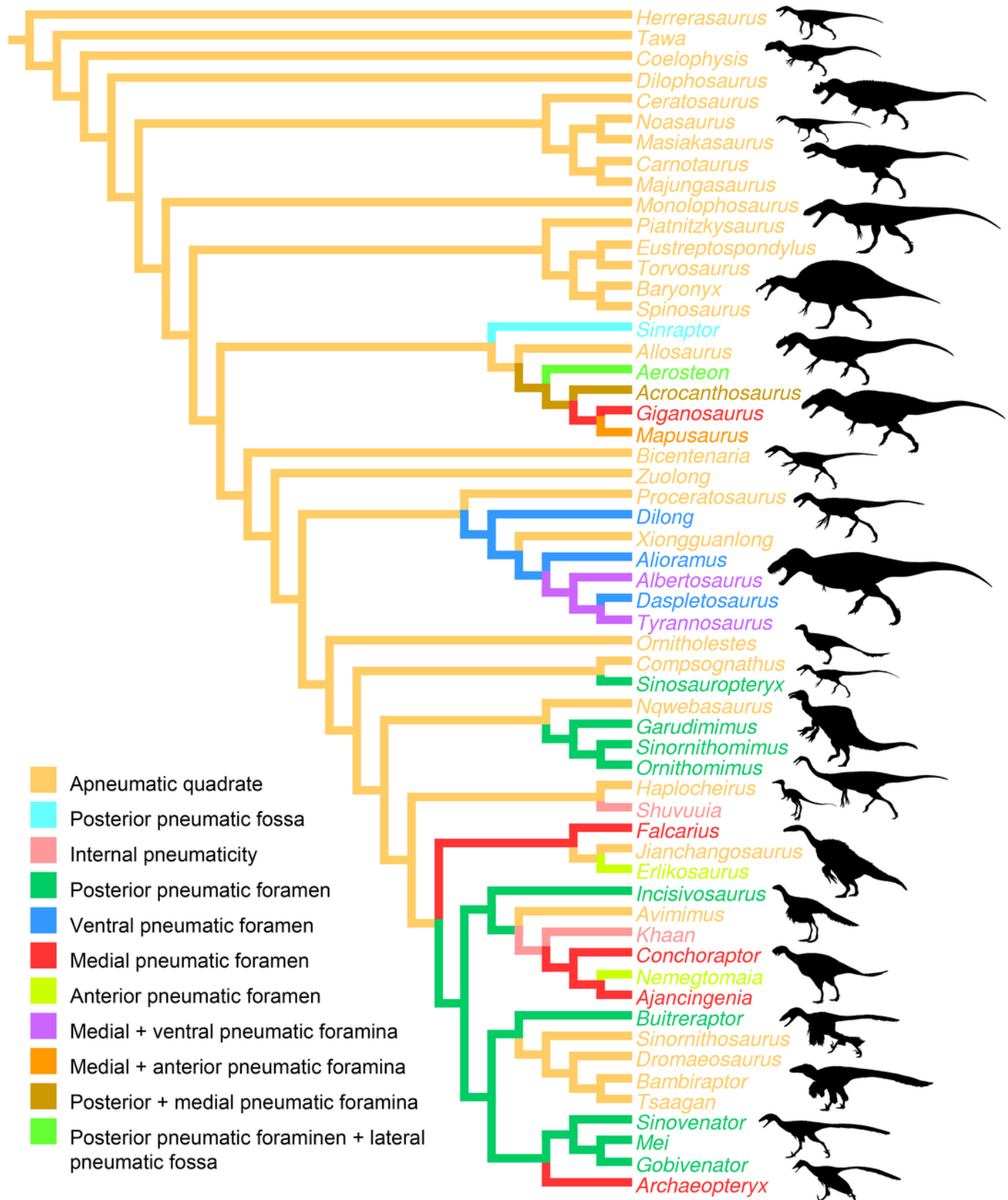



Table 1.

Standardized terminology and abbreviation of the non-avian 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) .

1   **TABLE 1.** Standardized terminology and abbreviation of the non-avian theropod quadrate and

2   comparison with the terminology of the avian quadrate based on Baumel and Witmer (1993),

3   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 quadratojugalis
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
Anterior intercondylar notch	ain	/
Posterior intercondylar notch	pin	/
Pterygoid flange	pfl	Processus orbitalis
Pterygoid contact	ptc	Condylus pterygoideus/Facies articularis pterygoidea
Medial fossa	mfq	Fossa basiorbitalis
Ventral shelf	vsh	/
Quadrate 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
Posterior pneumatic fossa	ppfo	/
Lateral pneumatic fossa	lpfo	/