1   **The nonavian theropod quadrate I: standardized terminology and**

2   **overview of the anatomy, function and ontogeny**

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4   **Keywords:** quadrate; terminology; anatomy; ontogeny; theropod; dinosaur

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ABSTRACT

24

25   By allowing the articulation of the mandible with the cranium, the quadrate of diapsids

26   and most other tetrapods plays an important role morphofunctionally. In Theropoda, its

27   morphology is particularly complex and varies importantly among different clades of

28   nonavian theropods so that the quadrate possesses a strong taxonomic potential.

29   Inconsistencies in the notation and terminology used in discussions of the theropod quadrate

30   anatomy have been noticed, a number of no less than height different terms being sometimes

31   given to a same structure. A standardization list of terms and notation for each quadrate

32   anatomical entity is here proposed, with the goal of facilitating future descriptions of this

33   important cranial bone.

34   An overview of the quadrate function, pneumaticity and ontogeny in nonavian

35   theropods is also given. The quadrate of the large majority of nonavian theropod is akinetic

36   and the diagonally oriented sulcus of the mandibular articulation allowed both rami of the

37   mandible to move laterally when opening the mouth in many of them. Pneumaticity of the

38   quadrate is also present in most of tetanuran clades and the pneumatic chamber, invaded by

39   the quadrate diverticulum of the mandibular arch pneumatic system, was connected to one or

40   several pneumatopores on the medial, lateral, posterior, anterior or ventral sides of the

41   quadrate. Absence of a quadrate foramen in allosauroid embryos and a poor delimitation of

42   mandibular condyles in both embryonic and juveniles tetanurans seems to be ontogenetic

43   features of some theropods. Finally, the numerous morphological differences existing in the

44   quadrates of the two specimens of *Shuvuuia deserti*, interpreted by some as juvenile and adult

45   individuals, are considered as ontogenetic, taphonomic, and perhaps also taxonomic

46   variations.

47

48

INTRODUCTION

49

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

51 endochondral origin that articulates with the mandible in all gnathostomes except mammals,

52 in which it evolved into the incus (Carroll 1988; Benton 2005; Brusatte 2012). In theropods,

53 this bone plays many important functions such as a structural support for the basicranium,

54 articulatory element with the lower jaws, attachment for several muscles, audition and hosting

55 important nerves and vascular passages (e.g., Witmer 1990, 1997; Bakker 1998; Sedlmayr

56 2002; Kundrát and Janáček 2007; Holliday and Witmer 2008; Tahara and Larsson 2011);

57 Appendix 1).

58   Its rather simple architecture, an elongated body bearing an anteriorly projected blade,

59 therefore tends to vary significantly in the structure of its head, mandibular articulation,

60 quadratojugal contact and the presence of pneumatic openings, quadrate foramen and lateral

61 processes, among theropods with a large variability of feeding strategies (e.g., Holtz 2003;

62 Therrien et al. 2005; Hone and Rauhut 2010; Zanno and Makovicky 2011). Such

63 morphological variation has been recognized in avian theropods in particular, revealing the

64 great taxonomical utility of the quadrate in this clade (e.g., Lowe 1926; Samejima and Otsuka

65 1987; Barbosa 1990; Elzanowski et al. 2001; Elzanowski and Stidham 2010). Likewise but to

66 a lesser degree, the systematic potential of the quadrate bone has also been noted for nonavian

67 theropods (Maryańska and Osmólska 1997; Currie 2006), witnessing the particular

68 importance that should be accorded to the description of this bone in the literature on

69 nonavian theropod anatomy. Nevertheless, the terminology and abbreviations of the quadrate

70 anatomy has been inconsistent in nonavian theropods, several different anatomical terms for

71 the same quadrate sub-entity being often used (Appendix 2). Although a thorough list of

72 anatomical terms has been given by Elzanowski et al. (2001) and Elzanowski and Stidham

73 (2010) for the avian quadrate, the terminology proposed by these authors has never been

74 followed in the description of the nonavian theropod quadrate hitherto. Indeed, the quadrate

75 of birds has greatly changed in its morphology throughout the evolution of this clade and

76 therefore displays many features absent in more primitive theropods, so that many anatomical

77 terms coined by Elzanowski et al. (2001) and Elzanowski and Stidham (2010) cannot be

78 applied for the nonavian theropod quadrate. Likewise, some quadrate entities such as the

79 quadrate foramen and the lateral process observable in nonavian theropods are absent in their

80 avian descents and do not appear in the list of these authors.

81   The present paper has two major aims. The first is to propose a standardization of the

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

83 abbreviation and followed by a definition, in order to facilitate future description of this bone

84 in the literature. The second is to give a general overview of the function, pneumaticity and

85 ontogeny of this important bone in nonavian theropods.

86

87 **Institutional Abbreviations**

88 **AMNH,** American Museum of Natural History, New York, U.S.A.; **BMNH,** The Natural

89 History Museum, London, U.K.; **BYUVP,** Brigham Young University Vertebrate

90 Paleontology, Provo, Utah, U.S.A.; **CMNH,** Carnegie Museum, Pittsburgh, Pennsylvania,

91 U.S.A.; **FMNH,** Field Museum of Natural History, Chicago, Illinois, U.S.A.; **IGM,**

92 Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **IVPP,** Institute for Vertebrate

93 Paleontology and Paleoanthropology, Beijing, China; **MACN,** Museo Argentino de Ciencias

94 Naturales, Buenos Aires, Argentina; **MCF PVPH,** Museo Municipal Carmen Funes,

95 Paleontologia de Vertebrados, Plaza Huincul, Argentina; **MCNA,** Museo de Ciencias

96 Naturales y Antropológicas de Mendoza, Mendoza, Argentina; **MIWG,** Dinosaur Isle, Isle of

97 Wight Museum Services, Sandown, U.K.; **ML,** Museu da Lourinhã, Lourinhã, Portugal;

98 **MNHN,** Muséum national d'Histoire Naturelle, Paris, France; **MNN,** Musée National du

4

99   Niger, Niamey, Niger; **MSNM,** Museo di Storia Naturale di Milano, Milan, Italy; **MUCPv,**

100   Museo de Ciencias Naturales de la Universidad Nacional de Comahue, Neuquén, Argentina;

101   **NH,** Horniman Museum & Gardens, London, U.K.; **OUMNH,** Oxford University Museum,

102   Oxford, U.K.; **PVSJ,** Instituto y Museo de Ciencias Naturales, San Juan, Argentina; **SMA,**

103   Sauriermuseum Aathal, Aathal, Switzerland; **SMNS,** Staatliches Museum für Naturkunde,

104   Stuttgart, Germany; **RTMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta,

105   Canada; **UCMP,** University of California Museum of Paleontology, Berkeley, California,

106   U.S.A.; **UC,** University of Chicago Paleontological Collection, Chicago, U.S.A.; **UMNH,**

107   Utah Museum of Natural History, Salt Lake City, Utah, U.S.A.; **USNM,** United State

108   National Museum Vertebrate Paleontology, Washington, D. C., U.S.A.; **WDIS,** Wyoming

109   Dinamation International Society, Casper, Wyoming, U.S.A.

110

111   **PROPOSED TERMINOLOGY OF THE QUADRATE ANATOMY**

112   Figure 1

113   Table 1

114   **Quadrate body (qb).** Part of the quadrate that includes the mandibular articulation, the

115   quadrate shaft, the quadrate ridge, the quadrate head, the lateral contact (quadratojugal and/or

116   squamosal contact), and the lateral process, and excludes the pterygoid flange. In posterior

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

118   the medial margin of the quadrate foramen, the ventral margin of the mandibular articulation,

119   the dorsal margin of the quadrate head, and a medial margin mostly formed by the quadrate

120   shaft and the medial fossa of the pterygoid flange. The quadrate body corresponds to the

121   corpus ossis quadrati of Baumel and Witmer (1993), and the corpus quadrati of Elzanowski et

122   al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

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

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

125 mandibular articulation). The quadrate shaft, as called by Welles (1984), Sereno and Novas

126 (1994), Norell et al. (2006), Sampson and Witmer (2007), Sereno et al. (2008), Carrano et al.

127 (2011), and Brusatte et al. (2012), is also referred as the quadrate pillar by Madsen and Welles

128 (2000), and the ascending process by Colbert (1989).

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

130 body and visible in posterior view. Although the quadrate ridge is present in the large

131 majority of nonavian theropods, a description of the structure is often omitted in the literature.

132 The quadrate ridge is referred as 'a column' for Welles (1984), a 'ridge-like mediodorsal

133 edge' for Carr (1996), 'a prominent rounded ridge' for Smith et al. (2007), a 'columnar ridge'

134 for (Rauhut et al. 2010) and a 'robust ridge' for Brusatte et al. (2012).

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

136 two-thirds, or more dorsally, of the quadrate body height. A quadrate ridge groove exists in

137 some allosauroid theropods.

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

139 squamosal and touching other bones of the braincase in some theropod taxa. The quadrate

140 head, as it is called by Britt (1991), Charig and Milner (1997), Madsen and Welles (2000),

141 Sampson and Witmer (2007), Sereno et al. (2008), Norell et al. (2009) and Brusatte et al.

142 (2012) among others, has also been termed quadrate cotylus (Currie 2003; Coria and Currie

143 2006) quadrate cotyle (Currie 2003; Coria and Currie 2006), squamosal condyle (Coria and

144 Salgado 1998), squamosal articulation (Turner et al. 2011), otic process (Maryańska and

145 Osmólska 1997; Burnham 2004; Holliday and Witmer 2008), squamosal capitulum (Zanno

146 2010) and, processus oticus (Baumel and Witmer 1993; Fig. 2), and caput quadrati

6

147   (Elzanowski et al. 2001; Elzanowski and Stidham 2010). When the quadrate head is double, it

148   divides into otic and squamosal capitula.

149   **Otic capitulum (otc).** Medial capitulum of the quadrate head articulating with the braincase.

150   The otic capitulum corresponds to the capitulum (condylus) oticum of Baumel and Witmer

151   (1993; Fig. 2), Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian

152   theropods.

153   **Squamosal capitulum (sqc).** Lateral capitulum of the quadrate head articulating with the

154   squamosal. The squamosal capitulum corresponds to the capitulum (condylus) squamosum of

155   Baumel and Witmer (1993; Fig. 2), Elzanowski et al. (2001) and Elzanowski and Stidham

156   (2010) for avian theropods.

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

158   capitulum on the dorsal surface of the quadrate head. The intercapitular sulcus (sensu Witmer

159   1990) corresponds to the incisura intercapitularis of Baumel and Witmer (1993; Fig. 2), and

160   the vallecula intercapitularis of Elzanowski et al. (2001) and Elzanowski and Stidham (2010)

161   for avian theropods.

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

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

164   the dorsal quadratojugal contact and its ventral projection in some theropod taxa. Most

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

166   and Novas 1994; Charig and Milner 1997; Maryańska and Osmólska 1997; Currie and

167   Carpenter 2000; Coria and Currie 2006; Currie 2006; Norell et al. 2006; Zanno 2010;

168   Choiniere et al. 2010; Foth and Rauhut 2012; Brusatte et al. 2012) but it can be also called the

169   paraquadratic foramen (e.g., Barsbold and Osmólska 1999; Kobayashi and Lü 2003;

170   Kobayashi and Barsbold 2005), the paraquadrate foramen (Sampson and Witmer 2007; Dal

171   Sasso and Maganuco 2011), the paraquadrate fenestra (Smith et al. 2007) or the quadrate

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

173   foramen exists in all nonavian theropods but Ceratosauria and Megalosauridae.

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

175   mandible and fitting in the glenoid fossa of the lower jaw. It includes the ectocondyle,

176   entocondyles, sometimes a mediocondyle, and an intercondylar sulcus. Corresponds to the

177   pars or processus mandibularis of Baumel and Witmer (1993; Fig. 2), Elzanowski et al.

178   (2001) and Elzanowski and Stidham (2010) for avian theropods. Although most authors (e.g.,

179   Currie 2006; Sampson and Witmer 2007; Rauhut et al. 2010; Brusatte et al. 2012) referred the

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

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

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

183   some theropods is here coined mediocondyle.

184   **Ectocondyle (ecc).** Lateral condyle of the mandibular articulation. The ectocondyle

185   corresponds to the condylus (mandibularis) lateralis of Baumel and Witmer (1993; Fig. 2),

186   Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

187   **Entocondyle (enc).** Medial condyle of the mandibular articulation. The entocondyle

188   corresponds to the condylus (mandibularis) medialis of Baumel and Witmer (1993; Fig. 2),

189   Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

190   **Mediocondyle (mdc)**. Median condyle of the mandibular articulation. The mediocondyle is

191   referred as the third condyle by Clark et al. (1994) and Xu and Wu (2001), the accessory

192   condyle by Kobayashi and Lü (2003), and the condyles caudalis of Baumel and Witmer

193   (1993) and Elzanowski et al. (2001) for avian theropods.

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

195   sliding along the interglenoid ridge of the articular. The intercondylar sulcus, a term also used

196   by Carrano et al. (2011), can be referred as a groove (e.g., Madsen 1976; Britt 1991; Madsen

197 and Welles 2000; Currie 2006), swelling (Charig and Milner 1997), sulcus (e.g., Kobayashi

198 and Lü 2003; Norell et al. 2006; Sadleir et al. 2008), trochlea (Brochu 2003; Brusatte et al.

199 2010), trochlear surface (Brusatte et al. 2010, 2012), and intercondylar bridge (Zanno 2010).

200 The intercondylar sulcus corresponds to the sulcus intercondylaris (Baumel and Witmer 1993)

201 and the vallecula intercondylaris (Elzanowski et al. 2001; Elzanowski and Stidham 2010) of

202 the quadrate of avian theropods.

203 **Intercondylar notch (icn).** Notch located in between the ectocondyle and entocondyle, either

204 on the anterior or posterior margin of the mandibular articulation, and corresponding to the

205 depressio praecondylaris of Elzanowski et al. (2001) for avian theropods.

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

207 body. Also known as the dorsal wing (Welles 1984; Currie 2006), the anterolateral wing

208 (Madsen and Welles 2000), the lateral lamina (Coria and Salgado 1998) and the lateral ramus

209 (Sampson and Witmer 2007), this process can contact the quadratojugal and/or the squamosal

210 and therefore either be referred to the quadratojugal ramus by Sampson and Witmer (2007) or

211 the squamosal ramus Norell et al. (2006).

212 **Quadratojugal contact (qjc)**. Contact of the quadrate with the quadratojugal on the lateral,

213 anterolateral or, posterolateral margin of the quadrate body. The quadratojugal contact, which

214 corresponds to the cotyla quadratojugalis of Baumel and Witmer (1993), Elzanowski et al.

215 (2001) and Elzanowski and Stidham (2010) for avian theropods, can be divided into a ventral

216 and a dorsal quadratojugal contact when the quadrate foramen is present and delimited by

217 both quadrate and quadratojugal.

218 **Ventral quadratojugal contact (vqjc)**. ventral contact of the quadrate with the

219 quadratojugal. The ventral quadratojugal contact of the quadrate always receives the

220 quadratojugal bone.

221   **Dorsal quadratojugal contact (dqjc)**. dorsal contact of the quadrate with the quadratojugal.

222   The ventral quadratojugal contact of the quadrate can either receive the quadratojugal or both

223   quadratojugal and squamosal in some theropod taxa.

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

225   dorsal quadratojugal contact delimiting the dorsolateral margin of the quadrate foramen.

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

227   quadrate.

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

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

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

231   quadrate ridge. The posterior fossa can include or exclude the quadrate foramen.

232   **Quadrate diverticulum (qdi).** Air sac invading the pneumatic chamber inside the quadrate

233   body and communicating with other diverticula by the quadrate pneumatopores.

234   **Dorsal pneumatopore (dpne).** Pneumatic foramen or recess located on the dorsal part of the

235   quadrate, beneath the quadrate head. The dorsal pneumatopore corresponds to the foramen

236   pneumaticum caudomediale of Elzanowski et al. (2001) and Elzanowski and Stidham (2010)

237   for avian theropods.

238   **Medial pneumatopore (mpne).** Pneumatic foramen or recess situated on the medial side of

239   the quadrate, typically in the ventromedial part of the pterygoid flange. The medial

240   pneumatopore corresponds to the foramen pneumaticum basiorbitale of Elzanowski et al.

241   (2001) and Elzanowski and Stidham (2010) for avian theropods.

242   **Posterior pneumatopore (ppne).** Pneumatic foramen or recess on the posterior side of the

243   quadrate body, typically at one-height of the quadrate. The posterior pneumatopore

244   corresponds to the 'foramen pneumaticum rostromediale' of Elzanowski et al. (2001) and

245   Elzanowski and Stidham (2010) for avian theropods.

246   **Ventral pneumatopore (vpne).** Pneumatic foramen or recess on the ventral side of the

247   quadrate. The ventral pneumatopore corresponds to the foramen pneumaticum adventitium of

248   Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian theropods.

249   **Pterygoid flange (pfl).** Sheet-like projection attached to the quadrate body and extending

250   anteriorly or anteromedially to contact the pterygoid bone. The pterygoid flange, a term also

251   used by Charig and Milner (1997), Brochu (2003), Currie (2006), Coria and Currie (2006)

252   and (Rauhut et al. 2010), is also known as the quadrate/anterior flange (e.g., Colbert 1989;

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

254   1994; Sampson and Witmer 2007; Choiniere et al. 2010), the pterygoid wing (e.g., Welles

255   1984; Madsen and Welles 2000; Eddy and Clarke 2011), the pterygoid ala (e.g., Currie 2003,

256   2006; Sadleir et al. 2008; Dal Sasso and Maganuco 2011), the pterygoid process (Molnar

257   1991; Carr 1996; Sereno et al. 2008), the optic wing (Balanoff and Norell 2012), the orbital

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

259   Witmer 1993; Elzanowski et al. 2001; Elzanowski and Stidham 2010; Fig. 2) for avian

260   theropods.

261   **Pterygoid contact (ptc).** Contact on the medial margin of the pterygoid flange, or the

262   quadrate body, with the pterygoid. The pterygoid contact corresponds, for avian theropods, to

263   the facies pterygoidea in Elzanowski et al. (2001) and the facies articularis pterygoidea in

264   Elzanowski and Stidham (2010), as well as the condylus pterygoideus, located on the

265   quadrate body, in Baumel and Witmer (1993; Fig. 2), Elzanowski et al. (2001) and

266   Elzanowski and Stidham (2010).

267   **Medial fossa (mfq).** Depression or concavity situated ventroposteriorly on the pterygoid

268   flange. It is delimited by the quadrate shaft and the ventral shelf in some theropod taxa. The

269   medial fossa corresponds to the fossa corporis quadrati of Fuchs (1954) and the fossa

270   basiorbitalis of Elzanowski et al. (2001) and Elzanowski and Stidham (2010) for avian

271   theropods.

272   **Ventral shelf (vsh).** a medial or medioposterior fold of the ventral margin of the pterygoid

273   flange. The term 'shelf' was employed by Sereno and Novas (1994) and 'ventral shelf' was

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

275

276   Figure 2

277   **Inter-taxic Topological Homologies**

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

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

280   of the variability within different anatomical sub-units of the quadrate and by following the

281   criteria summarized in Rieppel (2006).

282   The quadrate ridge (Figure 1, qr) is easily distinguishable in many theropod taxa such

283   as *Aerosteon riocoloradensis* (MCNA-PV 3137) and *Proceratosaurus bradleyi* (NHM

284   R.4860) but the limits of this structure on the quadrate body can be subtle like in *Noasaurus*

285   *leali* (PVL 4061), *Majungasaurus crenatissimus* (FMNH PR 2100), and *Eustreptospondylus*

286   *oxoniensis* (OUMNH J.13558). The quadrate ridge corresponds to a columnar ridge in many

287   theropod clades like in *Dilophosaurus wetherilli* (Welles 1984), *Allosaurus* (SMA 005/02)

288   and *Eotyrannus lengi* (MIWG, 1997.550) but can also corresponds to a thin crest as in

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

290   of the quadrate ridge is usually demarcated just above the medial condyle of the mandibular

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

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

293   of the quadrate such as in *Albertosaurus sarcophagus* (Currie 2003:fig. 10B). Despite being

294   the same structure, the quadrate ridge can be separated by a deep groove like in *Allosaurus*

295   *fragilis* (AMNH 600) and *Allosaurus europaeus* (ML 415) or flare and reappear more

296   dorsally at the second third of the quadrate such as in some derived Spinosauridae (pers.

297   observ.). Likewise, the ventral portion can also be divided in two parts separated by a

298   concavity such as in the tyrannosaurids *Albertosaurus sarcophagus*, *Daspletosaurus* sp.

299   (Currie 2003:fig. 10 and 28) and *Tyrannosaurus rex* (AMNH 5027).

300   The pterygoid flange (Figure 1, pfl) contacts the quadrate process of the pterygoid

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

302   *Herrerasaurus ischigualastensis* (PVSJ 407), the basipsphenoid and prootic in *Erlikosaurus*

303   *andrewsi* (Clark et al. 1994), and the squamosal in *Khaan mckennai* (Balanoff and Norell

304   2012). Although the pterygoid flange can be easily homologized between taxa, it may acquire

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

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

307   *walkeri*, *Tyrannosaurus rex*) or get attached to the quadrate body well-above the mandibular

308   articulation (e.g., *Majungasaurus crenatissimus*). This single structure can in some instances

309   be divided into two ridges delimited by a deep pneumatic fossa facing ventrally (e.g.,

310   *Alioramus altai*, Brusatte et al. (2012), figure 23c; *Tyrannosaurus rex* FMNH PR2081). In

311   anterior view, the pterygoid flange can be straight and only directed anteriorly like in the

312   carcharodontosaurid *Shaochilong maortuensis* (Brusatte et al. 2010:fig. 7a), or completely

313   recurved anteromedially and its anteroventral margin can be either straight, or fold medially

314   and dorsally, forming the ventral shelf, such as in *Majungasaurus crenatissimus* (FMNH PR

315   2100), *Carnotaurus sastrei* (MACN-CH 894) and *Allosaurus fragilis* (Madsen 1976:plate 3d).

316   The medial fossa of the quadrate (Figure 1, mfq) can be easily recognizable between

317   taxa as it is always situated on the pterygoid flange, usually on the ventral part of it. This

318   fossa is posteriorly delimited by the quadrate body in nonavian theropods and sometimes by

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

320 *Cryolophosaurus* and shallow in *Eustreptospondylus*), pneumatized (e.g., *Falcarius*), and

321 situated in the ventralmost part of the pterygoid flange (e.g., *Tsaagan*) or at mid-height of it

322 and just above a large pneumatic recess like in *Mapusaurus roseae* (MCF PVPH-108.102).

323   The posterior fossa of the quadrate (Figure 1, pfq) can be located either in between the

324 quadrate and the quadratojugal, being centred on the lateral margin of the quadrate (e.g.,

325 *Ceratosaurus*); or in the middle of the quadrate shaft and between the quadrate ridge and the

326 lateral margin of the quadrate (e.g., '*Syntarsus*'; *Majungasaurus*; *Tsaagan*). Difficulties to

327 recognize this structure between taxa may arise because it is not always well-delimited (e.g.,

328 *Shaochilong*). The posterior fossa can either be strongly ventrodorsally elongated like in the

329 megalosaurid *Torvosaurus tanneri*, or form an oval concavity lateromedially wide (e.g.,

330 *Majungasaurus*). Similarly to the medial fossa, the posterior fossa can have a large pneumatic

331 recess positioned dorsally (e.g., *Sinornithomimus*) or ventrally (e.g., *Garudimimus*) inside the

332 fossa.

333   Due to the highly variable morphology of the quadrate foramen (Figure 1, qf), this

334 structure deserves special attention. It can be completely absent (e.g., *Carnotaurus*,

335 *Torvosaurus*), or form a very small aperture (e.g., '*Syntarsus*') to a large opening (e.g.,

336 *Tsaagan*). In most nonavian theropods, the quadrate foramen is mostly delimited by the

337 quadrate and only its lateral margin is bounded by the quadratojugal (e.g., *Sinraptor*). In some

338 nonavian theropods, however, the medial margin of the quadrate foramen and part of the

339 ventral and dorsal margins are formed by the quadrate, the other lateral half being delimited

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

341 completely enclosed in the quadrate (e.g., *Aerosteon*).

342   The quadratojugal contact of the quadrate (Figure 1, qjc) can either be a single

343 extensive contact or made of two contacts separated by the quadrate foramen. In the latter

344 case, the ventral quadratojugal contact and the dorsal quadratojugal contact of the quadrate

14

345 are not always clearly separated and their dorsal and ventral margins, respectively, can

346 overlap like in the sinraptorid *Sinraptor dongi* (IVPP 10600). If the quadrate foramen is

347 absent or located inside the quadrate, the lateral quadratojugal contact is an elongated line of

348 variable width along the lateral margin of the quadrate. If separated by the quadrate foramen,

349 the ventral and dorsal contacts can display a wide variety of shapes that, nevertheless, are

350 easily recognizable inter-taxically. Both quadratojugal contacts may face laterally, anteriorly

351 or posteriorly and their articulating surface can be smooth, irregular or deeply grooved by

352 several radiating ridges as in *Allosaurus fragilis* (Madsen 1976). The ventral quadratojugal

353 contact is usually D-shaped or ovoid and its anterior margin can extend far anteriorly, forming

354 the quadratojugal process occasionally forming a large subtriangular projection (Norell et al.

355 2006). The dorsal quadratojugal contact can vary from a very thin line to a broad surface and

356 its dorsal extension can reach the dorsal condyle or terminate well beneath it. A ventral

357 projection of this contact may be present, and such projection delimiting part of the lateral

358 border of the quadrate can either be short, like in *Daspletosaurus* sp. (Currie 2003:fig. 28A),

359 or formed an elongated ramus, like in the therizinosaurid *Falcarius utahensis* (Zanno

360 2010:fig. 1H) and the coelurosaur *Zuolong salleei* (Choiniere et al. 2010:fig. 3B).

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

362 quadrate (Figure 1, lpq) forms a wing-like projection similar to the pterygoid flange. This

363 process is an extension of the quadrate body laterally so that it can be difficult to delimitate

364 and one can see the presence of such process in *Allosaurus 'jimmadseni'* (SMA 005/02),

365 *Sinraptor dongi* (Currie 2006:fig. 1D), and *Erlikosaurus andrewsi* (Clark et al. 1994:fig. 7).

366 The lateral process can also vary in shape and size, as it can be short and parabolic (e.g.,

367 *Carnotaurus*) or elongated and subtriangular (e.g., *Tsaagan*). Its ventral border can also

368 extend to the quadrate foramen (e.g., *Bambiraptor*) or more ventrally, sometimes reaching the

369 medial condyle of the mandibular articulation (e.g., *Ilokelesia*).

370   The quadrate head (Figure 1, qh) always articulates with the deep cotylus of the

371   squamosal and contacts more rarely other bones of the braincase such as the opisthotic in

372   oviraptorids (Maryańska and Osmólska 1997), the prootic in *Mononykus olecranus* (Perle et

373   al. 1994; Chiappe et al. 2002) and the postorbital in *Shuvuuia deserti* (Chiappe et al. 1998,

374   2002). The contact of the braincase between the dorsal part of the quadrate and the opistothic-

375   exoccipital or the paroccipital process is also present in *Herrerasaurus ischigualastensis*

376   (Sereno and Novas 1994), *Dilophosaurus wetherilli* (Welles 1984), *Ceratosaurus*

377   *magnicornis* (Madsen and Welles 2000; Sanders and Smith 2005), tyrannosaurids (Currie

378   2003), *Heyuannia huangi* (Lü 2005), and perhaps *Erlikosaurus andrewsi* (Clark et al. 1994),

379   but this contact occurs on a small medial surface just below the quadrate head and not with

380   the quadrate head itself. The large majority of nonavian theropods have a single headed

381   quadrate head (Rauhut 2003; pers. observ.); however, oviraptorids (Maryańska and Osmólska

382   1997:fig. 3B) and the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998) have a unique

383   double head. A bistylic quadrate head has also been observed in the dromaeosaurid *Mahakala*

384   *omnogovae* (Turner et al. 2007) but Turner et al. (2011:fig. 4) later reconsidered the head of

385   the quadrate as not being double headed. The morphology of the quadrate head is variable; it

386   may be subtriangular in most basal theropods (Sereno and Novas 1994; UCMP 37302), oval

387   or subcircular in megalosaurids (UC OBA1; BYUVP 9246) and allosauroids (MCNA-PV-

388   3137; IVPP 10600; IVPP V2885.3), subquadrangular in Spinosaurinae (SMNS 58022;

389   MSNM V6896) or conical in Oviraptoridae (Maryańska and Osmólska 1997:fig. 1B). Whilst

390   most nonavian theropods have either a convex or a flattened quadrate head, the quadrate of

391   some allosaurids (Bakker 1998:fig. 5C) and derived tyrannosaurids (FMNH PR208) can also

392   possess a well-marked concavity on the dorsal margin of the quadrate head. Despite this

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

394   location of this structure.

395   With the exception of the therizinosaur *Erlikosaurus andrewsi* and the

396   ornithomimosaur *Sinornithomimus dongi* which both seem to have a unique tricondylar

397   condition on the mandibular articulation (Clark et al. 1994; Kobayashi and Lü 2003), all other

398   nonavian theropods have two mandibular condyles. The presence of three mandibular

399   condyles was also noted in the alvarezsaurid *Avimimus portentosus* (Chatterjee 1995) and the

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

401   (2002) only found two condyles in the former and our observations confirm that the third

402   condyle of the latter seems to be part of the much broader lateral condyle (Xu and Wu

403   2001:fig. 4D).

404   The intercondylar sulcus (Figure 1, ics) varies in orientation, size and depth. It can be

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

406   articulation as in *Tyrannosaurus rex* (FMNH PR2081); or narrow, deep and strongly

407   lateromedially-oriented as in some derived spinosaurids (pers. observ.).

408   The shape of the mandibular articulation (Figure 1, mar) in posterior view can vary

409   from the biconvex condition known in most theropods, to the W-shaped articulation typical of

410   *Citipati osmolskae* (Clark et al. 2002:fig. 6) or a unique convex articulation seen in some

411   dromaeosaurids such as *Tsaagan manga* (IGM 100/1015). The intercondylar notch (Figure 1,

412   icn) is present in *Allosaurus 'jimmadseni'* (Bakker 1998:fig. 5B, C; SMA 005/02) and

413   *Suchomimus tenerensis* (MNN GAD 502) on the posterior side of the mandibular articulation,

414   and in *Majungasaurus crenatissimus* (FMNH PR 2100) and *Carnotaurus sastrei* (MACN-CH

415   894) on its anterior margin. The ectocondyle (Figure 1, ecc) and entocondyle (Figure 1, ent)

416   are highly variable among each clade of nonavian theropods in terms of shape, size and

417   orientation.

418   Pneumaticity of the quadrate can either be internal or, obviously expressed externally

419   by pneumatopores. The establishment of inter-taxic homologies is difficult to assess, because

420 these structures have very diverse interspecific variability. Nevertheless, as in other

421 saurischian taxa (Schwarz et al. 2007), these pneumatic structures have phylogenetic signal.

422 These openings can appear on different views and portions of the quadrate. The medial and

423 posterior pneumatopores (Figure 1, ppne) usually occur in the medial and posterior fossa

424 respectively, and their position inside the fossae is again quite variable. Pneumatopores can

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

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

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

428 septum.

429

430 **OVERVIEW OF THE FUNCTION, PNEUMATICITY AND ONTOGENY**

431 Figure 3

432 **Function of the Quadrate**

433   Although in all archosaurs, and all amniotes except mammals, the main function of the

434 quadrate is the articulation of the cranium with the mandible, this bone can also play an

435 important role in the mobility of the skull in many extant theropods. Quadrate movement

436 inside the skull, known as streptostyly, is a fundamental property of all avian theropods, and

437 cranial kinesis in birds, known already in the beginning of the, 19th century (Nitzsch 1816),

438 has been extensively studied in the past sixty years (e.g., Fisher 1955; Bock 1964, 1999, 2000;

439 Bühler 1981; Zusi 1984, 1993; Bühler et al. 1985, 1988; Chatterjee 1991, 1997; Hoese and

440 Westneat 1996; Zweers et al. 1997; Zweers and Vanden Berge 1998; Bout and Zweers 2001;

441 Gussekloo and Bout 2005; Meekangvan et al. 2006). Streptostyly consists of the rotation of

442 the quadrate at its dorsal articulation against the squamosal and/or supratemporal and usually

443 corresponds to a transversal movement, although a lateral movement of the quadrate around

444 an anteroposteriorly directed axis occurs in some lepidosaurs taxa (Metzger 2002). Cranial

445 kinesis in avian theropods with a streptostylic quadrate includes upward (protraction) and

446 downward (retraction) rotation of the upper jaw relative to the braincase and three main types

447 of kinesis are recognized relative to the position of the dorsal flexion zone of the cranium and

448 the nature of the nasal opening in modern theropods (Bock 1964; Bühler 1981; Zusi 1984;

449 Meekangvan et al. 2006). There are the prokinesis where the flexion occurs at the nasofrontal

450 joint and the upper jaw thereby moves as one unit, the amphikinesis where the flexion occurs

451 in two zones of flexibility and the upper jaw and its tip are bent upward, and finally the

452 rhynchokinesis where the flexion happens forward from the nasofrontal joint, allowing its

453 rostral part to be moved.

454   Inference of the cranial kinesis and quadrate mobility in nonavian theropods has been

455 recently investigated by Holliday and Witmer (2008) which regard the cranium of this group

456 of dinosaurs as partially kinetically competent, since synovial joints and protractor muscles

457 are present, but not fully kinetic like in birds. The strong suture of the quadrate to the

458 quadratojugal and the immobile contact of the quadrate and the pterygoid on the medial side

459 of the pterygoid flange in most nonavian theropods seem to indicate a very limited movement,

460 and perhaps even the total absence of movement of this bone within the cranium. Although

461 the synovial quadrate head joint existing in theropods, and all other archosaurs, is necessary to

462 infer cranial kinesis, its presence in akinetic taxa such as crocodiles and thyreophorans

463 demonstrates that the synovial joint cannot be considerate alone as an argument for cranial

464 kinesis. Synovial joints have actually been interpreted as growth zones rather than articular

465 surfaces of mobile joints based on the presence of very thin articular cartilage covering the

466 end of this joint (Holliday and Witmer 2008). According to Holliday and Witmer (2008)

467 "articular cartilage persists in loading environments that exert hydrostatic pressures (which

468 result in a change in volume but not shape) but exert low shear stresses". Indeed, one of the

469 key centres of deformation during normal biting is the quadrate-squamosal contact, which

470   would have experienced large shear stresses associated with torque and asymmetrical loading

471   during biting (Rayfield 2005), and the presence of a minimal amount of cartilage between the

472   quadrate and squamosal would therefore suggest that the synovial zone was rather a growth

473   zone than a mobile one. A streptostylic quadrate in *Tyrannosaurus rex* (Molnar 1991, 1998),

474   *Oviraptor philoceratops* (Smith 1992), *Heyuannia huangi* (Lü 2005) and *Dromiceiomimus*

475   *brevitertius* (Russell 1972) based on the saddle joint between the quadrate and squamosal only

476   is thereby unlikely.

477   Nevertheless, and more convincingly, a streptostylic quadrate has also been proposed

478   in the alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998) in which the quadratojugal/jugal

479   (Dufeau (2003) suggested that the quadratojugal may be absent in *Shuvuuia deserti*), rather

480   than being firmly sutured to the quadrate, like in other nonavian theropods, would have

481   contacted the quadrate though a movable joint (Chiappe et al. 1998, 2002; Fig.3). According

482   to Chiappe et al. (1998), the absence of a latero-dorsal contact of the quadrate with the

483   quadratojugal/jugal, as well as a ventro-lateral process of the squamosal, would have

484   permitted to the quadrate of this mononykine to pivot antero-posteriorly, and the upper jaw to

485   rotate ventro-dorsally thanks to this transversal movement. Although these authors have

486   implied the existence of a bending zone between the frontals and the nasal–preorbital bones in

487   *S. deserti*, allowing the flexion of the snout as a single unit when the quadrate displaced

488   forward, like in prokinetic birds, the complex contacts between the nasal, frontal and

489   prefrontal illustrated by Sereno (2001:fig. 12B) makes assessment of Chiappe et al. (1998)

490   hypothesis quite dubious (Holliday and Witmer 2008). In addition, Holliday and Witmer

491   (2008) noted that a maxillojugal and palatal flexion zones authorizing a true prokinesis to be

492   present in alvarezsaurids is still not clear. Likewise, the contact between the pterygoid flange

493   of the quadrate and the pterygoid needs also to be better documented in order to imply any

494   specific movement of the quadrate inside the cranium of *S. deserti*.

495   A movable articulation between the quadrate and quadratojugal may also have been

496   present in the oviraptorids *Heyuannia huangi* (Lü 2003) and *Nemegtia huangi* (Lü et al. 2004) in

497   which the quadrate and quadratojugal articulation of the former corresponds to a trochlea-like

498   structure (Lü 2003, 2005), while the quadratojugal contact of the latter is convex and fit into a

499   quadratojugal cotyle (Lü et al. 2004).

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

501   highly variable among nonavian theropods, therefore suggesting some variation in the

502   movement of the rami when the jaw opened. The helical intercondylar sulcus present in many

503   nonavian theropods, but not all of them (pers. observ.), was noticed by Bakker (1998) in

504   primitive theropod dinosaurs, Hendrickx and Buffetaut (2008) in spinosaurids, and Molnar

505   (1991) and (Larson 2008) in *Tyrannosaurus rex*. These authors suggested that such spiral

506   groove of the mandibular articulation constrained the diagonal ridge of the articular glenoid

507   fossa, which fitted into the intercondylar sulcus, to slide laterally, therefore forcing the rami

508   of the mandible to displace laterally when the lower jaw was depressed, enlarging the width

509   of the larynx in order to swallow food of large size (Hendrickx and Buffetaut 2008).

510   In allosaurid quadrates, the marked constriction of the intercondylar sulcus, associated

511   with the enlargement of the mandibular condyles, the backward bent of the ventral part of the

512   quadrate, and the intercondylar notch, were interpreted by Bakker (1998) as joint-stabilization

513   zones. According to this author, the enlargement of the articulating surface would improve the

514   stability of the joint when the mouth was widely opened, while the posterior depression would

515   correspond to the area for attachment of one or several ligaments within the quadrate-

516   mandibular articulation ((Bakker 1998). An intercondylar notch has also been noticed in the

517   abelisaurids *Carnotaurus sastrei* (MACN-CH 894) and *Majungasaurus crenatissimus*

518   (FMNH PR 2100), and the spinosaurid *Suchomimus tenerensis* (MNN GAD 502), implying a

519   similar mechanic of the mandibular articulation than *Allosaurus*.

520

522   **Pneumaticity in the Quadrate**

523   Pneumatization of the quadrate bone has long been recognized for its phylogenetic

524   value (e.g., Gauthier 1986; Holtz 1998; Chiappe 2001; Rauhut 2003; Holtz et al. 2004; Smith

525   et al. 2007; Benson 2010; Carrano et al. 2012; Turner et al. 2012; Novas et al. 2013;

526   Choiniere et al. 2014). Pneumatopores within the quadrate are widespread among

527   avetheropod clades (Gold et al. 2013; Fig. 4). The presence of one or several pneumatopores

528   has indeed been recorded in carcharodontosaurids (e.g., Coria and Currie 2006; Eddy and

529   Clarke 2011), neovenatorids (Sereno et al. 2008), tyrannosauroids (e.g., Molnar 1991; Brochu

530   2003; Currie 2003; Xu et al. 2004; Brusatte et al. 2012; Gold et al. 2013), compsognathids

531   (Currie and Chen 2001), therizinosauroids (Clark et al. 1994; Zanno 2010), oviraptorids (e.g.,

532   Maryańska and Osmólska 1997; Lü 2003; Kundrát and Janáček 2007; Balanoff and Norell

533   2012), ornithomimoids (Witmer 1997; Tahara and Larsson 2011), dromaeosaurids

534   (Makovicky et al. 2005) and troodontids (Barsbold et al. 1987; Currie and Zhao 1993;

535   Varricchio 1997; Xu et al. 2002; Xu and Norell 2004). An incipient development of a

536   pneumatic recess also exists in the basal allosauroid *Sinraptor dongi* (Currie 2006), and

537   quadrate pneumaticity therefore seems to be an avetheropod synapomorphy (Fig. 4). Among

538   nonavian avetheropods, there is however no evidence of a pneumatic quadrate in

539   Alvarezsauroidea hitherto.

540   The pneumatic foramen is particularly large in some allosauroids such as *Aerosteon*

541   *riocoloradensis* (Sereno et al. 2008) and *Acrocanthosaurus atokensis* (Eddy and Clarke

542   2011), and the therizinosaur *Falcarius utahensis* (Zanno 2010; Fig. 5). It however

543   corresponds to a small rounded or oval aperture lodged in the posterior fossa of the quadrate

544   body in most avetheropods (Fig. 5). Indeed, a posterior pneumatopore exists in the

545 tyrannosauroid *Dilong paradoxus* (Xu et al. 2004), the compsognathid *Sinosauropteryx prima*

546 (Currie and Chen 2001:fig. 3f), the ornithomimids *Garudimimus brevipes* (the 'paraquadrate

547 foramen' or 'paraquadratic foramen' of Kobayashi and Barsbold 2005), *Sinornithomimus*

548 *dongi* (the 'paraquadratic foramen' of Kobayashi and Lü 2003) and *Ornithomimus*

549 *edmontonicus* (Tahara and Larsson 2011), the dromaeosaurid *Buitreraptor gonzalezorum*

550 (Makovicky et al. 2005), and the troodontids *Mei long* (Xu and Norell 2004), and *Sinovenator*

551 *changii* (Xu et al. 2002). A pneumatopore can also be located in the ventral corner of the

552 pterygoid flange, as observed in the carcharodontosaurids *Acrocanthosaurus atokensis* (Eddy

553 and Clarke 2011), *Mapusaurus roseae* (Coria and Currie 2006), *Giganotosaurus carolinii*

554 (MUCPv-CH-1), and the tyrannosaurid *Albertosaurus sarcophagus* (Currie 2003:fig. 10B). A

555 pneumatic opening is also present anteroventrally, within a recess on the posteroventral part

556 of the pterygoid flange ('funnellike external opening on the rostral surface of the quadrate,

557 above the condyles' of Gold et al., 2013, p. 37) like in the therizinosauroid *Falcarius*

558 *utahensis* (Zanno 2010) and the tyrannosaurids *Alioramus altai* ((Brusatte et al. 2012; Gold et

559 al. 2013), *Daspletosaurus* sp. (Currie 2003:fig. 28C) and *Tyrannosaurus rex* (Brochu 2003).

560 This ventral pneumatopore has also been reported in the basal tyrannosauroid *Dilong*

561 *paradoxus* (Gold et al. 2013) but was not observed in the closely related taxa *Guanlong*

562 *wucaii*, *Proceratosaurus lengi*, and *Xiongguanlong baimoensis* (Gold et al. 2013), and its

563 presence cannot be established in *Eotyrannus lengi* (contra Gold et al. 2013; pers. obs.). More

564 rarely, a pneumatic opening can be situated on the lateral surface of the quadrate body, as in

565 *Aerosteon riocoloradensis* (MCNA-PV 3137), and in the anterior part of the quadrate, as in

566 *Mapusaurus roseae* (Coria and Currie 2006), *Troodon formosus* (Currie and Zhao 1993),

567 *Heyuannia huangi* (Lü 2005), and perhaps *Tyrannosaurus rex* (Molnar 1991).

568 Figure 5

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

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

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

572   pneumatic foramina usually enter a large pneumatic chamber within the quadrate bone such as

573   in *Tyrannosaurus rex* (Molnar 1991; Brochu 2003), *Alioramus altai* (Gold et al. 2013),

574   *Conchoraptor gracilis* (Kundrát and Janáček 2007) or *Ornithomimus edmontonicus* (Tahara

575   and Larsson 2011). The neovenatorid *Aerosteon riocoloradensis* also possess a large posterior

576   pneumatopore leading to a pneumatic chamber, as well as a shallow pneumatic recess on the

577   lateral surface of the quadrate shaft (pers. obs.).

578   These pneumatopores and the pneumatic chamber associated with them are invaded

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

580   the periotic pneumatic system, forms the tympanic sinus of archosaurs (Tahara and Larsson

581   2011). The mandibular arch pneumatic system includes the quadrate and/or the articular

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

583   mandibular) arch, like the middle ear sac itself (Witmer 1997). As nonavian theropods, the

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

585   pneumatize the quadrate by entering through a single medial or anteromedial foramen or not

586   (Witmer 1990; Tahara and Larsson 2011). In the basal theropods that do not have a pneumatic

587   quadrate, both medial and posterior fossae of the quadrate correspond to the osteological trace

588   of the quadrate diverticulum. In nonavian theropods with a pneumatic quadrate, the position

589   of the quadrate diverticulum is variable such as in ornithomimids (Tahara and Larsson 2011),

590   carcharodontosaurids and oviraptorids (pers. observ.). The quadrate diverticulum of nonavian

591   theropods may also have communicated with other diverticula such as the squamosal

592   diverticulum as in *Conchoraptor gracilis* (Kundrát and Janáček 2007), and the siphoneal

593   diverticulum of the articular as in *Dilong paradoxus*, *Aerosteon riocoloradensis* and perhaps

24

594   other nonavian maniraptorans (Sereno et al. 2008; Tahara and Larsson 2011). In

595   *Tyrannosaurus rex*, however, the siphoneal diverticulum does not pass through the quadrate

596   and the quadrate diverticulum only enters the ventral opening of the pterygoid flange, and

597   then passes with or without the siphoneal diverticulum along the medial fossa of the pterygoid

598   flange. Likewise, the quadrate diverticulum only pneumatizes two distinct regions of the

599   quadrate in *Acrocanthosaurus atokensis* and *Mapusaurus roseae* (Tahara and Larsson 2011).

600

601   Figure 6

602   **Quadrate Ontogeny**

603   Skull ontogeny has been generally poorly studied in nonavian theropod, especially in

604   their early stage of development (Rauhut and Fechner 2005), but the ontogeny of the quadrate

605   bone has particularly received very little attention when compared to other cranial bones (see

606   Carr 1999; Loewen 2010). Although the quadrate of embryonic and juvenile specimens has

607   been reported in many nonavian theropod clades such as basal Megalosauroidea (Rauhut et al.

608   2012), Spinosauridae (Hendrickx and Mateus 2012), basal Avetheropoda (Hendrickx and

609   Mateus 2012), Tyrannosauridae (e.g. Bakker et al. 1988; Carr and Williamson 2010; Tsuihiji

610   et al. 2011), Compsognathidae (Dal Sasso and Maganuco 2011), alvarezsaurid (Dufeau 2003),

611   Oviraptoridae (Norell et al. 1994, 2001; Weishampel et al. 2008) and Troodontidae

612   (Varricchio et al. 2002), the ontogenic variations of the nonavian theropod quadrate has only

613   been investigated by Hendrickx and Mateus (2012) hitherto. These authors reported two

614   incomplete quadrates belonging to embryos of *Lourinhanosaurus autunesi* (Fig. 6) from the

615   Upper Jurassic of Portugal (Mateus et al. 1998; de Ricqlès et al. 2001; Mateus 2005).

616   Comparison of these two bones with the quadrates of the closest relative of

617   *Lourinhanosaurus*, *Sinraptor dongi* (Benson 2010; Benson et al. 2010) allowed Hendrickx

618   and Mateus (2012) to suggest that the absence of a quadrate foramen and the poor

619   delimitation of the two mandibular condyles and the intercondylar sulcus were most likely

620   ontogenetical features present in the allosauroid quadrate. Hendrickx and Mateus (2012) also

621   examined the ontogenic changes of the quadrate in spinosaurids from the Cenomanian of

622   Eastern Morocco. Based on five quadrates belonging to juvenile, subadult and adult

623   specimens of *Spinosaurus* sp., they were able to propose a list of ontogenetical steps that they

624   divided into juvenile, subadult and adult stages. The ontogenetical transformation occurring in

625   the *Spinosaurus* quadrate are the clear delimitation of the ento- and ectocondyle, the

626   intercondylar sulcus and the quadrate head, as well as the development of a ventral projection

627   of the dorsal quadratojugal contact and the excavation of both ventral and dorsal

628   quadratojugal contacts, allowing a firm contact between the quadrate and quadratojugal to be

629   present in sub-adults and adults specimens.

630   Well-preserved quadrates are present in a small and large specimens of the

631   alvarezsaurid *Shuvuuia deserti* (Chiappe et al. 1998; Dufeau 2003). Dufeau (2003), who

632   interprets the small skull (IGM 100-1001) and the larger one (IGM 100-977) as belonging to a

633   juvenile and adult specimens of *Shuvuuia deserti*, respectively, comprehensively described

634   the quadrate bone but did not investigate the ontogenetic variation occurring in the skull of

635   *Shuvuuia deserti*. Personal examination of the two specimens allowed to observe major

636   differences in the quadrate morphology (Fig. 3.3-3.6) that could be interpreted as ontogenetic

637   variations. The quadrate body of IGM 100-1001 is extremely ventro-dorsally elongated, with

638   a prominent and narrow quadrate ridge along the dorsal half of the quadrate bone. On the

639   other hand, the quadrate body of the larger specimen IGM 100-977 is shorter, with a

640   relatively shallow quadrate ridge. The mandibular articulation of IGM 100-1001 is

641   lateromedially expanded and the lateral part of the articulation is subtriangular in outline and

642   strongly projects laterally. The mandibular articulation of IGM 100-977 is particularly short,

643   subrectangular in outline in posterior view, and lacks a lateral projection (Fig. 3.3, 3.5). This

644 projection may however be broken and present as an isolated piece of bone displaced on the

645 ventrolateral surface of the pterygoid flange (pers. obs.). In IGM 100-1001, the lateral process

646 is ventro-dorsally long, subtriangular in lateral view, almost subrectangular in posterior view,

647 and reaches the quadrate head dorsally. The most lateral corner projects anteriorly to contact

648 the postorbital, and the postorbital contact of the quadrate extends along the anterodorsal

649 surface of the lateral process. The ventral most part of the lateral process forms a small corner

650 dorsal to the parabolic outline of the ventral part of the quadrate body. On the contrary, the

651 lateral process of IGM 100-977 only projects laterally and does not extend to the quadrate

652 head dorsally. The lateral margin of the lateral process is parabolic in outline, and neither

653 includes a small corner ventrally, nor an important projection anteriorly. The quadrate

654 foramen of IGM 100-1001, forms a large fenestra delimited by the quadrate, jugal and,

655 postorbital. If an articulation between the postorbital and the lateral corner of the lateral

656 process was present in IGM 100-977 as well, the quadrate foramen of this specimen would

657 have been much smaller, and delimited by the ventral half of the quadrate only. The quadrate

658 head of the small specimen (IGM 100-1001) is incipiently bistylic and oriented

659 posteromedially to contact the squamosal dorsally, and the braincase posteromedially (Fig.

660 3.3). The quadrate head of IGM 100-977 is strongly inclined laterally and seems to include a

661 single condyle only, although Dufeau (2003) noted that the quadrate head was also divided by

662 a very weak intercondylar sulcus in the adult specimen.

663 Dufeau (2003) interpreted these differences in the two specimens of *Shuvuuia deserti*

664 as ontogenetic and taphonomic variations (Dufeau pers. comm.). According to Dufeau (2003),

665 the contact between the quadrate head and the junction of the squamosal and postorbital,

666 which is unique in IGM 100-1001 among nonavian theropods, is, for instance, interpreted as a

667 taphonomic condition where the quadrate head would be taphonomically displaced laterally.

668 Nevertheless, both left and right quadrate of IGM 100-1001 occupy the same position and

669   share similar contact with the postorbital and squamosal, and the skull suffered neither

670   compressional nor shear distortions (Dufeau 2003; pers. obs.). A taphonomic displacement of

671   the quadrate of IGM 100-1001 seems therefore unlikely, and the postorbital contact of the

672   quadrate is an autapomorphy of *Shuvuuia deserti*. Despite the fact that the right quadrate of

673   the larger specimen IGM 100-977 may have been subject to important postmortem

674   compression (as the rest of the skull which is ventro-dorsally flattened), the numerous

675   differences existing between IGM 100-1001 and IGM 100-977 suggests that these variations

676   may be taphonomic, ontogenetic, but also perhaps taxonomic. The ontogenetic variations

677   occurring in the spinosaurid quadrates are subtle and only concern the delimitation of the

678   condyles and quadrate head, and the reinforcement of the quadrate and quadratojugal suture,

679   so that the general morphology of the quadrate bone does not change at all. If the features

680   differentiating IGM 100-1001 and IGM 100-977 are mostly ontogenetic, the quadrate of

681   *Shuvuuia deserti* would therefore undergo a major metamorphosis during its development,

682   including a dorsoventral shortening of the quadrate bone, rotation of the quadrate head from a

683   medial to a lateral orientation, posterior displacement of the lateral process, and

684   morphological transformation of the lateral process from a subtriangular to a parabolic

685   process. Although plausible, these ontogenetic transformations seem a bit extreme, and it is

686   reasonable to suggest that IGM 100-977 and IGM 100-977 may belong to two taxa, perhaps

687   two species of *Shuvuuia*.

688   Quadrate pneumaticity appears early in ontogeny as it has been reported in the embryo

689   of *Troodon formosus* (Varricchio et al. 2002) and the juvenile *Tarbosaurus baatar* (Tsuihiji et

690   al. 2011). Although absent in the embryonic specimen of *Lourinhanosaurus autunesi*, a

691   quadrate foramen exists in many juvenile specimens of theropods such as the hatchling

692   *Scipionyx samniticus* (Dal Sasso and Maganuco 2011) and the early posthatchling

693   *Sciurumimus albersdoerferi* (Rauhut et al. 2012). Although the quadrate and quadratojugal

694   are weakly articulated to each other in immature tetanurans (Hendrickx and Mateus 2012), a

695   fusion between the quadrate and pterygoid was already present in oviraptorid embryos (Norell

696   et al. 2001).

697

698   **CONCLUSIONS**

699   A revised nomenclature of the quadrate bone, along with a corresponding set of

700   abbreviations, is here proposed and provides a standard set of terms for describing this cranial

701   bone in nonavian theropod dinosaurs. The quadrate can be divided into two regional

702   categories, the quadrate body and the pterygoid flange, and twelve anatomical sub-units, the

703   quadrate shaft, quadrate head, quadrate ridge, quadrate foramen, lateral process, quadratojugal

704   contact, squamosal contact, pterygoid contact, mandibular articulation, medial fossa, and

705   posterior fossa. Although being highly variable in shape, all of these quadrate entities, with

706   perhaps the exception of the posterior fossa, are easily recognisable inter-taxa and a

707   description of their morphology should be provided in the literature.

708   A summary of the current knowledge on the quadrate function, pneumaticity

709   and ontogeny in nonavian theropods allows some evidence about this bone to be highlighted.

710   The quadrate of large majority of nonavian theropods is akinetic and a streptostylic quadrate

711   may have been present in some derived coelurosaurs such as the alvarezsaurid *Shuvuuia*

712   *deserti* and the oviraptorid *Nemegtia huangi*. A lateral movement of the rami while the

713   mandible was depressed was permitted in many theropods such as spinosaurids thanks to a

714   helicoidal and diagonally oriented intercondylar sulcus of the mandibular articulation.

715   Likewise, the presence of an intercondylar notch constricting the intercondylar sulcus in

716   allosaurids was interpreted to be a joint-stabilization zone that would improve the stability of

717   the mandibular articulation when the mouth was widely opened.

A pneumatic quadrate was present in members of most nonavian avetheropod clades

such as allosauroids, tyrannosaurids, compsognathids, therizinosauroids, ornithomimoids,

oviraptorids, troodontids and dromaeosaurids, in which pneumatopores typically open in the

ventral part of the pterygoid flange and in the medial and lateral fossae. Although the

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

system was linked to only one pneumatopore in most avetheropods, the presence of several

pneumatic openings perforating different sides of the quadrate have been recorded in

Neovenatoridae, Carcharodontosauridae and Tyrannosauridae.

A poorly delimited mandibular condyles, intercondylar sulcus and quadrate head, and

a quadratojugal contact with a smooth surface have been interpreted as ontogenetical features

in the quadrate of embryonic and juvenile basal tetanurans. The development of a quadrate

foramen and a ventral projection of the dorsal quadratojugal contact seem also to happen

during ontogeny in allosauroids and spinosaurids, respectively. On the other hand,

pneumaticity and a strong suture between the quadrate and quadratojugal appear early in

ontogeny, in the embryonic stage of coelurosaurs. Finally, based on the quadrate morphology,

the two specimens assigned to *Shuvuuia deserti*, considered by some as juvenile and adult

specimens, may belong to two distinct taxa.

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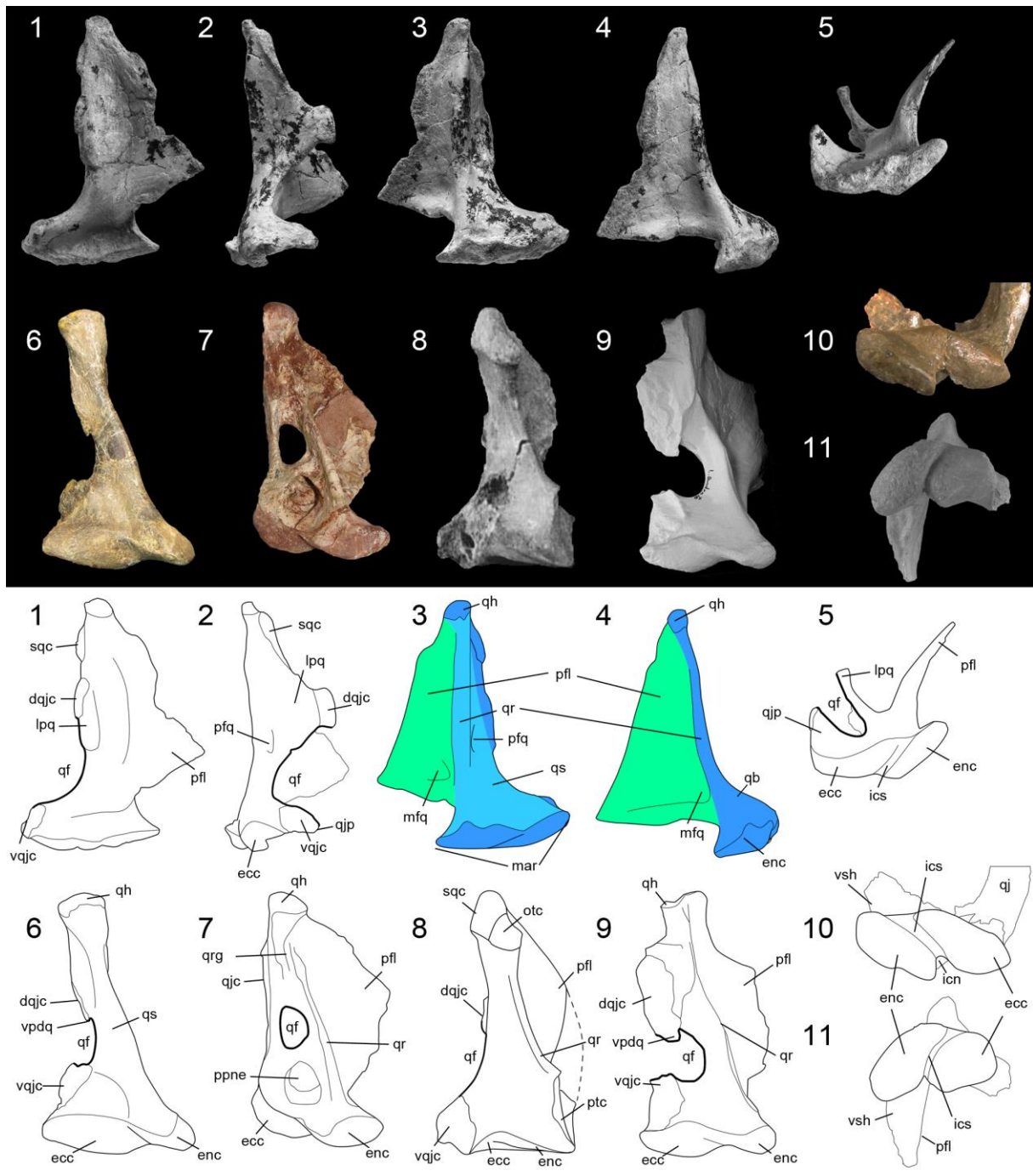1162   trophic diversification. *Zoology* 100:25–57.

1163

FIGURE CAPTIONS AND TABLES

1165

FIGURE 1. Anatomy of nonavian theropod quadrates. Right (**1–5**) quadrate of *Tsaagan*

mangas (IGM 100-1015; courtesy shared by Mick Ellison © AMNH) in (**1**) anterior, (**2**)

lateral, (**3**) posterior, (**4**) medial and (**5**) ventral views; left (**6–10**) and right (**11**) quadrates of

(**6**) *Baryonyx walkeri* (BMNH R9951), (**7**) *Aerosteon riocoloradensis* (MCNA-PV-3137;

courtesy shared by Martín Ezcurra), (**8**) an indeterminate Oviraptoridae (GIN A; Maryańska

1171 and Osmólska 1997:fig. 1), (**9**) *Tyrannosaurus rex* (BHI 3333, cast; Larson and Carpenter,

1172 2008), (**10**) *Allosaurus 'jimmadseni'* (SMA 005/02), and (**11**) *Majungasaurus crenatissimus*

1173 (FMNH PR 2100, cast; courtesy shared by Lawrence Witmer) in (**6–9**) posterior and (**10–11**)

1174 ventral views. Abbreviations: **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**,

1175 entocondyle; **icn**, intercondylar notch; **ics**, intercondylar sulcus; **lpq**, lateral process of the

1176 quadrate; **mar**, mandibular articulation; **mfq**, medial fossa of the quadrate; **pfl**, pterygoid

1177 flange (in green); **pfq**, posterior fossa of the quadrate; **ppne**, posterior pneumatopore; **qb**,

1178 quadrate body (in blue); **qf**, quadrate foramen (delimited by a broader line); **qh**, quadrate

1179 head; **qj**, quadratojugal; **qjp**, quadratojugal process; **qr**, quadrate ridge; **qrg**, quadrate ridge

1180 groove; **qs**, quadrate shaft (in light blue); **sqc**, squamosal contact; **vqjc**, ventral quadratojugal

1181 contact; **vpdq**, ventral projection of the dorsal quadratojugal contact; **vsh**, ventral shelf.
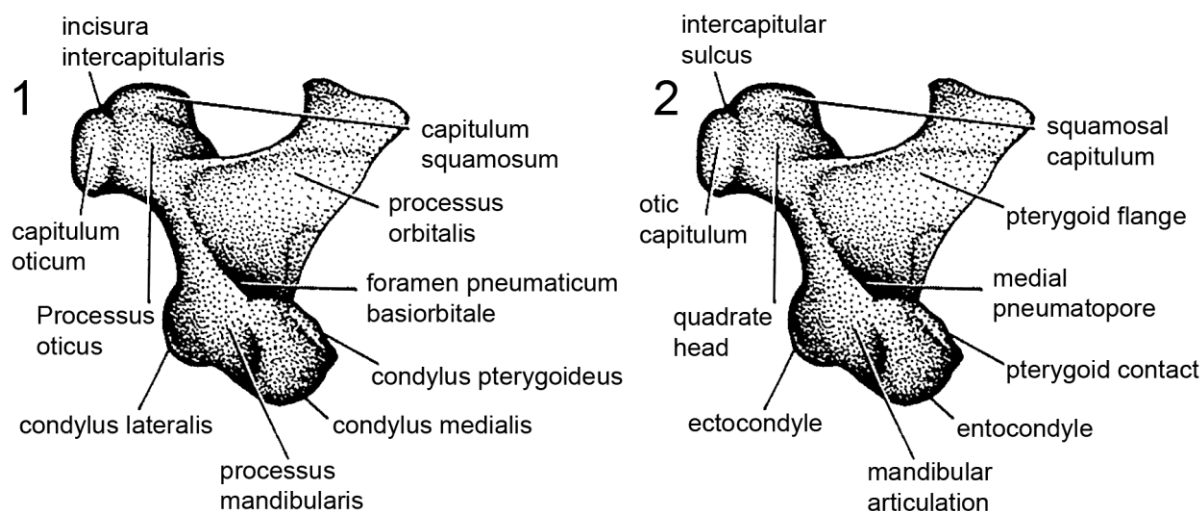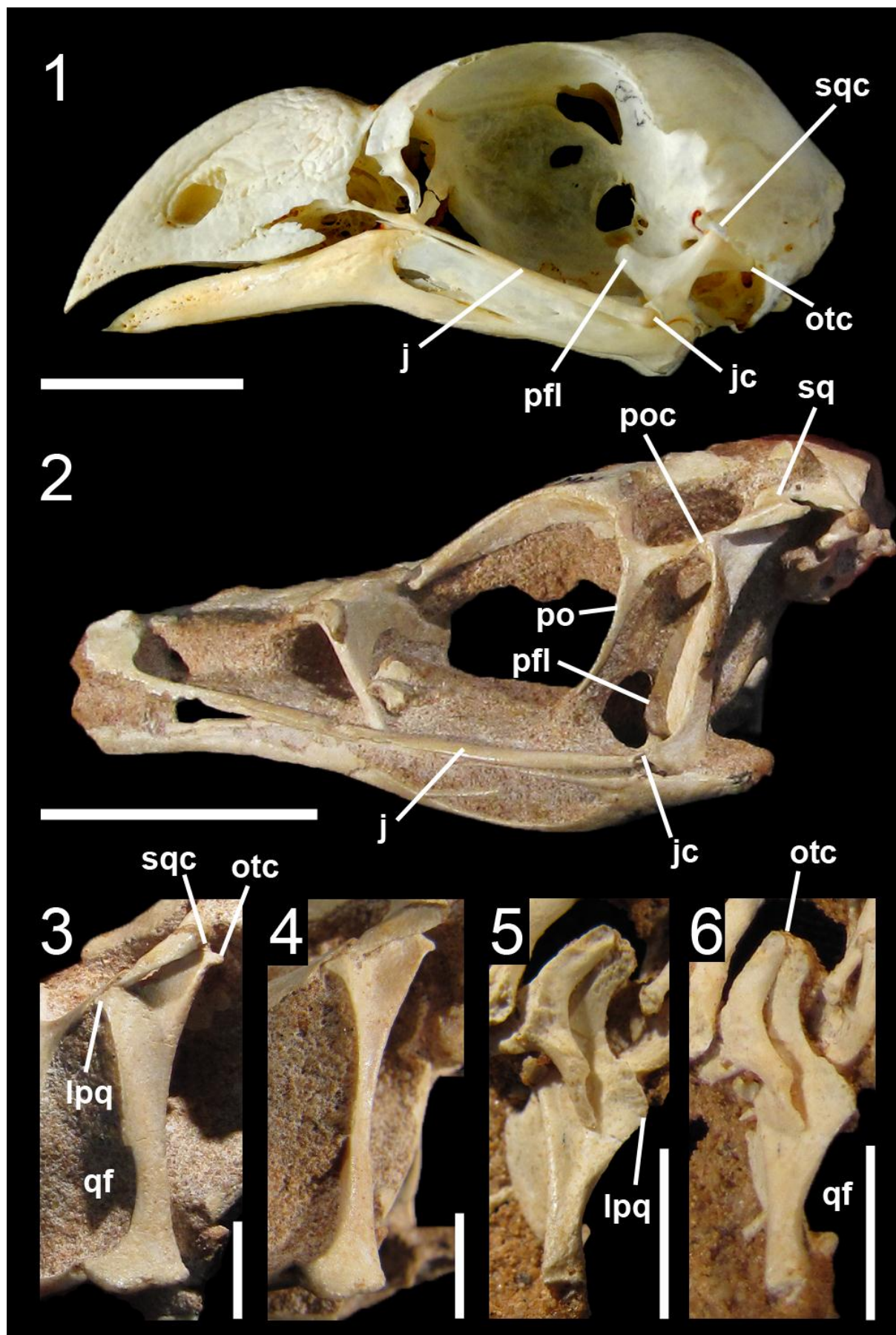
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1184 **FIGURE 2.** Avian and non-avian theropod terminology of the quadrate bone. Left quadrate

1185 of *Fregata minor* (Great Frigatebird) in medial view annotated with (**1**) Baumel and Witmer

1186 (1993) terminology, and (**2**) the here proposed terminology for the nonavian theropod

1187 quadrate (image from Witmer 1990 and Baumel and Witmer (1993); modified).

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1190   **FIGURE 3.** Skull comparison between (**1**) the bird *Corythaeola cristata* (Great Blue Turaco;

1191   NH.34.26; courtesy of the Horniman Museum & Gardens), and (**2**) the alvarezsaurid

1192   *Shuvuuia deserti* (IGM 100-1001; reversed) in lateral view. Comparison between the left

1193   quadrate of the juvenile? specimen of *Shuvuuia deserti* (IGM 100-1001) in (**3**) posterior, and

1194   (**4**) lateral view, and the right quadrate of the adult specimen of *Shuvuuia deserti* (IGM) in (**5**)

1195   posterior, and (**6**) posterolateral views. Abbreviations: **j**, jugal; **jc**, jugal contact; **lpq**, lateral

1196   process; **otc**, otic capitulum; **pfl**, pterygoid flange; **po**, postorbital; **poc**, postorbital contact;

1197   **qf**, quadrate foramen; **sq**, squamosal; **sqc**, squamosal capitulum. Scale bars = 2 cm (1-2), 1

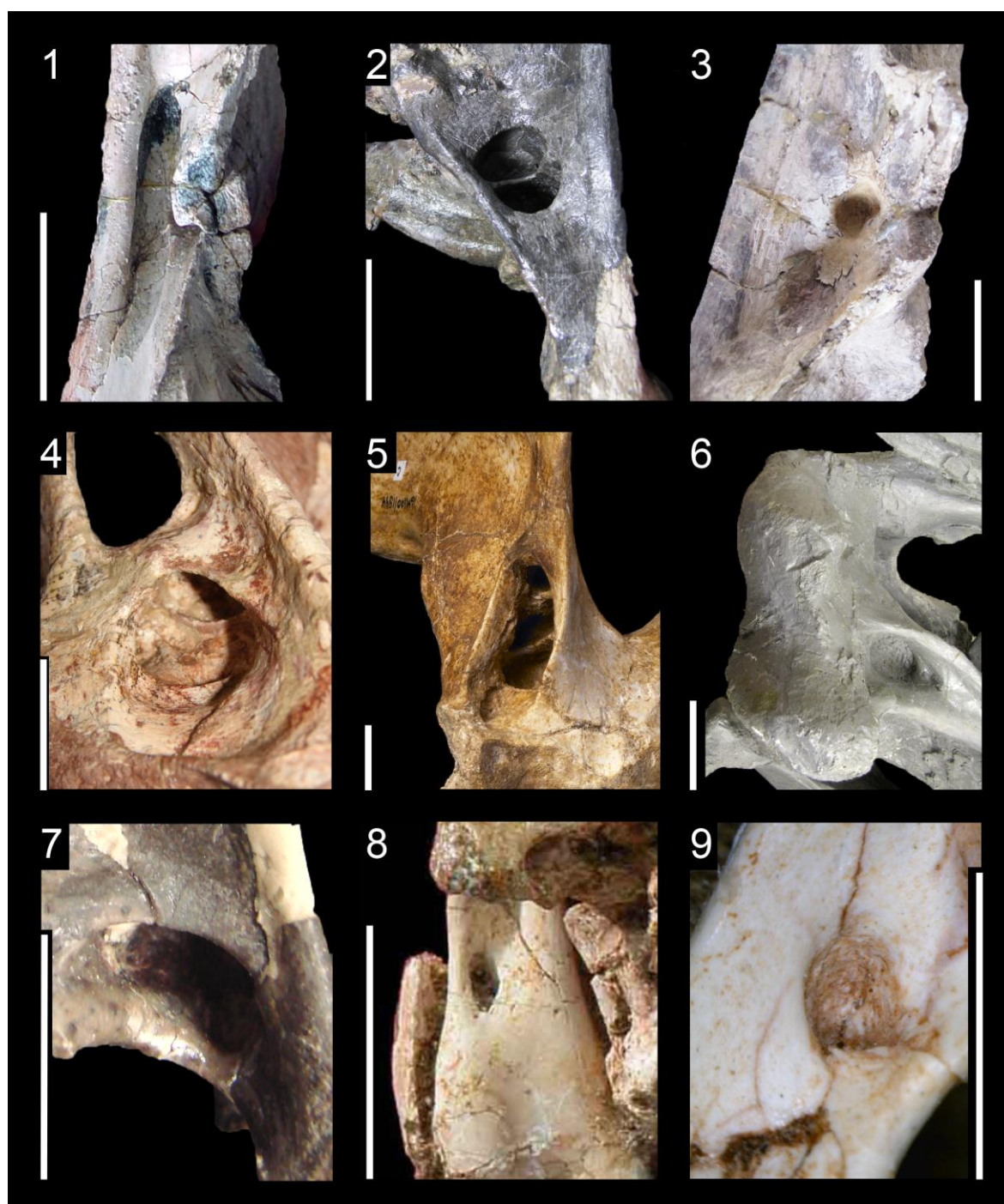1198   cm (5-6), and 5 mm (3-4).

1199

FIGURE 4. Morphology and position of pneumatic openings in the quadrate of nonavian

Theropoda. Pneumatic fossa (**1**) of the right quadrate of the metriacanthosaurid *Sinraptor*

dongi (IVPP 10600) in posterior view (courtesy of Philip Currie). Medial pneumatopore (**2**) of

the right quadrate of the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345) in

medial view. Medial pneumatopore (**3**) of the left quadrate of the carcharodontosaurid

1206 *Giganotosaurus carolinii* (MUCPv CH 1) in medial view. Posterior pneumatopore (**4**) of the

1207 left quadrate of the neovenatorid *Aerosteon riocoloradensis* (MCNA PV 3137) in posterior

1208 view (courtesy of Martín Ezcurra). Ventral pneumatopore (**5**) of the right quadrate of the

1209 tyrannosaurid *Alioramus altai* (IGM 100–844) in ventral view (courtesy of Mick Ellison).

1210 Ventral pneumatopore (**6**) of the left quadrate of the tyrannosaurid *Tyrannosaurus rex*

1211 (FMNH PR2081; cast) in ventral view. Medial pneumatopore (**7**) on the right quadrate of the

1212 therizinosauroid *Falcarius utahensis* (UMNH VP 14559) in medial view (courtesy of Lindsay

1213 Zanno). Posterior pneumatopore (**8**) of the left quadrate of the ornithomimid *Garudimimus*

1214 *brevipes* (IGM 100–13) in posterior view (courtesy of Yoshitsugu Kobayashi). Posterior

1215 pneumatopore (**9**) of the right quadrate of the dromaeosaurid *Buitreraptor gonzalezorum*

1216 (MPCA 245) in posterior view. Scale bars = 5 cm (1–3,6), 2 cm (4,8), 1 cm (5,7), 5 mm (9).
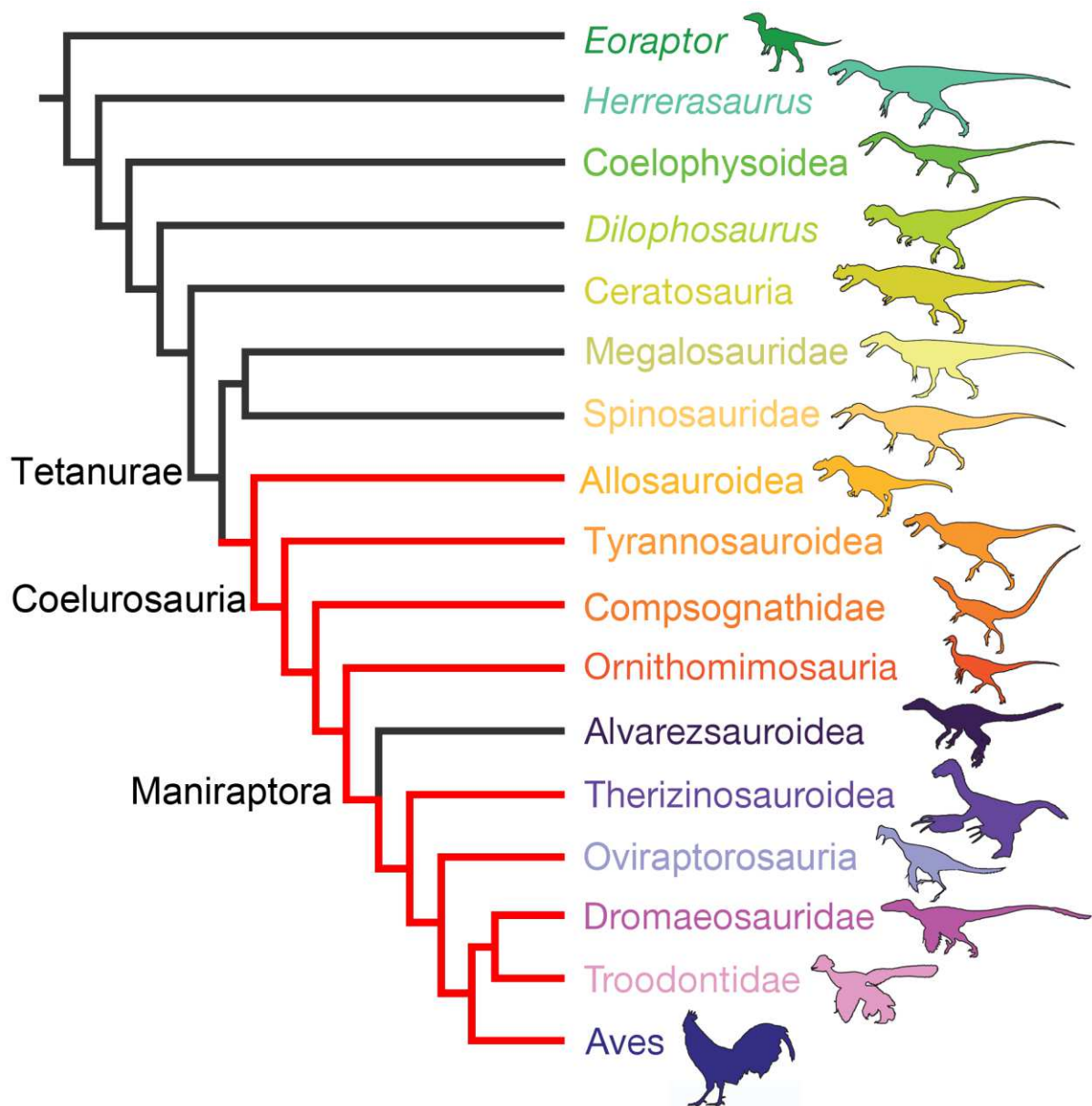
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FIGURE 5. Distribution of quadrate pneumaticity in Theropoda. Simplified cladogram of

theropod dinosaurs showing the phylogenetic distribution of a pneumatic quadrate denoted in

red (from Bhullar et al., 2012; Modified). Pneumaticity is present in the quadrate of

Allosauroidea (*Acrocanthosaurus*, *Mapusaurus*, *Giganotosaurus*), Tyrannosauroidea

(*Alioramus*, *Albertosaurus*, *Tyrannosaurus*), Compsognathidae (*Sinosauropteryx*),

Ornithomimosauria (*Ornithomimus*), Therizinosauria (*Falcarius*), Oviraptorosauria

(*Conchoraptor*), Troodontidae (*Sinovenator*), Dromaeosauridae (*Buitreraptor*) and many

birds. There is no evidence of a pneumatic quadrate in Alvarezsauroidea hitherto. When

1227 optimized onto this simplified tree, a pneumatic quadrate is a synapomorphy of

1228 Avetheropoda.

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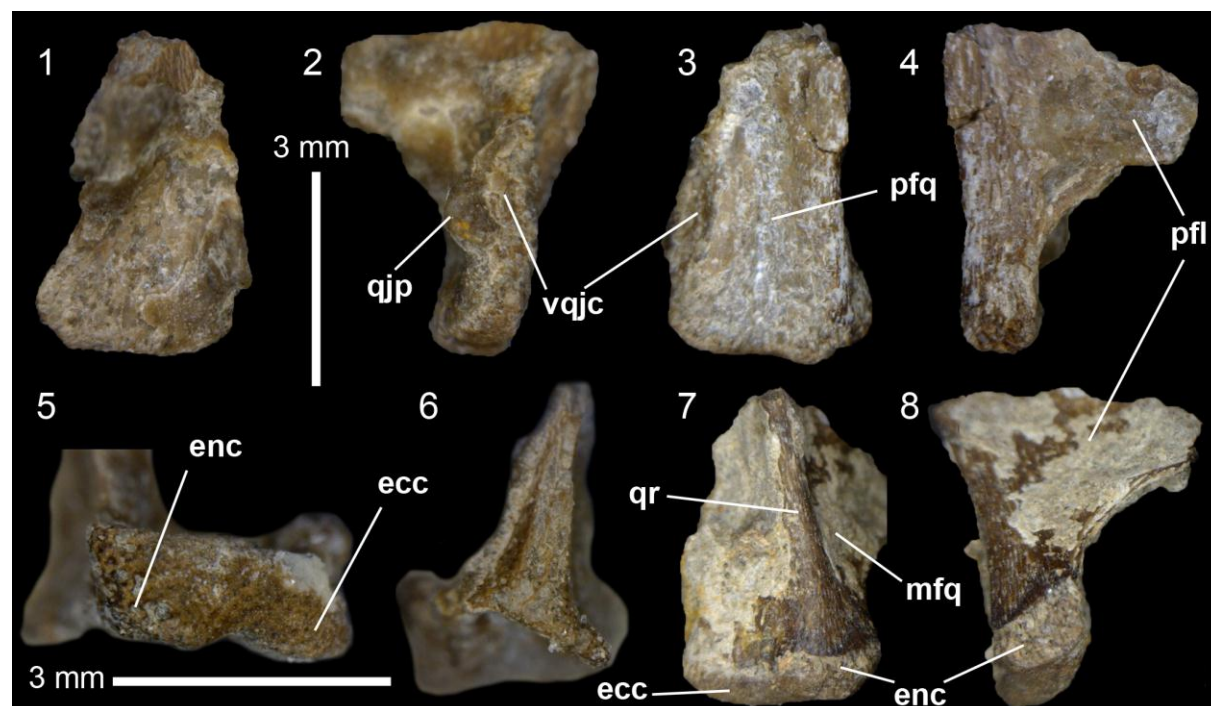
1231 **FIGURE 6.** Quadrate of *Lourinhanosaurus antunesi* embryo. Incomplete left (**1–8**) quadrate

1232 (ML565-150) in (**1**) anterior, (**2**) lateral, (**3**) posterior, (**4**) medial, (**5**) ventral, (**6**) dorsal, (**7**)

1233 posteromedial, and (**8**) ventromedial views (the quadrate in (**7**) and (**8**) was photographed

1234 before preparation). Abbreviations: **dqjc**, dorsal quadratojugal contact; **ecc**, ectocondyle; **enc**,

1235 entocondyle; **mfq**, medial fossa; **pfl**, pterygoid flange; **pfq**, posterior fossa; **qjp**, quadratojugal

1236 process; **qr**, quadrate ridge; **vqjc**, ventral quadratojugal contact.

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1238 **TABLE 1.** Standardized terminology and abbreviation of the nonavian theropod quadrate and

1239 comparison with the terminology of the avian quadrate based on Baumel and Witmer (1993),

1240 Elzanowski et al. (2001) and Elzanowski and Stidham (2010).

Nonavian theropod quadrate (q)		Avian theropod quadrate
Quadrate body	qb	Corpus quadrati
Quadrate shaft	qs	/
Quadrate ridge	qr	/
Quadrate ridge groove	qrg	/
Quadrate head	qh	Processus oticus/Pars otica/Caput quadrati
Otic capitulum	otc	Capitulum oticum
Squamosal capitulum	sqc	Capitulum squamosum
Intercapitular sulcus	icas	Incisura/Vallecula intercapitularis
Quadrate foramen	qf	/
Mandibular articulation	mar	Pars/Processus mandibularis
Ectocondyle	ecc	Condylus (mandibularis) lateralis
Entocondyle	enc	Condylus (mandibularis) medialis
Mediocondyle	mec	Condylus caudalis
Intercondylar sulcus	ics	Vallecula intercondylaris
Intercondylar notch	icn	Depressio praecondylaris
Lateral process	lpq	/
Quadratojugal contact	qjc	Cotyla quadratojugalis
Ventral quadratojugal contact	vqjc	/
Dorsal quadratojugal contact	dqjc	/

Quadratojugal process	qjp	/
Ventral projection of the dorsal quadratojugal contact	vpdq	/
Squamosal contact	sqc	/
Posterior fossa	pfq	/
Quadrate diverticulum	qdi	/
Dorsal pneumatopore	dpne	Foramen pneumaticum caudomediale
Medial pneumatopore	mpne	Foramen pneumaticum basiorbitale
Posterior pneumatopore	ppne	Foramen pneumaticum rostromediale
Ventral pneumatopore	vpne	Foramen pneumaticum adventitium
Pterygoid flange	pfl	Processus orbitalis
Pterygoid contact	ptc	Condylus pterygoideus/Facies articularis pterygoidea
Medial fossa	mfq	Fossa basiorbitalis
Ventral shelf	vsh	/

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1242

1243 **APPENDIX**

1244 Appendix 1: Function of quadrate sub-entities.

1245 Appendix 2: Quadrate sub-units terminology.

1246

1247 **APPENDIX 1A.** Function of quadrate sub-entities.

Anatomical component	Nature	Anatomical sub-entity	Function
Quadrate diverticulum	Tympanic sinus, mandibular arch pneumatic system	Lateral, medial and posterior pneumatopores	Auditory function?
Siphoneal diverticulum	Tympanic sinus, mandibular arch pneumatic system	Ventromedial pneumatopore?	Auditory function?
Dorsal tympanic diverticulum	Tympanic sinus	Cotylus, separated into otic and squamosal capitula	Auditory function
Musculus Protractor Pterygoideus (MPPt)	Orbitotemporal muscle	Medial surface of the pterygoid ramus	Insertion for the MPPt
Musculus Adductor Mandibulae Externus Medialis (MAMEM)	Temporal muscle	Quadrate body between otic and orbital processes	Origin for the MAMEM
Musculus Adductor Mandibulae Externus Superficialis	Temporal muscle	Ootic process	Origin for the MAMES

(MAMES)			
Musculus Adductor Mandibulae Posterior (MAMP)	Palatal muscle	Lateral surface of the pterygoid ramus	Origin for the MAMP
Musculus Pterygoideus Ventralis (MPTv)	Palatal muscle	Lateral surface of the pterygoid ramus	Insertion for the MPTv
Musculus Pseudotemporalis Profundus (MPsTP)	Palatal muscle	Anterior surface of the ootic process	Origin for the MPsTP
Otic joint	Synovial joint	Otic process of cotylus	Articulation with squamosal
Articular process of quadrate	Synovial joint	Mandibular condyles	Articulation with mandible
Intercondylar sulcus	Synovial joint	Groove between ectocondyle and entocondyle	Ventral or ventrolateral displacement of mandible rami
Branches of maxillomandibular vessels	Neurovascular bundle	Quadrate foramen	Neurovasculature transmission between the occiput and adductor chamber

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1249   **APPENDIX 1B.** Function of quadrate sub-entities.

Anatomical component	Theropod clades involved	Publication
Quadrate diverticulum	All Theropoda	(Witmer 1990; Kundrát and Janáček 2007; Tahara and Larsson 2011)
Siphoneal diverticulum	Allosauroidea? Tyrannosauroidea?	(Tahara and Larsson 2011)
Dorsal tympanic diverticulum	Neognathae	(Witmer 1990)
Musculus Protractor Pterygoideus (MPPt)	All Theropoda	(Holliday 2009)
Musculus Adductor Mandibulae Externus Medialis (MAMEM)	Avian and non-avian? Theropoda	(Sedlmayr 2002)
Musculus Adductor Mandibulae Externus Superficialis (MAMES)	Avian and non-avian? Theropoda	(Sakamoto 2008)
Musculus Adductor Mandibulae Posterior (MAMP)	All Theropoda	(Molnar 1998; Sakamoto 2008; Holliday 2009)
Musculus Pterygoideus Ventralis (MPTv)	Tyrannosauridae?	(Sakamoto 2008; Holliday 2009)
Musculus Pseudotemporalis Profundus (MPsTP)	Neornithes	(Holliday and Witmer 2008; Sakamoto 2008; Holliday

		2009)
Otic joint	All Theropoda	(Holliday and Witmer 2008)
Articular process of quadrate	All Theropoda	(Holliday and Witmer 2008)
Intercondylar sulcus	All Theropoda	(Molnar 1991; Bakker 1998; Hendrickx and Buffetaut 2008)
Branches of maxillomandibular vessels	Some Theropoda	(Sampson and Witmer 2007)

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1251　**APPENDIX 2A.** Terminology of nonavian theropod quadrate sub-unit by authors.

Source	Referred taxa	Quadrate shaft	Quadrate ridge	Pterygoid flange
(Sereno and Novas 1994)	*Herrerasaurus*	Shaft	/	Pterygoid ramus
(Colbert 1989)	*Coelophysis*	Ascending process	/	Quadrate flange
(Welles 1984)	*Dilophosaurus*	Shaft	Column	Pterygoid wing
(Smith et al. 2007)	*Cryolophosaurus*	Body	Rounded ridge	/
(Gilmore 1920)	*Ceratosaurus/ Allosaurus*	/	/	Sheet/projection
(Madsen and Welles 2000)	*Ceratosaurus*	Pillar	/	Pterygoid wing
(Carrano et al. 2011)	*Masiakasaurus*	Shaft/body	/	Pterygoid articular flange
(Coria and Salgado 1998)	*Ilokelesia*	/	/	Medial process
(Bonaparte et al. 1990)	*Carnotaurus*	/	/	Anteromedial projection
(Sampson and Witmer 2007)	*Majungasaurus*	Shaft	/	Pterygoid ramus
(Sadleir et al. 2008)	*Eustreptospondylus*	Shaft	/	Pterygoid ala

(Britt 1991)	*Torvosaurus*	Shaft	/	Pterygoid blade
(Charig and Milner 1997)	*Baryonyx*	Shaft	/	Pterygoid flange
(Madsen 1976)	*Allosaurus*	Shaft/body	/	Contact with the pterygoid
(Sereno et al. 2008)	*Aerosteon*	Shaft	/	Pterygoid process
(Currie 2006)	*Sinraptor*	Column	/	Pterygoid flange/ala
(Currie and Carpenter 2000)	*Acrocanthosaurus*	/	/	/
(Eddy and Clarke 2011)	*Acrocanthosaurus*	/	/	Pterygoid wing/contact
(Brusatte et al. 2010)	*Shaochilong*	Shaft	/	Quadrate flange
(Coria and Currie 2006)	*Mapusaurus*	/	/	Pterygoid flange
(Rauhut et al. 2010)	*Proceratosaurus*	/	Columnar ridge	Pterygoid flange
(Li et al. 2010)	*Xiongguanlong*	Shaft	/	Quadrate wing
(Brusatte et al. 2012)	*Alioramus*	Shaft	Robust ridge	Quadrate flange
(Carr 1996)	*Albertosaurus*	Quadrate body	Ridge	Pterygoid flange/process

(Currie 2003)	*Albertosaurus/ Daspletosaurus*	/	/	Pterygoid ala
(Molnar 1991)	*Tyrannosaurus*	Vertical bar	/	Pterygoid process
(Brochu 2003)	*Tyrannosaurus*	/	/	Pterygoidal flange
(Dal Sasso and Maganuco 2011)	*Scipionyx samniticus*	/	/	Pterygoid ala
(Kobayashi and Lü 2003)	*Sinornithomimus*	/	/	Pterygoid wing
(Kobayashi and Barsbold 2005)	*Garudimimus*	/	/	Pterygoid wing
(Zanno 2010)	*Falcarius*	/	/	Pterygoid process/flange/ wing
(Clark et al. 1994)	*Erlikosaurus*	Body	/	Orbital process
(Maryańska and Osmólska 1997)	*Oviraptoridae*	Shaft	/	Pterygoid ramus
(Choiniere et al. 2010)	*Zuolong*	Shaft	Ridge	Pterygoid ramus
(Burnham 2004)	*Bambiraptor*	/	/	/
(Norell et al.	*Tsaagan*	Shaft	/	Anterior/pteryg

2006)			oid flange
(Colbert and Russell 1969)	*Dromaeosaurus*	Shaft	Pterygoid flange/wing
(Currie 1995)	*Dromaeosaurus*	/	Anterodorsal lamina
(Norell and Hwang 2004)	*Saurornithoides*	Shaft	Pterygoid flange
(Norell et al. 2009)	*Zanabazar*	Shaft	/

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1253   **APPENDIX 2B.** Terminology of nonavian theropod quadrate sub-unit by authors.

Referred taxa	Lateral process	Quadrate foramen	Quadrate head	Ento-/Ectocondyles
Herrerasaurus	/	Quadrate foramen	Head	Distal condyles
Coelophysis	Smaller surface/wing	/	Upper extremity	Quadrate condyle
Dilophosaurus	Dorsal wing	Quadrate foramen	Head	Ento/Ectocondyles
Cryolophosaurus	/	Paraquadrate fenestra	Dorsal head	Medial/Lateral condyles
Ceratosaurus/Allosaurus	/	Quadrate foramen	/	articular surfaces
Ceratosaurus	Anterolateral wing	Quadrate foramen	Head	Ento/Ectocondyles
Masiakasaurus	/	Foramen	/	Medial/Lateral condyles
Ilokelesia	Lateral lamina/process	/	Squamosal condyle	Medial/Lateral condyles
Carnotaurus	/	/	/	Lower condyles
Majungasaurus	Lateral/quadratojugal ramus	Paraquadrate foramen	Head	Medial/Lateral condyles
Eustreptospondylus	/	/	Head	Medial/Lateral condyles

Torvosaurus	/	Quadrate foramen	Head	Medial/Lateral condyles
Baryonyx	/	Quadrate foramen	Head	Quadrate condyle
Allosaurus	/	Quadrate foramen	Head	Condyles
Aerosteon	/	Quadrate foramen	Head	Distal condyles
Sinraptor	Wing-like process	Quadratic foramen	Quadrate cotyle	Medial/Lateral condyles
Acrocanthosaurus	/	Quadrate foramen	Head	Condyles
Acrocanthosaurus	/	Quadrate foramen/fenestra	Quadrate cotylus	Medial/Lateral condyles
Shaochilong	/	Quadrate foramen	Quadrate cotylus/head	Medial/Lateral condyles
Mapusaurus	/	Quadratic foramen	Quadrate cotyle	Mandibular articulation
Proceratosaurus	/	Quadrate foramen	Head	Medial/Lateral condyles
Xiongguanlong	/	Quadrate foramen	/	Medial/Lateral condyles
Alioramus	/	Quadrate	Head	Medial/Lateral

		foramen		condyles
Albertosaurus	/	Quadrate fenestra	Quadrate cotyle	Medial/Lateral condyles
Albertosaurus/ Daspletosaurus	/	Quadrate fenestra	Quadrate cotylus	Mandibular condyles
Tyrannosaurus	/	Quadrate foramen	Hemispherical surface	Quadrate condyle
Tyrannosaurus	/	Quadrate foramen	Head	Medial/Lateral hemicondyles
Scipionyx samniticus	/	Paraquadrate foramen	Quadrate head	Medial/Lateral condyles
Sinornithomimus	/	Paraquadratic foramen	/	Medial/Lateral condyles
Garudimimus	/	Paraquadratic foramen	/	Mandibular condyles
Falcarius	/	Quadrate foramen	Head/Squamosal capitulum	Medial/Lateral condyles
Erlikosaurus	/	Quadrate foramen	Dorsal process	Mandibular process
Oviraptoridae	/	Quadrate foramen	Otic process	Medial/Lateral condyles
Zuolong	/	Quadrate foramen	Dorsal condyle	Medial/Lateral condyles
Bambiraptor	/	/	Otic process	Medial/Lateral

	Squamosal ramus	Quadrate foramen	Dorsal articulation	condyles
Tsaagan	Squamosal ramus	Quadrate foramen	Dorsal articulation	Articular ramus
Dromaeosaurus	/	Quadrate foramen	Head	Medial/Lateral condyles
Dromaeosaurus	/	Quadrate fenestra	Head	/
Saurornithoides	/	/	/	Medial/Lateral condyles
Zanabazar	/	/	Head	/

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