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1 **Title:** Expression of myosin heavy chain isoforms mRNA transcripts in the temporalis

2 muscle of common chimpanzees (Pan troglodytes)

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ABSTRACT

Purpose: The common chimpanzee (Pan troglodytes) is the primate that is phylogenetically most closely related to humans (Homo sapiens). In order to shed light on the anatomy and function of the temporalis muscle in the chimpanzee, we have analyzed the expression patterns of the mRNA transcripts of the myosin heavy chain (MyHC) isoforms in different parts of the muscle.

Basic procedures: We dissected the superficial, deep and sphenomandibularis portions of the temporalis muscle in five adult Pan troglodytes and quantified by real-time quantitative polymerase chain reaction the expression of the mRNA transcripts of the MyHC isoforms in each portion.

Main findings: We observed significant differences in the patterns of expression of the mRNA transcripts of the MyHC-IIM isoform between the sphenomandibularis portion and the anterior superficial temporalis (33.6% vs 47.0%; P=0.032) and between the sphenomandibularis portion and the anterior deep temporalis (33.6% vs 43.0; P=0.016). We also observed non-significant differences between the patterns of expression in the anterior and posterior superficial temporalis.

Principal conclusions: The differential expression patterns of the mRNA transcripts of the MyHC isoforms in the temporalis muscle in Pan troglodytes may be related to the functional differences that have been observed in electromyographic studies in other species of primates. Our findings can be applicable to the fields of comparative anatomy, evolutionary anatomy, and anthropology.

Keywords: temporalis muscle, Pan troglodytes, myosin heavy chain, RT-qPCR, sphenomandibularis

1. INTRODUCTION

The temporalis, masseter, and medial pterygoid muscles are the jaw-closing muscles that produce the occlusion of the mandible and other movements associated with chewing and biting (Taylor and Vinyard, 2013). The temporalis arises from the side of the skull and inserts onto the coronoid process of the mandible and the anterior edge of the mandibular ramus (Aiello and Dean, 1990). In the common chimpanzee (Pan troglodytes), the temporalis comprises a superficial and a deep portion that can be easily separated (Aiello and Dean, 1990; Oxnard and Franklin, 2008). In contrast, in humans (Homo sapiens), the temporalis has the equivalent of the deep temporalis in Pan troglodytes, while the superficial temporalis is either completely lacking or only vestigially present (Oxnard and Franklin, 2008; Lee et al., 2012). This loss of the superficial temporalis in humans is a result of the general reduction of the masticatory apparatus that occurred in the evolution of the genus Homo (Aiello and Dean, 1990), which may in turn be due to a relatively soft diet (Oxnard and Franklin, 2008).

Some authors make a distinction between the sphenomandibularis and the temporalis muscles in humans and consider the sphenomandibularis to be a separate muscle arising from the maxillary surface of the sphenoid bone and inserting on the temporal crest of the mandible (Dunn et al., 1996). Others, however, consider the sphenomandibularis to be a part of the temporalis, without its own specific vascularization and innervation (Türp et al., 1997; Shimokawa et al., 1998; Schön-Ybarra and Bauer, 2001; Geers et al., 2005; Sedlmayr et al., 2009). In non-human primates, such as the Macaca mulatta, the sphenomandibularis has been described as part of the deep temporalis (Skinner and Aziz, 2003).

72   Electromyographic studies of the temporalis in Homo sapiens and in the non-

73   human primates Macaca fuscata and Papio anubis have found that the temporalis acts

74   in the occlusal phase of the masticatory cycle, with different fibers acting at different

75   points of the cycle (Blanksma et al., 1997; Hylander et al., 2005; Wall et al., 2008). The

76   contraction of the anterior fibers, which run vertically, results in elevation of the

77   mandible, closing the mouth. The anterior fibers reach their peak of maximum activity

78   during the power stroke (Blanksma et al., 1997; Hylander et al., 2005; Vinyard et al.,

79   2008; Vinyard and Taylor, 2010). The posterior fibers run horizontally and their

80   contraction retracts the mandible, pulling the jaw posteriorly. The posterior fibers act

81   during a later phase of the power stroke in which the mandible moves laterally to

82   reposition the molar teeth (Ahlgren et al., 1985; Blanksma et al., 1997; Hylander et al.,

83   2005; Wall et al., 2008; Williams et al., 2011). The consistency of the food being

84   chewed also influences which muscle fibers are called into play (Grünheid et al., 2009).

85   In Macaca fuscata, Papio anubis, and Homo sapiens, more muscle fibers in the anterior

86   than in the posterior temporalis are used when chewing tough food (Blanksma et al.,

87   1997; Ross and Hylander, 2000; Hylander et al., 2005; Vinyard et al., 2008). In Papio

88   anubis, the increase in electromyographic activity in the anterior region of the

89   temporalis occurred primarily in the superficial temporalis, which has a greater capacity

90   to produce force (Wall et al., 2008). However, when chewing relatively softer food,

91   there was greater electromyographic activity in the posterior temporalis in Macaca

92   fuscata and Papio anubis (Hylander et al., 2005; Vinyard et al., 2008). In

93   electromyographic studies in Homo sapiens, the sphenomandibularis portion of the deep

94   temporalis worked together with the lateral pterygoid muscle to produce lateral

95   movements of the mandible and also helped maintain the mandible in a stable position

96   (Wood, 1986; Fuentes et al., 2012).

97   The functional characteristics of the temporalis can also be analyzed in terms of

98   the expression of the myosin heavy chain (MyHC) isoforms (Bottinelli and Reggiani,

99   2000). Different types of muscle fibers have different contractile properties (force,

100   contraction velocity, and resistance to fatigue) that are related to the expression patterns

101   of MyHC isoforms (Pette and Staron, 2000; Bottinelli et al., 1996; Harridge et al.,

102   1996). The main MyHC isoforms expressed in the skeletal muscles of mammals are

103   MyHC-I, MyHC-IIA, and MyHC-IIX (Sciote and Morris, 2000). The MyHC-I isoform

104   is mainly expressed in slow-twitch oxidative fibers and is the predominant isoform in

105   slow-twitch (type I) muscles (Schiaffino and Reggiani, 2011), which are characterized

106   by low force production and high resistance to fatigue. The MyHC-IIA and MyHC-IIX

107   isoforms are primarily expressed in fast-twitch oxidative glycolytic fibers and fast-

108   twitch glycolytic fibers, respectively, and are the predominant isoforms in fast-twitch

109   (type II) muscles (Schiaffino and Reggiani, 2011). Type IIX fibers are characterized by

110   very high force production and low resistance to fatigue, while type IIA fibers fall in

111   between the type I and type IIX fibers. In addition to the MyHC-I, MyHC-IIA, and

112   MyHC-IIX isoforms, the masticatory muscles of non-human primates also express the

113   MyHC-IIM isoform in type IIM muscle fibers (Rowlerson et al., 1983), which have a

114   moderate contraction velocity, similar to that of the type IIA fibers, and a high force

115   production, greater than that of the type IIX fibers (Hoh, 2002; Toniolo et al., 2008).

116   The composition of muscle fibers and the expression patterns of the MyHC

117   isoforms in the temporalis muscle of non-human primates have been studied by

118   histochemistry in Macaca mulatta (Maxwell et al., 1979; Miller and Farias, 1988) and

119   Cebus apella (Andreo et al., 2002), by immunohistochemistry in Macaca irus

120   (Rowlerson et al., 1983), and by sodium dodecyl sulfate polyacrylamide gel

121   electrophoresis (SDS-PAGE) in Papio anubis (Wall et al., 2013). Using ATPase

staining, Miller and Farias (1988) found that the temporalis muscle of Macaca mulatta

had 47.9-58.5% of type IIX fibers, 27.3-42.6% of type IIA fibers, and 6.6-21.3% of type

I fibers. When they compared the anterior and posterior superficial temporalis, they

found no significant differences in the percentage of type IIA and IIX fibers, while the

percentage of type I fibers was greater in the anterior than in the posterior superficial

temporalis (13.1% vs 6.6%). They also found that the posterior superficial temporalis

had a lower proportion of type I and IIA fibers (6.6% and 34.9%, respectively) than the

posterior deep temporalis (9.5% and 42.6%, respectively). Maxwell et al. (1979) also

used ATPase staining to study the temporalis muscle in Macaca mulatta and found a

higher proportion of type I fibers in the anterior than in the posterior superficial

temporalis (49.95% vs 20.65%). In contrast, Andreo et al. (2002), using ATPase

staining to study the Cebus apella, found no significant differences between the anterior

and posterior superficial temporalis. Importantly, none of these studies examined type

IIM fibers, which are the most frequent type in the temporalis of non-human primates

(Rowlerson et al., 1983). Using ATPase staining together with indirect

immunoperoxidase staining, Rowlerson et al. (1983) found that the central temporalis in

Macaca irus had 86% of type IIM fibers and 14% of type I fibers. A study using SDS-

PAGE to analyze the temporalis in Papio anubis found 87-88.7% expression of the

MyHC-IIM isoform in the anterior and 85.2-90.8% expression in the posterior

superficial temporalis, while the MyHC-I isoform was the only other isoform expressed

(Wall et al., 2013). In the deep temporalis, the MyHC-IIM isoform was expressed at

60.7% in males and 14.4% in females, while the MyHC-IIA isoform was expressed at

less than 5% and the MyHC-I isoform at 38.1% in males and 83.3% in females (Wall et

al., 2013).

146   To the best of our knowledge, no electromyographic or molecular studies have

147   examined the temporalis muscle in Pan troglodytes, which together with Pan paniscus,

148   is the primate that is phylogenetically most closely related to Homo sapiens. In order to

149   shed further light on the anatomy and function of the temporalis muscle in the common

150   chimpanzee, we have dissected the temporalis muscles of five adult chimpanzees and

151   quantified the mRNA transcripts of the MyHC-I, MyHC-IIA, MyHC-IIX, and MyHC-

152   IIM isoforms by real time quantitative polymerase chain reaction (RT-qPCR) in the

153   anterior and posterior portions of the superficial and deep temporalis as well as in the

154   sphenomandibularis portion of the temporalis. Our primary objective was to identify

155   differences in the expression patterns of the MyHC isoforms among the different parts

156   of the temporalis muscle, especially in the sphenomandibularis portion, which could be

157   associated with the functional differences identified by electromyographic studies in

158   humans and other primates.

159 **2. MATERIAL AND METHODS**

160   **2.1 Muscle samples**

161   A total of five adult Pan troglodytes were included in the study – two males and

162   three females. All five chimpanzees came from Spanish zoos and had died from causes

163   unrelated to the present study. All bodies had been cryopreserved without chemical

164   fixation within 24-48 hours after death. We dissected the right temporalis muscles of

165   four of the chimpanzees and the left temporalis muscle of one female chimpanzee

166   (specimen 03), since the right temporalis of this female had been damaged in a prior

167   necroscopy. All dissections were performed by the same investigator at the Anatomy

168   Museum of the University of Valladolid (Valladolid, Spain) (Table 1).

169   The investigator removed the adipose and conjunctive tissue to identify and

170   isolate the superficial, deep, and sphenomandibularis portions of the temporalis muscle

171   (Figures 1 and 2). He then weighed each of these portions on a precision scale, with the

172   exception of specimen 03, in which it was not possible to weigh the different portions.

173   In all five specimens, the investigator also obtained 0.5-cm^3 samples of the anterior and

174   posterior regions of the superficial and deep portions of the temporalis and of the

175   sphenomandibularis portion, which were cryopreserved in physiological saline solution

176   for later molecular analysis at the Unit of Human Anatomy and Embryology of the

177   University of Barcelona (Barcelona, Spain).

178   **2.2 RNA isolation and cDNA synthesis**

179   We extracted the RNA from the muscle samples using the commercial RNeasy

180   mini kit (Qiagen, Valencia, CA) according to the manufacturer's protocol. We used a

181   NanoDrop 1000 Spectrophotometer to determine the concentration, purity and amount

182   of RNA.

183   We used TaqMan Reverse Transcription Reagent Kit (Applied Biosystems,

184   Foster City, CA) to synthesize cDNA. We performed reverse transcription using 330 ng

185   of total RNA in 10 µl of RT Buffer, 22 ml of 25 mM magnesium chloride, 20 µl dNTPs,

186   5 µl Random Hexamers, 2 µl RNAse Inhibitor, 2.5 µl MultiScribe Reverse

187   Transcription and RNA sample plus RNAse-free water, for a final volume of 100 µl, in

188   the following thermal cycler conditions: 10 min 25ºC, 48 min 30 ºC and 5 min 95 ºC.

189   **2.3 Gene expression and quantification by RT-qPCR**

190   Applied Biosystems supplied primers and probes. Primers are labeled at the 5'

191   end with the reporter dye molecule FAM. MYH-I (Hs00165276_m1), MYH-IIA

192   (Hs00430042_m1), MYH-IIX (Hs00428600_m1) and MYH-IIM (Hs01385213_m1)

193 genes were analyzed. We used human ACTB (Beta Actin) gene probe labeled at the 5'

194 end with the reporter dye molecule FAM (Hs99999903_m1) as endogenous control.

195 We performed RT-qPCR in a total volume of 20 µl in the ABI Prism 7700

196 Sequence Detection System (Applied Biosystems) using the following master mix

197 conditions: 10 µl of the TaqMan Universal PCR Master Mix, 1 µl of the primers and

198 probes, 2 µl of the cDNA and 7 µl of the RNAse-free water. We ran all samples for

199 each gene in duplicate using this thermal cycler conditions: two min 50 ºC, 40x (10 min

200 95 ºC, 15 s 95 ºC) and 1 min 60 ºC. We used genomic DNA as negative control in each

201 run. We captured fluorescent emission data and quantified mRNA concentrations by

202 using the critical threshold value and $2^{-\Delta\Delta Ct}$. In order to avoid any possible effects of

203 post-mortem mRNA degradation, the mRNA values for each of the MyHC isoforms

204 were normalized using the endogenous gene human ACTB.

205 Finally, we calculated the percentage of expression of the mRNA transcript of

206 each of the MyHC isoforms relative to the mRNA transcript of all the MyHC isoforms

207 (%MyHC-I, %MyHC-IIA, %MyHC-IIX and %MyHC-IIM).

208 **2.4 Statistical analyses**

209 We used the non-parametric Mann-Whitney U test to compare the expression

210 patterns of the MyHC isoforms mRNA in the regions analyzed of the temporalis. We

211 used PASW Statistics 18 for all statistical analyses and set statistical significance at

212 $P<0.05$.

213 **3. RESULTS**

214 In the four specimens in which it was possible to weigh the different portions of

215 the temporalis, the average total weight of the temporalis was 120.5±45.9 grams. On

average, the superficial temporalis accounted for 33.1±9.2% of the total weight, the deep temporalis 57.0±6.1%, and the sphenomandibularis 9.9±3.5%. In all four specimens, the sphenomandibularis portion was clearly separate from the deep temporalis, arising from the temporal surface of the greater wing of the sphenoid bone and inserting in the temporal crest of the internal surface of the coronoid process of the mandible (Figures 2 and 3).

The expression of the mRNA transcripts of the MyHC isoforms followed the pattern MyHC-IIM > MyHC-IIA > MyHC-I > MyHC-IIX in all the portions of the temporalis except the posterior superficial temporalis, where the pattern was slightly different, with a higher percentage of the MyHC-I isoform and a lower percentage of the MyHC-IIA isoform: MyHC-IIM > MyHC-I > MyHC-IIA > MyHC-IIX. Although the expression of the MyHC isoforms in the sphenomandibularis followed the general pattern, the actual percentage of expression of the MyHC-IIM isoform was lower than in other portions of the temporalis. This difference was significant when comparing the sphenomandibularis with the anterior superficial temporalis (33.6±3.2% vs 47.0±10.4%; P=0.032) and with the anterior deep temporalis (33.6±3.2% vs 43.0±4.9%; P=0.016). In addition, the percentage of expression of the MyHC-IIA isoform in the sphenomandibularis was higher than in other portions of the temporalis and showed a trend towards significance when comparing the sphenomandibularis with the anterior superficial temporalis (31.5±8.0% vs 22.5±5.6%; P=0.056) and with the posterior superficial temporalis (31.5±8.0% vs 18.6±7.5%; P=0.056). Although there were no significant differences between the anterior and posterior superficial temporalis in the expression pattern of the mRNA transcripts of the MyHC isoforms, interestingly, the percentage of expression of the MyHC-IIM isoform was higher in the anterior than in the posterior superficial temporalis (47.0% vs 40.5%), while the percentage of

241   expression of the MyHC-I isoform was lower in the anterior than in the posterior

242   superficial temporalis (19.9% vs 26.9%) (Tables 2 and 3).

243   **4. DISCUSSION**

244   The average weight of the temporalis muscle in our Pan troglodytes specimens

245   (120.5 grams) is similar to that reported by other authors (111 grams) (Taylor and

246   Vinyard, 2013). Interestingly, the deep temporalis accounted for 57.0% of the total

247   weight, while the superficial temporalis accounted for only 33.1%. In Homo sapiens,

248   the temporalis has only the equivalent of the deep temporalis in Pan troglodytes without

249   the superficial portion (Oxnard and Franklin, 2008; Lee et al., 2012), and it is much

250   smaller than in Pan troglodytes, with an average weight of only 34.79 grams (Taylor

251   and Vinyard, 2013). This reduced size is the result of a generalized process of reduction

252   of the masticatory apparatus during the evolution of the genus Homo (Aiello and Dean,

253   1990). Stedman et al. (2004) attribute this reduction in size to a frameshifting mutation

254   in the MYH16 gene that inactivated the gene, causing it to lose its ability to encode the

255   MyHC-IIM protein isoform. The loss of this protein is associated with a marked

256   reduction in the size of type II fibers and in the overall size of the masticatory muscles

257   (Stedman et al., 2004).

258   We observed a clear predominance of the mRNA transcripts of the MyHC-II

259   isoforms (>70%) in the temporalis muscle of our Pan troglodytes specimens. This

260   expression pattern is to be expected in a muscle that produces the force necessary for

261   the chimpanzee to chew food. The muscular force needed for the dietary habits and life

262   style of Pan troglodytes is reflected in the high percentage of expression of the MyHC-

263   IIM isoform, especially in the anterior superficial temporalis (47.0%). The MyHC-IIM

264   isoform has been shown to have a high ATPase activity, which is related to the capacity

265 of type IIM muscle fibers to produce a contractile force greater than that produced by

266 type IIX fibers (Hoh, 2002; Toniolo et al., 2008).

267 The functional differences between the anterior and posterior temporalis

268 observed in electromyographic studies of humans and other primates (Blanksma et al.,

269 1997; Ross and Hylander, 2000; Hylander et al., 2005; Vinyard et al., 2008; Wall et al.,

270 2008) are reflected in the mRNA transcripts of the MyHC isoforms in our Pan

271 troglodytes specimens. Although the differences were not significant, the MyHC-IIM

272 isoform was expressed at a higher percentage in the anterior than in the posterior

273 superficial temporalis (47.0% vs. 40.5%), while the MyHC-I isoform was expressed at a

274 higher percentage in the posterior than in the anterior superficial temporalis (26.9% vs.

275 19.9%). While the MyHC-IIM isoform is related to greater muscle force, the MyHC-I

276 isoform is related to a lesser degree of muscle force, a slower contraction velocity and a

277 greater resistance to fatigue. These characteristics are in line with the function of the

278 posterior superficial temporalis in recentering the mandible that has been observed in

279 electromyographic studies (Hylander et al., 2005). The functional differences observed

280 in electromyographic studies may also be related to structural differences between the

281 anterior and posterior temporalis identified in humans. The anterior temporalis has a

282 greater physiological cross sectional area than the posterior temporalis, which is related

283 to its greater capacity of force production (Van Eijden et al., 1997). Interestingly, there

284 were no differences between the anterior and posterior deep temporalis in the expression

285 patterns of the MyHC isoforms.

286 The sphenomandibularis is considered by some authors to be an independent

287 muscle in humans (Dunn et al., 1996), while others consider it to be the deep bundle of

288 the temporalis (Türp et al., 1997; Shimokawa et al., 1998; Schön-Ybarra and Bauer,

289 2001; Geers et al., 2005; Sedlmayr et al., 2009). In our five chimpanzees, we were able

12

290   to identify a clearly differentiated sphenomandibularis separate from the deep

291   temporalis. However, the innervation of the sphenomandibularis in our specimens was

292   not separate from the anterior temporalis; rather, it was innervated by a branch of the

293   anterior deep temporal nerve (Figure 4). The mRNA transcripts of the MyHC-IIM

294   isoform was significantly lower in the sphenomandibularis than in the anterior

295   superficial temporalis (33.6% vs. 47.0%, P=0.032) and in the anterior deep temporalis

296   (33.6% vs. 43.0%, P=0.016). This expression pattern suggests that the

297   sphenomandibularis has less capacity of force production, which may be related to its

298   role in the lateral movement and stabilization of the mandible observed in

299   electromyographic studies in Homo sapiens (Wood, 1986; Fuentes et al., 2012).

300   Our findings on the mRNA transcripts of the MyHC isoforms in Pan troglodytes

301   are markedly different from those of other investigators analyzing the percentages of

302   different types of muscle fibers by histochemistry and immunohistochemistry in

303   Macaca mulatta (Maxwell et al., 1979; Miller and Farias, 1988), Macaca irus

304   (Rowlerson et al., 1983), Cebus apella (Andreo et al., 2002), and Papio anubis (Wall et

305   al., 2013). These differences may be due to the presence of hybrid fibers expressing

306   more than one MyHC isoform, which can hinder the determination and quantification of

307   each type of fiber (Pette and Staron, 2000; Korfage and Van Eijden, 2003). Moreover,

308   the studies using ATPase staining did not identify or quantify type IIM fibers (Maxwell

309   et al., 1979; Miller and Farias, 1988; Andreo et al., 2002), while in the study by Wall et

310   al. (2013) using SDS-PAGE, the MyHC-IIX isoform was not detected. The MyHC-IIX

311   isoform had the lowest percentage of expression in our specimens, which may have

312   limited the capacity of SDS-PAGE to detect it.

313   In summary, when comparing the sphenomandibularis with the anterior

314   superficial and deep temporalis, we found significant differences in the mRNA

315 transcripts of the MyHC-IIM isoform, which may be related to the specific functional

316 role of the sphenomandibularis observed in electromyographic studies of other species

317 of primates. Moreover, we identified differences in the pattern of the mRNA transcripts

318 of the MyHC isoforms between the anterior and posterior superficial temporalis that

319 may also be related to the functional differences observed in electromyographic studies

320 of other species of primates. The fact that the differences we observed are not

321 statistically significant may be due to the small number of specimens included in our

322 study, which in turn is the result of the difficulty inherent in obtaining cadavers of

323 chimpanzees with undamaged temporalis muscles. Further studies with larger samples

324 and other analytical techniques are warranted to determine if the functional differences

325 between the anterior and posterior superficial temporalis are due to molecular or

326 structural factors or both.

327 **5. CONCLUSIONS**

328   The use of RT-qPCR to quantify the mRNA transcripts of the MyHC isoforms

329 has enabled us to identify differences between the portions of the temporalis muscle in

330 Pan troglodytes that may be related to functional differences observed in other species

331 of primates in electromyographic studies. These findings provide further knowledge of

332 the anatomical and functional characteristics of this muscle in the primate that is

333 phylogenetically most closely related to Homo sapiens. Our results can thus be

334 applicable to the fields of comparative anatomy, evolutionary anatomy, and

335 anthropology.

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338   like to thank the two anonymous reviewers for their helpful comments and suggestions,

339   which have greatly improved the manuscript.

345   **ETHICAL NOTE**

346   The research complied with protocols approved by the Ethical Committee for

347   Animal Experimentation of the University of Barcelona and adhered to the legal

348   requirements of Spain.

349   **CONFLICTS OF INTEREST**

350   The authors declare no conflicts of interest.

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457

458 **FIGURE LEGENDS**

459 **Figure 1.** Dissection of the superficial (a) and deep (b) temporalis muscle in a male Pan

460 troglodytes.

461 **Figure 2.** Dissection of the sphenomandibularis portion of the temporalis in a female

462 Pan troglodytes.

463 **Figure 3.** Detailed image of the origin and insertion point of the sphenomandibularis.

464 The origin is in the temporal surface of the greater wing of the sphenoid bone (a) and

465 the insertion is in the temporal crest of the mandible (b).

466 **Figure 4.** Dissection of a female Pan troglodytes showing the innervation of the

467 sphenomandibularis by a branch of the anterior deep temporal nerve. (a)

468 sphenomandibularis; (b) medial pterygoid muscle; (*) anterior deep temporal nerve.

469

470   **TABLE LEGENDS**

471   **Table 1.** Characteristics and sources of specimens included in the study.

472   **Table 2.** Means and standard deviations (SD) of the expression of the MyHC isoforms

473   mRNA transcripts in the different portions of the temporalis muscle of Pan troglodytes

474   (AST=anterior   superficial   temporalis;   PST=posterior   superficial   temporalis;

475   ADT=anterior   deep   temporalis;   PDT=posterior   deep   temporalis;

476   SMP=sphenomandibularis portion).

477   **Table 3. S**tatistical significance (P) of the expression of the MyHC isoforms mRNA

478   transcripts   in   the   different   portions   of   the   temporalis   muscle   of   Pan   troglodytes

479   (AST=anterior   superficial   temporalis;   PST=posterior   superficial   temporalis;

480   ADT=anterior   deep   temporalis;   PDT=posterior   deep   temporalis;

481   SMP=sphenomandibularis portion). * Statistical significance at P<0.05

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