

Osteological revision of the holotype of the Middle Jurassic sauropod dinosaur Patagosaurus fariasi (Sauropoda: Cetiosauridae) BONAPARTE 1979

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1	Osteological revision of the holotype of the Middle Jurassic sauropod
2	dinosaur <i>Patagosaurus fariasi</i> (Sauropoda: Cetiosauridae)
3	BONAPARTE 1979
4	
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30	ABSTRACT

31 Middle Jurassic sauropod taxa are poorly known, due to a stratigraphic bias of localities 32 yielding body fossils. One such locality is Cerro Cóndor North, Cañadón Asfalto Formation, 33 Patagonia, Argentina, dated to latest Early-Middle Jurassic. From this locality, the holotype 34 of Patagosaurus fariasi Bonaparte 1986 is revised. The material consists of the axial 35 skeleton, the pelvic girdle, and the right femur. Patagosaurus is mainly characterised by a 36 combination of features mainly identified on the axial skeleton, including the following: (1) 37 cervical centra with low Elongation Index, (2) high projection of the postzygodiapophyseal 38 lamina, (3) deep anterior pleurocoels that are sometimes compartmentalized in cervicals, (4) 39 high projection of the neural arch and spine in dorsal vertebrae and anterior(most) caudal 40 vertebrae, (5) deep pneumatic foramina in posterior dorsals which connect into an internal 41 pneumatic chamber, (6) anterior caudal vertebrae with 'saddle'shaped neural spines. 42 Diagnostic features on the appendicular skeleton include (7) a transversely wide and 43 anteroposteriorly short femur, (8) a medial placement of the fourth trochanter on the 44 femur, and (9) an anteroposteriorly elongated ilium with a rounded dorsal rim, with hook-45 shaped anterior lobe. The characters that are diagnostic for *Patagosaurus* are discussed, and 46 the osteology of *Patagosaurus* is compared to that of Early and Middle Jurassic 47 (eu)sauropods from both Laurasia and Gondwana. 48 49 Keywords: Sauropoda, Eusauropoda, Patagosaurus, Gondwana, Middle Jurassic, 50 pneumaticity 51

52 INTRODUCTION

The late Early to Middle Jurassic is an important time window for sauropod evolution, as phylogenetic studies indicate this was the time when most major lineages diversified and spread worldwide. Even though the Late Jurassic shows a diversity peak, the earlier stages of the Jurassic (or perhaps even the latest Triassic) seem to have been the time of the start of this rise in sauropods (Yates 2003; Barrett & Upchurch2005; Irmis *et al.* 2007; Allain &
Aquesbi 2008; Mannion & Upchurch 2010; Yates *et al.* 2010; McPhee *et al.* 2014, 2015,
2016; Xu et al. 2018). Not many terrestrial deposits remain from the specific time window
that is the Early - Middle Jurassic, and fewer still contain diagnostic basal sauropod or basal
non-neosauropod eusauropod material.

Notable Early Jurassic examples are *Isanosaurus attavipachi* from Thailand Buffetaut et al.,
2002, (Laoyumpon et al. 2017); *Sanpasaurus yaoi* McPhee et al., 2016 from China; *Barapasaurus tagorei* Jain et al., 1975, *Kotasaurus yamanpalliensis* Yadagiri, 1988 from India,
(Yadagiri 2001; Bandyopadhyay et al. 2010); and indeterminate non-neosauropodan
material from Morocco (Nicholl et al. 2018); *Vulcanodon karibaensis* Raath, 1972 from
Zimbabwe (Cooper 1984); and the Elliot Formation ?sauropodiform/sauropodomorph
fauna from South Africa and Lesotho (McPhee et al. 2017).

69 Notable Middle Jurassic examples are the cetiosaurs from the UK, e.g. Cetiosaurus 70 oxoniensis Phillips, 1871, the Rutland Cetiosaurus and cetiosaurid and gravisaurian material 71 from England, Scotland and Germany (von Huene 1927; Upchurch and Martin 2002, 2003; 72 Liston 2004; Galton 2005; Barrett 2006; Buffetaut et al. 2011; Brusatte et al. 2015; Stumpf et 73 al. 2015; Clark and Gavin 2016; Holwerda et al. 2019); Datousaurus bashanensis Dong & 74 Tang 1984, Nebulasaurus taito Xing et al., 2015, Lingwulong shenqi Xu et al., 2018, and 75 the mamenchisaur fauna from China (Young and Zhao 1972; Russell and Zheng 1993; Pi et al. 76 1996; Moore et al. 2018; Wang et al. 2018); Tazoudasaurus naimi Allain et al., 2004, 77 Spinophorosaurus nigerensis Remes et al., 2009 and Chebsaurus algeriensis Mahammed et 78 al., 2005 from North Africa (Allain and Aquesbi 2008); indeterminate non-neosauropodan 79 material and Lapparentosaurus madagascariensis Bonaparte 1986a from Madagascar (Läng 80 2008; Mannion 2010), and finally, Patagosaurus fariasi Bonaparte, 1979, Volkheimeria

chubutensis Bonaparte 1979 and *Amygdalodon patagonicus* Cabrera, 1947 (Bonaparte
1986b; Rauhut 2003) from Argentina.

Some sauropods that were traditionally considered to be Middle Jurassic might originate from the Late Jurassic; (*Rhoetosaurus brownei* Longman, 1926 from Australia (Nair and Salisbury 2012; Todd et al. 2019), *Shunosaurus lii* Dong et al., 1983 and *Omeisaurus junghsiensis* Young, 1939 from China (He et al. 1984, 1988; Zhang 1988; Tang et al. 2001; Chatterjee and Zheng 2002; Peng et al. 2005; and see Wang et al. 2018 for refined ages). For a short overview of some of these Early and Middle Jurassic sauropods, see Holwerda and Pol (2018).

90

91 In Patagonia, Argentina, the Cañadón Asfalto Formation (Stipanicic et al. 1968; Tasch and

92 Volkheimer 1970), is one of the few geological units worldwide to contain several latest

93 Early to early Middle Jurassic eusauropod fossils. It crops out in west-central Patagonia,

94 Argentina, and has recently been dated as ranging from the Toarcian to the

Aalenien/Bajocian (Cúneo et al. 2013). The sauropod fauna of this unit includes

96 Patagosaurus fariasi, Volkheimeria chubutensis (Bonaparte 1979), and at least two

97 undescribed taxa (Rauhut 2002, 2003; Pol et al. 2009; Holwerda et al. 2015; Becerra et al.

98 2016; Carballido et al. 2017a).

99 Patagonia first came under the attention of vertebrate palaeontologists by the discovery of 100 the basal sauropod *Amygdalodon patagonicus* by Cabrera (1947), and later by Casamiquela 101 (1963) from the Pampa de Agnia locality, Cerro Carnerero Formation (Rauhut 2003a). These 102 beds were revisited in 1976, but no further discovery was made, until another excursion in 103 Patagonia, about 50 Km further away in the Cañadón Asfalto Formation, in 1977, was 104 successful. José Bonaparte led numerous additional expeditions to the region between 1977

105 and 1986, during which *Patagosaurus fariasi*, *Volkheimeria chubutensis* and the theropod

106 *Piatnitzkysaurus floresi* Bonaparte, 1979 were found and described (Bonaparte 1979, 1986b,

107 1996; Rauhut 2004). Since then, numerous other dinosaurs and other vertebrates have been
108 discovered in the Cañadón Asfalto Formation; see Escapa et al. (2008), Cuneo et al (2013)
109 and Olivera et al. (2015). The MPEF in Trelew has more recently visited the locality of Cerro
110 Cóndor South to uncover more material, of which only one element has been described
111 (Rauhut 2003b).

112 Thus far, Patagosaurus is the only well-known sauropod taxon from this area, and one of the 113 few sauropods from the Middle Jurassic outside of China, known from abundant material. It 114 was coined by Bonaparte in 1979; Patagosaurus for Patagonia, and fariasi to honour the 115 owners of the Farias farmland, on which it was discovered. It has been included in numerous 116 phylogenetic studies (e.g. Upchurch 1998; Wilson 2002; Upchurch et al. 2004; Harris 2006; 117 Allain and Aguesbi 2008; Wilson and Upchurch 2009; Carballido et al. 2011, 2012; Holwerda 118 and Pol 2018). However, the only description of this taxon published so far (Bonaparte, 119 1986b) is not only based on the holotype, but also draws information from a selection of 120 associated material, representing several individuals from different localitites, therefore not 121 guaranteeing these are all Patagosaurus individuals. Some of the associated material comes 122 partially from the same bonebed as the holotype, but others come from a nearby bonebed 123 (Bonaparte 1979; Bonaparte 1986a). Since this description, new sauropod finds from the 124 Cañadón Asfalto Formation show a higher sauropod diversity for this unit than previously 125 assumed (Pol et al. 2009). Furthermore, recent studies of Patagosaurus material revealed 126 the probable presence of another taxon in the associated material (Rauhut 2002; Rauhut 127 2003). In light of this, a revision of *Patagosaurus* is needed.

128

129 MATERIAL AND METHODS

130

131 ANATOMICAL ABBREVIATIONS

132

Terminology: Wilson (1999) is followed for the terminology of vertebral laminae, with some
 modifications based on Carballido and Sander (2014). The terminology of vertebral fossae

135 follows Wilson *et al.* (2011).

- 136 As was already pointed out by Wedel (2003) and Carballido and Sander (2014), the term
- 137 pleurocoel has not been rigourously defined. The term, however, was used in that paper for
- 138 a lateral excavation on the vertebral centrum with clearly defined anterior, ventral and
- dorsal margins, and a usually less clearly defined but still visible posterior margin (Carballido
- and Sander 2014). As this description is applicable for the lateral pneumatopores found in
- 141 *Patagosaurus,* it will be used in this sense.
- 142 The use of 'anterior' and 'posterior' is preferred instead of 'cranial' and 'caudal'. This is to
- avoid confusion when describing, for instance, the caudal vertebrae.
- 144
- 145 *Laminae:* acdl: anterior centrodiapophyseal lamina; acpl: anterior centroparapophyseal
- 146 lamina; **cpol**: centropostzygapophyseal lamina; **cprl**: centroprezygapophyeseal lamina; **pcdl**:
- 147 posterior centrodiapophyseal lamina; **podl**: postzygadiapophyseal lamina; **posl**: postspinal
- 148 lamina; **ppdl**: parapodiapophyseal lamina; **prdl**: prezygodiapophyseal lamina; **prsl**: prespinal
- 149 lamina; **spdl**: spinodiapophyseal lamina; **spol**: spinopostzygapophyseal lamina; **sprl**:
- spinoprezygapophyseal lamina; **stpol**: single intrapostzygapophyseal lamina; **stprl**: single-
- 151 intraprezygapophyseal laminal; **tprl**: intraprezygapophyseal lamina; **tpol**:
- 152 intrapostzygapophyseal lamina;
- 153
- 154 Fossae: cdf, centrodiapophyseal fossa (fenestrae for some posterior dorsals); cpof,
- 155 centropostzygapophyseal fossa; **cprf**, centroprezygapophyseal fossa; **ivf**, intervertebral
- 156 fossa; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **posdf**, postzygapophyseal
- 157 spinodiapophyseal fossa; prcdf, prezygapophyseal centrodiapophyseal fossa; prsdf,

- 158 prezygospinodiapophyseal fossa; sdf, spinodiapophyseal fossa; spof, spinopostzygapophseal
- 159 fossa; **sprf**, spinoprezygapophseal fossa

160

- 161 Institutional abbreviations: LEICT: New Walk Museum and Art Gallery, Leicester Arts and
- 162 Museum Service, Leicester, UK. MACN: Museo Argentino de Ciencias Naturales 'Bernardino
- 163 Rivadavia', Buenos Aires, Argentina. MNHN-MAA: Musee National d'Histoire Naturelle,
- 164 Paris, France. OUMNH: Oxford University Museum of Natural History, Oxford, UK. PVL:
- 165 Paleovertebrados, Instituto Miguel Lillo, Tucuman, Argentina.
- 166

167 Systematic Paleontology

- 168 SAURISCHIA SEELEY 1887
- 169 SAUROPODA MARSH 1878
- 170 EUSAUROPODA UPCHURCH 1995
- 171 CETIOSAURIDAE LYDEKKER 1888
- 172 *PATAGOSAURUS* BONAPARTE 1979
- 173 PATAGOSAURUS FARIASI BONAPARTE 1979
- 174
- 175 Holotype: PVL 4170, consisting of several anterior, middle and posterior cervical vertebrae,
- 176 PVL 4170 1-9, anterior, mid- and posterior dorsals, PVL 4170 10-17, anterior caudals 19-25
- and middle to posterior caudals 26-32, sacrum, PVL 4170 18, fused ischia, PVL 4170 36, right
- 178 ilium, PVL 4170 34, right pubis, PVL 4170 35, and right femur, PVL 4170 37. See Table 1 and 2
- 179 for vertebral measurements, and Table 3 for appendicular measurements. The holotype was
- 180 said to also contain a scapula and coracoid (Bonaparte, 1986a), but these could
- 181 unfortunately not be located in the collections. In the collections of the MACN we found two
- elements labelled as MACN-CH 1986 scapula 'A' and coracoid 'B', which might be these
- 183 holotypic elements; however, at present the association of these bones with the holotype is

184 uncertain, and the association with another Patagosaurus specimen, MACN-CH 935, is also 185 likely, due to close association of these elements with MACN-CH 935 on the excavation map. 186 A large humerus is also indicated in the original quarry map for the holotype, however, the 187 only large humerus retrieved from the PVL collections is from another locality, Cerro Cóndor 188 South. Originally, associated teeth with typical eusauropod wrinkled enamel were 189 mentioned (Bonaparte 1986b). However, no directly associated teeth or tooth-bearing 190 bones are known for the holotype specimen, so that these teeth are not regarded as part of 191 the holotype here and were not used in the diagnosis, even though some are ascribed to 192 Patagosaurus (Holwerda et al. 2015). Ribs and chevrons appear on the quarry map of the 193 holotype, but are mixed in with ribs and chevrons of other Patagosaurus specimens, and will 194 therefore be omitted from the holotype description.

195

196 Original Diagnosis (Bonaparte 1986b): Cetiosaurid of large size, with tall dorsal vertebrae; 197 posterior dorsals with elevated neural arches and well-developed neural spines, formed 198 from 4 divergent laminae and with a massive dorsal region; dorsoventrally-oriented neural 199 spine cavities, more expanded than in *Barapasaurus*. Anterior and lateral regions of the 200 neural arch similar to that of Cetiosaurus and Barapasaurus. Sacrum with 5 vertebrae, 201 elevated neural spines, and a large dilation of the neural canal forming a neural cavity. Pelvis 202 with pubis showing distal and proximolateral expansions, more developed than 203 in Barapasaurus, and a less expanded pubic symphysis than in Amygdalodon. Ischium 204 slightly transversely compressed, with a ventromedial ridge of sublaminar type, and with a 205 clear distal expansion. Ratio of tibia-femur lengths from 1:1.5 in juveniles, reaching 1:1.7 in 206 adults. Mandible with weak medial torsion. Spatulate teeth with occlusal traces. 207 208 Emended diagnosis: Patagosaurus fariasi is a non-neosauropodan eusauropod dinosaur that

209 can be diagnosed on the basis of the following morphological features, and the following

210 combination of characters (features with * are tentatively considered autapomorphies): 1) 211 cervical and anterior dorsal vertebrae with marked pleurocoel, which is deep in cervicals but 212 shallower in dorsals. In cervical vertebrae, the pleurocoel is deeper anteriorly with well 213 defined margins, but becomes shallow posteriorly and has only well defined dorsal and 214 ventral margins. 2) In several cervicals, a faint oblique accessory lamina is present, dividing 215 the pleurocoel into an anterior deeper part and a posteriorly shallower part. 3) The cervicals 216 have a relatively high neural spine, accompanied by high dorsal placement of 217 postzygapophyses, which results in a high angle between the postzygodiapophyseal and 218 posterior centrodiapophyseal laminae of about 55°. 4) Posterior dorsal neural arches with a 219 centrodiapopohyseal fossa that extends internally as a pneumatic structure, which is 220 separated by the mirroring structure by a thin septum, and both of which connect into a 221 ventral, oval shaped internal pneumatic chamber, which is dorsal to and well separated from 222 the neural canal*. 5) Posterior dorsals with small round excavations on the posterior side of 223 the distal extremity of the diapophyses*. 6) Posteriormost dorsals have rudimentary aliform 224 processes. 6) All dorsals display an absence of the spinodiapophyseal lamina in all dorsals, 225 with a contact between the lateral spol and podl in posterior-most dorsals instead. 7) Sacrals 226 with dorsoventrally high neural spine. 8) Ilium with round dorsal rim, hooks-shaped anterior 227 lobe and dorsoventrally elongated pubic peduncle. 9) Fused distal ischia with the paired 228 distal shafts creating an angle of 110° to the horizontal, 10) pubis with torsion and kidney-229 shaped pubic foramen. 11) Femur with posteromedially placed fourth trochanter, and 230 laterally convex surface of femoral shaft.

231

232 *Horizon, locality and age: Patagosaurus fariasi* was found in what are now considered latest

233 Early to early Middle Jurassic beds of the Cañadón Asfálto Formation in west-central Chubut,

234 Patagonia, South Argentina (Cúneo et al., 2013). The Cañadón Asfálto Formation is a

235 continental unit, consisting mainly of lacustrine deposits. *Patagosaurus* was found in the

Cerro Cóndor area. The type locality of the holotype of *Patagosaurus fariasi* is Cerro Cóndor
North, which lies approximately 2 Km north-east of the first discovery site of *Patagosaurus*remains: Cerro Cóndor South, close to the village of Cerro Cóndor, near the Chubut river, not
far from the town of Paso de Indios (Figure 1).

240

241 GEOLOGICAL SETTING

242 The Cañadon Asfálto Formation (west-central Chubut province, Patagonia, Argentina, see 243 Figure 1) was first studied by Piatnitzky (1936), after which it was formally described and 244 named by Stipanicic et al. (1968) and further described by Nullo (1983). It is part of the 245 sedimentary infill of the eponymous Cañadón Asfalto Basin, which consists of different 246 subunits of Lower Jurassic to Upper Cretaceous sediments. The Cañadon Asfálto Formation 247 is the uppermost unit of the lower megasequence of the Cañadón Asfalto basin, which has 248 sedimentary infill of the Lower Jurassic (Figari et al. 2015). This unit is exposed between the 249 Chubut province towns of Paso del Sapo and Paso de Indios (Olivera et al. 2015). The early 250 Middle Jurassic (Toarcian-Bajocian, possibly earliest Bathonian) Cañadón Asfalto Formation 251 conformably overlies the Early Jurassic (Pliensbachian-early Toarcian; Cúneo et al. 2013; 252 Figari et al. 2015; Volkheimer et al. 2015) Lonco Trapial Formation. It has been the subject of 253 numerous geological studies in recent years to determine its sedimentology and age, since 254 the age of the Cañadón Asfálto Formation has long been considered to be Callovian-255 Oxfordian (and thus the South American equivalent of several other Jurassic beds 256 worldwide, such as the Oxford Clay; Frenguelli 1949; Bonaparte 1979; Bonaparte 1986; 257 Rauhut 2003). However, a recent detailed chronostratigraphic study showed otherwise, 258 using zircon grains from several tuff samples from the Cañadón Asfálto Formation (Cuneo et 259 al. 2013). These were pre-treated by the chemical abrasion, or CA-TIMS technique, in order 260 to constrain radiation-induced Pb loss. This method (using U/PB isotopes) is considered to 261 be one of the most precise dating methods (Mattinson 2005). The U/Pb isotope ratios show

a latest Early (early-mid Toarcian), to early Middle Jurassic age range (Aalenian or Bajocian,

263 Cúneo et al. 2013), although the youngest radiometric age for this formation has been given

as Bajocian-Bathonian (Cabaleri et al. 2010a). This much older age of the formation is also

265 consistent with palynological and other radiometric studies (e.g. Volkheimer et al. 2008;

266 Cabaleri et al. 2010; Zavattieri et al. 2010; Olivera et al., 2015; Hauser et al. 2017).

267 Moreover, this new age also puts the vertebrate fossils found in the Cañadón Asfálto

268 Formation in a new light.

269

270 Since its discovery, over twenty species of different taxonomic groups (including sauropod,

theropod, and ornithischian dinosaurs, pterosaurs, sphenodontians, mammals, fishes, frogs,

turtles and crocodiles) have been discovered (Sterli et al. 2010; Olivera et al. 2015). This

273 makes it an important unit for the study of Middle Jurassic tetrapods, and the diversification

- 274 of Middle Jurassic dinosaurs in particular.
- 275

276 The outcrops of the Cañadón Asfálto Formation are dominated by microbial limestones,

277 often tuffaceous mudstones and shales with conchostracans, and conglomeratic

intercalations (Silva Nieto et al. 2002; Tasch and Volkheimer 1970). They provide mainly

disarticulated dinosaur remains, as well as a few articulated skeletons, as shown in the

280 quarry map of the sauropod bonebed of Cerro Cóndor North (Figure 1). The Cañadón Asfálto

281 Formation shows evidence of both folding and faulting, which makes correlation of the

282 different localities impossible, until further study is performed.

283 The region was dominated by a warm and relatively humid climate in the Middle Jurassic,

evidenced by palynology (Volkheimer et al. 2001) and by macrofloral remains (e.g.

285 Cheirolepidiaceae and Araucariaceae; Volkheimer et al. 2008, Volkheimer et al. 2015).

286 Lacustrine sedimentation cycles found in paleolakes in the Cañadón Asfálto Formation

provide evidence of climatic fluctuations and cyclicity (Cabaleri and Armella 2005; Cabaleri

288 et al. 2005).

289

290	José Bonaparte started excavations in the Cañadón Asfálto Formation with a team of
291	scientists and preparators, and with funding from the National Geographic Society, in 1977.
292	They found bones, on the Farias farm estate close to the river Chubut. After this, in 1978,
293	they found a sauropod skeleton 4-5 km north of Cerro Condor. This site was then dubbed
294	Cerro Cóndor Norte (North), and the original site Cerro Cóndor Sur (South). The Cerro
295	Cóndor North site was excavated until 1982; in 1980, however, most material was
296	uncovered and visible, as demonstrated in the quarry map of Figure 1. From this site, the
297	holotype PVL 4170 originates, as well as at least seven other individuals, most likely of
298	Patagosaurus.
299	
300	The sediments of Cerro Cóndor North are dark grey, and hard. The bones from this quarry
301	are similarly dark grey or dark brown in colour. The sediments of Cerro Cóndor North were
302	interpreted by Bonaparte as fluvial deposits; however, they have more recently been
303	interpreted as mainly lacustrine deposits.
304	Cerro Cóndor South was thought to be fluvial, but from observations by O.R. is now thought
305	to be originating from an alluvial fan within a shallow lacustrine environment. Sediments
306	from Cerro Cóndor South are fine-grained to paraconglomeratic, light-coloured and contain
307	small freshwater shell fragments of invertebrates. Bonaparte also hinted that this locality
308	consists of multiple layers of sediment with fossils.

309 **RESULTS**

310

311 AXIAL SKELETON

312

- 313 *Cervicals:* PVL 4170 has seven cervical vertebrae preserved, ranging from anterior to
- 314 posterior cervicals. The most anterior cervical preserved (PVL 4170 1) is probably the third or
- fourth cervical, based on comparisons with the Rutland *Cetiosaurus* (LEICT 468.1968.40;

316 Upchurch and Martin 2002).

317 Given the incomplete preservation of the neck in *Patagosaurus*, the exact cervical count in 318 this taxon cannot be established. At the very least, the atlas, axis and first one or two 319 postaxial cervicals are missing, given the high projection of the neural spine in the first 320 cervical preserved, and compared to the Rutland Cetiosaurus, where neural arches and 321 spines are low in the first 2-3 cervicals after the axis. Only very few non-neosauropodan 322 sauropods with complete cervical series are known, making a comparison of the preserved 323 elements difficult. Of the basal eusauropods with complete cervical series, Shunosaurus and 324 Jobaria tiguidensis Sereno et al., 1999 have 12 cervicals (Zhang 1988; Sereno et al. 1999), 325 whereas Spinophorosaurus has 13 (Remes et al. 2009). The Rutland Cetiosaurus was said to 326 have 14 cervicals by Upchurch and Martin (2002), but several of these vertebrae, including 327 the possibly last two cervicals, have only parts of the neural arch preserved, so that it cannot 328 be established with certainty if these two last vertebrae are cervicals or might already be 329 anterior dorsals (Upchurch & Martin 2002). The derived non-neosauropodan 330 mamenchisaurids apomorphically increased the cervical vertebral count to as much as 18 331 cervicals (Ouyang & Ye 2002). The primitive number of cervicals in basal eusauropods thus 332 seems to be either 12 or 13, and this is the condition we assume for Patagosaurus. As the 333 exact position of the different cervicals preserved can thus not be established, the

numbering used here starts with the first element preserved, therefore what is actually Cv 3

335 or 4 is numbered cervical 1 in the PVL collections. For convenience we will adhere to this336 numbering.

337 The cervical centra are longer than high (see Table 1) and opisthocoelous, as in most 338 sauropods. In comparison with other sauropods, cervicals are rather stout, with an average 339 elongation index (aEI; Chure et al., 2010) ranging from 1.9-2 in anterior to 1.2-1.4 in 340 posterior cervicals and the 'traditional' elongation index (EI, Upchurch 1998) ranging from 341 2.1 in anterior to 1.2 in posterior cervicals, compared to ~3.5 on average in 342 Spinophorosaurus (Remes et al. 2009b), ~3.1 in the only cervical known from Amygdalodon 343 (Rauhut 2003, MLP 46-VIII-21-1/8), and 2,1 in anterior to 5,3 in mid cervicals in an 344 undescribed sauropod from the Bagual site in the Cañadón Asfálto Formation (MPEF-PV 345 'Bagual' C2-4; Pol et al. 2009). This index is thus on average lower if compared to other non-346 neosauropod eusauropods (see Table 1). The condyle has an anterior protrusion slightly 347 dorsal to its center, and the condyle is 'cupped' by a ca. 1-2 cm thick rugose layer, similar to 348 that in the Rutland Cetiosaurus (see Upchurch and Martin 2003, LEICT 468.1968 cervical 349 series). The cotyles are concave; with the deepest concavity slightly dorsal to the midpoint. 350 As in most saurischians, the parapophyses are placed on the anteroventral end of the 351 centra. In lateral view, the centra are ventrally concave posterior to the parapophysis. The 352 posteriormost 1/3rd of the ventral side of the centra is convex, and the dorsoventral height 353 of the centra increases posteriorly. Pleurocoels are developed as large, but only partially 354 well-defined lateral depressions on the centra. In anterior cervicals, the pleurocoel is deeper 355 than in posterior cervicals, and has a well-defined anterior, dorsal and ventral margin. In 356 mid- and posterior cervicals the posterior margin of the pleurocoel is less clearly defined and 357 the depression gradually fades into the lateral surface of the centrum. In some mid- to 358 posterior cervicals, the left and right pleurocoels are only separated by thin septa (which are 359 damaged or broken in some elements), but they do not invade the centrum and ramify 360 within the bone, as is the case in neosauropods, (Wedel et al. 2005). Some cervicals show a

faint compartmentalization of anterior and posterior pleurocoels, but they generally lack the
 oblique lateral lamina that subdivides the cervical pleurocoels in neosauropods and some
 derived basal eusauropods.

364 In ventral view, the centra are constricted directly posterior to the condyle, as in most 365 sauropods. A prominent ventral keel is present, which extends to about 2/3rd of the length 366 of the ventral axial midline of the cervicals, after which it fades and disappears into the 367 ventral surface of the centrum. It is present in all cervicals preserved (and possibly in the 368 first dorsal as well as a marginally developed keel). The keel is developed as a thin, ventrally 369 protruding ridge, with a very small hypapophysis anteriorly. The latter is developed as a 370 transversely thin, rounded, sail-like ventral protrusion present immediately behind the 371 ventral rim of the condylar 'cup'. This structure is accompanied by elliptical lateral fossae, as 372 in Amygdalodon (Rauhut 2003), Tazoudasaurus (MNHM To1-64; 81; 112; 354) 373 Lapparentosaurus (MNHM MAA 13; 172; 5) and Spinophorosaurus (NMB-1699-R), but in 374 contrast to the Rutland Cetiosaurus (Leict 468.1968.40; 42; 7) and Mamenchisaurus 375 hochuanensis (Young and Zhao 1972) and derived sauropods. At the posterior end, the 376 cotyle extends further ventrally than it does dorsally, also seen in Lapparentosaurus, 377 Amygdalodon, Tazoudasaurus, and Spinophorosaurus. The dorsal side of the cotyle shows a 378 U-shaped notch in middle and posterior cervicals. 379 Neurocentral sutures are visible on the lateral side of the centrum in some cervical 380 vertebrae, a possible sign of morphological immaturity in archosaurs (Brochu 1996; Irmis 381 2007). The neural arches of the cervicals are axially elongated, transversely narrow and 382 higher posteriorly than the vertebral centrum, as in most sauropods. The diapophyses are 383 placed on ventrolaterally directed transverse processes, which are attached to the neural 384 arch by bony laminae, which are described in detail below for the individual vertebrae. The 385 prezygapophyses are more prominent than the postzygapophyses, being placed on stout, 386 elongated, beam-like stalks projecting anteriorly from the neural arch. They consistently

387 project anteriorly beyond the centrum in anterior cervical vertebrae, and show an increasing 388 incline towards posterior cervicals, as in basal sauropods Tazoudasaurus, the Rutland 389 Cetiosaurus, and in basal neosauropods such as Haplocanthosaurus priscus Hatcher, 1903. 390 Well-developed prezygapophyses apparently have a pre-epipophysis, however, a similar 391 structure is mentioned in a basal non-neosauropodan sauropod form the Early Jurassic of 392 Morocco, (Nicholl et al. 2018). The postzygapophyses are less prominent as they do not 393 project much posteriorly from the neural arch. With the increasing height of the neural arch 394 in more posterior cervicals, the postzygodiapophyseal lamina becomes more steeply 395 inclined. A relatively high posterior cervical neural arch is shared with mamenchisaurs 396 (Mannion et al. 2019). In mid cervicals, this inclination of the postzygodiapophyseal lamina is 397 approximately 45-50°, measured from the axial plane, which is larger than in most basal 398 sauropods, but comparable to the situation in diplodocids (see also McPhee et al 2015). 399 At the anterior end of the cervical neural arches the intraprezygapophyseal laminae are 400 separated medially, as in *Tazoudasaurus* (Allain and Aquesbi 2008) and the Rutland 401 Cetiosaurus (LEICT 468.1968). The intrapostzygapophyseal laminae (tpol) do meet at the 402 midline. However, there are no centropostzygapophyseal laminae, as in *Tazoudasaurus* 403 (Allain and Aquesbi 2008), but unlike the Rutland Cetiosaurus (Leict 468.1968). Cervical 404 vertebra PVL 4170 (7) is the only cervical with a single centropostzygapophyseal lamina 405 (stpol). This lamina is found more commonly in middle and posterior cervicals of 406 neosauropods, Haplocanthosaurus and Cetiosaurus (Upchurch et al. 2004). As this is the last 407 cervical before the cervico-dorsal transition (which happens at cervical PVL 4170 (8), this 408 could be a feature enabling ligament attachment for stability and strength at the base of the 409 neck, however, this would need more investigation with e.g. biomechanical modeling. 410 The cervical neural spines project higher than in most basal sauropods, especially in the 411 middle and posterior cervicals. The spines are connected to the zygapophyses by well-412 developed spinopre- and spinopostzygapophyseal laminae. Whereas the summit of the

413 spine is more or less flush with the spinopostzygapophyseal lamina (spol) in the

414 anteriormost vertebra, it protrudes dorsally beyond that lamina in more posterior elements.

415 The spol are robust in all cervicals, but the sprl is only extensive in anterior elements and

416 becomes short and thin in more posterior cervicals. From cervical 4 onwards the neural

417 spine forms a rounded protrusion which is transversely wider than long anteroposteriorly.

418 The neural spine is slightly anteriorly inclined in anterior cervicals (to at least the fifth

419 preserved element), but becomes more erect towards the end of the cervical series, with a

420 straight anterior margin; this is also seen in *Shunosaurus* (Zhang 1988, T5402).

421

422 *Cervical vertebra PVL 4170 (1):* This is the smallest and anteriormost of the cervical

423 vertebrae preserved. The element is generally complete and well-preserved, but the right

424 prezygapophysis is broken off at the base (see Fig. 2). A lump of sediment is still attached to

425 the anterior part of the neural arch, above the condyle.

426 The centrum is relatively shorter than in the mid-cervicals, with an EI of 1,55 and an aEI of

427 1,43. The articular ends are notably offset from each other, with the anterior end facing

428 anteroventrally in respect to the posterior cotyle (Fig. 2E, F). The cotyle is not as concave as

429 in the other cervicals of the series. The ventral keel is strongly developed in the anterior

430 1/3rd of the centrum, after which it gradually fades into ventral surface. In ventral view, the

431 parapophyses are visible as lateral oval bulges, the articular surfaces of which are confluent

432 with the condyle rim (Figure 2E).

433 The centrum shows a distinct pleurocoel, present laterally on the vertebral body (Figure 2A,

B). It is deeper anteriorly than posteriorly and developed as a rounded concavity that follows

the rim of the condyle on the lateral anterior side of the centrum. Posteriorly it extends

436 almost to the posterior end of the centrum; however, it fades gently into the lateral surface

437 from about 2/3rd of the centrum axial length. Within the pleurocoel there appears to be a

438 slight bulge at about the height of the diapophysis, which is similar to the oblique accessory

439 lamina in neosauropods (Upchurch 1998), dividing the pleurocoel in two subdepressions. 440 This subdivision is also seen to some extent in mamenchisaurids (e.g. Ouyang and Ye 2002; 441 Tang et al. 2001; Young 1939; Young and Zhao 1972; Zhang et al. 1998), and also in the 442 Rutland Cetiosaurus (Upchurch and Martin 2003). This incipient subdivision is also present in 443 some other cervicals of *Patagosaurus*, but it is best developed in this element. The 444 parapophysis is positioned anteroventrally on the lateral side of the centrum, and is 445 connected to the rugose rim of the condyle. The dorsal side is excavated, with the recess 446 being confluent with the deep anterior part of the pleurocoel. A stout lamina extends 447 horizontally posteriorly from the parapophysis and forms the ventral border of the 448 pleurocoel and the border between the lateral and the ventral side of the centrum. This 449 lamina becomes less prominent posteriorly (Figure 2A, B). 450 The posterior region of the neural arch is approximately as high as the posterior end of the 451 centrum. It extends over most of the length of the centrum, but is slightly offset anteriorly 452 from the posterior end of the latter. The neural canal is rather small and round in outline, 453 but only its posterior opening is visible, as the anterior end is still covered in matrix. Despite 454 the anterior position of the vertebrae, lateral neural arch lamination is well-developed, with 455 prominent prdl, podl and pcdl. The diapophysis is developed as a small, lateroventrally 456 projecting process on the anterior third of the neural arch (Figure 2A, C, D). It is connected 457 to the prezygapophysis by a slightly anterodorsally directed prezygadiapophyseal lamina 458 (prdl). The latter is in line with the pcdl, which meets the diapophysis from posteroventral. 459 The postygaydiapophyseal lamina (podl) is steeply anteroventrally inclined and meets the 460 prdl just anterior to the diapophysis. A short and stout acdl is present, but hidden in lateral 461 view by the diapophysis.

The prezygapophysis is placed on a stout, anteriorly and slightly dorsally directed process
that slightly overhangs the anterior condyle of the centrum (Figure 2A, C). The base of this
process is connected to the centrum by a short and almost vertical centroprezygapophyseal

lamina (cprl), which here meets the prdl in an acute angle; from this point onwards only a single, very robust lateroventral lamina continues anteriorly onto the stall and braces the prezygapophysis from lateroventral. The prezygapophyseal articular suface is flat, triangular to elliptic in shape and measures about 3 by 3 cm. It is inclined dorsomedially at an angle of approximately 30-40° from the horizontal. The intraprezygapophyseal lamina is very short and widely separated from its counterpart in the middle of the anterior surface of the neural arch.

472 A slightly asymmetrical centroprezygapophyseal fossa (cprf) is present below the

473 intraprezygapophyseal (tprl) and centroprezygapophyseal laminae on either side of the

474 neural arch, with the right fossa being hidden by sediment (Figure 2C). Anteroventral to the

475 diapophysis an axially elongated prezygapophyseal centrodiapophyseal fossa (prcdf) is

476 visible, contra Upchurch and Martin (2003), who reported this to be absent in *Patagosaurus*.

477 A slightly larger centrodiapophyseal fossa (cdf) is present posteroventral to the diapophysis,

478 and a very large, triangular pocdf is present between the pcdl and podl.

479 The postzygapophysis is placed on the posterodorsal edge of the neural arch, above the

480 posterior end of the centrum, which it does not overhang it posteriorly. It is developed as a

481 large, lateroventrally facing facet which is dorsally bordered by the slightly curved podl and

482 dorsally braced by the stout spinopostzygapophyseal lamina (spol). The stout and almost

483 vertical cpol connects the centrum to the medial margin of the postzagypophysis. The

484 intrapostzygapophyseal lamina (tpol) is directed ventromedially and connects the medial

side of the postzygapophysis to the dorsal margin of the neural canal, where it is separated

486 from its counterpart.

487 The neural spine is relatively low, barely extending dorsally beyond the postzygapophysis,

488 but it is anteroposteriorly elongate and robust, becoming wider transversely posteriorly

489 (Figure 2A, B, C, D). It is placed more over the anterior side of the centrum and is almost 2/3

490 of the length of the latter. Its anterior margin is inclined anterodorsally. The spine is

491 connected to the medial side of the prezygapophyseal process by a short

492 spinoprezygapophyseal lamina (sprl), which meets its counterpart at about one third of the

493 height of the neural spine, thus defining a small sprf. The spol is robust, but also short and

494 connects the posterior end of the spine with the dorsal surface of the postzygapophysis. A

495 large, diamond-shaped spof is bordered by the spols and tpols, with the latter being longer

than the former. The entire dorsal surface of the neural spine is rugose.

497

498 *Cervical vertebra PVL 4170 (2):* This anterior cervical vertebra is the second element

499 preserved after the anteriormost cervical, and appears to be directly sequential based on

500 the size similarity in cotylar and condylar size between PVL 4170 (1) and (3). It is incomplete,

501 missing the neural arch and neural spine, which are broken off (Fig 3). The centrum,

502 prezygapophyses and the right postzygapophysis, however, are complete. The left

503 postzygapophysis is also broken. The vertebra is slightly flattened/displaced towards the

right lateral side, most likely due to compression.

505 The centrum is stout and robust, although slightly more elongated than that of the previous

506 cervical PVL 4170 (1). Its EI is 1,64 and its aEI is 1,97. The overall shape is not as curved as in

507 PVL 4170 (1), but rather straight along the axial plane, with a slight concave curvature of the

508 ventral side of the centrum. The condyle is convex, although slightly more dorsoventrally

509 flattened than in the previous cervical. In lateral view it shows a slightly pointy 'nose', i.e. a

510 pointed protrusion, on its dorsal side (Fig. 3A, B). The cotyle is slightly flattened

511 dorsoventrally as well, and it is wider transversely than dorsoventrally. Because the condyle

and cotyle show a high amount of osteological detail, this flattening might be natural, and

513 not caused by compression. On the ventral side of the cotyle, a lateral flange extends on the

514 left side but not on the right (Fig. 3E). This flange extends further posteriorly than the dorsal

rim of the cotyle, extending posteriorly and laterally. The dorsal side of the rim of the cotyle

shows a U-shaped indentation in dorsal and posterior view, posterior to the neural canal. As

in the first preserved cervical, the parapophyses are placed at the anteroventral end of the
centrum and extend from the thick condylar rim to the lateral and posterior sides of the
condyle. They are generally conical in shape and elongated towards the rest of the centrum.
The parapophyseal articular surfaces are more elongated axially than in the previous cervical
(PVL 4170 1). In ventral view, the ventral keel on the centrum is clearly present anteriorly on
the vertebral body, but fades after about 2/3rd of the vertebral length towards the posterior
side where it is not clearly visible (Fig. 3E).

524 On the lateral sides of the centrum, pleurocoels are clearly visible as deep round anterior

525 depressions, directly behind the rim of the anterior condyle (Fig. 3A, C). These depressions

526 fade into the lateral side of the centrum posteriorly. In this cervical, as in the first preserved

527 cervical, the right pleurocoel slightly ramifies anteriorly near the right parapophysis;

however, this is not visible on the left side of the centrum. As in the previous cervical, the
ventrolateral side of the centrum and ventral border of the pleurocoel is formed by a stout

530 lamina that extends from the posterior edge of the parapophyses to the posterior end of the

531 cotyle.

The neural arch is only partially preserved (Fig. 3A, B). Its height is similar to the height ofthe cotyle. The neural arch in this element is limited to the middle/posterior end of the

vertebra; however, this is probably due to the fact that the neural spine is missing. The

neural canal, however, is clearly visible in this vertebra, being round to oval in anterior view

and more rounded triangular in posterior view. As in the previous vertebra, the lateral

neural arch lamination is well-developed, with the stoutest laminae being the prdl, the

posterior centrodiapophyseal lamina (pcdl), and the right podl. The anterior

539 centrodiapophyseal lamina (acdl) is also visible; however, it is smaller and shorter than the

540 pcdl. Both diapophyses are present on the neural arch, and are positioned dorsal and slightly

541 posterior to the parapophyses. The diapophyses are developed as small, lateroventrally

542 projecting protrusions of bone, being oval in shape in lateral view and conical in anterior

543 view. The left diapophysis is flexed more towards the centrum than the right, this is probably 544 due to deformation. The right prdl runs straight in a slight anterodorsal slope from the 545 diapophysis towards the prezygapophysis, where it meets with the cprl. Similarly, the right 546 sprI runs more or less parallel to the prdI. The left prdI, however, forms a much steeper 547 angle from the left diapophysis to the left prezygapophysis, due to the taphonomical 548 deformation. Towards the posterior end of the neural arch, the pcdl is in alignment with the 549 prdl. However, the former is directed slightly posteroventrally. The right podl is visible but is 550 damaged. It is a stout lamina and it forms a steep angle of 50° from the horizontal axis in its 551 course from the right diapophysis towards the right postzygapophysis.

552 553

(Fig. 3B, C). They project further anteriorly from the vertebral condyle than PVL 4170 (1) by
about 9 cm. Moreover, unlike in PVL 4170 (1), they project mostly anteriorly and only slightly

The prezygapophyses are much more elongated than in the previous cervical PVL 4170 (1),

dorsally from the neural arch. Once more the taphonomical deformation of this cervical is

apparent, as the left prezygapophysis is displaced and bent towards the vertebral body,

558 while the right projects more lateral and away from the vertebral body. The

prezygapophyses are supported by very stout stalks, which are formed by the prdl on the

560 dorsolateral side, the cprl on the lateral, and, partially, the sprl on their dorsal side. The prdl

561 meets the cprl in an acute angle, which is obscured from view by the prezygapophyseal

articular surfaces. A small, short, pair of tprl is present, which meet in a wide acute angle,

563 dorsal to the neural canal (Fig. 3C). Lateral to these laminae, small, paired, rounded to oval

564 prcdfs are visible underneath the prezygapophyses. They are also transversely convex.

565 The only preserved, right postzygapophysis is flexed slightly medially in dorsal view, and has

- its articular surface directed dorsally and tipped slightly anteriorly and laterally (Figure 3B,
- D). It is supported by the stout podl and an acutely angled, thin cpol, which together with
- 568 the pcdl creates a triangular, wing-like structure, which is offset from the neural arch

569	dorsally and posteriorly. The thin sheet of bone between the podl and the pcdl is pierced.
570	The distal end of the postzygapophysis is rounded to triangular in shape. A relatively deep
571	right pocdf is visible between the cpol and the podl. No tpol is visible here.
572 573	
5/4	<i>Cervical vertebra PVL 4170 (3):</i> This is the third cervical preserved in the series; it probably
575	corresponds to the 5-6th cervical (compared to the Rutland Cetiosaurus Leict LEICT
576	468.1968). It is well-preserved, but lacks both diapophyses, see Figure 4. The cervical is
577	stout, and is similar to PVL 4170 (2) in that the centrum is generally straight, and the anterior
578	and posterior ends are not as offset from each other as in the first preserved cervical.
579	Nevertheless, the cotyle is slightly offset to the ventral side, and the condyle bends slightly
580	ventrally from the relatively straight vertebral body (Fig. 4A, B). The prezygapophyses are
581	slightly displaced, the right projects further laterally than the left; this might be caused by
582	deformation.
583	Both the condyle and cotyle are larger in this cervical than in the previous two (Fig. 4A, B).
584	The condyle is oval in shape, and is transversely wider than dorsoventrally. It has a small
585	rounded protrusion, visible slightly dorsal to the midpoint of the condyle (Fig. 4E). A thick
586	rugose rim surrounds the condyle, from which the parapophyses protrude at the
587	lateroventral sides. The cotyle is more or less equally wide transversely as high
588	dorsoventrally. It has its deepest depression slightly dorsal to the midpoint. The cotyle does
589	not have a rugose rim; however, its ventral rim projects further posterior and slightly lateral
590	than its dorsal rim. In ventral view, (as well as in lateral view) the parapophyses are clearly
591	visible as rugose, oval structures that protrude from behind the condylar rim to the posterior
592	and lateral sides. Also emerging from this condylar rim is the ventral keel, which is
593	prominently visible for about 2/3rds of the length of the centrum, after which it fades into
594	the ventral body of the centrum. At the onset of the keel, a small round hypapophysis

protrudes ventrally from the centrum. Two oval depressions are visible on the lateral sidesof the hypapophysis.

597 In lateral view, the centrum shows neurocentral sutures between the lower part of the 598 centrum and the upper part of the vertebral body (Fig. 4A, B). The suture is better preserved 599 on the right side than on the left side of the centrum. On both lateral sides of the centrum, a 600 prominent pleurocoel is visible as a deep oval depression, which becomes shallower 601 posteriorly but spans almost the entire length of the vertebral body. Unlike in the previous 602 two cervicals, no compartmentalization of the pleurocoel is visible in this element. The 603 dorsal and ventral rim of the pleurocoels are marked by two stout laminae that define the 604 ventral and dorsal sides of the centrum.

605 The neural arch becomes more dorsoventrally elevated in this cervical, with the neural arch 606 being slightly higher than the dorsoventral height of the cotyle (Fig. 4A, B). The neural canal 607 is triangular to slightly teardrop-shaped in anterior view, in contrast to the previous two 608 cervicals. In posterior view, the neural canal is oval, with a flat ventral surface. Because the 609 diapophyses are damaged, the lamination underneath the diapophyses is clearly visible in 610 lateral view. The acdl is developed as a short lamina, running anteroventrally in an oblique 611 slope towards the anterodorsal end of the pleurocoel. The pcdl is a very stout, elongated 612 lamina in this cervical. It runs from directly underneath the diapophysis to the posterior end 613 of the vertebral body, but fades into the centrum shortly before the rim of the cotyle. The 614 acdl and pcdl delimit a small triangular centrodiapophyseal fossa (cdf), while a much wider 615 postzygapophyseal centrodiapophyseal fossa (pocdf) is bordered by the slightly convex, 616 stout podl (Figure 4A, B, C). This lamina runs at an oblique angle of about 40 degrees to the 617 horizontal from the diapophysis to the postzygapophysis. Shortly before reaching the 618 postzygapophysis, the curvature of the lamina changes from straight to slightly concave 619 (ventrally), giving the podl a slight sinusoidal appearance. The prdl runs from the 620 diapophyses to the prezygapophyses in an oblique angle similar to the podl. The four major

621 laminae on this cervical, prdl, acdl, pcdl, and podl, together create an X shape (in near

622 symmetrical oblique angles) on the midpoint of this cervical.

624 between each prezygapophyseal summit being about 110-120° (Fig. 4D). They project

The prezygapophyses project anteriorly, dorsally, and slightly laterally, with the angle

625 asymmetrically; this is probably due to taphonomical deformation. The stout stalks

626 supporting the prezygapophyses are concave ventrally, and convex dorsally, and project 9

627 cm anterior from the vertebral body (Fig. 4A, B, D). The articular surfaces are triangular in

628 shape. The prezygapophyses are supported by the prdl from the dorsolateral side, and by

629 the cprls ventrally. The cprls extend in a near vertical axis from the ventral side of the neural

630 arch, but at about the height of the neural canal project laterally towards the

631 prezygapophyseal articular surface in an angle of about 30°. In anterior view, the stout,

632 sinusoidal tprl join together from the medial articular surface of the prezygapophyses to the

633 ventral side of the prezygapophyses, just dorsal to the neural canal. Here a very short, stout,

634 single intraprezygapophyseal lamina (stprl) is present. The paired prcdfs, seen as triangular

635 depressions, bordered by the tprls and the cprls, are larger than in previous cervicals PVL

636 4170 (1) and (2).

623

637 The postzygapophyses are triangular in shape in posterior view, and their articular surfaces 638 in posterior/ventral view are rounded to triangular in shape (Fig. 4C). There is a slight V-639 shaped indentation on the medial side of each postzygapophysis between the posterior 640 termination of the podl and the cpol at the postzygapophyses. The cpols run in a curved, 641 oblique angle of about 55° to the horizontal, from the postzygapophyseal articular surfaces 642 to the dorsal rim of the posterior neural canal. No stpol is visible here. On each lateral side 643 of the paired cpols, large triangular paired pocdf are visible, bordered by the vertically 644 aligned podls.

645 The neural spine is already prominent in this cervical, more so than in PVL 4170 (1) and (2)
646 (Fig. 4A, B, F). In dorsal view, the neural spine appears solid, and is rounded in shape, and

647	the anterior, posterior and lateral rims are clearly visible and protrude slightly dorsally
648	(Figure 4F). The dorsalmost part shows rugosities, probably for ligament attachment. In
649	anterior view, the neural spine is kite-shaped, and shows rugosities on the anterior surface.
650	Relatively thin, paired sprl curve down from the anterior lateral sides of the neural spine,
651	where they extend in an inverted V-shape to the lateral sides of the prezygapophyses.
652	Medial to these laminae, an oval sprf is visible, ventrally bordered by the tprls. Similarly, in
653	posterior view, the spols form an inverted V towards the postzygapophyses, dorsally
654	bordering the spof, which is clearly visible as a deep and large fossa, which in turn is
655	bordered laterally by the paired cpols. The neural spine in lateral view as well as in posterior
656	view is seen to incline anteriorly, making the neural spine summit less prominent in
657	posterior view (Fig. 4A, B, C).
658	
659 660	Cervical vertebrae PVL 4170 (4): The fourth preserved cervical is generally well-preserved.
661	However, the left diapophysis and part of the neural arch are missing, and the right neural
662	arch, between the neural spine and the diapophysis, is partially reconstructed, see Figure 5.
663	The left prezygapophysis, and the articular surface of the postzygapophysis are also partially
664	missing. This cervical could have been more robust than the next one, and the neural spine
665	could have projected further dorsally, making this cervical in fact cervical (5), however, as it
666	is reconstructed, this cannot be ascertained for certain.
667	The centrum is more elongated then that of the previous cervical (Fig. 5A, B). The centrum
668	only shows a mild curvature, and the cotyle and condyle are not offset from one another;
669	the condyle bends slightly ventrally and the cotyle also mildly curves ventrally. The
670	lateroventral rims of the cotyle flare out slightly laterally and posteriorly, and are more
671	enlongated ventrally than dorsally. In anterior view, the condyle is oval and slightly
672	dorsoventrally flattened (Fig. 5D). It has a thick, prominent rim surrounding it, from which
673	the parapophyses are offset in anterior view. In posterior view, the cotyle is larger than the

674 condyle, and more or less equally wide transversely as dorsoventrally. In ventral view, the 675 thick rim that cups the condyle is clearly visible (Fig. 5E). From this rim, the hypapophysis 676 protrudes ventrally as a small rounded bulge. The ventral keel is prominently visible, and 677 runs along the ventral surface of the centrum until it fades into the posterior $1/3^{rd}$ of the 678 centrum, where it widens transversely towards its posterior end. This is also seen to some 679 extent in Lapparentosaurus (MNHM MAA 13; 172; 5), although this fanning includes a 680 dichotomous branching of the posterior end of the ventral keel in the latter taxon. In lateral 681 view, the ventral keel protrudes slightly more ventrally than the stout lamina that defines 682 the ventral lateral end of the centrum. In lateral view, the pleurocoels are visible as deep 683 depressions on the lateral side of the centrum, being deepest behind the rim of the condyle, and fading into the posterior $1/3^{rd}$ of the lateral centrum. Interestingly, this cervical shows 684 685 pleurocoels with well-defined posterior margins (as well as anterior, dorsal and ventral), 686 which differs from the pleurocoels in the previous cervicals (Fig. 5A, B). Moreover, the 687 pleurocoels in this element are slightly compartmentalized (a deeper depression of the 688 pleurocoel is visible anteriorly and posteriorly, while the mid section is less deep in the 689 lateral body of the centrum), as in the first two cervicals. 690 As in the previous three cervicals, the neural arch extends over most of the length of the 691 centrum, but ends a short way anterior to the posterior end of the centrum. The neural 692 canal is rounded to teardrop-shaped in anterior view, and oval to triangular in posterior 693 view, with an abrupt transverse ventral rim, as in PVL 4170 (3). The configuration of the four 694 prominent laminae on the lateral neural arch is similar to that of PVL 4170 (3) in that pcdl, 695 prdl, podl and acdl form an X-shaped structure. However, the right diapophysis (the left is 696 missing) of this element is larger than in the previous cervicals. The right diapophyis is 697 developed as a ventrolaterally projecting process, which is supported posteriorly by the very 698 stout pcdl, and anteriorly by a smaller, shorter acdl. The diapophysis is oval in shape and is 699 axially shorter than dorsoventrally.

700 The right prezygapophysis is supported laterally and dorsally by the stout prdl, which 701 extends from the anterodorsal side of the diapophysis to approximately 2/3rds of the length 702 of the stalk of the prezygapophysis (Fig. 5B, D). Ventrally, the prezygapophysis is supported 703 by the cprl, which is nearly vertically positioned on the neural arch. The prezygapophysis has 704 a triangular articular surface. As in the previous cervicals, the cprl and tprl meet at the distal 705 end of the prezygapophysis in an acute angle of approximately 30 degrees. The paired tprls 706 slope steeply down and meet on the dorsal rim of the anterior neural canal. The cprl and 707 tprls enclose paired, rhomboid prcdf.

708 In posterior view, the left postzygapophysis is only partially preserved, as the articular

surface is missing, but the right structure is present, showing a flattened articular surface

710 (Fig. 5C). The intrapostzygapophyseal laminae form a V shape with an angle of about 55 $^\circ$

from the sagittal plane of the centrum, which is similar to PVL 4170 (3). They meet only on

the dorsal rim of the posterior neural canal. The paired, triangular pocdfs, which are

713 demarcated by the cpols and the podls, are also similar to the third preserved cervical.

The neural spine is robust in anterior view (Fig. 5D). It is narrower at the base (at the onset

of the spinoprezygapophyseal lamina) and expands transversely towards the summit, which

in anterior view is shaped like a rounded hexagon. The right sprl is a near-vertically

positioned, prominent structure that extends from about 1/3rd under the neural spine

summit to the ventral pairing of the tprls. In lateral view, the neural spine is

anteroposteriorly shorter, with respect to the length of the centrum, than in previous

720 cervicals. Its anterior margin is slightly inclined anteriorly. In posterior view, the neural spine

summit has a more rounded, rectangular shape, and is clearly inclined towards the anterior

side of the cervical. The (only preserved) right spol curves concavely towards the

postzygapophysis (Figure 5A,B,C). The spinopostzygapophyseal fossa is deep and triangular

in shape.

725 In dorsal view, the neural spine summit is roughly quadrangular in outline, although it is 726 slightly wider transversely than long anteroposteriorly (Figure 5F). On the anterior rim of the 727 summit, the spine slightly bulges out convexly, with an indent on the midline, rendering the 728 anterior rim slightly heart-shaped. The posterior side of the neural spine summit is slightly 729 concave in dorsal view, with the spol sharply protruding from each lateral side. 730 731 732 Cervical vertebra PVL 4170 (5): This is a mid-posterior cervical, which is well-preserved, with 733 all zygapophyses and diapophyses intact, although the neural spine is slightly 734 taphonomically deformed, and the diapophyses are slightly asymmetrical, also probably due 735 to deformation. The left parapophysis is also missing (Fig. 6A). 736 The centrum is different from the previous cervicals in that it is more robust, less axially 737 elongated and the condyle, cotyle and neural spine are dorsoventrally larger (Fig. 6A, B). The 738 anterior condyle is rounded, robust and slightly dorsoventrally flattened. The anterior end of 739 the condyle has a rounded protrusion on the midpart. The rim of the condyle is clearly 740 visible and protrudes slightly dorsally (Fig. 6C). Posteriorly, the cotyle is deeply concave and 741 is larger transversely and dorsoventrally than the condyle. The posterior end of the centrum, 742 ventral to the cotyle, flares out laterally, however, it shows a U-shaped indent in the 743 midpart, seen in posterior view (Fig. 6D). In lateral view, the centrum is concavely 744 constricted anteriorly, directly posterior to the rim of the condyle. As in the other cervicals, 745 the dorsal end of the posterior cotyle extends a little further posteriorly from the neural 746 canal in lateral and ventral view. The right parapophysis is visible in lateral view at the 747 ventrolateral end of the condylar rim (Fig. 6B). It is oval in shape and protrudes ventrally and 748 posteriorly. The pleurocoel on the lateral side of the centrum is deeper anteriorly than 749 posteriorly, and spans almost the entire lateral side of the condyle anteriorly (Fig. 6A, B). 750 Posteriorly it fades into the centrum. In ventral view, the ventral keel is clearly visible, and

751 stretches over the entire length of the centrum, but flattens in the posteriormost part (Fig. 752 6E). The hypapophysis protrudes less in this cervical than in the previous ones. The 753 parapophysis is more elongated axially than transversely in ventral view, and less rounded 754 than in the previous cervicals; rather than having a rounded rectangular shape in ventral 755 view, it is more elliptical in shape, and is slightly more offset to the lateral sides of the 756 centrum (Fig. 6E). Both posterior centroparapophyseal laminae are clearly visible in this 757 element as short but strong laminae that are confluent with the ventrolateral edges of the 758 vertebral body.

759 The neural arch is higher dorsoventrally in this element than in the previous ones. In lateral 760 view, the neural arch spans almost the entire axial length of the centrum, however, as in the 761 previous cervicals, it is slightly offset from the anterior dorsal end of the centrum (Fig. 6A, B). 762 In anterior view, the neural canal is slightly teardrop-shaped, and dorsoventrally is more 763 elongated than transversely. In posterior view, the neural canal is also teardrop-shaped, 764 however here it is more dorsoventrally flattened and transversely widened at the base. The 765 diapophyses, in lateral view, appear as rounded appendices, which are offset from the 766 vertebral body as ventral and lateral projection. They are transversely thin and flattened. In 767 anterior view they are more complex in shape, created by a conjoining of the acdl, pcdl and 768 prdl in a triangular shape, which shows a ventral hook-shaped distal protrusion. In posterior 769 view the diapophyses are enclosed in sheets of bone. The prezygapophyses on this cervical 770 rest on more dorsoventrally elongate stalks than in previous cervicals (Fig. 6A, B, C). These 771 stalks have a pedestal-like appearance, and show lateral rounded bulges at their base, dorsal 772 and lateral to the thick condylar rim. The prezygapophyses project anteriorly and slightly 773 medially and dorsally, and are anteriorly triangular in shape. There are deep rhomboid 774 prcdfs visible as dorsoventrally narrow, slit-like fossae, ventral to the prezygapophyses. The 775 centroprezygapophyseal laminae form an oblique angle towards the centrum. The 776 prezygodiapophyseal laminae run ventrally from the prezygapophyses in a sharp angle.

777 These laminae meet dorsally in an acute angle. The tprl meet dorsal to the neural canal in a

The postzygapophyses and prezygapophyses are both more aligned with the axial column

778 wider angle than in the previous cervicals, showing a widening of the space between the

779 prezygapophyses towards more posterior cervicals in *Patagosaurus*.

781 than in previous cervicals (Fig. 6F). In lateral view, the articular surface of the 782 postzygapophyses is aligned with the horizontal axis, and in dorsal and posterior view the 783 articular surfaces are triangular in shape (Fig. 6A, B). In lateral view, the podl form a wide 784 angle with the axial column, owing to the further elongation of the cpol (producing more 785 elevated postzygapophyses). The cools show an acute angle from the postzygapophyses to 786 the anterior and ventral side, and are slightly ragged in appearance. They meet the centrum 787 anteriorly to the dorsal rim of the cotyle. In posterior view, the cool run at an acute angle, 788 and in a slightly concave way, to the ventral side of the postzygapophysis (Figure 6D). This 789 angle is smaller than in previous cervicals, being about 35°, due to the elongation of the 790 neural arch and higher dorsal position of the postzygapophyses. Between the cpol and podl,

791 large, triangular pocdf are visible.

780

792 The neural spine in anterior view is slightly sinusoidal, probably due to taphonomic

793 deformation (Fig. 6C). In lateral view, the neural spine is further reduced in its axial length 794 compared to the previous cervicals (Fig. 6A, B). The spine summit is prominent; it is seen to 795 protrude dorsally and anteriorly, clearly separated from the vertebral body as a rounded 796 rectangular bony mass. In dorsal view, the neural spine summit is wider than the neural 797 spine body, and is of a teardrop-shaped protuberant shape (Fig. 6F). It is also expanded 798 transversely. Anteriorly on the neural spine, a prominent protuberance is visible anteriorly, 799 possibly an attachment site for ligaments. The sprls are seen, in dorsal view, to protrude 800 from the anterior side of the neural spine summit (Fig. 6C). They run nearly vertically 801

towards the dorsal base of the prezygapophyseal stalks. At the base of the neural spine they

are slightly transversely constricted. The spol are positioned as near-horizontally aligned

803 with the axial plane of the cervical. They are thin, prominent laminae.

804

805 Cervical vertebrae PVL 4170 (6): This is a well-preserved posterior cervical with some 806 damaged/broken thin septa. The centrum is robust, as in PVL 4170 (5), but unlike the more 807 elongated anterior cervicals. The cervical is further distinguished by having an axially more 808 elongated neural arch than in the previous cervical, see Figure 7. 809 The centrum is shorter than in previous cervicals, and stouter, with a transversely flattened 810 condyle with a small rounded protrusion slightly higher than the midpoint (Fig. 7A, B). The 811 cotyle is slightly larger and higher dorsoventrally than the condyle, as in the other cervicals. 812 In ventral view, the ventral keel is developed as a protruding ridge between two concavities,

813 which are flanked by the ventrolateral ridges of the centrum (Fig. 7E). This keel flattens

814 towards the caudal end into a bulge and is no longer visible at the posterior end of the

815 ventral side of the centrum. Instead there is a slight depression on the distal end of the keel.

816 The centrum is constricted directly posterior to the parapophyses, which shows a deep

817 concavity of the centrum in lateral view, after which the centrum curves more gently

towards a convex posterior end of the centrum (Fig. 7A, B). The pleurocoel is anteriorly

819 deep, and the thin septum that separated it from its mirroring pleurocoel is broken, creating

an anterior fenestra. On the left side of the centrum the neurocentral suture is visible. In

anterior view, the neural canal is oval, being higher dorsoventrally than wide transversely,

and in posterior view, the neural canal is subcircular with a pointed dorsal side.

823 In anterior view, the prezygapophyses are a triangular shape, due to the tapering of both

824 cprl and prdl towards the dorsal tip of the prezygapophyses, where they meet in an inverted

825 V-shape, as in PVL 4170 (5), see Fig. 7C. The cprf are not as deep as in the previous cervicals.

826 The dorsal end of the prezygapophyses is not as convex as in the previous cervicals. In

827 ventral and posterior view, the postzygapophyseal articular surfaces are triangular (Fig. 7D,

828 E). In lateral view, the sprl is positioned less vertical than in PVL 4170 5, and instead slopes in

829 a gentle curve towards the prezygapophyses (Fig. 7A, B). In posterior view, the thick cpols

and the spols support the laterally canted, 'wing-tip'-shaped sheet of bones that are

831 supported by the podl and pcdl on the lateral side (Fig. 7D). The cpol do not meet, while

- there is no tpol. In dorsal view, the postzygapophyses and spol expand further beyond the
- 833 centrum than the prezygapophyses overhang the centrum anteriorly, which is the reversed

834 condition compared to the more anterior cervicals in PVL 4170. The

835 spinopostzygapophyseal lamina is also less oblique than in previous cervicals, and curves

836 gently concavely towards the postzygapophyses (Fig. 7D).

837 The neural spine is craniocaudally flattened but transversely broader than PVL 4170 (5). The 838 base of the neural spine is only supported by a rather thin bony sheet, both anteriorly and

posteriorly, as can be seen due to a break. The dorsal end and summit of the neural spine,

840 however, are formed by solid bone. In anterior view, the spine is not as teardrop-shaped as

in PVL 4170 (5), but is more rectangular, and widens towards its summit. The neural spine

842 does not tilt notably forward as in PVL 4170 (5), but cants only slightly anteriorly. The neural

spine summit extends dorsally beyond the spol as an oval to rhomboid protuberance. The

844 neural spine and the postzygapophyses, together with the podl are more axially elongated

and dorsally elevated in this cervical than in the previous ones. In dorsal view, the neural

spine summit is a stout, transverse strut. It is slightly transversely expanded, and thicker at

the lateral ends.

848

849

Cervical vertebra PVL 4170 (7): This is a partially reconstructed posterior cervical, with the
left diapophysis missing (Fig. 8). The vertebra is shorter axially and higher dorsoventrally
than previous cervicals (Fig. 8A, B). The centrum is stout. In anterior view, the condyle is
dorsoventrally compressed and transversely widened (Fig. 8 F). The 'cup' is very distinct. The
cotyle is larger than the condyle, more rounded, and shows an indentation dorsally for the

855 neural canal, making the cotyle slightly heart-shaped (Fig. 8E). In ventral view, this centrum 856 is less elongated and transversely wider than previous cervicals. The keel is still well 857 developed, as are the lateral concavities coinciding with the hypapophysis, which is present 858 as a sharp ridge (Fig. 8C). The posterior ventral side of the centrum is ventrally offset from 859 the anterior ventral side, due to the larger size of the cotyle in this specimen, and due to the 860 ventral bulge of the distal half of the centrum. The parapophyses are more aligned with the 861 centrum, in that they do not project ventrolaterally, but more posteriorly, in contrast to 862 previous cervicals (Fig. 8C). The parapophyses are oval in ventral view and more triangular in 863 lateral view. The neural canal is dorsoventrally flattened and teardrop-shaped (Fig. 8E, F). 864 The prezygapophyses differ from previous cervicals in that they form a more accute angle 865 with the vertebral body and have a flat, dorsally directed articular surface in lateral view 866 (Fig. 8A, B). The beams supporting the prezygapophyseal articular surface are stout, as in the 867 previous cervicals. The prezygapophyses are inverted V-shaped in anterior view (Fig. 8F). 868 However, this structure is wider transversely than in previous cervicals. The 869 intraprezygapophyseal laminae tilt ventromedially, whereas the distal tips of the 870 prezygadiapophyseal laminae tilt ventrolaterally, creating an inverted V-shape in anterior 871 view of each prezygapophysis, as in the previous cervical. The stprl is not present (see Table 872 2). In dorsal view, the articular surface of the prezygapophysis is more rounded than in 873 previous cervicals. The postzygapophyses are supported from the lateral and ventral sides 874 by the prominent podl, which project in a wide angle of about 70 degrees from the posterior 875 side of the diapophysis to the postzygapophyses; this lamina curves gently convexly (Figure 876 8A, B, E). In lateral view, the postzygapophyses are present as triangular structures at the 877 distal end of the thick podl. Dorsal to the postzygapophyses, triangular epipophyses are 878 visible (Fig. 8A, B, E). Also, in lateral view, the tools run ventral to the postzygadiapophyses 879 in a vertical line towards a U-shaped recess, formed by the stpol. In posterior view, the 880 intrapostzygapophyseal laminae form a V-shape. The tpol are much shorter than in PVL 4170 881 (6), which also limits the size of the spinopostzygapophyseal fossa (spof). The stpol is 882 present as a thin lamina that recedes towards the neural arch (Figure 8E). This is the only 883 cervical that has an stpol that is longer than 1 cm. It separates paired rhomboid cpof. These 884 are flanked by the thick podl, which are more elongated in this vertebra than in cervical PLV 885 4170 (6). The right diapophysis expands from the lateral side of the neural arch, and shows a 886 strong ventral bend towards its distal end. This strong bend could be the product of 887 deformation. The left diapophysis also bends ventrally and laterally, but not as strongly as 888 the right one (Fig. 8A, B, E, F). The diapophyses are clearly visible both in anterior and 889 posterior view. Ventrally and anteriorly they are concave, with elongated but axially short 890 prcdfs. They are dorsally supported by the convergence of the prdl and the podl, which form 891 a thick rugose, rounded plate of bone on the dorsal tips of the diapophyses. 892 The neural spine is transversely broad and axially short, and rectangular in shape (Fig. 8F). In 893 dorsal view, it fans out transversely at the apex, but, together with the sprl, becomes 894 constricted ventrally (Fig. 8D). This cervical is further distinguished from the previous 895 cervicals by the dorsoventral elongation of the neural spine, and the accompanying 896 elongation of the tpol in lateral view (Fig. 8A, B). 897 898 Cervicodorsal PVL 4170 (8): The neural arch is dorsoventrally elongated in this transitional 899 vertebra between cervicals and dorsals; a trend that persists throughout the anterior and 900 posterior dorsals. The posterior articular surface (cotyle) is dorsoventrally higher than the 901

anterior condyle, (Fig. 9).

902 The condyle is of similar shape to that in PVL 4170 (7) (Fig. 9A, B, C). The cotyle of this

903 vertebra is well-preserved and has an oval, slightly dorsoventrally flattened shape, with a

904 small concave recess at the base of the neural canal (Fig. 9D).
905 On the ventral side of the centrum, the ventral keel and adjacent fossae are still clearly 906 visible (Fig. 9F). In lateral view, the ventral margin of the centrum is strongly concave in the 907 first half of its length (slightly damaged but still visible) and in the posterior part becomes 908 more convex and robust (Fig. 9F). The ventral keel extends over the first 1/3 of the length, as 909 in the other vertebrae, and then becomes a bulge, adding to the convexity of the posterior 910 ventral end of the centrum. In lateral view, the pleurocoels of either side show a cut through 911 the centrum, creating a foramen (Fig. 9A, B). This supports the observation that the 912 pleurocoels are very deep in the cervicals of *Patagosaurus*, and that they are normally only 913 separated from the adjacent pleurocoel by a very thin midline septum (Carballido and 914 Sander 2014), which in this vertebra is not preserved. The parapophyses are present as 915 rounded to triangular extensions on the lateral sides of the condylar rim (Fig. 9F). They are 916 not clearly visible in anterior or lateral view, but are visible in ventral view. At the base of the 917 prezygapophyseal stalks, however, similar triangular protrusions exist (Fig. 9C). 918 The cprl project slightly laterally from the centrum (Figure 9A, B). The prdcf are larger than in 919 previous vertebrae, due to the wider lateral projection of the diapophyses. These fossae are 920 triangular in shape (Figure 9C). The prezygapophyses are roughly square with rounded edges 921 in dorsal view. The spinoprezygapophyseal fossa (sprf) is very deep. The prdl are 922 prominently developed as sinusoidal thick laminae, supporting the prdl from below and 923 from the lateral side, and supporting the diapophyses anteriorly. The prezygapophyseal 924 articular surfaces are flat and axially longer than in previous vertebrae (Fig. 9E). The angle of 925 lateral expansion of the sprl however, is greater than in previous vertebrae. 926 In posterior view, the postzygapophyses project to the lateral side (Fig. 9D). The tpols do not 927 meet, but run down parallel in the dorsoventral plane to the neural canal. A faint right cpol 928 seems to be present in this vertebra, however, it could also be an anomaly of the pocdf. This

elongates the spof. The podl project dorsally and posteriorly in a high angle. Towards about

929

930 2/3rd of the total vertebral height. These project in a straight line, after which they bend in a
931 convex curve to the posterior side. The pcdl make a similar bending curve towards the
932 centrum, due to the elongation of the posterior neural arch. Prominent pocdf are present as
933 shallow triangular fossae.

In dorsal view, as in PVL 4170 (7), the neural spine is transversely wide and axially short (Fig.
925 9E). It is constricted towards the postzygapophyses so that it 'folds' posteriorly. In anterior
view, the neural spine is ventrally more constricted than in the previous vertebra (Fig. 9C). It
is more elongated dorsoventrally, and the neural spine is transversely overall less wide than
the previous vertebra.

939

940 Dorsals: the holotype specimen has nine dorsals preserved, including a transitional 941 cervicodorsal vertebra. Dorsals are numbered PVL 4170 (9) – (17). Most of the anterior and 942 mid-dorsals are preserved, however, some may be missing, seen in the sudden transition 943 from anterior-mid dorsals PVL 4170 (10) - (11) and mid-posterior dorsals PVL 4170 (12) -944 (13). Most neural arches and spines are relatively complete; except dorsal PVL 4170 (15) has 945 only the centrum preserved. The number of missing dorsals can only be estimated. The 946 Rutland Cetiosaurus, thus far morphologically the closest sauropod to Patagosaurus (see 947 Holwerda and Pol 2018), shows the disappearance of the acdl at around vertebra nr 15. As 948 the acdl seems to disappear in anteriormost dorsals of *Patagosaurus*, assuming the 949 anteriormost dorsal is preserved, both sauropods could have had as few as 10 dorsal 950 vertebrae (see Table 2). However, (approximately) contemporaneous non-neosauropodan 951 eusauropods are reported to have 12 dorsals (Jobaria, mamenchisaurs) or 13 (Shunosaurus). 952 Barapasaurus is estimated to have had even 14 dorsal vertebrae. Diplodocids Apatosaurus 953 Marsh, 1877, Diplodocus Marsh, 1878, and Barosaurus Marsh, 1890 all had 10 dorsal

954 vertebrae, and basal neosauropod *Haplocanthosaurus* 13-14 (Hatcher 1903; Carballido et al.
955 2017).

956 The dorsal centra in PVL 4170 become axially shorter and dorsoventrally higher towards the 957 posterior dorsals, with mediolateral width increasing proportionally with height towards 958 posterior dorsals. Anterior-mid dorsal centra are therefore more rectangular in anterior and 959 posterior view, and the posteriormost dorsals more round with a higher mediolateral width. 960 The centra also change from being opisthocoelous to amphicoelous between anterior-mid 961 dorsals PVL 4170 (11)-(13), see Fig. 12 - 14. Opisthocoelus anterior dorsals are shared with 962 Cetiosaurus, Tazoudasaurus, and diplodocids (Tschopp et al. 2015). The pleurocoel on dorsal 963 vertebral centra in Patagosaurus remains visible on the lateral side of the centrum 964 throughout the dorsal series, but does gradually become more of an oval depression. The 965 ventral surface of the centra in anterior dorsals is similar to posterior cervicals in that there 966 is a vestigial ventral keel in anteriormost dorsals, but also in the constriction of the centrum 967 anteriorly, right behind the condyle. The cotyle flares out laterally. Towards mid and 968 posterior dorsals, the centrum in ventral view becomes more symmetrical, with a 969 constriction at the midpoint and flaring out of the centrum towards anterior and posterior 970 articular surfaces. In lateral view, the posterior dorsal centra show a strong curving inwards 971 more anteriorly than posteriorly. Towards the posterior end of the dorsal column, the neural 972 arches increase in height to twice that of the posterior cervicals. The neural spines become 973 axially shorter and transversely broader, however, the posteriormost dorsals have 974 protuberant neural spines that are nearly as high as the combined length of the neural arch 975 and centrum. The neural canal becomes elongated dorsoventrally in the elongated neural 976 arches, and is oval.

977 Anteriormost dorsals (PVL 4170 9-10) are already more elongated dorsoventrally than the978 cervicals, however, they are still opisthocoelous, and are morphologically distinct from the

posterior dorsals, in that they have transversely wide neural spines, which are flattened
axially. The neural canal is transversely wide and oval. The diapophyses are bent ventrally as
in the cervicals, and the prezygapophyses are placed higher dorsally than the diapophyses.
Prezygapophyses are also directed obliquely dorsally. The spol flare out ventrally, giving the
neural spine a broad exterior. As in the cervicals, the angle made between the podI and the
pcdI is high.

985 Middle dorsals (PVL 4170 11-12) become more transversely slender in the neural arch, and 986 the prezygapophyses have a more horizontally positioned articular surface. The transverse 987 processes are also more elongated than the anterior dorsals. The pedicels become more 988 elevated, and the neural spine more elongated dorsoventrally. spol still flare out, but less 989 posteriorly than in anterior dorsals, creating a more 'compact' neural spine complex. 990 At the transition from middle to posterior dorsals, anteriorly, cprl lengthen as the neural 991 arch and the pedicels elongate. Posteriorly, first the intrapostzygapophyseal laminae meet, 992 then the centropostzygapophyseal laminae disappear, and instead an stpol appears (see

993 Table 2).

994 The posterior dorsals (PVL 4170 13-17) possess the most discriminating combination of

995 features for *Patagosaurus*. The holotype posterior dorsals show an extensive elongation of

996 the neural arch, both at the pedicels as well as at the neural spine. Elongation of the neural

997 spine towards posterior dorsals is common for sauropods (e.g. *Cetiosaurus, Barapasaurus,*

998 *Haplocanthosaurus, Omeisaurus,* (Hatcher 1903; He et al. 1984; Upchurch and Martin 2003;

999 Bandyopadhyay et al. 2010), however this in combination with the elevation of the pedicels

1000 is not seen to this degree, save for *Cetiosaurus*, and then the elongation is still higher in

1001 *Patagosaurus*. The elongation of the neural arch and pedicels is only seen in

1002 *Mamenchisaurus youngi* (Pi et al. 1996). The lateral elongation of the transverse processes is

1003 reduced. Next to being elongated, the pedicels also show a lateral, ragged sheet of bone

1004 that stretches from the base of the prezygapophyses to the ventral end of the cprl. This is

1005 seen in a more rudimentary form in Cetiosaurus oxoniensis (Upchurch and Martin 2003, 1006 OUMNH J13644/2). The relatively horizontal lateral projection of the transverse processes 1007 also distinguishes Patagosaurus from many (more or less) contemporary basal non-1008 neosauropodan eusauropods, as these tend to project more dorsally in *Cetiosaurus*, 1009 Mamenchisaurus, Omeisaurus, and also in the basal neosauropod Haplocanthosaurus 1010 (Hatcher 1903; Young and Zhao 1972; Pi et al. 1996; Tang et al. 2001; Upchurch and Martin 1011 2002, 2003). In anterior view, the neural arch is characterized by two dorsoventrally 1012 elongated oval excavations; the cprf, which are separated by a stprl. The stprl runs down to 1013 the dorsal rim of the neural canal. This is also seen in Cetiosaurus oxoniensis OUMNH 1014 J13644/2, and to some extent in Tazoudasaurus (Allain and Aquesbi 2008), and 1015 Spinophorosaurus (Remes et al. 2009). However, in these taxa, this lamina is shorter, as the 1016 neural arch is less dorsoventrally elongated. In Patagosaurus dorsals, the neural canal itself 1017 is also dorsoventrally elongated and oval, this is also seen in Cetiosaurus oxoniensis OUMNH 1018 J13644/2, although not to the extent of *Patagosaurus*. It is not slit-like, as seen in 1019 Amygdalodon (Rauhut 2003a; Carballido et al. 2011) and Barapasaurus ISIR 700 1020 (Bandyopadhyay et al. 2010). In posterior view, the spol remain close to the body of the 1021 neural spine, i.e. they do not flare out laterally as in the anterior and mid-dorsals. The 1022 hyposphene appears here as a small, rhomboid structure, accompanied by very faint 1023 centropostzygapophyseal laminae which are embedded in the posterior neural arch. The 1024 hyposphene is a few cm more dorsal to the neural canal (about 5 cm). It is prominently 1025 visible below the postzygapophyses, which now are aligned at 90° with the neural spine, and 1026 have a horizontal articular surface. Posteriorly, during the transition from mid- to posterior 1027 dorsals, the tool becomes shorter, and eventually dissapears as the postzygapophyses 1028 approach each other medially. Instead, the stpol split into the medial and lateral 1029 spinopostzygapophyseal laminae (m.spol and l.spol, see Table 2). The podl include the l.spol. 1030 The stpol continues to run down to the hyposphene. Posterior dorsals have a very

1031 rudimentary aliform process, sensu Carballido and Sander (2014).

1032 The most noted autapomorphy of *Patagosaurus* is the presence of paired cdf, or fenestrae,

- 1033 which appear from dorsals PVL 4170 13 onwards. It was long thought that these were
- 1034 connected to the neural canal, however, recent CT data reveals that a thin septum which
- 1035 separates the adjacent fenestrae from each other, and from the neural canal. Ventrally
- 1036 these fenestrae form a central chamber, still well above the neural canal (see PVL 4170 13).
- 1037 The cpof is present in posterior dorsals of *Patagosaurus*, however it is only weakly
- 1038 developed. It is more developed in *Cetiosaurus*.
- 1039
- 1040 Dorsal PVL 4170 (9): Anterior-mid dorsal with the centrum drastically reduced in
- 1041 anteroposterior length, making it stouter than the cervicals, but still clearly opisthocoelous.,
- 1042 see Fig. 10. The left diapophysis, neural arch and part of the neural spine are partially
- 1043 reconstructed. The condyle has a slightly pointed protrusion on the midpoint, as in the
- 1044 cervicals (See Fig. 10A, B, F). Ventrally, the centrum constricts strongly immediately
- 1045 posterior to the anterior condyle (Fig. 10F). The ventral keel marginally visible, and exists
- 1046 more as a scar running down the midline from the small hypapophysis. The ventral side of
- 1047 the posterior cotyle is slightly deformed, with the left lateral end projecting further than the
- 1048 right. As in the other ventral posterior surfaces of the vertebrae, the lateral ends flare out
- 1049 slightly further posteriorly than the axial midpart (Fig. 10 A, B, F).
- 1050 The neural canal in anterior view is subtriangular in shape, and transversely wider than
- 1051 dorsoventrally high (Fig. 10C). Directly above it, there is a small protrusion present of the
- 1052 hypapophysis. In posterior view, the shape of the neural canal is similar, however, the
- 1053 posterior opening is less triangular and more rounded (Fig. 10D).
- 1054 The neural arch of this vertebra is still transversely wide, as in the cervicals. However, it is
- also becoming dorsoventrally higher (see Fig. 10A, B, C, D). Because of this, the

1056 centroprezygapophyseal fossae, which are placed medially to the prezygapophyseal stalks,

1057 are not as deep as in the cervicals (Fig. 10C). In lateral view, the prezygapophyseal pedestals

1058 are directed nearly vertically in the dorsoventral plane (Fig. 10A, B).

1059 The prezygapophyses are leaning slightly medially and ventrally towards the single

1060 intraprezygapophyseal lamina that runs along the midline of the vertebral neural arch on the

1061 anterior side (Fig. 10C). In dorsal view, the prezygapophyses are subtriangular in shape and

1062 are widely spaced apart, with about 1/3rd of the spinal summit width between them (Fig.

1063 10E).

1064 The postzygapophyses are raised even higher dorsally in this anterior dorsal than in the

1065 cervicals, at about 2/3rd of the height of the neural spine (Fig. 10A, B, D). Consequently, the

1066 podl are more elongated and makes a high angle, of about 130°, with respect to the axial

1067 plane and to the pcdl. Both podl's are slightly arched towards the postzygapophyses (Figure

1068 10A, B). Because of the extension of the podl, the posdf takes in a large portion of the

1069 posterior lateral surface of the vertebra (Fig. 10A, B). The tpols in posterior view are

1070 prominent, convexely curving laminae, which meet right above the posterior neural canal. In

1071 lateral view, the tpols show a triangular recess below the postzygapophyses, after which the

1072 tpols expand posteriorly before meeting the hypopshene dorsal to the neural canal (Fig.

1073 10D).

1074 In this vertebra, the cpol's are no longer clearly visible, and indeed, only the left cpol is seen

1075 as a thin lamina on the neural arch, lateral and ventral to the left tpol (Fig. 10D). Here, a

1076 rudimentary hyposphene is present as a small teardrop-shape ventral to the ventral fusion

1077 of the tpols. The fusion of the tpols and the hyposphene are also visible as a triangular

1078 protruding complex in dorsal view.

1079 The right diapophysis is prominent in anterior, posterior and lateral view as a stout,

1080 lateroventrally positioned element (Figure 10A, B, C, D). It is transversely broader than in the

1081 cervicals. In anterior view, the prdl and acdl/pcdl are all positioned in an inverted V-shape

- 1082 with oblique angles of about 45° to the horizontal. In anterior view, the cprl divides the cprf
- 1083 neatly from the prcdf, which is similarly inverted V-shaped as the outline of the
- 1084 diapophyseal laminae (Fig. 10C). In posterior view, the pocdf is confluent with the posterior
- 1085 flat surface of the diapophysis (Fig. 10D). The posterior centrodiapophyseal lamina in
- 1086 posterior view, curves convexly towards the ventral side of the vertebra.
- 1087 The articular surface of the diapophysis is flat to concave, and rounded to rectangular in
- 1088 shape. Posteriorly, they show small, elliptic depressions, on the distal end of the
- 1089 diapophyses (Fig. 10D).
- 1090 Note that the sprl are reconstructed, and will not be discussed here. The spol are clearly
- seen in anterior view; they flare out transversely in a steep sloping line (Fig. 10C). The spol
- are rugose, and the tpol as well, these appear ragged in lateral view. In this anterior dorsal,
- 1093 the spinopostzygapophyseal fossae (spof) are more rectangular than in the cervicals, and
- also deeper (Fig. 10D).
- 1095
- 1096 The neural spine is constricted transversely around the dorsoventral midlength, and fans out
- 1097 transversely towards the summit. The spine summit consists of a thick transverse ridge,
- 1098 which folds posteriorly on each lateral side, before smoothly transitioning to the spols (Fig.
- 1099 10E). The neural spine summit is positioned higher dorsally in this anterior dorsal than in the
- 1100 cervicals (so that the spol are consequently more elongated).
- 1101
- 1102

Dorsal PVL 4170 (10): This partially reconstructed anterior-middle dorsal (Fig. 11) is slightly
taphonomically distorted, in that the right transverse process is bent slightly more ventrally,
and the neural spine is slightly tilted to the left side (see Fig. 11). Parts of the centrum, the

- 1106 middle anterior part of the neural arch, and ventral parts of the diapophyses are partially
- 1107 reconstructed.

1108 The centrum is still slightly opisthocoelous in lateral view, as in PVL 4170 (9), and as in the 1109 cervicals, with the characteristic stout rim cupping the anterior condyle (Fig. 11A, B). It is 1110 noteworthy however, that the centrum and neural arch do not entirely match, possibly due 1111 to this vertebra being partially reconstructed. The centrum in ventral view is transversely 1112 constricted posterior to the rim that cups the condyle (Fig. 11F). The rim stands out 1113 transversely from the centrum body. The parapophyses are located dorsal to this this 1114 expansion, as triangular protrusions. The cotyle in posterior view is concave, and is slightly 1115 transversely wider than dorsoventrally high. 1116 The neural arch transversely narrows slightly, dorsal to the parapophyses (both at its

1117 anterior and posterior side; Fig. 11C). The anterior neural canal is embedded in this

1118 narrowing, and is rounded to rectangular in shape. It is less wide transversely as in the

1119 posterior cervicals (Fig. 11C). The posterior neural canal is equally rectangular to rounded in

shape. About 5 cm dorsal to it, the hyposphene is present as a rhomboid, small structure

1121 (Fig. 11D).

1122 The diapophyses in this dorsal are creating a wider angle with respect to the horizontal than 1123 in the last dorsal PVL 4170 (9), see Fig. 11C, D. The prdl, the acdl, and posteriorly, the pcdl, 1124 all arch into a less oblique angle, creating an inverted V-shape of about 50° (note that the 1125 right diapophysis is slightly distorted due to taphonomical damage). The diapophyseal 1126 articular surface is triangular, with the tip pointing ventrally, and the flat surface pointing 1127 dorsally, in lateral view (Fig. 11A, B). Ventral to the diapophyses, in lateral view, the anterior 1128 and pcdl are more or less equally distributed in length and spacing on the lateral surface of 1129 the neural arch. A roughly triangular but deep cdf can be seen between these laminae. 1130 The prezygapophyses in dorsal view make a wide wing-like structure together with the 1131 diapophyses and the prdls (Fig. 11E). There is a U-shaped, wide recess between the 1132 prezygapophyses. In anterior view, the prezygapophyses stand widely apart from one 1133 another, and are supported by stout cprl, creating thick pedicels that expand laterally above 1134 the centrum, dorsal to a slight recess right above the centrum (Fig. 11C). The articular

surface of the prezygapophyses is rounded to rectangular in shape, and in anterior view is

tilted ventrally towards the midline of the vertebra (Fig. 11C, E). The prezygapophyseal

spinodiapophyseal fossae (prsdf) are present between the prezygapophyseal pedicels, on

1138 the neural arch. They are rounded to rectangular in shape, dorsoventrally elongated, and

shallow, the deepest point being near the onset of the sprl (Fig. 11C).

1140 The postzygapophyseal articular surfaces are obliquely offset from the hyposphene. The

1141 articular surfaces are roughly triangular in shape (Fig. 11D). In posterior view, the tpol are

1142 distinctly flaring out from the dorsal end of the hyposphene to the postzygapophyses. The

1143 cpols are present only as very faint, low ridges embedding the hyposphene on the lateral

side (Fig. 11D). The postzygodiapophyseal lamina is short and stout, therefore dramatically

reduced in length and angle compared to dorsal PVL 4170 (9), (Fig. 11A, B), leading to

believe at least one dorsal between PVL 4170 (9) and (10) should have existed. The spof is

1147 deeply excavated, occupying about 1/3rd of the transverse length of the neural spine (Figure

1148 11D,E). The postzygapophyseal centrodiapophyseal fossae (pocdf) are shallow, and only a bit

1149 more excavated near the ventral rim of the postzygapophyseal pedicels.

1150 The sprl run from the top of the spine to the prezygapophyses in an oblique angle of about

1151 40°. They flank the entire length of the neural spine, creating roughly a V-shape (Fig. 11C, E).

1152 The spol are clearly visible in anterior view in this vertebra, as they flare out laterally from

1153 the neural spine, giving the neural arch and spine a triangular appearance.

1154 In anterior view, the neural spine is roughtly V-shaped, with a transversely broad dorsalmost

rim (Fig. 11C). In posterior view, the neural spine combined with spol and postzygapophyses

are slightly bell-shaped. The neural spine tapers dorsally to a point, exposing a stout rim. In

1157 dorsal view, the neural spine summit is clearly seen as an anteroposteriorly thin rim,

1158 transversely wide, reaching to the level of the onset of the postzygapophyses (Fig. 11E).

1159

1160 Dorsal PVL 4170 (11): Partially reconstructed dorsal; the centrum is a replica, which will not

1161 be described. The neural arch and spine and transverse processes, however, are original, see

1162 Figure 12. The diapophyses of this vertebra are elongated laterally compared to the other

dorsals, and the transition between this and the previous and next vertebrae, leads to

1164 believe a transitional dorsal could have existed originally.

1165

1166 The neural arch is mainly shaped by the acdl in anterior view, and the pcdl in posterior view.

1167 It is about as long and wide, as PVL 4170 (10), see Fig. 12A, B. The neural canal in anterior

view is rounded to rectangular in shape, with a dorsoventral elongation (Fig. 12C). The

1169 posterior neural canal is more flattened, and triangular to round in shape. The hyposphene

1170 is seen as a small rhomboid structure, about 5 cm dorsal to the posterior neural canal (Fig.

1171 12D).

1172 In this dorsal, the diapophyses are more prominent and extend wider transversely than in

1173 previous dorsals (Fig. 12C, D). Their shape in anterior and posterior view is near rectangular.

1174 They are directed laterally and slightly ventrally in anterior view (Fig. 12C). The articular

1175 surface of the diapophyses is more rounded than triangular (Fig. 12A, B). The diapophyses in

1176 posterior view are slightly expanded towards their extremities (Fig. 12D). The pcdl are

1177 slightly damaged and have a frayed appearance, but arch convexly towards the transverse

1178 processes.

The prezygapophyses are more or less perpendicularly placed towards the neural spine, and slightly canted medially in anterior view (Fig. 12C). Their articular surface lies in the dorsal plane. The articular surface of the prezygapophyses is roughly square in shape (Fig. 12E). In dorsal view, a U-shaped recess is seen between the prezygapophyseal articular surfaces. The prdl are stout and run in a convex arch transversely to the diapophyses. In this vertebra, the single intraprezygapophyseal lamina (stprl) is visible, as the interprezygapophyseal laminae (tprl) run down in a curved V-shape towards the neural canal (Fig. 12C). The paired cprf, positioned laterally to the stprl, are more excavated than in previous dorsals, and also havea more defined rim.

1188 The postzygapophyses are more pronounced in this vertebra than in previous dorsals, and 1189 also protrude posteriorly more than in previous dorsals (Fig. 12D). Their articular surface is 1190 triangular in shape. There is a similar U-shaped recess between the postzygapophyses, 1191 though not as wide, as with the prezygapophyses (Fig. 12C, D). The tpols are shorter in this 1192 vertebra, as they do not reach as far down ventrally to reach the hyposphene. Below the 1193 tpols, two cpols are seen to strut the hyposphene on lateral sides. The triangular and 1194 shallow pocdf's are positioned on each lateral side of the cools, and ventral to the tools (Fig. 1195 12D). 1196 The neural spine is transversely wide and anteroposteriorly short, but protrudes out 1197 posteriorly at both lateral sides and on the midline (Fig. 12D). This midline could be a 1198 rudimentary scar of a postspinal lamina (posl), but that is not clearly visible. In anterior view, 1199 the neural spine resembles that of PVL 4170 10, however the neural spine is more 1200 dorsoventrally elongated, and the spol are more dented than straight as they run down to 1201 the postzygapophyses. The morphology of the neural spine posteriorly, towards the 1202 postzygapophyses is similar to PVL 4170 10 in that the composition looks bell-shaped in 1203 posterior view, and the posterior half contains a deep V-shaped spof. The neural spine is 1204 more dorsally elevated however, and the summit is less transversely broad than in the 1205 previous dorsal (Fig. 12E). 1206

1207

Dorsal PVL 4170 (12): Mid-posterior dorsal with partially reconstructed neural spine (which
will therefore be omitted from description). The transition from middle to posterior dorsals
is perhaps the most drastic morphological transition in *Patagosaurus*, and hints at missing
vertebrae (Fig. 13).

1212 The centrum is clearly opisthocoelous, though the condyle is not as convex as in previous

- 1213 anterior dorsals (Fig. 13A, B). The centrum is posteriorly still wider transversely than
- 1214 anteriorly. The condyle still has a rugose rim, as in the cervicals. The parapophyses are
- 1215 positioned on the dorsolateral side of this rim, and are visible as rounded rugose
- 1216 protrusions. The pleurocoel is still clearly visible, and has a deep, rounded dorsal rim, and a
- 1217 clear rectangular posterior rim. The ventral side of the cotyle extends further posteriorly
- 1218 than the dorsal side (Fig. 13E). The cotyle is heart-shaped in posterior view, with a rounded
- 1219 'trench' below the neural canal (Fig. 13D). In ventral view, the centrum is not as constricted
- 1220 as in previous vertebrae; even though there is still a slight constriction posterior to the rim
- 1221 of the condyle. The ventral keel is no longer present.
- 1222 The neural canal in anterior view is elongated to an oval to teardrop shape, which is
- dorsoventrally longer than transversely wide (Fig. 13C). The neural canal in posterior view is
- 1224 oval to rectangular in shape, and is also dorsoventrally elongated.
- 1225 The neural arch in this dorsal is rather rectangular and straight in anterior and posterior
- 1226 view, widens axially in lateral view, towards the prezygapophyses (Figure 13 A, B, C, D). A
- 1227 fenestra is formed instead of the cdf. The centrodiapophyseal laminae run smoothly in a
- 1228 convex curve towards the centrum.
- 1229 The pedicels of the prezygapophyses are stout, and expand laterally towards the ventral side
- 1230 of the prezygapophyses (Fig. 13C). The tprl meet ventrally and at the midpoint between the
- 1231 prezygapophyses, where a rudimentary hypantrum is formed, below which a stprl runs
- down to the dorsal roof of the neural canal. This lamina separates two parallel, rhomboid,
- 1233 deep cprf.
- In posterior view, the postzygapophyses form a wide V-shape, and the tpols meet dorsal to a
 small diamond-shaped possible rudimentary hyposphene, below which a stpol runs down to
- 1236 the neural canal, which is oval and dorsoventrally elongated (Fig. 13D). The podl is a sharply
- 1237 curved, short lamina, not to be confused with the spdl, which is not present in this vertebra

1238 (Fig. 13A, B). Two parallel cpols might be present, but this is not entirely clear as the

1239 posterior part of this vertebra is partially reconstructed (Fig. 13D).

1240 In anterior view, the diapophyses are no longer ventrally and laterally positioned, but

dorsally and laterally, in an oblique angle dorsally (Figure 13C). In lateral view, pcdl runs in a

sinusoidal shape down from the diapophysis to the neural arch, while the prdl is convex (Fig.

1243 13A, B). The diapophyses extend a bit further ventrally in a subtriangular protrusion. The

diapophyses are slightly excavated between the podl and the pcdl. In dorsal view, the

diapophyses are seen to extend to nearly the entire width of the centrum (Fig. 13F). They

1246 are slightly pointed posteriorly as well.

1247

1248

1249 Dorsal PVL 4170 (13): This is the most complete posterior dorsal of the holotype (Fig. 14,

1250 15). It has consequently been scanned in order to elucidate on the pneumatic features

1251 present in the holotype (Fig. 14). The pneumatic opening ventral to the diapophyses, on the

1252 lateral surface of the neural arch, opens into an internal pneumatic chamber (Fig. 14 B, C),

1253 but is separated from the opening on the opposite neural arch by a thin septum (Fig. 14 I, J).

1254 The pneumatic chamber is situated ventral to this septum, and is round to squared in shape.

1255 It remains separated from the neural canal (see Discussion).

1256 The anterior articular surface of the centrum is oval in anterior view, with a slight

1257 constriction at about two-thirds of the dorsoventral height (Fig. 15C). Consequently, the

1258 ventral side is transversely wider than the dorsal side. In posterior view, the posterior

1259 articular surface of the centrum is heart-shaped at its dorsal side, and flattened on its

1260 ventral side. The articular surface itself is slightly oval, and is constricted towards the upper

1261 1/3rd as in the anterior side. In ventral view, the centrum is more or less equally flaring out

1262 at each articular surface, and slightly constricted in the midpoint. No keel is visible, but on

1263 the anterior ventral side of the centrum, a small triangular 'lip' is seen. In lateral view, the

1264 centrum is ventrally concave, with the posterior ventral side expanding further ventrally

than the anterior side (Fig. 15A, B). There is a slight depression on the lateral side of eachcentrum.

1267 The dorsal anterior side of the centrum is expanding a bit further anteriorly beyond the

1268 pedicels of the neural arch, but the dorsal posterior side of the centrum expands

1269 considerably further posteriorly from the neural arch.

1270 The parapophyses are not clearly visible in anterior view, however, they are visible in lateral

1271 and ventral view as rugose oval protrusions on the rugose lateral sides of the cprls.

1272 In anterior view, the neural canal is clearly visible in this specimen. It is oval and

1273 dorsoventrally much more elongated than in the previous vertebrae (Fig. 15A). It is

1274 transversely narrow, and slightly above the midpoint is constricted, so that the neural canal

1275 looks like a figure 8-shape. The neural canal is not clearly visible in posterior view; however,

1276 the neural arch is excavated in a triangular shape around the neural canal (Figure 15D). It is

1277 surrounded by stout centropostzygapophyseal laminae. Dorsal to this depression, the stpol

1278 supports the rhomboid hyposphene from below (see description of postzygapophyses).

1279 The neural arch itself is ventrally restricted transversely. The pedicels of the neural arch are

1280 equally dorsoventrally elongated and transversely narrow. The anterior side of the neural

1281 arch is characterised by a dorsoventrally oriented, long stprl, dividing two mirrored, shallow,

1282 oval to bean-shaped cprf. The lateral sides of the neural arch tilt towards the midline in

1283 posterior view, giving the neural arch a constricted look towards its dorsal end. On the

1284 lateral side of the neural arch, the centrodiapophyseal fossa (or more foramen in this

1285 vertebra) is visible as a dorsoventrally elongated oval, opening slightly posterior to the

1286 midpoint of the neural arch.

1287 The diapophyses project laterally in a near perpendicular angle from the neural arch (Fig.

1288 15A, D). They are ventrally excavated, with the prdl running concavely from the lateral side

1289 of the prezygapophyses to the diapophyses. In dorsal view, the diapophyses are seen to

1290 bend slightly posteriorly as well as laterally. The tips point sharply to the posterior side. The

1291 diapophyseal articular surfaces are triangular, with a rounded posterior rim, in lateral view. 1292 The dorsal distal ends of the diapophyses have a small triangular protrusion, projecting 1293 dorsally, in anterior view. The diapophyses show round excavations on the posterior side of 1294 their distal ends. The ventral side of the diapophyses is also concavely curved with a 1295 concave paradiapophyseal lamina (ppdl) running parallel to the prdl. The pcdl curve 1296 concavely from the diapophyses down to the ventralmost side of the neural arch. These 1297 sustain a thin sheet of bone that holds the diapophyses on each lateral side in posterior 1298 view.

1299 The prezygapophyses are transversely shorter than in previous dorsals, and are stout; 1300 almost as thick dorsoventrally as transversely (Fig. 15A, B, C). They tilt at an oblique angle 1301 anteriorly and dorsally from this narrow arch. The prezygapophyseal articular surfaces are 1302 horizontally aligned in the axial plane, and are near perpendicular to the neural spine. In 1303 dorsal view, prezygapophyses are directed mostly anteriorly, and there is a deep U-shaped 1304 recess between them. On the lateral side of the prezygapophyses, running from the lateral 1305 ends of the cdf, the cprl are characterized by laterally flaring, rugose, rugged bony flanges, 1306 that spread anteriorly as well as laterally. In anterior and lateral view, prdl and the ppdl run 1307 parallel in a convex arch at the ventral end of the neural spine. They are equally thin and 1308 dorsoventrally flattened.

1309 The postzygapophyses are triangular in shape, and are positioned slightly more dorsally on 1310 the neural arch than the prezygapophyses (Fig. 15D). The postzygapophyses are flat to 1311 slightly convex on articular surface, seen from lateral and ventral view. The stpol tapers 1312 dorsally and posteriorly in an oblique angle from the rhomboid hyposphene to the neural 1313 arch. The postzygapophyses are not visible in lateral view as they are obscured by the 1314 diapophyses. The postzygapophyses connect with the diapophyses through a strongly 1315 bending podl, which is often mistaken for a spinodiapophyseal lamina (spdl; Wilson, 2011a, 1316 Carballido and Sander, 2014).

1317 In this dorsal, the prdl and the podl are seen to support wide, but thin plates of bone

1318 between the prezyga- dia- and postzygapophyses.

The neural spine is roughly cone-shaped, and is constricted toward the summit both
anteriorly and posteriorly. In anterior view, the sprl flare out towards the ventral contact of
the prezygapophyses. The sprls are seen as sharply protruding thin laminae. The sprdfs,
bordered by the sprls, are visible as deep triangular depressions in dorsal view. The neural
spine shows a triangular excavated prezygospinodiapophyseal fossa (prsdf) on each lateral

1324 side, which have clear posterior rims.

1325 Similar to the sprls, in posterior view, the spol are seen to flare out towards the ventral side

1326 of the neural spine. In this dorsal, the spol has divided into a lateral spol and medial spol (l.

1327 spol and m. spol), visible as running from the ventral one-third of the neural spine to the

1328 postzygapophyses. On the midline between these laminae, a deep but transversely narrow

1329 rudimentary spof is present. The lateral spols flare out on the lateral sides, giving the spine a

1330 'rocket-shape' in posterior view. A slight transverse thickening of this stout lateral spol is

1331 visible at about two-thirds of the spinal dorsoventral length.

1332 On the dorsoventral midline of the spine, in posterior view, a rough scar is visible, which

1333 could be a very rudimentary postspinal (posl) lamina.

The spine itself tilts very slightly posteriorly, especially the most distal one-third part. This distal end is solid, and cone-shaped, with a rounded summit. The spine summit has a slight bulge on each lateral side, which might be a rudimentary aliform process (see Carballido and Sander, 2014), and the summit is more rounded than flattened. The summit of the neural spine in dorsal view is rounded, but has a constricted anterior end, where it points towards the sprls. The posterior end projects more posteriorly and is round, though with a slightly

1340 pointed end at the posterior midline.

1341

1342 Dorsal PVL 4170 (14): Posterior dorsal with preserved neural arch, spine and centrum.

Because of its fragile state, a ventral image could not be obtained. Parts of the diapophysesand neural arch are damaged.

1345 In anterior view, the anterior articular surface of the centrum is oval, and dorsoventrally 1346 flattened, so that the transverse width is greater than the dorsoventral height (Fig. 16D). The 1347 dorsal end is slightly heart-shaped. The anterior articular surface of the centrum is 1348 dorsoventrally longer than the posterior side. The posterior dorsal rim of the articular 1349 surface of the centrum extends further posteriorly than the ventral side. The extension is 1350 rounded and is visible on both lateral sides of this dorsal vertebra (Fig. 16A, B). The width of 1351 the centrum extends beyond the width of the pedicels of the neural arch. In posterior view, 1352 the centrum is dorsoventrally flattened and expands a little transversely on the midline 1353 (Fig.16C). The dorsal end of the posterior articular surface is slightly excavated dorsally, as 1354 are posterior surfaces of the pedicels surrounding the neural canal, embedding the neural 1355 canal. In lateral view, the centrum is ventrally concave. It is slightly reconstructed however, 1356 so there might not be more original curvature preserved. There are shallow, elliptical 1357 depressions visible on each lateral side of the centrum. 1358 The anterior side of the neural canal is oval and dorsoventrally elongated, and narrows in 1359 the upper one-third towards its dorsal end (Fig. 16D). The posterior side is more triangular in 1360 shape, but overall roughly similar to the anterior side (Fig. 16C). The medial sides of the 1361 pedicels of the neural arch are excavated, forming an oval excavation around the neural 1362 canal. 1363 The anterior central part of the neural arch is damaged, thereby revealing the pneumatic 1364 centrodiapophyseal fenestra, which connects to each lateral side of the neural arch below

1365 the diapophyses (Fig. 16A, B). These openings perforate the neural arch to the posterior

1366 side, indicating there must have been only a thin sheet of bone covering them. The neural

1367 arch tapers towards the midpoint on both the anterior and posterior sides in lateral view,

however, the anterior end expands towards the posterior side again together with the
parapophysis and the base of the prezygapophysis (Fig. 16A, B). The neural arch constricts
around the central part of the vertebra in posterior view. On the right lateral neural arch, a
neurocentral suture is present. Posteriorly, the hyposphene is visible as a clear triangular
protrusion below the postzygapophyses. The hyposphene is smaller than in the previous
dorsals (Fig. 16C).

1374 The left lateral side of this dorsal is missing the diapophyses, however, this does give a good 1375 view of the proximal bases of the diapophyseal laminae; the prdl is a relatively delicate and 1376 short lamina that runs obliquely to the ventral anterior base of the prezygapophysis; the 1377 podl lies on the same oblique sagittal plane and projects dorsally and posteriorly towards 1378 the postzygapophysis (Fig. 16B). The right lateral side in lateral view shows the partial right 1379 diapophysis, of which the distal end is broken, revealing two laminae, the distal side of the 1380 prdl and the distal side of the pcdl (Fig. 16A). Also, a thin short lamina runs from the 1381 posterior end of the diapophysis to the postzygapophyses; this lamina connects also to the 1382 lateral spol, therefore is the podl+lspol complex. On both lateral sides, ventral to the 1383 diapophyseal base, the centrodiapophyseal fenestra is clearly visible and perforates the 1384 neural arch completely; however, there would probably have been a thin septum separating 1385 them.

The right diapophysis is partially preserved; it is shorter than in the previous dorsals, and stout. It projects laterally, slightly dorsally and posteriorly, unlike the diapophyses of the previous dorsals (Fig. 16A, B, C, D). The diapophysis is wing-shaped in posterior view; the pcdl encircles a wide sheet of bone on its posterior side. The prezygodiapophyseal lamina is visible in anterior view, as it curves convexly to the lateral distal end of the diapophysis. The ventral lateral side of the transverse process is marked by the prcdf.

The only prezygapophysis present is reconstructed. On the right lateral side, a rugoseparapophysis is supported by an anterior centroparapophyseal lamina (cprl), which runs

- along a ragged lateral rim of bone from the prezygapophyses to the ventral end of the
- pedicel of the neural arch, which is similar to those in PVL 4170 (13), see Fig. 16A. The actual
- 1396 prezygapophyses are missing or reconstructed, therefore there is no information known

about these in this particular dorsal.

- 1398 Because most zygapophyseal structures are either broken or reconstructed, not much can
- 1399 be said about the shape of these in dorsal view, however, the wide sheet of bone between
- 1400 the prdl and the pcdl is clearly visible in dorsal view (Fig. 16F). The left pedicel of the neural

arch is partially visible. It is positioned slightly posterior to the anterior rim.

- 1402 The postzygapophyses are ventrally convex, and dorsally stand out from the neural spine,
- 1403 making the spols protrude from the spine in an equal fashion. The podl + lspol complex is
- 1404 seen curving sharply convexely from the lateral end of the right postzygapophysis to the
- 1405 distal end of the diapophysis (Fig. 16C).
- 1406 The neural spine in anterior view is straight and square in the upper one-third of its
- 1407 dorsoventral height, however, the anterior side tapers to a V-shaped point towards its
- ventral end (Fig. 16D). The 'V' is rugose. On each lateral side, slightly dorsal to this point, the
- 1409 spinoprezygapophyseal laminae widen the lowermost one-third of the neural spine. The
- summit of the neural spine is rugose and shows a small oval protrusion on its anterior
- 1411 midline (Fig 16F). The lower half of the neural spine shows a clear division between the
- 1412 lateral and medial spols, between which are evenly sized, slit-like fossae. The spof
- 1413 completely perforates the area between the postzygapophyses in an elliptical shape (Fig.
- 1414 16C). The top of the neural spine is cone-shaped and rugose. There is no trace of a
- 1415 postspinal scar, as in more anterior dorsals. The neural spine in lateral view is excavated by
- 1416 the prsdf, which is triangular and relatively deep (Fig. 16A, B). The lspol is thick in the ventral
- 1417 half of the neural spine, however, at the lateral sides of the dorsal half of the neural spine it
- 1418 is only a thin edge that protrudes posteriorly from the spine. The lateral spols form a bell-
- 1419 shaped sheet around the lower half of the neural spine in posterior view, whereas the upper

half has the base of the lateral spol only visible as a thin lateral ridge (Fig. 16C). As in the
previous dorsals, the distal end of the neural spine is massive, and cone-shaped. In this
posterior dorsal, however, the lower half of the spine is bending anteriorly, the upper half of
the spine is bending posteriorly (Fig. 16A, B). At the base of the upper half, a ridge is seen
curving from the anterior lateral side to the posterior lateral side. In dorsal view, the summit
of the neural spine is transversely wider posteriorly than anteriorly, giving it a trapezoidal
shape (Fig. 16 E). The surface is rugose.

1427

1428

1429 Dorsal PVL 4170 (15): This dorsal vertebra only has its centrum preserved (Fig. 17; 15). In 1430 anterior view, the anterior articular surface of the centrum is almost trapezoidal in shape, 1431 with lateral protrusions on the midline. The anterior articular surface is equally as high as it 1432 is wide. The posterior articular surface in lateral view is broken and not clearly visible. In 1433 lateral view, the centrum shows a concave ventral side, and a slightly more convex than flat 1434 anterior articular surface. Towards the dorsal middle part of the centrum, in lateral view, a 1435 shallow elliptical fossa is visible. The ventral floor of the neural canal is visible, and the 1436 lowermost lateral walls, indicating an elongated elliptical shape of the neural canal, as in the 1437 other posterior dorsals. In dorsal view, the neural canal is seen to cut deeply into the 1438 centrum, and shows a widening transversely towards the posterior opening. In dorsal view, 1439 the neurocentral sutures are either broken or unfused; the former is the more likely option, 1440 as the sutures are fused in the other dorsals of PVL 4170. 1441 1442 Dorsal PVL 4170 (16): This dorsal, though well-preserved, and only partially reconstructed, is 1443 unfortunately stuck behind a low bar on the ceiling of the Instituto Miguel Lillo, in the 1444 hallway where the holotype is mounted. As a result, only the right lateral side and some

1445 oblique views of the anterior side could be obtained (Fig. 17; 16).

1446The centrum is partially reconstructed; however, the dorsal end is original and is heart-1447shaped. In right lateral view, the centrum is almost quadrangular in shape. The dorsoventral1448height is slightly greater than the anteroposterior length. The posterior dorsal side of the1449centrum flares slightly laterally and posteriorly, and the neural canal creates a little 'gutter'1450on the dorsal surface of the centrum. On the lateral side of the centrum, dorsal to the axial1451midpoint, is an oval fossa, which is axially longer than dorsoventrally high. This fossa is1452dorsoventrally higher than in the previous dorsals, making it appear more round than

1453 elliptical.

1454 The neural arch is supported by lateral pedicels, which rest more on the anterior side of the

1455 centrum than on the posterior. The pedicels of the neural arch in anterior view are of

1456 irregular shape, and show an almost anastomosing structure. The posterior part of the

1457 pedicels rests a few centimeters medial to the dorsal posterior rim of the posterior articular

surface. From there, the posterior part of the pedicel inclines towards the medial side in

1459 lateral view. The dorsal end of the pedicels is axially constricted. The right lateral pedicel is

1460 broken off laterally. The anterior medial area, between the prezygapophyses, is excavated;

1461 this is probably due to a thin sheet of bone having been broken away, revealing the internal

1462 pneumatic structure.

1463 The diapophysis is not very clearly visible in anterior view. The diapophyses are located

1464 slightly posterior to the midline of the neural arch. In lateral view, the articular surface is a

1465 thin, semi-lunate dorsoventrally elongated ridge.

1466 The prezygapophyses are supported below by stout colums that project obliquely anteriorly

1467 and dorsally; these are also convex anteriorly.

1468 The prezygapophyses have a flat axial articular surface, and are supported from below by

stout convex columns.

1470 The postzygapophyses are situated at around the same elevation as the prezygapophyses.

1471 The articular surface of the postzygapophyses is slightly inclined ventrally. The hyposphene

extends further posteriorly than the postzygapophyses, and has a ragged outline in lateralview; this could however be caused by damage to the bone.

The neural spine is slightly inclined towards the posterior side in its lower half, the upper half is more or less erect in the dorsoventral plane. It is slightly wider at its base, however the upper 2/3rd is of an equal axial width. The summit is rod-shaped. The accessory lamina seen in the previous two dorsals is seen around halfway to the summit, running in a semicircular line from anterior dorsal to posterior ventral.

1479

1480 Dorsal PVL 4170 (17): The posteriormost dorsal is only partially preserved, and therefore is 1481 partially reconstructed (Fig. 17; 17). It is also not possible to unmount this dorsal, therefore 1482 the view is limited to the anterior side and the (partial) lateral side. The centrum shows deep 1483 lateral depressions, and is more oval than round, as in the previous dorsals. The neural arch 1484 is similar in morphology to the previous posterior dorsals, with stout problem and a deep 1485 depression between each lateral side of the neural arch. The prezygapophyses are inclined 1486 medially, rather than being horizontally aligned with the sagittal plane. The neural spine has 1487 very sharp outstanding sprls and spols between which the spine has deep depressions on 1488 anterior and lateral sides, which are oriented dorsoventrally. The spine summit is a massive 1489 block of bone, and has a square shape. Two rudimentary but clearly visible aliform processes 1490 are positioned slightly ventral to the dorsal spine summit on each lateral side.

1491

Sacrals PVL 4170 (18): The complete sacrum is well-preserved (see Bonaparte 1986b, Fig. 43 and 44, and this manuscript, Fig. 18, lower row, A-D). Unfortunately, because the holotype specimen is mounted, it is difficult to access. Most recent pictures can only show the neural arches and the spines, as the rest of the view is blocked by the ilium laterally (Fig. 18C), by the dorsal vertebrae anteriorly, and by the caudal vertebrae posteriorly, although the caudal vertebrae can be unmounted. Bonaparte's 1986 Patagosaurus description shows a detailed 1498 illustration, however; see Bonaparte (1986b), and Fig. 18D. The sacrum consists of five sacral 1499 vertebrae, of which all centra are fused. This is in contrast to Vulcanodon, Barapasaurus, 1500 Shunosaurus and Spinophorosaurus, who are reported to have had four sacral centra (Remes 1501 et al. 2009; Bandyopadhyay et al. 2010; Carballido et al. 2017b). Ferganasaurus and Jobaria 1502 tiguidensis had five sacral centra (Alivanov and Averianov 2003; Carballido et al. 2017b). 1503 Haplocanthosaurus, Camarasaurus and diplodocids had five (Although some have been 1504 reported to have had six, Tschopp et al. 2015; Carballido et al. 2017b). In PVL 4170 (18), the 1505 second, and third of the neural spines are fused together by their anterior and posterior 1506 sides. This is similar to Barapasaurus (Bandyopadhyay et al. 2010), but different from 1507 Ferganasaurus and neosauropods; e.g. Ferganasaurus verzilini Alifanov & Averianov, 2003 1508 and diplodocids fuse the sacral neural spines 2-4, whereas Camarasaurus Cope, 1877 and 1509 Haplocanthosaurus fuse sacral neural spines 1-3 (Alivanov and Averianov 2003; Upchurch 1510 2004). All neural spines are rugosely striated (Fig. 18B). They all possess sprI and spoI, which 1511 are roughly similar to the morphology of the posteriormost dorsal vertebrae. No spdl is 1512 present. The dorsal rim of the ilium terminates at about the diapophyseal height of the 1513 sacrum (Fig. 18C). The neural spines extend dorsally beyond the upper rim of the ilium for 1514 about 30 cm. In mamenchisaurids, as well as in Camarasaurus and basal titanosauriforms, 1515 the neural spines of the sacrum are much shorter (not as dorsoventrally high as the neural 1516 arch and centrum combined), and more robust (Ouyang and Ye 2002; Taylor 2009). In 1517 neosauropods such as Apatosaurus, Diplodocus and Haplocanthosaurus, however, the 1518 neural spines do extend further beyond the ilium. In *Haplocanthosaurus*, the neural spine is 1519 and are as dorsoventrally high as the neural arch and centrum together, like in 1520 Patagosaurus; however, some diplodocids have higher sacral neural spines. (Gilmore 1936; 1521 Hatcher 1901, 1903). The sacral ribs do not project over the ilium, as they do in 1522 neosauropods (Carballido et al. 2017b).

1523 The first sacral PVL 4170 18.1 is, as in most sauropods, relatively similar to the posteriormost 1524 dorsal (Upchurch 2004). The centrum is oval, and dorsoventrally elongated (Fig. 18D). The 1525 neural canal is oval and also dorsoventrally elongated, as in the posterior dorsals. The sacral 1526 rib is unattached to the diapophysis in this sacral vertebra. It is a lateral dorsoventrally 1527 elongated extension, as in most sauropods, a C-shaped plate that extends laterally towards 1528 the medial side of the ilium (Upchurch et al. 2004). The prezygapophyses are anteriorly 1529 elongated, and flat dorsally, and have a deep U-shaped recess between them, as in the 1530 posterior dorsals (Fig. 18A). They connect to the neural spine via the spinoprezygapophyeal 1531 laminae, which project as sharp ridges off the lateral sides of the anterior side of the neural 1532 spine. Lateral and anterior to the postzygapophysis, the podl runs to the transverse process 1533 of the first sacral. As in the posterior dorsals, dorsal to the postzygapophyses, a rudimentary 1534 aliform process is present. From here, the lateral spol flares out laterally and dorsally before 1535 it joins the postzygapophysis. The sprl encases a deep triangular depression, which is visible 1536 on the lateral side of the neural spine, which could be the sacral equivalent of the spdf in 1537 Patagosaurus (see Wilson et al. 2011).

1538 The neural spine inclines slightly anteriorly, as in the posteriormost dorsals. The anterior 1539 surface of the neural spine shows rugosities for ligament attachments. On the lateral side of 1540 the neural spine, a triangular depression runs over about 2/3rds of the dorsoventral length 1541 (Fig. 18A, D), with a sharp dorsal semicircular rim. Dorsal to this rim, the spine becomes 1542 solid. The spine summit is rounded laterally and has a crest-like shape in anterior view. 1543 The second and third sacral neural spines PVL 4170 18.2 and 18.3 are fused (Fig. 18A, C, D). 1544 Both the second and third sacral vertebrae have large C-shaped sacral ribs that connect to 1545 the medial side of the ilium. These sacral ribs project laterally and slightly posteriorly from 1546 the neural arch above the centra. Between these sacral ribs, dorsoventrally elongated and 1547 axially short intervertebral foramina (ivf; Wilson et al. 2011) are visible as slit-like apertures,

which in this sacrum are fenestrae that connect to large internal pneumatic chambers insidethe sacral centra.

The second sacral neural spine is projecting mainly dorsally, and only slightly anteriorly (Fig.

1551 18A, C, D). At the base of the spine, the sprl and spol and the dorsal side of the sacral

1552 transverse process border a triangular sdf, as in the first sacral. This fossa is more oval-to-

- triangular, which is different from the first sacral. This fossa is also present on the third
- 1554 sacral and is more pronounced there; being axially wider and more triangular. Between both
- 1555 neural spines, a thin plate of bone was probably present, as there is a small slit, which does
- 1556 not appear natural. The neural spines are dorsally connected by rugose bone tissue. In
- 1557 lateral view, this connection has a U-shaped concavity between both neural spine summits.
- 1558 The fourth sacral vertebra PVL 4170 18.4 inclines slightly more posteriorly than the previous
- sacrals (Fig. 18A, C, D). The sacral rib of this sacral is a C- or heartshaped laterally projecting
- bony plate. Between this sacral rib and the sacral rib of the third sacral, a large
- dorsoventrally elongated slitlike opening is seen to connect to the internal pneumatic
- 1562 chamber of the sacrum.

1550

- 1563 The prezygapophyses are not visible; the postzygapophyses are rhomboid, laterally
- 1564 projecting protrusions. The hyposphene is equally rhomboid.

1565 In anterior view, the neural spine is transversely shorter than the previous sacrals, however, 1566 axially it is equally wide, giving the spine summit a rhomboidal shape. At the anterior side of 1567 the base of the spine, a triangular protrusion is visible, which appears broken, therefore this 1568 sacral might have been connected to the third sacral by a bony protrusion at the bases of 1569 the neural spines. On the lateral side of the spine, a deep groove is seen to run concavely 1570 from the dorsal anterior lateral side to the ventral posterior lateral side, as in some anterior 1571 caudals (see caudals later). The dorsal lateral side of the neural spine shows a weakly 1572 developed aliform process. In posterior view, the lateral spinopostzygapophyseal laminae

are seen to protrude dorsally from the neural spine, which is very rugosely dorsoventrallystriated.

1575 The fifth sacral PVL 4170 18.5 is slightly different in morphology from the previous four, in 1576 that it is slightly posteriorly offset from the others (Fig. 18A, B). The posterior articular 1577 surface of the centrum is clearly visible in this last sacrum, and is flat to slightly 1578 amphicoelous. It is oval in shape, and slightly dorsoventrally elongated, and slightly 1579 transversely flattened. The neural canal is a dorsoventrally elongated oval shape. Directly 1580 dorsal to the neural canal, a small triangular and posteriorly projected protrusion is visible, 1581 which resembles the small anteriorly projected protrusions above the neural canal of some 1582 of the dorsal vertebrae. The lamina that projects laterally towards the sacral rib has a 1583 dorsolaterally directed bulge, so that the rib projects laterally in two stages (Fig. 18B). The 1584 main body of the sacral ribs of this last sacral are directed laterally, but also bend anteriorly 1585 towards the other sacrals. The postzygapophyses are diamond-shaped, as is the 1586 hyposphene. The spol in posterior view are slightly offset from the spine, and at about half 1587 of the dorsoventral height of the spine, protrude in a rounded triangular shape. This might 1588 have been a ligament attachment site. The spine itself is rugosely striated and resembles the 1589 fourth sacral in morphology.

1590

Caudals: The holotype PVL 4170 has a few anterior, mid, and mid-posterior caudals
preserved. The caudal numbering is rather discontinuous, indicating that the caudal series
was already incomplete when it was found. Two caudals are without collection reference
numbers, but will be described here for completeness, and positioned in the caudal series
relative to their size and morphology. Two caudals are repeated, as one is a cast of the
other.

Anterior- to anterior-mid caudals (PVL 4170 19-20-21) have dorsoventrally high and axially
short centra (Fig. 19), as seen in *Cetiosaurus, Tazoudasaurus* and *Chebsaurus*. They display

1599 rounded triangular-to-heart-shaped anterior vertebral articular surfaces, and slightly more 1600 heart-shaped posterior vertebral articular surfaces, the most acute tip being the ventral 1601 side. The centrum in lateral view is concavely curved on the ventral side, with the slope on 1602 the anterior half less acute than on the posterior half. A faint raised ridge of bone is seen in 1603 some caudals on the lateral centrum, ventral to the diapophyses. This is also seen in 1604 Cetiosaurus, and could be a rudimentary lateral ridge as seen in neosauropods (Tschopp et 1605 al. 2015). The posterior dorsal rim of the centrum shows an inlet for the neural canal, as in 1606 the cervicals and dorsals, and stretches slightly beyond the posterior end of the base of the 1607 neural spine.

1608 In ventral view, two parallel axially positioned struts are visible, between which is a 'gully'; 1609

an axially running depression. This feature is seen in other basal eusauropods (Cetiosaurus

1610 oxoniensis and the Rutland Cetiosaurus; (Upchurch and Martin 2002, 2003) as well as an

1611 unnamed specimen from Skye, UK (Liston 2004), though is not as prominently developed in

1612 Patagosaurus as in the latter taxa. This feature is named the 'ventral hollow' in

1613 neosauropods, and is also found in derived non-neosauropodan eusauropods (Mocho et al.,

1614 2016), as well as in a possible neosauropodan caudal centrum from the Callovian of the UK

1615 (Holwerda et al. 2019). Pronounced chevron facets are present, as in all sauropods (e.g.

1616 Cetiosaurus oxoniensis, Lapparentosaurus, 'Bothriospondylus madagascariensis' Bonaparte,

1617 1986b, Chebsaurus and in caudals from unnamed taxa from the Late Jurassic of Portugal

1618 (Upchurch & Martin 2003; Läng and Mahammed 2010; Mannion 2010; Mocho et al. 2016))

1619 but not as prominent as in Vulcanodon (Raath 1972; Cooper 1984) or Cetiosaurus.

1620 The transverse processes are short and blunt, and project slightly posteriorly as well as

1621 laterally. Below them, rounded shallow depressions are visible, which are a vestigial caudal

1622 remnant of the pleurocoels. These depressions are both in anterior and middle caudals

1623 bordered by slight rugosities protruding laterally from the centrum, which could be very

1624 rudimentary lateral and ventrolateral ridges, but this is unsure, and not recorded in non1625 neosauropodan eusauropods (Mocho et al. 2016). The neural arch is both dorsoventrally as 1626 well as axially shortened compared to the dorsals and sacrals. Lamination is rudimentarily 1627 present; in particular the sprl, spol, stpol and tprl are visible anteriorly and posteriorly. Small, 1628 blunt pre- and postzygapophyses are also present. The prezygapophyses rest on short, stout 1629 stalks that project anteriorly and dorsally. The postzygapophyses are considerably smaller 1630 than the prezygapophyses, and project only posteriorly as small triangular protrusions. 1631 These are, however, still prominent in anterior caudals; more so than in *Spinophorosaurus* 1632 (Remes et al. 2009). Prezygapophyses and postzygapophyses are strongly diminished in the 1633 anterior caudals and continue to do so towards the posterior caudals. Prezygapophyses are 1634 expressed as small oval protrusions, in anterior caudals still projecting from stalks, in middle 1635 and posterior simply projecting from the neural arch. The postzygapophyses are even 1636 further diminished, are only seen as small triangular protrusions from the base of the neural 1637 spine, and disappear completely in posterior caudals. The hypophsene remains visible, 1638 however, as a straight rectangular structure projecting at 90° with the horizontal. The neural 1639 spine is dorsoventrally high, and projects dorsally and posteriorly. 1640 The most distinctive features of this set of vertebrae, however, are the elongated neural 1641 spines. These taper posteriorly, and dorsally, in a gradual gentle curve, which becomes more 1642 straightened towards the dorsal end. Towards the tip of the neural spine, the lateral surface 1643 expands axially. The spine summit displays the same characteristic saddle shape as in the 1644 posterior dorsals, in that in lateral view both anterior and posterior dorsal ends bulge 1645 slightly, with a slight depression on the midline between these bulges. In lateral view, as well 1646 as posterior view, the posterior side of the spine shows long coarse rugose dorsoventrally 1647 running striations, probably for ligament attachments. In particular, one or two grooves of 1648 approximately 1 cm wide are seen aligned in the dorsoventral plane, a few centimeters from 1649 the posterior rim in lateral view. These run from the midline of the spine, a few centimeters 1650 below the spine summit, to the posterior rim of the spine, just above the hyposphene.

1651 Middle caudals (PVL 4170 22-25) are more elongated axially, with the axial length slightly 1652 higher than the height or width of the centrum (Fig. 20). However, the centrum height and 1653 width are still similar to the anterior-mid caudals (see Table 2). The centrum in lateral view 1654 shows a concave surface between two slightly raised ridges, as seen in *Cetiosaurus*. The 1655 ventral side of the centra is concavely and symmetrically curved, as opposed to the more 1656 anterior caudals. The base of the spine is axially wider than in the anterior caudals, and 1657 together with the base of the prezygapophyses, forming the simplified neural arch, rest 1658 more on the anterior half of the centrum, a feature commonly seen in non-neosauropodan 1659 eusauropods as well as in neosauropods (Tschopp et al. 2015). The posterior dorsal side of 1660 the centrum inclines slightly dorsally. The diapophyses are reduced to small rounded stumps 1661 that protrude laterally and slightly dorsally. They are positioned on the ventral and posterior 1662 side of the neural spine bases. Below the transverse processes a very shallow depression can 1663 be seen, unlike in *Tazoudasaurus* where well-defined round fossae are still present on the 1664 middle caudals (To1-288, Allain and Aquesbi 2008). Most prezygapophyses are broken; their 1665 bases are visible as broad stout bulges. The base of the neural spine bulges out laterally, and 1666 is extended axially to the base of the prezygapophyses, creating a broad stout pillar in lateral 1667 view. The spine is inclined posteriorly, and shows a gentle sinusoidal curvature on the 1668 posterior rim. The neural arch and spine shift towards the anterior side of the centrum in 1669 middle and posterior caudals.

Posterior-mid caudals (PVL 4170 (26) – (30) increase in axial centrum length and decrease in centrum height, giving the centrum a dorsoventrally flattened oval shape. The posterior articular surfaces of the centra have a small inlet on their dorsal rim, rendering them heartshaped. From PVL 4170 (26) the transverse processes diminish into slight bulges underneath which a small shallow elliptical depression is visible. The postzygapophyses are present as stunted, slightly square ventral protrusions on the neural spine; the prezygapophyses are more developed and protrude as short stout struts anteriorly and dorsally from just above 1677 the base of the neural spine. The neural spine inclines heavily posteriorly, and becomes

1678 rectangular; losing the sinusoidal curvature.

1680 posterior-most caudals of the skeleton, PVL 4170 (31) – (34) display an elongated centrum,

The last preserved, posteriormost caudals of the holotype (note that these are not the

1681 further decreased centrum height and a symmetrically curved concave ventral side. Most

1682 neural spines are broken off or damaged; only PVL 4170 (32) has a neural spine that curves

1683 posteriorly and aligns with the axial plane. The diapophyses are further reduced as small

1684 rugose stumps, and the elliptical depression below these is barely discernible. The

1685 prezygapophyses are short stunted protrusions on the anterior end of the spine, nearly

1686 equal in height with the spine. The articular surfaces are round rather than heart-shaped.

1687

1679

1688 PVL 4170 (19):

1689 The first caudal that is preserved is an anterior- to mid- caudal. The centrum is

dorsoventrally higher than transversely wide, and is axially short, as in the posterior dorsals

and sacrals (Fig. 21 A, B).

1692 In anterior view, the anterior articular surface of the centrum is oval, and dorsoventrally

1693 higher than transversely wide (Fig. 21D). However, the upper 1/3rd of the anterior articular

1694 surface is transversely broader than the transverse width of the midpoint, and towards the

1695 lower 1/3rd this width decreases further. The ventral side of the articular surface is slightly

1696 V-shaped (Fig. 21E). The dorsal section of the articular surface shows a protruding sharp 'lip-

1697 like' rim. 'Lips' on the dorsal rim of the articular surface of the caudals are an autapomorphy

1698 in Cetiosaurus (Upchurch and Martin 2003). However, Patagosaurus has less distinctive 'lips'

than *Cetiosaurus*, potentially hinting at a shared feature for Cetiosaurids. The articular

1700 surface is concave, with the deepest point slightly dorsal to the midpoint. In posterior view,

1701 the articular surface of the centrum is heart-shaped, due to two parallel elevations of the

dorsal rim between which a gully for the neural canal exists (Fig. 21C). The articular surface

1703 is less concave than its anterior counterpart, and also less extensive; the outer rim stretches 1704 towards the centre of the articular surface, which is flattened, and only the area slightly 1705 dorsal to the midpoint is slightly concave. In lateral view, the centrum is ventrally mildly 1706 concave, and the rims of both posterior and anterior articular surfaces show thick circular 1707 striations, seen in weight-bearing bones of sauropods, e.g. Cetiosaurus, Giraffatitan, 1708 Tornieria (H. Mallison pers. comm.; see Fig. 21A, B). The centrum is dorsoventrally much 1709 higher than it is axially long, however; this length has decreased with respect to the sacrals 1710 and the posterior dorsals. The neural canal is triangular to rounded in shape, both in anterior 1711 and posterior views. 1712 The diapophyses project laterally and dorsally in anterior view, and in dorsal view, they are 1713 also seen to project slightly posteriorly (Fig. 21D, F). Their shape is triangular with a stunted 1714 distal tip; the dorsal angle made with the centrum is less acute than the ventral one. 1715 Between the diapophyses and the neural arch, a raised ridge of bone is present, similar to 1716 that of anterior caudals of Cetiosaurus (Upchurch and Martin 2003). Whether this is a 1717 rudimentary lateral ridge, seen in neosauropods (Tschopp et al. 2015) is unsure. 1718 The neural arch is formed of a square elevated platform upon which the prezygapophysis 1719 and the neural spine rest (Fig. 21A, B, F). The prezygapophysis projects anteriorly and 1720 dorsally from the neural arch, at an angle of ±100° with the horizontal. The base of the 1721 prezygapophyses is stout, after which it tapers towards the distal end. The medial articular 1722 surface of the prezygapophysis is round with an internal rounded depression. In posterior 1723 and lateral view, the hyposphene is visible as a squared protrusion at the posterior base of 1724 the neural spine. It makes an angle of 90° with respect to the axial and dorsoventral planes. 1725 The postzygapophyses are only visible as raised oval facades, dorsal to the hyposphene. The 1726 postzygapophyses are formed as triangular lateral protrusions, which project from the base 1727 of the neural spine, between which is an oval depression, likely a rudimentary caudal spof.

1728 The neural spine is diverted to the left lateral side in anterior view; this is probably a 1729 taphonomic alteration (Fig. 21D). It has roughly the same morphology as in the dorsals; a 1730 constricted base and a widened summit, with gently curving lateral sides. The spine is 1731 heavily striated on the surface of the upper 2/3rds of the dorsoventral height. The neural 1732 spine in lateral view gently curves convexly posteriorly and concavely anteriorly. The summit 1733 has a distinct saddle shape in lateral view. The spine summit is elevated in the centre and 1734 has two anterior and posterior rims, which are at a lower elevation than the middle part, as 1735 is seen in the neural spine summits of the dorsal vertebrae. The neural spine is rugosely 1736 striated in the dorsoventral plane in posterior view, and is offset to the right (Figure 21C). 1737 Two spol are clearly visible.

1738

1739 PVL 4170 (20): This anterior caudal resembles PVL 4170 (19). In anterior view, the anterior 1740 articular surface is asymmetrically oval, with a slightly flattened dorsal rim, and a slightly 1741 triangular ventral one (Figure 22D). It is also transversely broadest slightly dorsal to the 1742 midline. The dorsal edge shows lateral elevations, between which a slight rounded 1743 indentation exists on the midline. In posterior view, the articular surface of the centrum is 1744 more heart-shaped than oval (Fig. 22C). It has a thick rim, showing circular striation marks, 1745 which is not as concave as the inner part of the articular surface. This concave surface, 1746 however, is less concave than the anterior articular surface. The posterior dorsal rim of the 1747 centrum does not extend posteriorly, but it faces ventrally in an oblique angle towards the 1748 axial plane, as in PVL 4170 (19), however, the posterior dorsal rim of the centrum extends 1749 further ventrally in PVL 4170 (20). In lateral view, the centrum is axially short and 1750 dorsoventrally elongated as in the posterior dorsals and the sacrals. The ventral side of the 1751 centrum, however, is symmetrically concavely curved, with posterior and anterior rims 1752 bulging out concavely towards the ventral side.

1753 The neural canal is visible as a semi-circular indentation in the neural arch. It is much

1754 broader ventrally than in PVL 4170 (19), see Fig. 22C, D.

1755 In ventral view, the anterior chevron facets are broken off Fig. 22F). The centrum is concave

- 1756 on both lateral sides, and shows a slight depression beneath the diapophysis. Right at the
- 1757 base of the diapophysis however, it shows a slight convexity.
- 1758 The centrum is anteriorly slightly convex, and posteriorly slightly convex, in dorsal view.
- 1759 The left diapophysis is preserved, and this projects laterally in anterior view, with an angle of
- 1760 90° with respect to the dorsoventral plane (Fig.22C, D). The diapophysis in dorsal view
- projects posteriorly and slightly dorsally. The diapophysis is flat and rectangular in dorsal
- 1762 view, with the anterior edge being convex and the posterior one concave.
- 1763 The prezygapophyses are visible above the neural canal as short rounded triangular stubs,
- 1764 which project dorsally and slightly laterally (Fig. 22A, B, D). In dorsal view, the
- 1765 prezygapophyses are rounded-triangular protrusions that fork from the base of the neural
- arch, and which bend slightly medially, towards each other. The postzygapophyses are
- 1767 broken off, although the bases are present, showing a dorsoventrally elongated, dorsally
- triangular and ventrally oval shape (Fig. 22C).
- 1769 The neural spine is stout and cone-shaped in anterior view, and displays paired sprl (Fig.
- 1770 22D). The base of the neural spine is axially constricted; the neural spine broadens axially
- towards its dorsal end. The spine shows rugose longitudinal striations on its lateral sides (Fig.
- 1772 22A, B). Though possibly broken and damaged, it shows a similar curve as in PVL 4170 (19),
- 1773 in that the posterior side curves convexly and the anterior concavely, allowing the neural
- spine to curve gently in a sort of L-shape. The tip of the neural spine is not as saddle-shaped
- as in PVL 4170 (19), however, there is still a slight curvature of the neural spine summit
- 1776 visible on its posterior side (Fig. 22A, B). The spine summit is similar in shape to those of the
- 1777 posterior dorsals of PVL 4170 (19), in that the sides of the summit are tapering slightly

ventrally from a 'platform' that is the dorsalmost part. The summit is a rhomboid-shaped

1779 knob, which is transversely broader anteriorly than posteriorly (Fig. 22E).

1780

1781	PVL 4170 (21): This anterior - mid caudal has a much more heart-shaped anterior articular
1782	surface than PVL 4170 (19-20), however, the lower half of the articular surface is
1783	reconstructed, therefore it is not certain that the original form persists (Fig. 23D). The
1784	deepest concavity is not at the midpoint but slightly above it, about 1/3rd of the
1785	dorsoventral length of the articular surface down from its dorsal rim. The dorsal rim has a
1786	slight 'lip'; an anteriorly protruding part of the rim that cups the articular surface. The
1787	midpart of this lip is bent ventrally with two lateral bulges, giving it a heart-shape, as in PVL
1788	4170 (19-20), see Fig. 23C. In posterior view, the articular surface of the centrum is
1789	rounded-to-triangular in shape. The posterior articular surface is less concave than the
1790	anterior articular surface. In lateral view the centrum is more elongated than in PVL 4170
1791	(19-20). In ventral view, the posterior edge of the centrum shows slightly developed chevron
1792	facets (Fig. 23E). The lateral sides of the centrum are strongly concave, the axial centrum
1793	length is increased in this caudal vertebra, compared to PVL 4170 (19-20).
1794	The neural canal is near semi-circular with the horizontal axis on the ventral side. In dorsal
1795	view, the posterior dorsal rim of the centrum retreats towards the neural arch in a U-shaped
1796	recess, posterior to the neural canal opening (Fig. 23C).
1797	The left diapophysis is preserved; the right is broken off (Fig. 23C, D). The left diapophysis is
1798	a stout straight element in anterior view, and is slightly tilted towards the anterior and
1799	dorsal side. The extremity is roughly triangular in outline (Fig. 23B). In dorsal view, the
1800	diapophysis is seen to bend posteriorly as in PVL 4170 (19-20). The prezygapophyses are
1801	flattened in dorsal view, and slightly spatulate. The diapophysis is seen to deflect slightly
1802	posteriorly Fig. 23F).

1803 The prezygapophyses are stout dorsoventrally broad struts (Fig. 23A, B, D). They are

1804 triangular in shape, with dorsoventrally elongated struts, and are directed dorsally. The

1805 neural arch is tilted, probably due to taphonomical alteration. The postzygapophyses are

1806 small rounded triangular bosses posterior to a large bulge on the neural spine (Fig. 23A, B,

1807 C). This bulge is set right ventral to an axial constriction of the neural spine, after which it

1808 constricts slightly again.

1809 The spine summit is similar to PVL 4170 (19) - (20). It constricts transversely at about $1/3^{rd}$

1810 of the dorsoventral length towards the summit, after which it slightly transversely widens

- 1811 towards the summit; the sprl follow a similar pattern (Fig. 23A, B, F). Dorsal to the
- 1812 postzygapophyses, the spine also bends more posteriorly after this bulge, similar to PVL

1813 4170 (20). The top 1/3rd of the spine shows ligament attachment sites in lateral view. The

1814 neural spine expands slightly towards the summit in a rhomboid shape, with dorsoventrally

1815 deep striations for ligament attachments. The summit is 'saddle shaped', as in the other

1816 anterior caudals PVL 4170 (19-20), see Fig. 23F.

1817

1818 *PVL 4170 (22):* This anterior middle caudal has a partially broken neural spine and partially

1819 broken right prezygapophysis Fig. 24A, B). In anterior view, the articular surface of the

1820 centrum is oval, with the dorsal edge similar to PVL 4170 (19) – (21), see Fig. 24D. In

1821 posterior view, the articular surface is oval to round, with the long axis on the dorsoventral

1822 plane (Fig. 24C). The rim that cups the articular surface is thinner than in PVL 4170 (19) –

1823 (21). In lateral view, the ventral side of the centrum is concave, and in ventral view the

1824 anterior rim showing chevron facets (Fig. 24A, E). Because the ventral side of the centrum

1825 slopes down, the posterior end lies lower than the anterior end (Fig. 24A). In ventral view,

1826 the centrum is symmetrically concave transversely. The axial midline is smooth, with no keel

1827 or struts, however, anteriorly two large, rugose semi-circular chevron facets are visible, and

1828 posteriorly two smaller semi-circular ones (Fig. 24E).
1829 The neural canal is triangular to semi-circular. In posterior view, the neural canal is semi-oval1830 (Fig. 24C, D).

1831 The prezygapophyses are less triangular than in PVL 4170 (21), rather they are blunted

triangular to rounded (Fig. 24A, D). The prezygapophyses are stout struts that protrude

- 1833 anteriorly and dorsally from the neural arch. They have a rounded tip at their extremities. In
- dorsal view, the prezygapophyses show stout beams and stout sprl. Posteriorly, the same U-
- 1835 shaped recess is visible as in PVL 4170 (19) (21), ventral to the hyposphene and
- 1836 postzygapophyses, which together have the same morphology as the previous caudals PVL

1837 4170 (19) – (21) and the posterior dorsals PVL 4170 (16) - (17), see Fig. 24A, C.

- 1838 The diapophyses bend towards the posterior side (Fig. 24B). The centrum is broadened
- 1839 transversely around the diapophyses.
- 1840 The neural spine is inclined posteriorly, directly dorsally from an axial thickening of the
- 1841 neural spine (Fig. 24A). This part however, is broken off.
- 1842
- 1843 *PVL 4170 (23):* In anterior view, this middle caudal has a round articular surface (Fig. 25C).
- 1844 The articular surface is concave, with the deepest point in the center. The same thick rim is
- 1845 present as in PVL 4170 (19) –(22), however it is less rugose in this caudal. In posterior view,
- 1846 the articular surface is round (Fig. 25D). The rim surrounding the articular surface shows
- rounded striations as in the previous caudals. In ventral view, the centrum is of a similar
- 1848 morphology to in PVL 4170 (22), see Fig. 25E. It has two well-developed chevron facets on
- 1849 the anterior ventral rim of the anterior articular surface. These chevron facets are connected
- 1850 medially by a rugose elevated ridge of bone. On the posterior rim two small semi-circular
- 1851 chevron facets are discernible.
- The neural canal is rounded to triangular in shape, with the horizontal plane on the ventralside (Fig. 25C, D).

1854 The prezygapophyses are directed more dorsally than anteriorly (Figure 25A, C). In dorsal

1855 view, the prezygapophyses are bent towards their medial side, as in PVL 4170 (22), see Fig.

1856 25B. In lateral view, the neural arch is of similar morphology as in PVL 4170 (22), however,

1857 the prezygapophyses are directed more dorsally than ventrally and the diapophyses are

1858 shorter in length (Fig. 25A).

1859 The diapophyses are thickened axially compared to previous caudals, and remain closer to

1860 the central body, where the centrum is thickened transversely (Fig. 25B). Both the

1861 diapophyses and postzygapophyses are reduced in size compared to previous caudals. The

1862 postzygapophyses are present as small triangular bosses (Fig. 25A, D).

1863 The neural spine is of equal transverse width, unlike the previous caudals (Figure 25A). The

1864 neural spine is still elongated as in previous caudals; however, it is straighter and does not

1865 bend dorsally more than $1/3^{rd}$ of its dorsoventral length onwards. The axial thickening

1866 however, is still visible as in the previous caudals. The spine summit is slightly saddle shaped

1867 as in the previous anterior caudals (Fig. 25B). The neural spine summit does still show the

1868 elevated rhomboid morphology as in the previous anterior caudals and in the posterior

1869 dorsals of PVL 4170.

1870

1871 PVL 4170 (24): In anterior view, this caudal has a more oval than round articular surface,

1872 with the long axis in the dorsoventral plane (Fig. 26D). This is different to the other caudals;

1873 however, it and its surrounding thick rim are also partially damaged on the anterior surface.

1874 In posterior view, the articular surface of the centrum is oval, with the long axis in the

1875 transverse axis, giving the articular surface a more flattened appearance (Fig. 26C). In lateral

1876 view, the centrum shows an elliptical fossa ventral to the diapophyses (Fig. 26A, B). In

1877 ventral view, the centrum is smooth, without a keel or rugosities, with only a faint ventral

1878 groove, and is transversely concave (Fig. 26F). The anterior chevron facets are similar to

those in PVL 4170 (23), however they are less developed (Fig. 26F).

- 1880 The neural canal is more semi-circular than triangular (Fig. 26C, D). The neural arch
- 1881 supporting the posterior neural canal opening is triangular in shape, and the neural canal
- itself is oval with an elongation on the dorsoventral plane (Fig. 26C).
- 1883 The right prezygapophysis is slightly damaged; the left is complete (Fig. 26A, B, E). Its
- 1884 articular surface bends towards the lateral side, unlike in the previous caudals. The
- 1885 prezygapophyses are more elongated, and the postzygapophyses (Fig. 26C) are more
- 1886 pronounced in this caudal, unlike PVL 4170 (23), which might mean that this caudal should
- 1887 be switched with the former caudal, in terms of vertebral order.
- 1888 The neural spine is straight and rectangular in shape in anterior, posterior and lateral view,
- 1889 showing a more basal morphology than the previous caudals (Fig. 26A, B, E). The spine
- 1890 summit has a faint saddle shape, however not as pronounced as in previous anterior
- 1891 caudals; the summit shows a flatter surface, with only a slight posterior elevation (Fig. A, B,
- 1892 E).
- 1893
- 1894 *PVL 4170 (25):* In anterior view, the dorsal rim of the anterior articular surface is well
- 1895 developed, and shows a slight indentation below the neural canal, giving it a small
- 1896 heartshape as in the more anterior caudals (Fig. 27D). In posterior view, the articular surface
- 1897 of the centrum is round, and shows pronounced round striations on the rim (Fig. 27E). In
- 1898 lateral view, the centrum displays a larger anterior articular surface than posteriorly
- 1899 (Fig.27A, B), as in other middle caudals of eusauropods (Upchurch 2004). The anterior rim is
- also more rugose than the posterior one. In ventral view, the centrum shows two large
- 1901 chevron facets on the anterior side, and two smaller ones on the posterior side (Fig. 27C).
- 1902 The neural canal is similar in morphology to that of PVL 4170 (23) (24), see Fig. 27D, E.
- 1903
- The prezygapophyses are connected medially by a ridge of bone, which is different from the
 previous caudal vertebrae, where a deep U-shaped gap between the prezygapophyses exists

1906 (Fig. 27A, B, D, F). The prezygapophyses themselves are damaged. In dorsal view, the

1907 prezygapophyses and spinoprezygapophyseal laminae are clearly visible as stout beams, as

in PVL 4170 (22). The posterior dorsal rim of the centrum shows a sharp U-shaped recess

1909 towards the postzygapophyses, which are positioned in an angle at almost 90° to the

1910 horizontal, Fig. 27A, B, E). The postzygapophyses are visible as lateral triangular protrusions

1911 ventral to the neural spine.

1912 The diapophyses in this caudal are reduced to small protrusions on the more dorsal side of

1913 the centrum, indicating the transition from the middle caudals to a more posterior caudal

1914 morphology (Fig. 27E, F). They are shaped as round bosses on the lateral sides of the

1915 centrum, in dorsal view.

1916 The neural spine is straight, and increases in axial width towards the summit (Fig. 27A, B, F).

1917 It is more inclined posteriorly than dorsally, confirming its middle-posterior caudal position.

1918 On the lateral side, rugose dorsoventrally positioned striations are visible. The spine summit

1919 is not straight, but shows a faint saddle shape (Fig. 27A, B).

1920

1922	PVL 4170 (26): In anterior view, the articular surface of the centrum is oval and
1923	dorsoventrally flattened as in PVL 4170 (25), see Fig. 28B. In posterior view, the articular
1924	surface is oval and elongated in the dorsoventral axis (Fig. 28A). It has rough circular
1925	striations as in the other caudals. In lateral view, the centrum is axially elongated, suggesting
1926	a possibly more posterior position than the numbering might indicate (Fig. 28C, D). In dorsal
1927	view, the axial elongation of the centrum is apparent, again indicating this caudal might be
1928	more posterior than middle (Fig. 28F). This could also imply that some caudals that originally
1929	existed between PVL 4170 (25) and (26) are missing here. The outline of the centrum is
1930	symmetrical in dorsal view; the flaring of the extremities and the constriction of the centrum
1931	in the middle (Fig. 28F). In ventral view, the centrum is smooth and concave, and the
1932	chevron facets are not pronounced (Fig. 28E).

- 1933 The same indentation as in most caudals, ventral to the neural canal, is visible, however, this
- 1934 part is also partially broken. The anterior neural canal is large and triangular to oval in shape
- 1935 (Fig. 28B). It occupies most of the anterior surface of the neural arch. The posterior neural
- 1936 canal is oval and also dorsoventrally elongated (Fig. 28A).
- 1937 The prezygapophyses are still protruding anteriorly, however as in PVL 4170 (25), the recess
- 1938 between them is not pronounced (Fig. 28B, C, D). The prezygapophyses are inclined dorsally
- and medially, and make an angle of about 45 degrees with respect to the centrum, with the
- 1940 triangular articular surface on the medial side. The postzygapophyses are reduced to
- triangular bosses, ventral to the neural spine (Fig. 28A, C, D).
- 1942 The diapophyses are reduced to bulges on the lateral side of the centrum, beneath which a
- 1943 slight depression still remains (Figure 28C, D, F).
- 1944 The neural spine is partially broken off at the base. Dorsal to the postzygapophyses, the
- 1945 neural spine displays rough dorsoventrally elongated striations (Fig. 28C, D). The neural
- spine is projecting dorsally and posteriorly, being parallel to the centrum. In dorsal view, all
- 1947 extremities are symmetrical, giving the caudal the outline of a cross in dorsal view (Fig. 28F).
- 1948
- 1949 PVL 4170 (27): The centrum of this middle-posterior caudal amphicoelus and symmetrically
- 1950 shaped. In anterior view, the articular surface is oval and dorsoventrally flattened as in PVL
- 1951 4170 (25) (26), see Fig. 29F. Similarly, the dorsal rim of the articular surface is heart-
- 1952 shaped. In lateral view, the anterior articular surface is slightly longer dorsoventrally than
- 1953 the posterior one (Fig. 29C, D). The anterior also shows the chevron facets clearly as ventral
- rugose protrusions. The centrum on the ventral side is concave, and on the lateral axial
- 1955 surface the centrum seems to be slightly transversely flattened (Fig. 28B). In posterior view,
- 1956 the articular surface is oval, with the elongation in the dorsoventral plane (Fig. 28E). It is also
- 1957 flattened transversely. In ventral view, no chevron facets are visible, however, the centrum
- 1958 shows a flattening in the axial midline, which is slightly concave (Fig. 29B).

1959 On the lateral sides of the centrum, the diapophyses are visible as rudimentary, rugose

rounded bulges (Fig. 29C, D). The prezygapophyses are damaged, however, this renders the

neural canal clearly visible as a semi-circular/triangular structure (Fig. 29E, F).

1962 The neural spine is broken; however, it is straight and directed posteriorly and dorsally, it

being more flattened towards the centrum than in previous caudals, indicating again a more

1964 posterior caudal morphology (Fig. 29C, D). In dorsal view, the spine is clearly flattened

1965 towards the centrum (Fig. 29A).

1966

1967 PVL 4170 (30 / 31 /32): The last preserved caudals are middle/posterior caudals. They are 1968 dorsoventrally and transversely smaller than previous caudals, and show an even more 1969 simplified morphology than middle caudals. The anterior articular surface is oval with the 1970 elongation axis on the dorsoventral plane, see Fig. 30A. The posterior articular surface is 1971 smaller in size and more rounded than oval (Fig. 30B). These caudals do not have the 1972 prezygapophyses, postzygapophyses or neural spines preserved (Fig. 30), except for PVL 1973 4170 (32). In lateral view, PVL 4170 (32) has prezygapophyses present as small rounded 1974 protrusions that project anteriorly. The postzygapophyses are no longer visible. PVL 4170 1975 (32) has a short, robust spine. It is inclined posteriorly and ventrally, back towards the 1976 centrum, indicating a posterior caudal position. 1977

1978 APPENDICULAR SKELETON

1979

Ilium PVL 4170 (34): According to the Cerro Cóndor Norte quarry map (Fig 1), two ilia were recovered in the original excavations. However, the whereabouts of the second ilium are unknown. Even though the MACN in Buenos Aires hosts several ilia, which can be attributed

1983 to *Patagosaurus*, none of these are large enough to match the holotype ilium in the

1984 collections of the Instituto Miguel Lillo in Tucuman.

1985 The right ilium is axially longer than dorsoventrally high (Fig. 31C). The dorsal rim is convex

- as in most sauropods, however, the curvature resembles the high dorsal rim of basal
- 1987 neosauropods/derived eusauropods (e.g. Apatosaurus, Haplocanthosaurus, Diplodocus,
- 1988 *Cetiosaurus*) more than those of more basal forms, which tend to be less convex, as seen in
- 1989 *Tazoudasaurus* (Allain et al. 2004; Allain and Acquesbi 2008). The iliac body is not entirely
- straight; it is offset from the axial plane to the lateral side at the anterior lobe, whereas the
- 1991 midsection is axially aligned, and the posterior end is slightly offset to the medial side. The
- 1992 ilium of the eusauropod *Lapparentosaurus* also follows this curvature. *Cetiosaurus*
- 1993 *oxoniensis* shows a more or less straight anterior half of the iliac body, though the posterior
- 1994 half is also slightly offset medially.
- 1995 The preacetabular process in lateral view is hook-shaped (Fig. 31C); a common feature
- among sauropods, and found in the eusauropods *Cetiosaurus*, *Barapasaurus*, *Omeisaurus*
- *junghsiensis,* and *Shunosaurus lii* (Tang et al. 2001; Upchurch and Martin 2003;
- 1998 Bandyopadhyay et al. 2010), although not in *Tazoudasaurus* (Allain and Aquesbi 2008). The
- anteriormost part of the process has a thickened rugose dorsal side, which is much thicker
- 2000 than the dorsal edge of the more posterior part of the ilium, and is slightly constricted
- 2001 dorsoventrally. However, the posteriormost dorsal rim of the iliac blade shows another
- thickened ridge. Ventrally the preacetabular process slopes down gently, not in a sharp
- 2003 curve, towards the pubic peduncle of the ilium.
- The preacetabular process in anterior view (Fig. 31A) is dorsally rugose and pitted for muscleand cartilage attachment. It is slightly bent towards the lateral side, thus not entirely aligned
- 2006 in the axial plane. The pubic peduncle in anterior view is a stout element, which flares out
- 2007 distally and is less wide at its proximal base. The articular surface of the distal end of the
- 2008 pubic peduncle is not symmetrical, but slightly triangular in shape. The dorsal part of the
- 2009 preacetabular lobe is similar to *Haplocanthosaurus* in that it has a similar thickening rugosity
- 2010 of the anteriormost hook-shaped process, but differs from *Haplocanthosaurus* in that it

- 2011 constricts slightly behind this process, whereas in *Haplocanthosaurus* the dorsal rugosity
- 2012 behind the anterior process continues smoothly (Hatcher 1903; Upchurch et al. 2004). The

2013 constriction does seem to be natural and not due to damage.

2014 The pubic peduncle is a slender rod-shaped element, which widens towards the distal end,

2015 both anteriorly and posteriorly, in lateral view (Fig. 31C). The anterior distal side of this

2016 peduncle bulges slightly convexly. The posterior side of the pubic peduncle (or the anterior

- 2017 edge of the acetabulum) is concave. The extremity of the peduncle is convex anteriorly and
- 2018 flat posteriorly, and the surface is rugose.
- 2019 The acetabulum is relatively wide as in *Barapasaurus, Haplocanthosaurus,* and diplodocids
- 2020 (Hatcher 1903; Upchurch et al. 2004; Bandyopadhyay 2010), but differs in width from
- 2021 Cetiosaurus, Tazoudasaurus and titanosauriforms (Upchurch and Martin 2003; Allain and
- Aquesbi 2008; Díez Díaz et al. 2013; Poropat et al. 2015), see Figure 31C. Its dorsal rim is
- transversely acute towards the medial side. The rim itself is concave.
- 2024 The ischial lobe is clearly visible as the ventral half of the heart-shaped posterior end of the
- 2025 illiac blade (Fig. 31B, C). In lateral view it is a semi-round structure. The surface of the ischial
- 2026 peduncle bulges out laterally, giving it a slight offset from the iliac blade to the lateral and
- 2027 ventral side. It is also offset ventrally and posteriorly from the acetabulum (Fig. 31B). The
- 2028 articular surface for the ischium is oval in shape and rugosely pitted and striated. The ischial
- 2029 peduncle of the ilium in lateral view is a semi-round, non-prominent lobe.
- 2030
- 2031 *Pubis PVL 4170 (35):* The right pubis is almost complete. In lateral view, the pubic shaft
- 2032 shows a slightly convex dorsal side and a slightly concave ventral side of the shaft, providing
- 2033 the shaft with a slight curvature in lateral view (Fig. 32A). The shaft is gracile, taking up
- 2034 approximately 2/3rds of the entire pubic length. The shaft is more compressed
- 2035 lateromedially than that of *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003)
- 2036 Mamenchisaurus youngi (Pi et al. 1996), or Bothriospondylus madagascariensis (Mannion

2037 2010). Moreover, the length of the pubis is more or less similar to that of the ischium. In this 2038 way it more resembles that of Haplocanthosaurus than other sauropods (Hatcher 1903). The 2039 shaft and proximal part are aligned (Fig. 32A); in that there is no torsion of the pubis as in 2040 more derived sauropods (Upchurch and Martin 2003; Upchurch et al. 2004). Interestingly, 2041 the African and Malagasi basal eusauropods Spinophorosaurus and 'Bothriospondylus' have 2042 a much more 'robust' pubis than Patagosaurus (Remes et al. 2009; Läng 2010). The pubis of 2043 Tazoudasaurus appears to be of the more robust type as well, however this is not entirely 2044 clear, as it belongs to a juvenile (Allain et al. 2008). The elongated and slender shaft is also 2045 seen in Vulcanodon (Cooper 1984), however in this taxon the pubic apron is smaller. Also, in 2046 Vulcanodon, the pubis is much shorter than the ischium, as in most sauropods (Cooper 1984; 2047 Upchurch et al. 2004).

- 2048 The distal expansion of the pubis in lateral view flares more dorsally than ventrally, and
- tapers acutely to a point (Fig. 32B, D). This distal shape is similar to that of *Barapasaurus*
- 2050 (Bandhyopadhyay 2010) is more flared than *Haplocanthosaurus* (Hatcher 1903). The distal

2051 end of the pubis in distal view is suboval in shape (Fig. 32B, D).

- 2052 The pubic apron is slightly convex ventrally in lateral view, with the ischial peduncle tapering
- 2053 obliquely (Fig. 32A). The pubic peduncle of the pubis projects medially and slightly ventrally.
- 2054 Even though the mirroring pubis is not present, the pubic basin can be estimated to be wider
- than that of *Barapasaurus,* in which the pubic basin is narrow.
- 2056 The pubic foramen is 'pear-shaped' in lateral view; a dorsoventrally elongated oval that is
- 2057 constricted slightly dorsal to the middle (Fig. 32A).
- 2058 The pubic rim of the acetabulum is a steeply sloping surface from the iliac peduncle to the
- ischial peduncle in lateral view. This rim tapers ventrally and posteriorly towards the
- acetabulum.
- 2061 The ischial peduncle has a roughly triradiate, transversely narrow and dorsoventrally
- 2062 elongated articulation surface, with the narrowest point on the ventral side. The length of

2063 the ischial peduncle of the pubis is less than 33% of the length of the entire pubis; further 2064 reinforcing the elongation of this pubis. In Haplocanthosaurus the length of the ischial 2065 peduncle is also less than 33%, in Cetiosaurus as well (Hatcher 1903; Upchurch and Martin 2066 2003). The iliac peduncle is dorsally elevated from the pubic apron and the shaft, as in 2067 Cetiosaurus. The iliac articulation surface is rugose, and curves slightly medially and 2068 posteriorly. There is no 'hook'-shaped ambiens process present as in Lapparentosaurus, 2069 Bothriospondylus or derived sauropods (Mannion 2010). The pubic symphysis projects 2070 medially and ventrally, as in most sauropods (Upchurch et al. 2004)

2071

2072 *Ischia PVL 4170 (36):* The fused distal parts of both ischia are preserved, with fusion

2073 occurring at around 2/3 of the shaft length (Fig. 33). The proximal parts are recreated in

2074 plaster; therefore, these will not be described. However, part of the shaft of the right

ischium is preserved (Fig. 33C). In lateral view, the ventral side is concave, and the shaft

2076 expands both dorsally and ventrally towards the limit of the distal end (as far as it is

2077 preserved).

There is a peculiar oval depression on the lateral side of the right ischium, approximately at the height of the fusion with the left ischium (Fig. 33A). This could be a pathology, however, seeing as the femur originally was overlaying the ischium in situ during excavations (see Fig. 1), this depression is most probably taphonomic in nature. The extremities of the fused ischia flare out distally towards the sagittal plane. In posterior view, the distal ends are directed laterodorsally and medioventrally (Fig. 33B). The fusion forms a wide V-shape with an angle of 110° with the horizontal; an intermediate stage between the coplanar

2085 *Camarasaurus* ischial fusion state and that of diplodocoids, *Cetiosaurus, 'Bothriospondylus*

2086 madagascariensis' and Vulcanodon (Janensch 1961; Cooper 1984; Upchurch and Martin

2087 2003; Mannion 2010; Tschopp et al. 2015). In dorsal view, the shaft of the right ischium

2088 bends and bulges slightly towards the lateral side at 2/3rd of shaft length, but this is probably

due to the taphonomic/pathological damage, as the left ischial shaft is concave laterally indorsal view. The surfaces of the ischial extremities are convex and rugose (Fig. 33B).



2115 In posterior view, the curvature of the femur is still visible (Fig. 34). A deep longitudinal 2116 muscle attachment scar is visible at around the midpart of the shaft. The greater trochanter 2117 is clearly visible in posterior view, as a small rounded protrusion, projecting dorsally from 2118 the proximolateral end of the femur. Directly medial to this, the proximal end of the femur 2119 shows a slight depression, before the medial onset of the femoral head. Distally, in posterior 2120 view, the tibial condyle is slightly damaged. It expands strongly medially, and 2121 medioposteriorly; this is also seen in Cetiosaurus (Upchurch and Martin 2003). Between the 2122 tibial and fibular condyles, the distal end of the posterior part of the femur shows a deep 2123 depression, also seen in Cetiosaurus, and possibly Lapparentosaurus (MNHN-MAA 64). The 2124 fibular condyle is offset to the lateral side, and clearly protrudes posteriorly as a teardrop-2125 shaped solid structure. The distal lateral condyle flares to the lateral side. 2126 In dorsal view, the proximal end of the femur is strongly rugose and pitted, for cartilage and 2127 muscle attachments. Medial to the greater trochanter, the proximal end is axially 2128 constricted, after which the femoral head widens again. Unfortunately, the femoral head is 2129 not very clearly visible due to the mounting of the specimen, however, it is rounded, 2130 standing out medially at about 20 cm. The medial end of the femoral head is not completely 2131 rounded, but a little pointed, though not as abruptly as in Cetiosaurus. 2132 2133 DISCUSSION 2134 2135 **COMPARATIVE MORPHOLOGICAL CHARACTERS OF PATAGOSAURUS FARIASI** 2136 2137 *Cervicals:* the number of cervicals of *Patagosaurus* is possibly closer to that of *Cetiosaurus* 2138 and Spinophorosaurus, and possibly slightly lower than that of the Rutland Cetiosaurus. It is

- 2139 most likely also lower than in neosauropods, placing it within known derived non-
- 2140 neosauropodan eusauropods (Mannion et al. 2019).

2141 One feature that differentiates *Patagosaurus* from other sauropods is the wide angle 2142 between the postzygodiapophyseal laminae and the posterior centrodiapophyseal lamina. 2143 This angle is as wide as 55° to the horizontal (contra McPhee et al. (2016) who measured 2144 41°) and is not found in any basal non-neosauropodan eusauropod (all have an angle 2145 between the podl and pcdl of between 30 and 40°). In basal sauropods and 2146 sauropodomorphs, this angle is much lower, and even in many and even in many 2147 eusauropods the angle is less wide (McPhee et al 2015). Thus, this elevation seems to mark 2148 the transition from sauropodomorphs to sauropods. Shunosaurus and Kotasaurus (Tang et 2149 al. 2001; Yadagiri 2001), have a high projection of the podl, but not a lower projection of the 2150 pcdl, therefore still not equating the high angle of Patagosaurus. Potentially in Jobaria 2151 (Wilson 2012), and certainly in neosauropods, such as Haplocanthosaurus and Diplodocus 2152 (Hatcher 1901; 1903), higher angles are reached with higher projections of the podl 2153 (Upchurch et al 2004). In general, high posterior cervical neural arches are achieved by 2154 mamenchisaurs and titanosauriforms (Mannion et al. 2019). 2155 The cervicals of Patagosaurus are different from most other Early and Middle Jurassic non-2156 neosauropodan eusauropods in that they are rather stout and short but high dorsoventrally. 2157 The aEI is on average lower than most other eusauropods (*Cetiosaurus, Spinophorosaurus*, 2158 Lapparentosaurus, Amygdalodon, see Table 1). However, as the cervical series is not 2159 complete, some cervicals that are missing might have had a higher aEI. The aEI is possibly 2160 similar to that of Tazoudasaurus, however, the morphology of the cervicals between these 2161 two taxa is different, and also Tazoudasaurus does also not have a complete cervical series 2162 (Allain and Aquesbi 2008). 2163 The anterior condyle of the cervicals is most comparable to those of *Cetiosaurus*, especially 2164 as there is a rugose rim that cups the condyle, and as there is a protrusion on the condyle.

2165 The condylar rim of *Cetiosaurus*, however, is more rugose than in *Patagosaurus* (Upchurch

and Martin, 2002; 2003). The cervicals of *Cetiosaurus* used in this study belong to the

2167 Rutland Cetiosaurus, which itself might be a slightly more derived, separate taxon than the 2168 holotype of Cetiosaurus oxoniensis (Läng 2008; P. Upchurch & M. Evans pers.comm.). 2169 The other cervical features, such as a pronounced ventral keel and posteriorly extending 2170 ventral end of the posterior cotyle, are more plesiomorphic features shared with 2171 Lapparentosaurus, Amygdalodon, Tazoudasaurus, and Spinophorosaurus. Cetiosaurus 2172 oxoniensis (Upchurch and Martin 2003; 2002) does not seem to have a ventral keel on its 2173 anterior cervicals. Lapparentosaurus shows a posterior V-shaped forking of the keel, which is 2174 not seen in Patagosaurus. Moreover, some more derived sauropods possess ventral keels, 2175 such as the titanosaurs Opisthocoelicaudia and Diamantinasaurus (Poropat et al. 2015). 2176 The next outstanding cervical feature is the non-juncture of the intrapostzygapophyseal 2177 laminae. This is a feature that distinguishes Patagosaurus from Cetiosaurus, and unites it 2178 with Tazoudasaurus, therefore a connection between this non-juncture and the elevation of 2179 the neural spine can be ruled out. Whether or not this is a feature shared between 2180 Gondwanan sauropods is uncertain. The single intraprezygapophyseal lamina is a feature 2181 shared with Cetiosaurus and Tazoudasaurus. The centrodiapophyseal fossa, as seen in 2182 Patagosaurus, is not shared with Tazoudasaurus, rather, it is shared with Mamenchisaurus. 2183 The centroprezygapophyseal fossa is shared with *Tazoudasaurus* (To1-354, contra Wilson 2184 2011). 2185 Dorsals: 2186

2187 The slightly rectangular shape of anterior and middle dorsal centra is shared with non-

2188 neosauropodan sauropods, and differs from neosauropods (Mannion et al. 2019). The

2189 slightly more mediolaterally wide posterior dorsal centra are not as wide as in

titanosauriforms (Mannion et al. 2019). The inconspicuous small round depressions on the

2191 posterior side of some of the more well preserved posterior dorsals is a feature thus far not

seen in any other sauropod, and could be an autapomorphy. However, as it is a small

2193 feature, it might have been missed in osteological descriptions of contemporaneous 2194 sauropods to Patagosaurus. Most (eu)sauropods do have a rectangular fossa or depression 2195 at the posterior side of the transverse process of (posterior) dorsals, bordered by the pcdl, 2196 and the podl, which is named the pocdf, or postzygocentrodiapophyseal fossa (Wilson 2197 2011). Whether this has compartmentalized in *Patagosaurus* is not clear, as the pocdf is 2198 rather prominently present, however, in *Patagosaurus* this fossa is more expressed towards 2199 the neural arch than towards the distal end of the diapophysis, as is the case in 2200 Spinophorosaurus and Cetiosaurus (Rutland Cetiosaurus as well as C. oxoniensis; Upchurch 2201 and Martin 2002, 2003; Remes et al. 2009). One observation is that these latter taxa have 2202 more dorsally projecting diapophyses, at an angle of about 45° to the horizontal, compared 2203 to a more horizontal and lateral projection in Patagosaurus. Whether or not the extra fossa 2204 in Patagosaurus is correlated to the projection of the diapophyses (e.g. as extra ligament 2205 attachement site for additional support) remains an unanswered question. In Barapasaurus, 2206 no such fossa is seen, whilst the diapophyses of that taxon also project laterally as in 2207 Patagosaurus. 2208 The rudimentary aliform process in the neural spines of dorsal vertebrae is seen in high 2209 ontogenetic stages of development in Europasaurus holgeri Sander et al., 2006, where it 2210 projects as a triangular protrusion dorsal to the spinal onset of the sprl in anterior view, and 2211 dorsal to the lateral spdl + spol complex in posterior view (Carballido and Sander 2014). In 2212 Patagosaurus, this feature is seen dorsal to the lspol+podl complex. This feature could be a 2213 convergence of a laterally projecting triangular process for ligament attachement, found in 2214 basal eusauropods in the configuration as in *Patagosaurus*, and in neosauropods in the

2215 configuration of *Europasaurus*. Note also that this feature develops more in mature

specimens of *Europasaurus* and that the holotype of *Patagosaurus* PVL 4170 is a (sub)adult

and still growing (as evidenced by fused but visible neurocentral sutures), and in

2218 *Patagosaurus* the feature is only seen in posteriormost dorsals as a very rudimentary form.

2219 Posterior dorsal neural arches with rudimentary aliform processes are now known for

2220 *Patagosaurus*, and are also seen in more distinct form in basal macronarians such as

2221 Europasaurus, and also in Bellusaurus sui Mo, 2913 and Haplocanthosaurus (Hatcher 1903;

- 2222 Upchurch 1998; Mo 2013; Carballido and Sander 2014; Foster and Wedel 2014).
- 2223

2224 The absence of a spinodiapophyseal lamina on dorsal vertebrae is another characteristic 2225 dorsal feature in *Patagosaurus*. This lamina is seen in dorsals of basal sauropods such as 2226 Tazoudasaurus and Barapasaurus, then disappears in Patagosaurus, C. oxoniensis and the 2227 Rutland Cetiosaurus, then reappears in neosauropods such as Apatosaurus, Diplodocus, 2228 Haplocanthosaurus, Camarasaurus, Dicraeosaurus and Amargasaurus (Wilson 1999). It's 2229 absence is therefore interpreted as an apomorphic character uniting the cetiosaurids 2230 (Holwerda and Pol 2018). In Patagosaurus, the diapophyses are supported solely by the acdl, 2231 pcdl from the ventral and lateral sides, and prdl and podl from the lateral and dorsal sides. In 2232 posterior dorsals, the diapophysis is additionally supported by the lspol+podl complex, 2233 which is sometimes mistaken for the spdl (Allain et al. 2008). This podl+lspol complex is also 2234 seen in the Rutland Cetiosaurus. This complex could possibly be the 'replacement' of the 2235 spdl found in basal sauropods and neosauropods. In any case, the absence of the spdl in 2236 Patagosaurus and Cetiosaurus cannot be connected with either neural spine elongation, as 2237 neosauropods (and especially diplodocids) display similar spine elongation. Neither can the 2238 spdl be correlated with neural spine bifurcation, as the spdl is found in basal non-2239 neosauropodan sauropods. 2240 2241 Whereas anterior dorsals and middle dorsals of Patagosaurus resemble other non-

2242 neosauropodan eusauropods, particularly *Cetiosaurus*, *Tazoudasaurus* and

2243 *Lapparentosaurus*, the posterior dorsals display non-neosauropodan eusauropod features

such as unbifurcated neural spines, simple hyposphene/hypantrum complexes (hyposphene

rhomboid and small, hypanthrum a rugose scar) and unexcavated parapophyses. The neural
spine summit, however, resembles more those of the non-neosauropodan eusauropod *Lapparentosaurus* and also of the basal neosauropod *Haplocanthosaurus*. The phylogenetic
position of *Lapparentosaurus* is not completely resolved, as the type specimen is a juvenile,
and has been retrieved as either a brachiosaurid by Bonaparte (1986a), as a titanosauriform
(Upchurch 1998), and as non-neosauropodan eusauropod (Läng 2008; Mannion et al. 2013),
therefore it is not possible to draw any conclusions from this.

2252 The lamination of the anterior dorsals is largely similar to that of *Cetiosaurus* and

2253 *Tazoudasaurus*, in that the spol flare out laterally and ventrally, broadening the neural spine. 2254 However, the transition from anterior to middle to posterior dorsal vertebrae brings some 2255 changes in lamination. The centroprezygapophyseal laminae extend dorsoventrally as the 2256 neural arch, pedicels and neural canal extend in dorsoventral height. This is seen in several 2257 other sauropods, although not in the same degree as in *Patagosaurus*. The configuration of 2258 the intrapostzygapophyseal laminae shifts from a non-juncture to a juncture, and then these 2259 laminae disappear. Instead, a single intrapostzygapophyseal lamina appears. This seems to 2260 be unique for a select group of eusauropods (see Allain and Aquesbi 2008; Carballido and 2261 Sander 2014). The posterior dorsals also display a split in the spol, into a medial and a lateral 2262 running lamina. This is described for *Europasaurus* (Carballido 2012), a basal macronarian. 2263 However, this pattern is also observed in the Rutland Cetiosaurus. It is therefore possibly a 2264 more widespread configuration than for solely (basal) macronarians, and also existed in non-2265 neosauropodan eusauropods. Throughout the dorsal vertebral column, the cpol becomes a 2266 rather secondary lamina to the tools and stool. In Europasaurus, this feature coincides with 2267 a division of the cpol into a lateral and medial one, however, in *Patagosaurus*, only one cpol 2268 exists, which matches the description of the medial cpol of *Europasaurus*. 2269 Posterior dorsals show the dorsoventrally elongated neural spine seen in Cetiosaurus, and

also in *Haplocanthosaurus* and flagellicaudatans (Hatcher 1901; 1903). The posterior

- inclination of the neural spines of posterior dorsals is also seen in *Klamelisaurus sui* Zhao,
- 2272 1993, *Mamenchisaurus* and *Omeisaurus* (Xijing 1993; Tang et al. 2001; Ouyang and Ye 2002;
- 2273 Moore et al. 2017). The deep excavations of the fossae on the posterior dorsal neural spines,
- especially on the lateral sides, noted by Bonaparte (1986a), is also seen in *Cetiosaurus*,
- 2275 mamenchisaurids and neosauropods, suggesting a widespread character (Upchurch and
- 2276 Martin 2002, 2003; Upchurch et al. 2004).
- 2277 The presence of a single intraprezygapophyseal and single intrapostzygapophyseal lamina is
- a relatively newly named feature for sauropods, as this was named a median strut or single
- lamina below the hypantrum/hyposphene (Upchurch et al. 2004; Wilson 1999) before
- 2280 Carballido and Sander (2014) named it the stprl. These laminae are noted only for
- 2281 *Camarasaurus* and the titanosauriform *Tehuelchesaurus benetezii* Rich et al., 1999
- (Carballido et al. 2011; Carballido and Sander 2014); however, they appear to also be
- 2283 present in *Patagosaurus*. The presence of a small stprl accompanied by a large oval cprf on
- 2284 either lateral side, is shared with many other eusauropods, showing this to be a
- 2285 plesiomorphic character common in the cetiosaurids, and reappearing in Macronaria and
- basal titanosauriforms.
- 2287
- 2288 Sacrum: One possible source of bias in the comparison of the sacrum of Patagosaurus with
- 2289 other sauropods is that not many sacra of basal sauropods or non-neosauropodan
- 2290 eusauropods are preserved. Sacral elements are known from *Lapparentosaurus* and
- 2291 *Tazoudasaurus*, but mostly from juvenile individuals. Neither show the neural spine
- elongation of PVL 4170 (18). The sacral count of Patagosaurus shows one more sacral
- vertebra than the basal eusauropods *Barapasaurus*, *Spinophorosaurus* and *Shunosaurus*,
- and resembles that of derived non/neosauropodan eusauropods such as Ferganasaurus and
- 2295 *Jobaria*, as well as basal neosauropods such as *Haplocanthosaurus* (Lang and Mahammed
- 2296 2010, Tschopp et al. 2015, Carballido et al. 2017b). The fusion of sacral neural spines

- number 2-3, however, shows a more basal non-neosauropodan state. The morphology of
- the neural spines resembles that of *Haplocanthosaurus* in particular (Hatcher 1903). The
- neural spine elongation of PVL 4170 (18) is at an intermediate stage between *Shunosaurus*,
- 2300 *Camarasaurus, Haplocanthosaurus* and diplodocids, but without the sacral ribs extending
- beyond the ilium, the sacral neural spines of *Patagosaurus* do not resemble those of
- neosauropods.
- 2303
- 2304 *Caudals:* The anterior caudal vertebrae of *Patagosaurus* strongly resemble those of
- 2305 Spinophorosaurus and Cetiosauriscus (P. Upchurch pers. comm., Charig 1993; Heathcote and
- 2306 Upchurch 2003, Noè et al. 2010). *Cetiosauriscus* is currently under revision, and its
- 2307 phylogenetic position is debated. According to <u>Heathcote and Upchurch (2003)</u>; <u>Rauhut</u>
- 2308 <u>et al. (2005</u>); and <u>Tschopp et al. (2015</u>), it is a non-neosauropodan eusauropod, although in
- the last analysis, it is also recovered as a basal diplodocoid as well. Holwerda et al. (2019)
- 2310 recover it as a diplodocimorph in some analyses. A formal redescription is ongoing
- 2311 (P.Upchurch pers. comm.). The middle and posterior caudals of *Patagosaurus* are more
- 2312 resembling those of the holotype of *Cetiosaurus*.
- 2313 The elongated neural spines of PVL 4170, which are not straight but curve convexly
- posteriorly at 2/3rd of the height of the spine, are possibly a diagnostic feature that is not
- 2315 seen in other sauropods, even though anterior neural spine elongation is seen in
- 2316 *Cetiosauriscus*, and diplodocids (Charig 1980; Upchurch et al. 2004; Noè et al. 2010).
- 2317
- 2318 Appendicular elements: The round dorsal rim and hook-shaped anterior lobe of the ilium,
- together with the elongated pubic peduncle are diagnostic features for the ilium of
- 2320 Patagosaurus. Whereas Cetiosaurus oxoniensis displays a more flattened dorsal rim
- 2321 (Upchurch and Martin 2002), and Chebsaurus possibly as well (Läng and Mahammed 2010),
- 2322 *Barapasaurus* does share a rounded ilium (Bandyopadyay 2010), but not as highly dorsally

2323 projecting as in *Patagosaurus*. The morphology of PVL 4170 is more similar to

Haplocanthosaurus, and with diplodocids (Hatcher 1903, Wedel and Taylor 2013; Tschopp etal. 2015).

2326 Together with the sacrum, which is similar to (basal) neosauropods (Haplocanthosaurus,

2327 Diplodocus and Apatosaurus), the sacricostal complex of Patagosaurus is more of a

2328 neosauropod build, supporting a phylogenetic position as a derived eusauropod (Holwerda

and Pol 2018). Similarly, the 110° angle with the horizontal of the fused distal ischia, shows

an intermediate stage between neosauropods and basal eusauropods. Finally, the

intermediate morphology of the pubis, showing a torsion similar to that seen in

2332 neosauropods like *Tornieria* (Remes 2009), but showing a kidney-shaped pubic foramen as *in*

2333 Cetiosaurus oxoniensis, adds to the pelvic complex of Patagosaurus resembling a derived

2334 non-neosauropodan eusauropod, or basal neosauropod.

2335 The femur of the holotype of *Patagosaurus* is a stout element, which does not resemble the

2336 elongated femora of neosauropods, but rather that of *Cetiosaurus, Tazoudasaurus* and

2337 Barapasaurus. The slightly convex femur towards the lateral side shows a possible gait

2338 modification that is diagnostic for *Patagosaurus* and that has not been found in the other

aforementioned Jurassic sauropods. While the femoral morphology of *Cetiosaurus* is similar

to that of *Patagosaurus*, the femur of the former is straighter. A wide-gauge, which might be

inferred from the femoral morphology of *Patagosaurus*, is more common in titanosaurs

2342 (Henderson 2006) and Titanosauriformes (Wilson and Carrano 1999). There are, however,

2343 earlier ichnological indications of a possible wide-gauge: a footprint site from the early

2344 Middle Jurassic from the UK shows the presence of both a narrow-, as well as wide-gait

sauropod track (Day et al. 2004), and also footprints from the Late Jurassic of Morocco show

a wide-gauge (Marty et al. 2010). The trackmaker from these sites unfortunately cannot be

identified.

2349 **PNEUMATICITY IN BASAL EUSAUROPODS**

2350 The cervicals of *Patagosaurus* show anteriorly deep pleurocoels with a gradual shallowing 2351 towards the posterior end, and with clearly defined anterior, dorsal and ventral rims, but no 2352 clearly defined posterior rim. The anteriorly deep part of the pleurocoel is visible as a 2353 circular concavity. Damage in some cervicals show that only a thin plate of bone divided 2354 mirroring pleurocoels (e.g PVL 4170 6). Bonaparte (1979, 1986a, 1999) already noted the 2355 presence of a pleurocoel. Note that the pleurocoel is present, but is shallower in the dorsals, 2356 as is also noted by Bonaparte (1986a). The pleurocoel is defined for sauropods either as a 2357 pneumatopore or as a pneumatic structure (Wilson 2002; Wedel 2003, 2005, 2013; 2358 Upchurch et al. 2004), however, Carballido and Sander (2014) defined the structure using 2359 Patagosaurus as an example, as a lateral excavation on the centrum, with clear anterior, 2360 dorsal and ventral margins, and a posterior margin that could be either well-defined or more 2361 gradually merging with the lateral body of the centrum (Carballido & Sander 2014). As 2362 already remarked on by Bonaparte (1986a, 1999) and Carballido and Sander (2014), 2363 *Patagosaurus* does not show the internal pneumatic structure that neosauropods display. 2364 This type of pleurocoel outline is seen in other Jurassic non-neosauropodan eusauropods, 2365 such as the Rutland Cetiosaurus, Barapasaurus, Tazoudasaurus, Spinophorosaurus, 2366 Lapparentosaurus (Bonaparte 1986c; Upchurch and Martin 2003; Allain and Aquesbi 2008; 2367 Remes et al 2009). The lack of a clear posterior margin of the pleurocoel is also common, 2368 except in the Rutland Cetiosaurus (Upchurch and Martin 2003). The anterior depth of the 2369 pleurocoel in Patagosaurus, however, is probably unique to this taxon. In Spinophorosaurus 2370 (Remes et al., 2009), as well as Lapparentosaurus (MNHN-MAA 13), the pleurocoel is shallow 2371 at its anterior margin, and even shows a shallowing at its anterior ventral margin. In 2372 Barapasaurus (Bandyopadhyay 2010), the entire pleurocoel is shallow. In Shunosaurus, the 2373 pleurocoel is anteriorly deep, but the concavity is more elongated and elliptic in shape, while 2374 in *Patagosaurus* this is circular and restricted to the anterior-most part of the pleurocoel. In

2375 Klamelisaurus (Zhao 1993) the pleurocoel is entirely shallow, and in the mamenchisaurids 2376 Mamenchisaurus youngi (Ouyang and Ye 2002), Zigongosaurus (Hou et al. 1976), 2377 Tonganosaurus Liu et al., 2010, and Qijianglong Xing et al., 2015 the pleurocoel is 2378 compartmentalized by one or more accessory laminae into small deep pockets over the 2379 length of the centrum. Only in the Rutland Cetiosaurus (Upchurch and Martin 2003), the 2380 pleurocoel is anteriorly deep as well. In some cervicals, an oblique accessory lamina, which 2381 divides the pleurocoel into a deeper anterior section and a shallower posterior section, is 2382 faintly present. This feature is also seen in the Rutland Cetiosaurus, in mamenchisaurids, and 2383 in neosauropods like Apatosaurus (Upchurch and Martin 2003; Xing et al. 2015; Taylor and 2384 Wedel 2017). The poor development of this oblique accessory lamina, however, and the 2385 irregularity of its presence are probably not enough to make it a character. Note that in the 2386 roughly contemporaneous Rutland Cetiosaurus (Upchurch and Martin 2003) this lamina is 2387 more consistently present.

2388

2389 Dorsals: The pneumatic structure on dorsal neural arches, appearing first in the middle 2390 dorsal neural arches and expanding in the posterior dorsal neural arches, is the key feature 2391 that Bonaparte mentioned for *Patagosaurus*, also using it to distinguish it from 2392 Volkheimeria, the other sauropod described from Cerro Cóndor (Bonaparte 1979, 1986b, 2393 1999). This feature is still the main autapomorphy for Patagosaurus, and marks new 2394 pneumatic features for basal eusauropods that were previously unknown. Pneumaticity in 2395 sauropods is well-known for neosauropods (Wedel 2003; Wedel et al. 2005; Schwarz and 2396 Fritsch 2006; Schwarz et al. 2007; Fanti et al. 2013; Taylor and Wedel 2013). It is not well 2397 understood for basal non-neosauropod eusauropods, and Patagosaurus is the first taxon to 2398 give conclusive evidence for this structure. However, other basal sauropods may have this 2399 structure (e.g. Cetiosaurus, Barapasaurus, Tazoudasaurus, see Figure 35B). The 2400 centrodiapophyseal fenestrae, which extend ventrally in a pneumatic chamber separated

- from the neual canal, is a feature possibly shared with *Cetiosaurus* and *Barapasaurus*
- 2402 (Bandyopadhyay et al. (2010); this feature often pairing these taxa with *Patagosaurus* as
- sister-taxa in phylogenetic analyses, e.g. Remes et al. (2009a)); however, it is not clearly
- shown whether these latter taxa possess the same ventral pneumatic chamber as in
- 2405 *Patagosaurus*. This feature has however been shown to be present in the basal neosauropod
- 2406 *Haplocanthosaurus* (Foster and Wedel 2014).
- A preliminary phylogenetic analysis using the holotype PVL 4170 by Holwerda & Pol (2018)
- 2408 and implementing the dorsal neural spine pneumaticity shows a close affinity of
- 2409 *Patagosaurus* with the Rutland *Cetiosaurus*, and *Patagosaurus* being nested within
- specimens referred to *Cetiosaurus*. It is furthermore more derived than *Barapasaurus*, and
- 2411 more basal to mamenchisaurids, and neosauropods (see Figure 35A).

2412

2413

2414 CONCLUSIONS

2415 To summarize and conclude, the holotype of the Middle Jurassic sauropod *Patagosaurus* 2416 fariasi shows a set of morphological features that are typically broadly non-neosauropodan 2417 eusauropod and are shared with other non-neosauropodan eusauropods. This includes 2418 features in the cervical vertebrae, such as unbifurcated neural spines, presence of a ventral 2419 keel, unexcavated parapophyses and the absence of neosauropodan laminae. In the dorsal 2420 vertebrae, these features include amphicoelus middle and posterior dorsal centra, the 2421 absence of the spdl and unbifurcated neural spines. In caudal vertebrae, this includes simple 2422 lamination, and small transverse processes. In the pelvis and femur, these include V-shaped 2423 fusion of distal ischia, and a stout femur. However, some elements seem to be slightly more 2424 derived, and are found in derived eusauropods and/or (non)-neosauropods. These include 2425 deep excavations in cervical and dorsal vertebrae, elongated neural spines in dorsal, sacral 2426 and anterior caudal vertebrae, and convex femur. The dorsal vertebral pneumaticity

- 2427 patterns found in *Patagosaurus* may unite it with other derived non-neosauropodan
- 2428 eusauropods such as *Cetiosaurus*. Finally, the main diagnostic characters for *Patagosaurus*
- 2429 *fariasi* are low (a)EI for cervical vertebrae, high neural spines in dorsal, sacral and anterior
- 2430 caudal vertebrae, cervical and dorsal vertebral pneumaticity, and convex femur.
- 2431

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2441

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2866 FIGURE AND TABLE CAPTIONS

2867

2868 Figures



2869 2870 Figure 1: Geological setting of the locality Cerro Cóndor Norte, and bonebed with holotype highlighted 2871



- Figure 2: Cervical PVL 4170 (1) in lateral (A,B), anterior (C), posterior (D), ventral (E) and
- 2874 dorsal (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl =
- 2875 centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis,
- 2876 hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior
- 2877 centrodiapophyseal lamina, pp = parapophysis, po = postzygapophysis, prcdf =
- 2878 prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal
- 2879 fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, spof =
- 2880 spinopostzygapophyseal fossa, spol = spinopostzygapophyseal lamina, sprf =
- spinoprezygapophyseal fossa, sprl = spinoprezygapophyseal lamina, vk = ventral keel.



2882 2883 2884 2885 2886 2887 2888 2889 2890 2891 2892	Figure 3: Cervical PVL 4170 (2) in lateral (A,B), anterior (C), posterior (D), ventral (E) and dorsal (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl = centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis, hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior centrodiapophyseal lamina, pp = parapophysis, po = postzygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, spof = spinopostzygapophyseal fossa, spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, wk = ventral keel
2888	prezygapophyseal centrodiapophyseal tossa, pocdf = postzygapophyseal centrodiapophyseal
2889	fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, spof =
2890	spinopostzygapophyseal fossa, spol = spinopostzygapophyseal lamina, sprf =
2891	spinoprezygapophyseal fossa, sprl = spinoprezygapophyseal lamina, tprl =
2892	intraprezygapophyseal lamina, vk = ventral keel.


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2894	Figure 4: Cervical PVL 4170 (3) in lateral (A,B), posterior, (C) anterior, (D), ventral (E) and
2895	dorsal (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl =
2896	centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis,
2897	hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior
2898	centrodiapophyseal lamina, pp = parapophysis, po = postzygapophysis, prcdf =
2899	prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal
2900	fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf =
2901	spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, spol =
2902	spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl =
2903	spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, vk = ventral keel.
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2705	
2906	Figure 5: Cervical PVL 4170 (4) in lateral (A,B), posterior (C), anterior (D), ventral (E) and
2907	dorsal (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl =
2908	centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis,
2909	hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior
2910	centrodiapophyseal lamina, pp = parapophysis, po = postzygapophysis, prcdf =
2911	prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal
2912	fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf =
2913	spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, spol =
2914	spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl =
2915	spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, vk = ventral keel.
2916	



- 2917 2918 2919 (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl =
- 2920 centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis,
- 2921 hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior
- 2922 centrodiapophyseal lamina, pp = parapophysis, po = postzygapophysis, prcdf =
- 2923 prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal
- 2924 fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf =
- 2925 spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, spol =
- 2926 spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl =
- 2927 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, vk = ventral keel.



- 2928 2929 2930 dorsal (F) view. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl =
- 2931 centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis,
- 2932 hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior
- 2933 centrodiapophyseal lamina, pp = parapophysis, po = postzygapophysis, prcdf =
- 2934 prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal
- 2935 fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf =
- 2936 spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, spol =
- 2937 spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl =
- 2938 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, vk = ventral keel.





2939 2940 Figure 8: Cervical PVL 4170 (7) in lateral (A,B), ventral (C), dorsal (D), anterior (E) and 2941 posterior (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl = 2942 centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis, 2943 hypa = hypapophysis, nc = neural canal, ns = neural spine, pp = parapophysis, po = 2944 postzygapophysis, prcdf = prezygapophyseal centrodiapophyseal fossa, pocdf = 2945 postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina, 2946 pre = prezygapophysis, sdf = spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, 2947 spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = 2948 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol = 2949 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, vk = ventral 2950 keel.



2951 2952 Figure 9: Cervicodorsal PVL 4170 (8) in lateral (A,B), anterior (C), posterior (D), dorsal (E) and 2953 ventral(F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl = 2954 centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis, 2955 hypa = hypapophysis, nc = neural canal, ns = neural spine, pp = parapophysis, po = 2956 postzygapophysis, prcdf = prezygapophyseal centrodiapophyseal fossa, pocdf = 2957 postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina, 2958 pre = prezygapophysis, sdf = spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, 2959 spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = 2960 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol = 2961 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, vk = ventral 2962 keel. 2963



2964 2965 Figure 10: Dorsal PVL 4170 (9) in lateral (A,B), anterior (C), posterior (D), dorsal (E) and 2966 ventral (F) views. Note part of this vertebra is reconstructed. Abbreviations: acdl = anterior 2967 centrodiapophyseal lamina, cprl = centroprezygapophyseal lamina, cpol = 2968 centropostzygapophyseal lamina, dp = diapophysis, hypa = hypapophysis, nc = neural canal, 2969 ns = neural spine, pcdl = posterior centrodiapophysesal lamina, pp = parapophysis, po = 2970 postzygapophysis, prcdf = prezygapophyseal centrodiapophyseal fossa, pocdf = 2971 postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina, 2972 pre = prezygapophysis, sdf = spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, 2973 spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = 2974 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol = 2975 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, stprl = single 2976 intrapostzygapophyseal lamina, vk = ventral keel. 2977



2978 2979 Figure 11: MACN-CH 4170 (10) dorsal vertebra in lateral (A,B) anterior (C), posterior (D), 2980 dorsal (E) and ventral (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, 2981 cdf = centrodiapophyseal fossa, cprl = centroprezygapophyseal lamina, dp = diapophysis, 2982 hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior 2983 centrodiapophyseal fossa, pp = parapophysis, po = postzygapophysis, prcdf = 2984 prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal 2985 fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf = 2986 spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, spol = 2987 spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = 2988 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol = 2989 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, stprl = single 2990 intrapostzygapophyseal lamina, vk = ventral keel.



2991 2992 Figure 12: Dorsal MACN-CH 4170 (11) in lateral (A,B) anterior (C), posterior (D), and dorsal 2993 (E) views. Note that the centrum is reconstructed, and a ventral view is therefore not given. 2994 Abbreviations: acdl = anterior centrodiapophyseal lamina, cdf = centodiapophyseal fossa, 2995 cpol = centropostzygapophyseal lamina, cprl = centroprezygapophyseal lamina, dp = 2996 diapophysis, hypa = hypapophysis, nc = neural canal, ns = neural spine, pcdl = posterior 2997 centrodiapophyseal lamina, pp = parapophysis, po = postzygapophysis, prcdf = 2998 prezygapophyseal centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal 2999 fossa, prdl = prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf = 3000 spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, spol = 3001 spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = 3002 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol = 3003 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, stprl = single

3004 intrapostzygapophyseal lamina, vk = ventral keel.



3005 3006 Figure 13: Dorsal MACN-CH 4170 (12) in lateral (A,B) anterior (C), posterior (D), ventral (E) 3007 and dorsal (F) views. Note that a large part of the posterior neural arch and spine is 3008 reconstructed. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl = 3009 centroprezygapophyseal lamina, dp = diapophysis, hypa = hypapophysis, nc = neural canal, 3010 ns = neural spine, pcdl = posterior centrodiapophyseal lamina, pp = parapophysis, po = 3011 postzygapophysis, prcdf = prezygapophyseal centrodiapophyseal fossa, pocdf = 3012 postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina, 3013 pre = prezygapophysis, sdf = spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, 3014 spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl = 3015 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol = 3016 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, stprl = single 3017 intrapostzygapophyseal lamina, vk = ventral keel. 3018



3019 3020 Figure 14: CT scan of PVL 4170 (13) in anterior (A), lateral (B,C) and posterior (D) views, with 3021 the shape of the internal pneumatic feature highlighted in light blue, in dorsal (E), ventral (F) 3022 lateral (G,H), anterior (I) and posterior (J) views.



- 3023 3024 Figure 15 (previous page): Dorsal MACN-CH 4170 (13) in lateral (A,B), anterior (C), dorsal (D), 3025 posterior (E) and ventral (F) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, 3026 cprl = centroprezygapophyseal lamina, dp = diapophysis, hypa = hypapophysis, nc = neural3027 canal, ns = neural spine, pcdl = posterior centrodiapophyseal lamina, pp = parapophysis, po 3028 = postzygapophysis, prcdf = prezygapophyseal centrodiapophyseal fossa, pocdf = 3029 postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina, 3030 pre = prezygapophysis, sdf = spinodiapophysal fossa, spof = spinopostzygapophyseal fossa, 3031 spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa,
- 3032 lat.spol/med.spol = lateral/medial spinopostzygapophyseal lamina, sprl =
- 3033 spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol =
- 3034 intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, stprl = single
- 3035 intrapostzygapophyseal lamina, vk = ventral keel.



- 3036 3037
- Figure 16: Dorsal MACN-CH 4170 (14) in lateral (A,B), posterior (C), anterior (D), and dorsal
- 3038 (E) views. Abbreviations: acdl = anterior centrodiapophyseal lamina, cprl =
- 3039 centroprezygapophyseal lamina, dp = diapophysis, hypa = hypapophysis, nc = neural canal,
- 3040 ns = neural spine, pp = parapophysis, po = postzygapophysis, prcdf = prezygapophyseal
- 3041 centrodiapophyseal fossa, pocdf = postzygapophyseal centrodiapophyseal fossa, prdl = 3042 prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf = spinodiapophysal
- prezygapophyseal diapophyseal lamina, pre = prezygapophysis, sdf = spinodiapophysal
 fossa, spof = spinopostzygapophyseal fossa, spol = spinopostzygapophyseal lamina, sprf =
- 3044 spinoprezygapophyseal fossa, sprl = spinoprezygapophyseal lamina, tprl =
- 3045 intraprezygapophyseal lamina, tpol = intrapostzygapophyseal lamina, lat.spol/med.spol =
- 3046 lateral/medial spinopostzygapophyseal lamina, stpol = single intrapostzygapophyseal
- 3047 lamina, stprl = single intrapostzygapophyseal lamina, vk = ventral keel.
- 3048





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3050	Figure 17: Dorsals PVL 4170 (15,16,17). PVL 4170 (15) in lateral, dorsal, anterior, posterior
3051	(oblique) view. PVL 4170 (16) in lateral and anterior view. PVL 4170 (17) in lateral view.
3052	Abbreviations: acdl = anterior centrodiapophyseal lamina, ali = aliform process, cprl =
3053	centroprezygapophyseal lamina, cpol = centropostzygapophyseal lamina, dp = diapophysis,
3054	hypa = hypapophysis, nc = neural canal, ns = neural spine, pp = parapophysis, po =
3055	postzygapophysis, prcdf = prezygapophyseal centrodiapophyseal fossa, pocdf =
3056	postzygapophyseal centrodiapophyseal fossa, prdl = prezygapophyseal diapophyseal lamina,
3057	pre = prezygapophysis, sdf = spinodiapophysal fossa, spof = spinopostzygapophyseal fossa,
3058	spol = spinopostzygapophyseal lamina, sprf = spinoprezygapophyseal fossa, sprl =
3059	spinoprezygapophyseal lamina, tprl = intraprezygapophyseal lamina, tpol =
3060	intrapostzygapophyseal lamina, stpol = single intrapostzygapophyseal lamina, stprl = single
3061	intrapostzygapophyseal lamina, vk = ventral keel.
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Figure 18: Upper row: All presacral vertebrae of MACN-CH 4170 (1-17) in left lateral view 3065 (not to scale). Lower row: all sacral vertebrae of PVL 4170 (18) sacrum. A: PVL 4170 (18.1-5) 3066 sacral neural arches and spines in right lateral view with dorsal PVL 4170 (17) on the right. B: 3067 PVL 4170 (18) in posterior view. C: PVL 4170 (18) associated with ilium PVL 4170 (34). D: 3068 Original drawing of PVL 4170 (Bonaparte, 1986b). Abbreviations: hypo = hyposphene, pre = 3069 prezygapophysis, post = postzygapophysis, spol = spinopostzygapophyseal lamina.



3070 3071

Figure 19: Anterior Caudals PVL 4170 (19-20-21) in lateral view.





Figure 20: Middle Caudals PVL 4170 (22-23-24) in lateral view.



- 3074 3075
- Figure 21: Caudal PVL 4170 (19) in lateral (A,B), posterior (C), anterior (D) and ventral (E)
- 3076 and dorsal (F) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
- 3077 postzygapophysis, pre = prezygapophysis, tv = transverse process.



- 3078 3079
- Figure 22: Caudal PVL 4170 (20) in lateral (A,B), posterior (C), anterior (D), dorsal (E) and 3080 ventral (F) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
- 3081 postzygapophysis, pre = prezygapophysis, tv = transverse process.



3082 3083 Figure 23: Caudal PVL 4170 (21) in lateral (A,B), posterior (C), anterior (D), ventral (E) and

- 3084 dorsal (F) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
- 3085 postzygapophysis, pre = prezygapophysis, tv = transverse process.
- 3086



3	0	8	7
~	~	\sim	~

3088	Figure 24: Caudal PVL 4170 (22) in lateral (A), dorsal (B), posterior (C), anterior (D) and
3089	ventral (E) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
3090	postzygapophysis, pre = prezygapophysis, tv = transverse process.



3092	9.0012		
3093	Figure 25: Caudal PVL 4170 (23) in lateral (A), dorsal (B), anterior (C), posterior (D) and		
2004	······································		

- 3094 ventral (E) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
- 3095 postzygapophysis, pre = prezygapophysis, tv = transverse process.
- 3096



3	0	9	7
0	v	-	

- 3098Figure 26: Caudal PVL 4170 (24) in lateral (A,B), posterior(C), anterior (D), dorsal (E) and
- 3099 ventral (F) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
- 3100 postzygapophysis, pre = prezygapophysis, tv = transverse process.
- 3101



3102	
3103	Figure 27: Caudal PVL 4170 (25) in lateral (A,B), ventral (C), anterior (D), posterior (E), and

- dorsal (F) views. Abbreviations: hypo = hyposphene, ns = neural spine, post =
- 3105 postzygapophysis, pre = prezygapophysis, tv = transverse process.
- 3106



3107 3108

Figure 28: Caudal PVL 4170 (26) in posterior (A), anterior (B), lateral (C,D), ventral (E), and 3109 dorsal (F) views. Abbreviations: ns = neural spine, post = postzygapophysis, pre = 3110 prezygapophysis, tv = transverse process.

3111



- 3112 3113 3114 3115 Figure 29: Caudal PVL 4170 (27) in dorsal (A), ventral (B), lateral (C,D), posterior (E), anterior (F) views.



- 3116 3117 3118 3119 Figure 30: Caudal PVL 4170 (30) in anterior (A), posterior (B), ventral (C), dorsal (D), lateral E,F) views.



3120 3121 3122 Figure 31: PVL 4170 (34) ilium in anterior (A) posterior (B) and lateral (C) view.



3123 3124 Figure 32: PVL 4170 (35) Pubis in lateral (A), distal (B), dorsal (C) and distal-most (D) view.

3125 Note that D is not to scale.

3126











Figure 35: Simplified phylogenetic tree based on Holwerda & Pol, (2018) (A), with posterior
dorsal vertebrae of *Tazoudasaurus, Barapasaurus, Cetiosaurus oxoniensis* and the Rutland *Cetiosaurus* showing possible analogous pneumatic features with *Patagosaurus* highlighted
in grey (B).

3144 Table 1: EI and aEI for several sauropod cervicals

Table 2: measurements of all presacral (1-17, blue), sacral (18, red), and caudal (19-30,

3147 green) vertebrae.

Tables

- Table 3: Measurements on appendicular elements of PVL 4170.