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***Xenoposeidon* is the earliest known rebbachisaurid sauropod dinosaur**

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Xenoposeidon proneneukos is a sauropod dinosaur represented by a single partial dorsal vertebra, NHMUK R2095, which consists of the centrum and the base of a tall neural arch. Despite its fragmentary nature, it is recognisably distinct from all other sauropods, and is here diagnosed with five unique characters. One character previously considered unique is here recognised as shared with *Rebbachisaurus garasbae*: an “M”-shaped arrangement of laminae on the lateral face of the neural arch. Following the more complete *Rebbachisaurus garasbae*, these laminae are now interpreted as ACPL and lateral CPRL, which intersect anteriorly; and PCDL and CPOL, which intersect posteriorly. Similar arrangements are also seen in some other rebbachisaurid specimens (though not all, possibly due to serial variation), but never in non-rebbachisaurid sauropods. *Xenoposeidon* is therefore referred to Rebbachisauridae. Due to its elevated parapophysis, the holotype vertebra is considered a posterior dorsal despite its elongate centrum. Since *Xenoposeidon* is from the from the Berriasian–Valanginian (earliest Cretaceous) Ashdown Beds Formation of the Wealden Supergroup of southern England, it is the earliest known rebbachisaurid by some 10 million years. Electronic 3D models were invaluable in determining *Xenoposeidon*'s true affinities: descriptions of complex bones such as sauropod vertebrae should always provide them where possible.

1 *Xenoposeidon* is the earliest known rebbachisaurid 2 sauropod dinosaur

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6 Abstract

7 *Xenoposeidon proneneukos* is a sauropod dinosaur represented by a single partial dorsal vertebra,
8 NHMUK R2095, which consists of the centrum and the base of a tall neural arch. Despite its
9 fragmentary nature, it is recognisably distinct from all other sauropods, and is here diagnosed
10 with five unique characters. One character previously considered unique is here recognised as
11 shared with *Rebbachisaurus garasbae*: an “M”-shaped arrangement of laminae on the lateral face
12 of the neural arch. Following the more complete *Rebbachisaurus garasbae*, these laminae are
13 now interpreted as ACPL and lateral CPRL, which intersect anteriorly; and PCDL and CPOL,
14 which intersect posteriorly. Similar arrangements are also seen in some other rebbachisaurid
15 specimens (though not all, possibly due to serial variation), but never in non-rebbachisaurid
16 sauropods. *Xenoposeidon* is therefore referred to Rebbachisauridae. Due to its elevated
17 parapophysis, the holotype vertebra is considered a posterior dorsal despite its elongate centrum.
18 Since *Xenoposeidon* is from the from the Berriasian–Valanginian (earliest Cretaceous) Ashdown
19 Beds Formation of the Wealden Supergroup of southern England, it is the earliest known
20 rebbachisaurid by some 10 million years. Electronic 3D models were invaluable in determining
21 *Xenoposeidon*'s true affinities: descriptions of complex bones such as sauropod vertebrae should
22 always provide them where possible.

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23 Introduction

24 *Xenoposeidon proneneukos* is a neosauropod sauropod dinosaur from the Berriasian–Valanginian
25 (earliest Cretaceous) Ashdown Beds Formation of the Wealden Supergroup of southern England.
26 It is represented by a single partial mid-to-posterior dorsal vertebra, NHMUK R2095 (BMNH
27 R2095 at the time of the original description by Taylor and Naish 2007). This element consists of
28 the centrum and the base of a tall neural arch, broken off below the transverse processes and
29 zygapophyses. Despite its fragmentary nature, it is recognisably different from all other
30 sauropods, and Taylor and Naish (2007) diagnosed it on the basis of six characters that they
31 considered unique among sauropods.

32 D’Emic (2012:651) asserted that “the absence of diagnostic features renders *Xenoposeidon* a
33 nomen dubium”. However, his assessment was mistaken in several respects. For example, the
34 extension of the base of the neural arch to the posterior extremity of the centrum is clearly not, as
35 he asserted, due to damage. D’Emic claimed that dorsal vertebrae illustrated by Osborn and
36 Mook (1921:plates LXIX and LXXII) have forward-sloping neural arches resembling those of
37 *Xenoposeidon*: in reality, only one posterior dorsal vertebrae out of four complete dorsal columns
38 illustrated in that monograph shows a forward slope, and it differs so much from its fellows that
39 this can only be interpreted as the result of crushing. D’Emic further claimed that the lamina
40 patterns observed in *Xenoposeidon* can be recognised in other sauropods, but I have been unable
41 find morphology resembling them in the descriptions he suggests: Osborn and Mook 1921 for
42 *Camarasaurus*, Riggs 1903 for *Brachiosaurus* (probably a typo for Riggs 1904, which also does
43 not depict similar patterns), Carballido et al. 2011 for *Tehuelchesaurus*. A similar pattern does
44 appear in *Rebbachisaurus*, as will be discussed below. D’Emic (2012:651) is probably correct
45 that the “asymmetric neural canal” described by Taylor and Naish (2007:1553–1554) is a
46 misreading of the tall centroprezygapophyseal fossae as being the anterior portion of the neural
47 canal: as Taylor and Naish pointed out, “The vacuity is filled with matrix, so the extent of its
48 penetration posteriorly into the neural arch cannot be assessed”. Nevertheless, the shape and size
49 of the fossa is unique among sauropods, and it is bounded by laminae which do not seem to be
50 medial CPRLs. In summary, *Xenoposeidon proneneukos* is a valid, diagnosable taxon, *contra*
51 D’Emic (2012).

52 Taylor and Naish (2007:1554–1557) compared the *Xenoposeidon* vertebra to those of the main
53 neosauropod groups — Diplodocoidea, Camarasauridae, Brachiosauridae and Titanosauria —
54 and concluded that it could not be convincingly referred to any of these groups. Their
55 phylogenetic analysis (pp. 1157–1558 and figure 6) corroborated this by recovering
56 *Xenoposeidon* as a neosauropod in all most parsimonious trees, but in a polytomy with all other
57 neosauropods, wholly unresolved save that the clade Flagellicaudata was preserved in all MPTs.

58 In light of Wilson and Allain’s (2015) redescription of *Rebbachisaurus garasbae*, and the
59 availability of more photographs and models of rebbachisaurid material, it has now become
60 possible to reinterpret the idiosyncratic system of laminae found in *Xenoposeidon*, and to refer it
61 confidently to an existing family-level clade.

62 Anatomical Abbreviations

- 63 • aEI — average elongation index *sensu* Chure et al. 2010: length of a centrum divided by
64 the average of the height and width of the posterior articular surface.

- 65 • ACPL — anterior centroparapophyseal lamina.
- 66 • CPOL — centropostzygapophyseal lamina.
- 67 • CPRF — centroprezygapophyseal fossa.
- 68 • CPRL — centroprezygapophyseal lamina.
- 69 • EI — elongation index *sensu* Wedel et al. 2000: length of a centrum divided by the height
- 70 of the posterior articular surface.
- 71 • PCDL — posterior centrodiapophyseal lamina.
- 72 • PCPL — posterior centroparapophyseal lamina.
- 73 • POSL — postspinal lamina.
- 74 • Postzyg — postzygapophysis.
- 75 • PPDL — paradiapophyseal lamina.
- 76 • Prezyg — prezygapophysis.
- 77 • PRPL — prezygaparapophyseal lamina.
- 78 • PRSL — prespinal lamina.
- 79 • SDL — spinodiapophyseal lamina.

80 Institutional Abbreviations

- 81 • IWCMS — Isle of Wight County Museum Service at Dinosaur Isle, Sandown, Isle of
- 82 Wight, England.
- 83 • MIWG — Museum of Isle of Wight Geology (now Dinosaur Isle Visitor Centre),
- 84 Sandown, Isle of Wight, England.
- 85 • MNHN — Muséum National d'Histoire Naturelle, Paris, France.
- 86 • NHMUK — the Natural History Museum, London, England.
- 87 • NMC — Canadian Museum of Nature (previously National Museum of Canada), Ottawa,
- 88 Ontario, Canada.
- 89 • “WN” — “without number”, an informal designation for specimens awaiting accession.

90 Reinterpretation

91 Taylor and Naish’s (2007) history, geography, geology and description of the *Xenoposeidon*
92 specimen requires no revision, and should continue to be considered definitive: this paper does
93 not supersede it, but should be read in conjunction with it.

94 The illustrations of the specimen in the original paper, however, were in monochrome and
95 omitted the dorsal and ventral views. The present paper supplements these illustrations with a
96 colour depiction from all six cardinal directions (Figure 1), and a high-resolution 3D model of the
97 specimen (supplementary file AA).

98 More importantly, Taylor and Naish’s (2007) interpretation of some features of the vertebra,
99 particularly the “M”-shaped complex of laminae on the lateral faces of the neural arch, was
100 mistaken. Although the neural spine and dorsal part of the neural arch are missing, including the
101 pre- and postzygapophyses and lateral processes, they wrote that “sufficient laminae remain to
102 allow the positions of the processes to be inferred with some certainty”. But their inferences were
103 incorrect. Taylor and Naish (2007:1553) interpreted the cross-shaped structure on the
104 anterodorsal part of the left lateral face of the neural arch as the site of the parapophysis, despite
105 the lack of any articular facet in that location. This influenced their interpretation of the four
106 laminae that met at that point as the ACPL below, the PPDL above, the PRPL anteriorly and an

107 unnamed accessory infraparapophyseal lamina posteroventrally, which they interpreted as
108 homologous with a PCPL (Figure 2A). Similarly, they did not attempt to identify either the long
109 lamina running up the posterior edge of the lateral face of the neural arch (designating it only
110 “posterior lamina”) or the lamina forming a shallow “V” with the “accessory infraparapophyseal
111 lamina”, simply calling it an “accessory postzygapophyseal lamina” (Figure 2A)

112 Among the various unusual features of the *Xenoposeidon* vertebra, the “M”-shaped set of laminae
113 is immediately apparent in lateral view (Figure 3A): a line can be traced from the anterior margin
114 of the neural arch’s lateral face up the ACPL to the cross that was interpreted as the parapophysis,
115 then posteroventrally down the “accessory infraparapophyseal lamina”, then posterodorsally up
116 the “accessory postzygapophyseal lamina” and finally down the posterior margin of the neural
117 arch’s lateral face, along the “posterior lamina”. Photographs of other specimens that were
118 available to us at this time did not apparently manifest similar features.

119 But subsequent work on *Rebbachisaurus garasbae* (Wilson 2012:100, Wilson and Allain 2015)
120 — and an associated video of the rotating vertebra (see acknowledgements) — show that
121 *Rebbachisaurus* has a similar complex of laminae (Figure 3B), which are described by Wilson
122 and Allain (2015:6) as the second of the eight autapomorphies that they listed for the species:
123 “infrazygapophyseal laminae (lat. CPRL, CPOL) that intersect and pass through neighbouring
124 costal laminae (ACPL, PCDL) to form an ‘M’ shape”.

125 Because the illustrated dorsal vertebra of *Rebbachisaurus* — MNHN MRS 1958 — is
126 substantially complete, it is possible to follow the trajectories of the laminae that participate in
127 the “M” to their apophyses, and so determine their true identities. The two vertically oriented
128 laminae — the outer pillars of the “M” — continue up past the top of the “M”. The anterior one
129 supports the parapophysis, and the posterior supports the diapophysis. And the two laminae that
130 form the valley in the middle of the “M” support the prezygapophyses and postzygapophyses: in
131 both cases, as noted by Wilson and Allain, they intersect the vertical lamina before continuing to
132 meet their respective zygapophyses. The four laminae that make up the “M”, from anterior to
133 posterior, are therefore the ACPL, posterior part of the lateral CPRL, anterior part of the CPOL
134 and PCDL. Of these, the intersection between the ACPL and lateral CPRL is clearly visible in left
135 lateral view of MNHN MRS 1958. The intersection between the CPOL and PCDL is less
136 apparent in this view, though clear in three dimensions. Both laminae continue dorsally beyond
137 this intersection, but their paths are somewhat changed at the point of contact, with the dorsal
138 portion of the PCDL inclining more anteriorly, and the rod-like CPOL apparently passing through
139 the sheet of bone formed by the PCDL to meet the postzygapophysis.

140 The referred *Rebbachisaurus garasbae* specimen NMC 50844 described and illustrated by
141 Russell (1996:388–390 and figure 30) is also broadly consistent with this morphology. It is not
142 possible to be definite about the laminar intersection based only on line drawings of the specimen
143 from the four cardinal directions, but, as illustrated in Russell’s figure 30c, the lateral CPRL does
144 appear to pass through the ACPL. The CPOL seems in this specimen to originate posterior to the
145 PCDL, not intersecting with it. But this difference from the holotype dorsal may be serial
146 variation since, as Russell notes, the relatively longer centrum of his specimen indicates a more
147 anterior serial position than for the holotype’s dorsal vertebra; and this interpretation is
148 corroborated by the observation than, based on lamina trajectories, the anteroposterior distance
149 between the parapophysis and diapophysis was less in NMC 50844 than in the holotype.

150 In light of these *Rebbachisaurus* specimens, the mysterious laminae of *Xenoposeidon* are easily
151 explained. It is now apparent that the cross on the side of the *Xenoposeidon* vertebra is not the
152 site of the parapophysis, as Taylor and Naish (2007:1553) proposed, but merely the intersection

153 of two laminae that pass right through each other: the ACPL, running dorsolaterally, and the
154 lateral CPRL, extending anterodorsally to the (missing) prezygapophysis (Figure 2B). Similarly,
155 the “posterior lamina” is the PCDL, and it intersects with the CPOL, though the intersection is
156 lost in NHMUK R2095 (Figure 2B). Both the parapophysis and diapophysis of the *Xenoposeidon*
157 vertebrae would have been located some distance above the preserved portion, the former
158 anterior to the latter.

159 It appears from Dalla Vecchia (1999:figure 47, left part) that in the holotype and only vertebra of
160 *Histriasaurus boscarollii*, “WN-V6”, the CPOL on the right side of the vertebra intersects with
161 the PCDL in the same way as in *Rebbachisaurus*, though it is not possible to determine whether
162 the lateral CPRL similarly intersects the ACPL. Dorsal vertebrae of other rebbachisaurid
163 sauropods, however, do not appear to feature the distinctive “M” and intersecting laminae of
164 *Rebbachisaurus* and *Xenoposeidon*:

- 165 • The 3D model of a dorsal vertebra of *Nigersaurus* (Serenó et al. 2007) shows that the
166 lateral CPRLs originate anterior to the ACPLs and the CPOLs posterior to the PCDLs, so
167 that there is no intersection. A subtle “V” shape does appear high up on the lateral faces of
168 the neural arch, between the ACPL and the PCDL, but it seems unrelated to the lateral
169 CPRL and CPOL.
- 170 • Unpublished 3D models of an anterior dorsal neural arch and a more posterior dorsal
171 vertebra of *Katpensaurus* (pers. comm., Lucio M. Ibiricu) as illustrated in figures 3A and
172 5A of Ibiricu et al. (2017) show that in both vertebrae, the lateral CPRLs originate anterior
173 to the ACPLs, and the CPOLs seem to originate posterior to the PCDLs — though
174 damage to the posterior portion makes the latter uncertain.
- 175 • The laminae do not appear to intersect in the illustrated dorsal vertebra of
176 *Demandasaurus* (Fernández-Baldor et al. 2011:figure 9).
- 177 • The sole known vertebra of *Nopcsaspondylus* seems to have an entirely different pattern
178 of lamination (Mannion 2010:figure 5) with no lamina intersections like those of MNHN
179 MRS 1958.

180 No determination can be made for other rebbachisaurids as they are insufficiently preserved (e.g.
181 *Limaysaurus*, *Amazonsaurus*), or illustrated (e.g. *Cathartesaura*), or simply lack posterior dorsal
182 vertebral material (e.g. *Rayososaurus*, *Tataouinea*, *Comahuesaurus*, *Zapalasaurus*).

183 However, we cannot rule out the possibility that complete and well-preserved posterior dorsal
184 vertebrae of most or all rebbachisaurids have *Rebbachisaurus*-like intersecting laminae: even in
185 those species for which a well-preserved vertebra lacks them, this could be due to serial variation,
186 with these features only fully developing in the most posterior dorsals.

187 *Xenoposeidon*, then, resembles *Rebbachisaurus* in the possession of a distinctive “M” on the
188 lateral face of the neural arch, in the intersecting lateral CPRL and ACPL, and in the elevation of
189 the parapophysis above the level of the prezygapophysis — a complex of related features.
190 Although at first glance they appear rather different, *Xenoposeidon* and *Rebbachisaurus*, while
191 geometrically different, are topologically similar.

192 Regarding the significance of the elevated parapophysis, since no complete or nearly complete
193 rebbachisaurid dorsal column has been described, comparisons with other, better represented
194 sauropods are warranted. In the probable basal diplodocoid *Haplocanthosaurus*, the dorsal
195 margin of the parapophyseal facet reaches the level of, and is coincident with, the
196 prezygapophyseal facet around dorsal vertebra 7 or 8, but never rises any higher than this in more

197 posterior vertebrae (Hatcher 1903:plate I). In the more distantly related diplodocid diplodocoids
198 *Apatosaurus* and *Diplodocus*, the parapophysis never migrates far enough dorsally to reach a
199 position level with the prezygapophyses, even in the most posterior dorsals (Gilmore 1936:plate
200 XXV; Hatcher 1901:plates VII, VIII).

201 Taylor and Naish (2007:1554) argued that *Xenoposeidon* could not at that time be convincingly
202 referred to Rebbachisauridae because *Rebbachisaurus* differs from NHMUK R2095 in five ways:
203 “possession of a very prominent PCPL, large and laterally diverging prezygapophyses,
204 depressions at the base of the neural arch (Bonaparte 1999:173), lateral foramina not set within
205 fossae, and a strongly arched ventral border to the centrum.” Of these features, the first is now
206 recognised as occurring in *Xenoposeidon*; the second appears to be an outright error, as the
207 prezygapophyses of *Rebbachisaurus* meet on the midline, and in any case the situation in
208 *Xenoposeidon* is not known. “Depressions at the base of the neural arch” seems to be a
209 mistranslation of Bonaparte’s original Spanish, “profundas depresiones en la base de la espina
210 neural”, which refers not to the neural arch but the neural spine, and since this portion is not
211 preserved in *Xenoposeidon*, it is not informative for our purposes. The 3D model of the
212 *Rebbachisaurus* dorsal shows that in fact its lateral foramina are set in shallow depression,
213 similar in quality if not in degree to those of *Xenoposeidon*. This leaves the stronger arching of
214 the ventral border of the centrum in *Rebbachisaurus*, a feature that in isolation is not convincing.

215 In conclusion, the weight of morphological evidence supports including *Xenoposeidon* within
216 Rebbachisauridae. This is in accordance with the observation of Taylor and Naish (2007:1557), in
217 whose phylogenetic analysis “various most-parsimonious trees also recover *Xenoposeidon* in
218 many other positions, including as a ... rebbachisaurid.”

219 Serial position

220 The serial position of the *Rebbachisaurus garasbae* holotype dorsal vertebra MNHN MRS 1958
221 is not definitely known. However, it has been uniformly referred to as a posterior dorsal, most
222 likely due to the very elevated position of its parapophyses and Lavocat’s (1954) initial
223 assessment of it as “une des dernières dorsales” (one of the last dorsals) — perhaps made with
224 knowledge of the spatial relation of bones in the quarry.

225 The position of the *Xenoposeidon proneneukos* holotype vertebra NHMUK R2095 is of course
226 even more difficult to determine in light of the limited nature of the specimen, though its
227 similarity to MNHN MRS 1958 suggests a similar position. Taylor and Naish (2007:1553) wrote
228 that “the high position of the parapophysis on the neural arch of R2095 indicates a mid to
229 posterior placement of the vertebra within the dorsal column, but, because the prezygapophyses
230 must have been dorsal to it, it was probably not among the most posterior vertebrae in the
231 sequence.” With the location of the parapophysis now interpreted as significantly higher than
232 previously thought, and probably well above the prezygapophysis, an even more posterior
233 position is indicated.

234 This posterior serial position is surprising in light of the anteroposterior length of the
235 *Xenoposeidon* centrum. Its posterior articular surface measures 160 mm high by 170 mm wide,
236 while the length of even the preserved portion of the centrum is 190 mm, and it must have been at
237 least 200 mm long when complete (Taylor and Naish 2007:table 1). As noted by Taylor and Naish
238 (2007:1554), “the length of the centrum, especially in so posterior a dorsal vertebra, argues
239 against [a diplodocoid identity]: the posterior dorsal centra of diplodocoids typically have $EI <$
240 1.0, compared with 1.25 for R2095” — or 1.21 using the aEI of Chure et al. (2010:384).
241 However, rebbachisaurids may be unusual among diplodocoids in this respect — perhaps

242 unsurprisingly, as they diverged early from the line leading to diplodocids, with their
243 characteristically short dorsal centra, and likely retained something more similar to the ancestral
244 neosauropod condition. Wilson and Allain (2015:8) give the centrum measurements of MNHN
245 MRS 1958 as posterior height 231 mm, posterior width 220 mm and length 220 mm. This yields
246 an aEI of 0.98, meaning that the *Xenoposeidon* centrum is only 24% more elongate than that of
247 *Rebbachisaurus*. This is a significant difference, but not an outlandish one. For comparison, the
248 centrum of the basal rebbachisaurid *Histriasaurus boscarollii* holotype “WN-V6” is relatively
249 elongate, with its posterior articular surface measuring 150 mm high and centrum length of “more
250 than 200 mm” (Dalla Vecchia 1998:122) yielding an EI of > 1.33. Also, the aEIs of the last four
251 dorsal vertebrae of the *Brachiosaurus altithorax* holotype FMNH PR 25107 are 1.34, 1.27, 1.19
252 and 0.96 (calculated from the table of Riggs 1904:34): so aEIs of sauropod dorsals can vary,
253 within two serial positions of the same individual, from values below that of MNHN MRS 1958
254 to above that of NHMUK R2095.

255 In conclusion, while the evidence regarding the serial position of NHMUK R2095 remains
256 equivocal, it suggests a more posterior position than previous inferred — it can be fairly
257 confidently described as “posterior” rather than “mid-to-posterior” — but it is unlikely to be the
258 very last dorsal.

259 Revised Reconstruction

260 In light of the reassignment of *Xenoposeidon* to Rebbachisauridae, and the reinterpretation of its
261 laminae, I present a new reconstruction of how the vertebra NHMUK R2095 might have looked
262 when complete (Figure 4). As in MNHN MRS 1958, the parapophysis and diapophysis are both
263 elevated above the zygapophyses. The lateral CPRL and ACPL meet at a point where they
264 project outwards about the same distance from the vertebra, as is apparent from the preserved
265 portion of the vertebra; but the CPOL is assumed to pass through a sheet-like PCDL as in
266 *Rebbachisaurus*, because it is clear from breakage in NHMUK R2095 that the PCDL extended
267 further from the body of the neural arch than the preserved portion indicates. The neural spine,
268 composed as in *Rebbachisaurus* of pre- and post-spinal laminae together with the left and right
269 SDLs, is shown fading out at the top, as there is no way to determine its height. The condyle that
270 is the centrum’s anterior articular surface is reconstructed as only slightly convex, as in
271 *Rebbachisaurus*.

272 It is instructive to compare this with the original reconstruction of the vertebrae (Taylor and
273 Naish:figure 5). The new reconstruction has a taller neural arch, a far more elevated
274 parapophysis, a more posteriorly located diapophysis (no longer dorsal to the parapophysis) and a
275 shallower condyle, as that of the original reconstruction was drawn with those of brachiosaurs in
276 mind.

277 Systematic Palaeontology

278 Dinosauria Owen, 1842
279 Saurischia Seeley, 1888
280 Sauropodomorpha Huene, 1932
281 Sauropoda Marsh, 1878
282 Neosauropoda Bonaparte, 1986
283 Rebbachisauridae Sereno et al., 1999
284 *Xenoposeidon* Taylor and Naish, 2007

285 *Xenoposeidon proneneukos* Taylor and Naish, 2007

286 **Holotype.** NHMUK R2095, the Natural History Museum, London. A mid posterior dorsal
287 vertebra consisting of partial centrum and neural arch.

288 **Revised diagnosis:** Differs from all other sauropods in the following characters:

- 289 1. neural arch covers dorsal surface of centrum, with its posterior margin continuous with
290 that of the centrum;
- 291 2. neural arch slopes anteriorly 35 degrees relative to the vertical;
- 292 3. broad, flat area of featureless bone on lateral face of neural arch;
- 293 4. very large, teardrop-shaped centroprezygapophyseal fossa.
- 294 5. arched laminae form vaulted boundary of centroprezygapophyseal fossa.

295 The “arched laminae” of #5 are not the medial CPRLs, as these arise from the neural arch
296 pedicels — and the laminae arising from the pedicels cannot instead be regarded lateral CPRLs,
297 as those laminae are located on the lateral face of the neural arch, intersecting with the ACPLs.
298 Furthermore, the point where the supporting laminae meet at the top of their arch is located some
299 way posterior to the inferred location of the prezygapophyses (Figure 5).

300 Discussion

301 Age

302 As shown by the Wilson and Allain (2015:table 1), the 19 then-recognised rebbachisaurids (of
303 which 13 had been named) span the middle third of the Cretaceous. The earliest recognised taxon
304 is *Histriasaurus boscarollii* from the upper Hauterivian or lower Barremian limestones of
305 southwest Istria, Croatia. Seven taxa, of which five are named, survived at least to the
306 Cenomanian (earliest Late Cretaceous), of which two (*Katepensaurus goicoecheai* and
307 *Limaysaurus tessonei*) may be from the Turonian age.

308 As discussed by Taylor and Naish (2007:1547–1548), the precise location and horizon where
309 NHMUK R2095 was excavated was not recorded in the specimen’s original brief description,
310 which only said “the Wealden of Hastings” (Lydekker 1893:276). However, records of the
311 collection of Philip James Rufford, who collected the specimen, indicate that the most likely
312 location is Ecclesbourne Glen, a mile or two east of Hastings, East Sussex (see discussion in
313 Taylor and Naish 2007:1548). The units exposed at Ecclesbourne Glen are part of the Ashdown
314 Beds Formation, which straddles the Berriasian/Valanginian boundary; but the part of the
315 formation at that location is from the earlier Berriasian age. If this assessment is correct, then
316 *Xenoposeidon* is from the very earliest Cretaceous, giving it an age of around 140 million years
317 — about 10 million years earlier than *Histriasaurus*.

318 This early age is consonant with a basal position within Rebbachisauridae, a possibility that is
319 corroborated by *Xenoposeidon*’s camerate internal morphology compared with the camellate
320 centra of most rebbachisaurids. However, further material will be required before numerical
321 phylogenetic work can firmly establish its position within the group.

322 Wealden Rebbachisaurids

323 Although *Xenoposeidon* is the first named Rebbachisaurid from the Wealden Supergroup of
324 southern England, other material from this unit has been referred to Rebbachisauridae. Naish and
325 Martill (2001:plate 36, opposite page 236) illustrated some isolated sauropod teeth
326 IWCMS.2001.201–203, and these were referred to Rebbachisauridae by Sereno and Wilson
327 (2005:174). Mannion (2009) described a partial rebbachisaurid scapula MIWG 6544. Finally,
328 Mannion et al. (2011) described a proximal caudal neural arch MIWG 5384, which they also
329 interpreted as rebbachisaurid. All of these specimens are from the Barremian Wessex Formation
330 of the Isle of Wight, so they could all belong to the same species or genus. However, since the
331 likely Berriasian age of NHMUK R2095 makes it 10–15 Mya older than these specimens, it is
332 unlikely that they belong to *Xenoposeidon*, but to some other as yet-unnamed rebbachisaurid.
333 Thus it is likely that the Wealden Supergroup contains at least two rebbachisaurid sauropods.

334 3D models of complex bones

335 Electronic 3D models were invaluable in determining *Xenoposeidon*'s true affinities. Most
336 obviously, the model of the *Xenoposeidon* vertebra itself, created by Heinrich Mallison, has
337 functioned as an invaluable proxy for the fossil itself when I am unable to visit the NHMUK, and
338 I have consulted it many times in writing this paper. I would also have been unable to determine
339 to my own satisfaction whether the *Katepensaurus* dorsals feature intersecting laminae like those
340 of *Rebbachisaurus* without the models provided by Lucio M. Ibiricu. Although no true model is
341 available for the *Rebbachisaurus* dorsal itself or for the dorsal vertebrae of *Nigersaurus*, rotating
342 videos were crucial in enabling me to understand their morphology. When interpreting specimens
343 for which no such models exist, such as Russell's (1996) referred *Rebbachisaurus* specimen
344 NMC 50844, the conclusions reached using only 2D representations — whether photographs or
345 drawings — are much less well founded.

346 Techniques such as photogrammetry (see e.g. Falkingham 2012; Mallison and Wings 2014) are
347 reducing the barriers to the creation of high-quality 3D models in full colour. Doing so is now
348 inexpensive in both time and money. In light of our discipline's goal of making palaeontology
349 more accessible and reproducible, then, it should become increasingly routine in the 21st Century
350 to provide 3D models as a standard part of the description of complex bones such as sauropod
351 vertebrae.

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353 I thank Sandra D. Chapman (Natural History Museum, London) for access to the *Xenoposeidon*
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355 3D model of NHMUK R2095 and talking me through aspects of photogrammetry. I am also
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357 Naturelle, Paris) for sharing high-resolution photographs of the French *Rebbachisaurus* vertebra,
358 and to Mathew J. Wedel (Western University of Health Sciences) and Darren Naish (University
359 of Southampton) for helpful discussion. Lucio M. Ibiricu kindly provided access to unpublished
360 3D models of an anterior dorsal neural arch and a more posterior dorsal vertebra of
361 *Katepensaurus*.

362 As noted in Taylor (2015), this project began when I recognised the true identity of the curious
363 laminae on the *Xenoposeidon* vertebra while viewing a rotating video of the *Rebbachisaurus*
364 *garasbae* holotype dorsal vertebra MNHN MRS 1958 on the University of Michigan Museum of

365 Paleontology's UMORF web-site (University of Michigan Online Repository of Fossils) at
366 <https://umorf.ummp.lsa.umich.edu/wp/gallery/vertebrate-animations/>. This video was based on a
367 3D reconstruction created from CT scans performed at the AST-RX (Accès Scientifique à la
368 Tomographie à Rayons X) of the MNHN by F. Goussard.

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474 **Figure Captions**

- 475 **Figure 1.** NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, shown
476 from all six cardinal directions. Top row: **A.** dorsal view, with anterior to the left. Middle row, left
477 to right: **B.** anterior, **C.** left lateral, **D.** posterior and **E.** right lateral view. Bottom row: **F.** ventral
478 view, with anterior to the left. Scale bar = 200 mm.
- 479 **Figure 2.** NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left
480 lateral view, with interpretative drawing. **A.** The incorrect interpretation of the laminae from
481 Taylor and Naish (2017:figure 4A), with identifying captions greyed out since they are largely
482 incorrect. **B.** The revised interpretation of the same laminae, based on the similar arrangement in
483 *Rebbachisaurus garasbae*. Scale bar = 200 mm.
- 484 **Figure 3.** Centra and neural arches of posterior dorsal vertebrae from two rebbachisaurid
485 sauropods (not to scale), highlighting the distinctive “M” shape formed by laminae high on the

486 neural arch. **A.** NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*.
487 **B.** MNHN MRS 1958, a posterior dorsal vertebra from the holotype specimen of *Rebbachisaurus*
488 *garasbae*.

489 **Figure 4.** NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left
490 lateral view, interpreted as a rebbachisaurid. This interpretation is modelled primarily on MNHN
491 MRS 1958, a posterior dorsal vertebra from the holotype specimen of *Rebbachisaurus garasbae*.
492 The CPOL passes through a sheetlike PCDL, as in *Rebbachisaurus*; but the lateral CPRL forms a
493 cross-shaped junction with the ACPL, each of these laminae equally interrupting the trajectory of
494 the other. Abbreviations as used in the text. Scale bar = 200 mm.

495 **Figure 5.** NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left
496 anteroventrolateral view, highlighting the three sets of laminae related to the prezygapophyses.
497 The trajectories of the medial CPRLs (which emerge from the neural arch pedicels) and the
498 lateral CPRLs (which intersect with the APCLs) indicate the approximate position of the
499 prezygapophyses. The additional arched laminae form the margins of the large, teardrop-shaped
500 CPRF, but meet at a position some way below and posterior to the presumed location of the
501 prezygapophyseal facets. Breakage of both medial CPRLs and the left ACPL and PCDL is
502 indicated by cross-hatching. Note that, from this perspective, the lateral CPRL appears to turn a
503 corner where it intersects with the ACPL, such that the posteroventral portion of the lateral CPRL
504 appears contiguous with the dorsal portion of the ACPL. This is an illusion brought about by the
505 eminence at the point of intersection. As always, this is much easier to see in three dimensions.
506 Abbreviations as used in the text.

507 **Supplementary Files**

508 **Supplementary file 1.** Three-dimensional surface model (11 million polygons) of NHMUK
509 R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*. A 3D polygon mesh file
510 was created by Heinrich Mallison in Agisoft Photoscan Pro version 1.3.0 (agisoft.com), from 95
511 high resolution digital photographs by the author. All 95 images aligned, and resulted in a dense
512 point cloud at maximum resolution of 20,900,043 points and 44,871,128 polygons. Scaling was
513 based on a single 10 cm scale bar created from a high quality scale bar placed in the pictures with
514 the specimen. Available from <https://doi.org/10.6084/m9.figshare.5605612.v2>

Figure 1

NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, shown from all six cardinal directions.

Figure 1. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, shown from all six cardinal directions. Top row: **A.** dorsal view, with anterior to the left. Middle row, left to right: **B.** anterior, **C.** left lateral, **D.** posterior and **E.** right lateral view. Bottom row: **F.** ventral view, with anterior to the left. Scale bar = 200 mm.

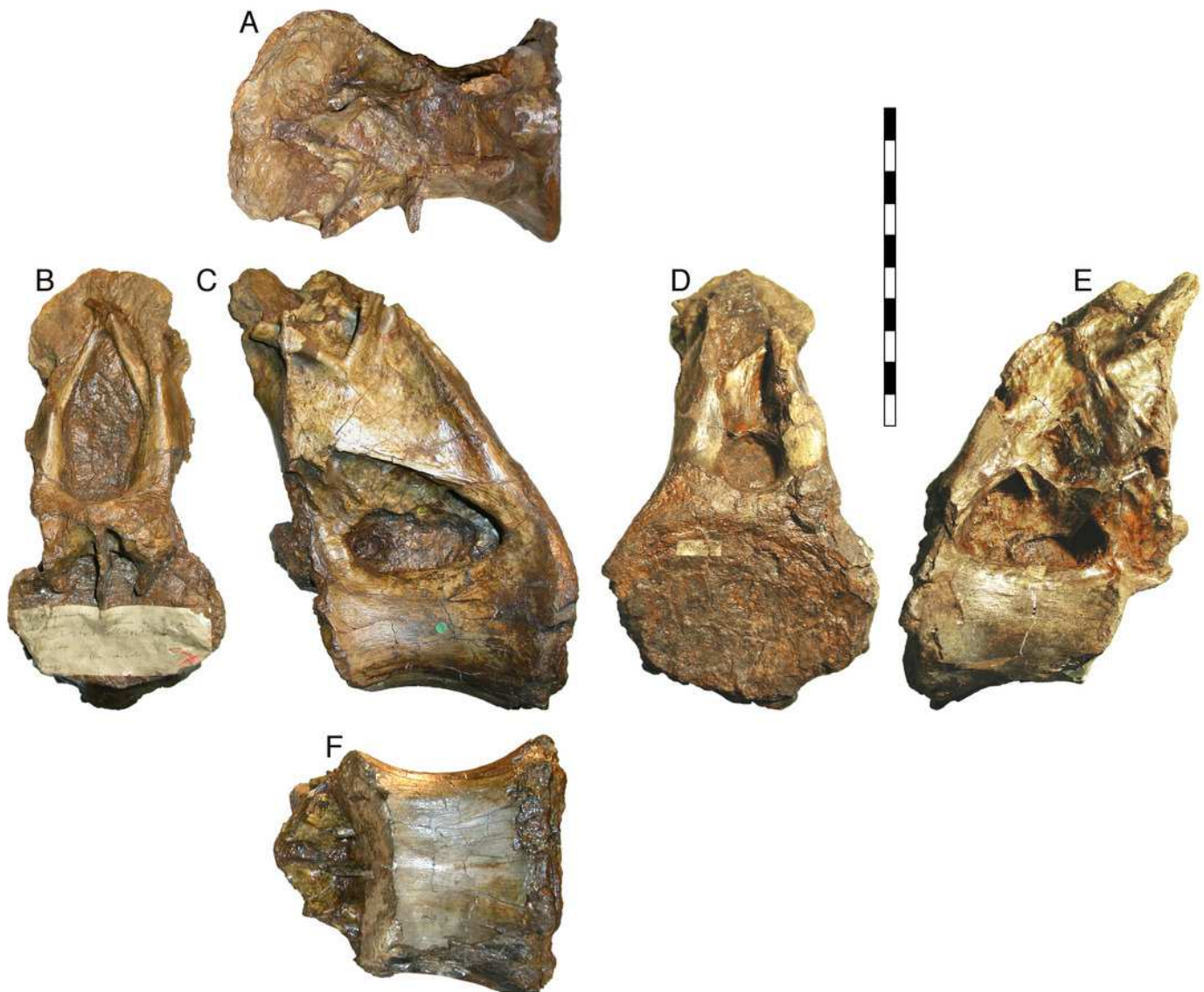


Figure 2

Figure 2. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left lateral view, with interpretative drawing.

Figure 2. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left lateral view, with interpretative drawing. **A.** The incorrect interpretation of the laminae from Taylor and Naish (2017:figure 4A), with identifying captions greyed out since they are largely incorrect. **B.** The revised interpretation of the same laminae, based on the similar arrangement in *Rebbachisaurus garasbae*. Scale bar = 200 mm.

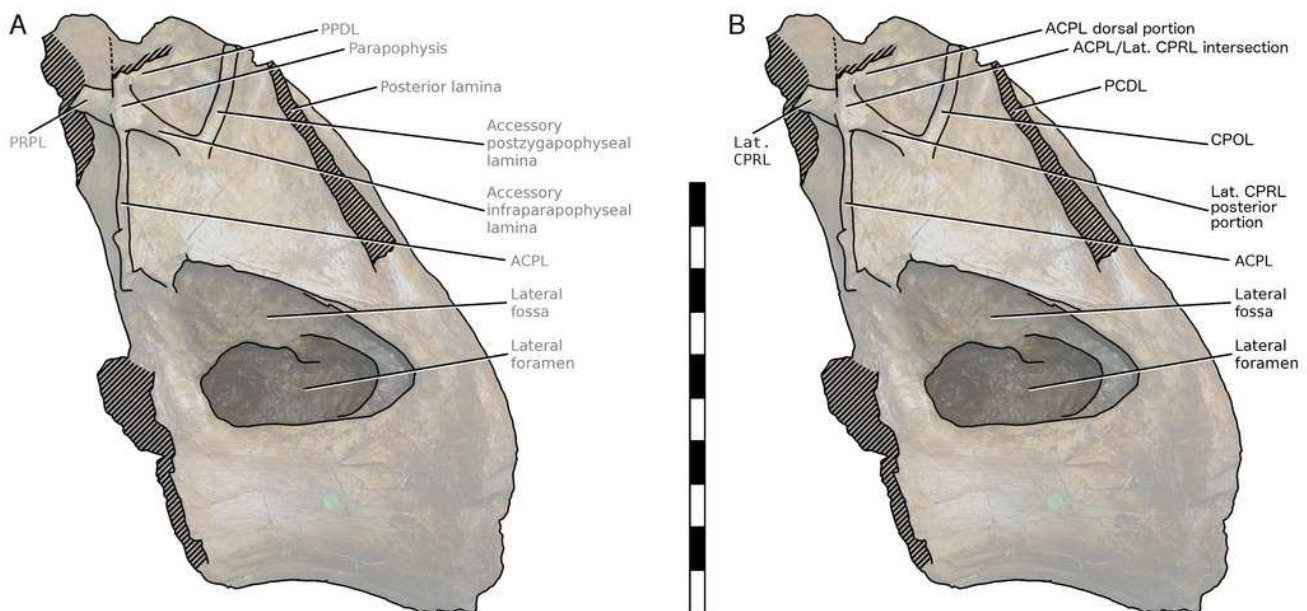


Figure 3

Figure 3. Centra and neural arches of posterior dorsal vertebrae from two rebbachisaurid sauropods (not to scale), highlighting the distinctive “M” shape formed by laminae high on the neural arch.

Figure 3. Centra and neural arches of posterior dorsal vertebrae from two rebbachisaurid sauropods (not to scale), highlighting the distinctive “M” shape formed by laminae high on the neural arch. **A.** NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*. **B.** MNHN MRS 1958, a posterior dorsal vertebra from the holotype specimen of *Rebbachisaurus garasbae*.

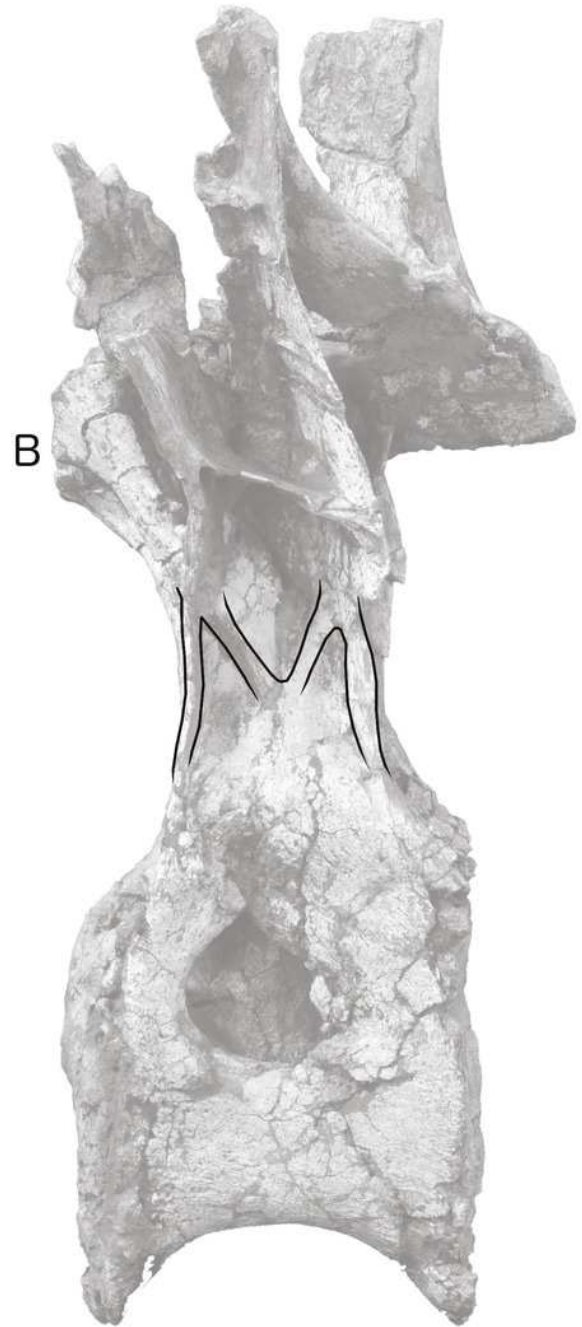


Figure 4

Figure 4. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left lateral view, interpreted as a rebbachisaurid.

Figure 4. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left lateral view, interpreted as a rebbachisaurid. This interpretation is modelled primarily on MNHN MRS 1958, a posterior dorsal vertebra from the holotype specimen of *Rebbachisaurus garasbae*. The CPOL passes through a sheetlike PCDL, as in *Rebbachisaurus*; but the lateral CPRL forms a cross-shaped junction with the ACPL, each of these laminae equally interrupting the trajectory of the other. Abbreviations as used in the text. Scale bar = 200 mm.

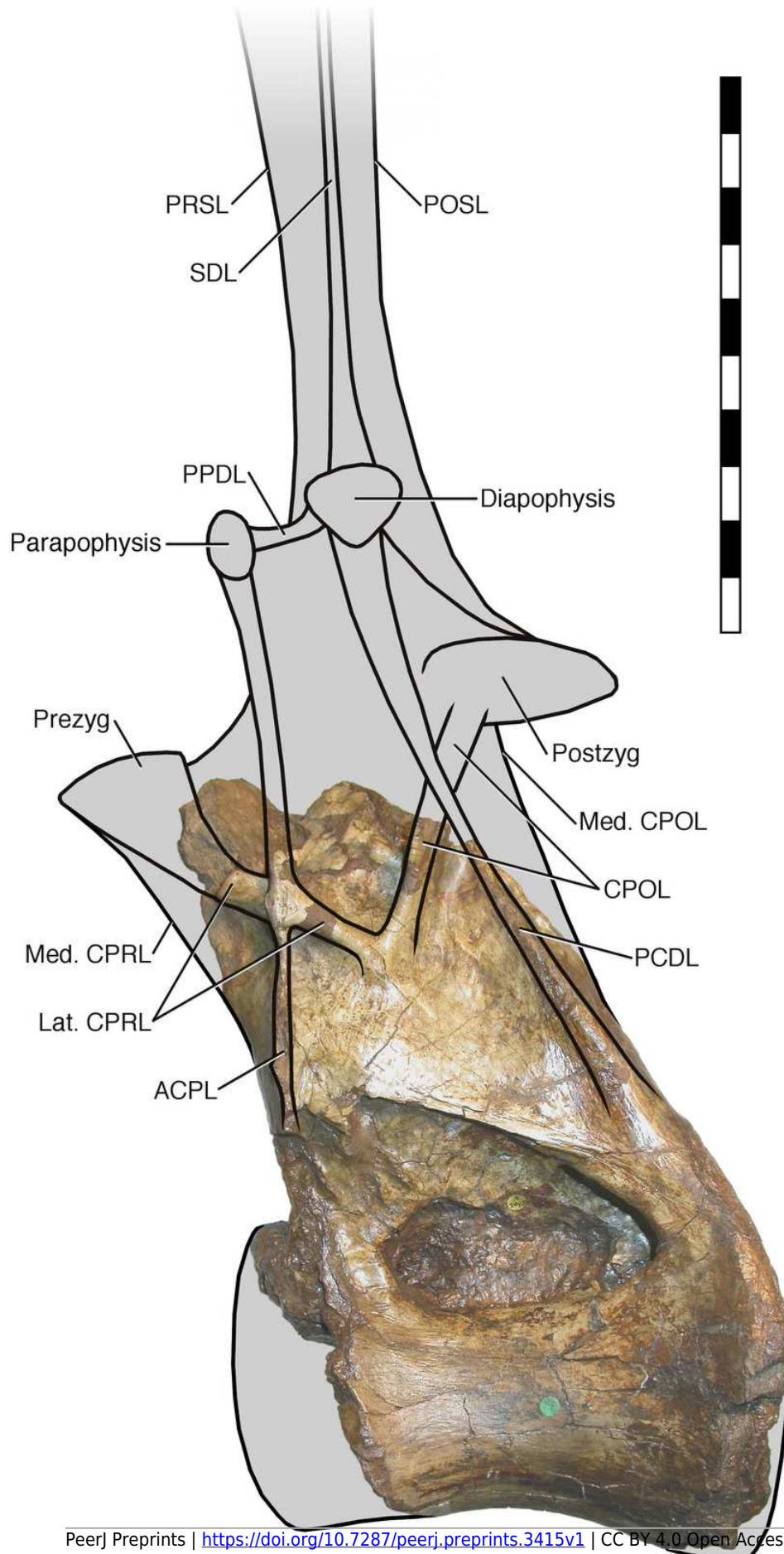


Figure 5

Figure 5. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left anteroventrolateral view, highlighting the three sets of laminae related to the prezygapophyses.

Figure 5. NHMUK R2095, the holotype and only vertebra of *Xenoposeidon proneneukos*, in left anteroventrolateral view, highlighting the three sets of laminae related to the prezygapophyses. The trajectories of the medial CPRLs (which emerge from the neural arch pedicels) and the lateral CPRLs (which intersect with the APCLs) indicate the approximate position of the prezygapophyses. The additional arched laminae form the margins of the large, teardrop-shaped CPRF, but meet at a position some way below and posterior to the presumed location of the prezygapophyseal facets. Breakage of both medial CPRLs and the left ACPL and PCDL is indicated by cross-hatching. Note that, from this perspective, the lateral CPRL appears to turn a corner where it intersects with the ACPL, such that the posteroventral portion of the lateral CPRL appears contiguous with the dorsal portion of the ACPL. This is an illusion brought about by the eminence at the point of intersection. As always, this is much easier to see in three dimensions. Abbreviations as used in the text.

