

1 Edentulous pterosaurs from the Cretaceous Cambridge Greensand of
2 eastern England with a review of *Ornithostoma* Seeley, 1871

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9 ABSTRACT

10 A re-examination of all UK pterosaur material from the Late Cretaceous Cambridge Greensand
11 Member (CGM) of the West Melbury Marly Chalk Formation revealed a number of new specimens of
12 edentulous pterosaur jaw fragments previously identified as shark fin spines and jaws and
13 accessioned under the epithet 'Cestraciontid Finray' and 'jaws of fish'. These are now recognised as
14 pterosaurian jaw tips and referred to *Ornithostoma* Seeley, 1891 and *Azhdarchoidea* indet. This
15 material increases the diversity of edentulous pterosaur in the CGM.

16 The edentulous pterosaur *Ornithostoma sedgwicki* Seeley, 1891 also from the Cretaceous Cambridge
17 Greensand of eastern England is reviewed. The holotype specimen is identified as a mandibular
18 fragment of a ?chaoyangopterid on account of a conspicuous expansion of the lateral margins
19 posteriorly and the presence of small neural foramina on the lateral margins. This combination of
20 features is not seen on the mandibles or rostra of *Azhdarchidae* or *Pteranodontia*, both groups to
21 which *Ornithostoma* is thought to have had affinities in the past. If referral to *Chaoyangopteridae* is

22 correct, then this records for the first time Chaoyangopteridae in Europe. Postcranial material
23 referred to *Ornithostoma* from the type horizon is regarded as indeterminate Pterosauria.

24

25 *Keywords:* Pterosauria, Chaoyangopteridae, Azhdarchidae, *Ornithostoma* Cretaceous, eastern
26 England.

27

28 **1. Introduction**

29 In the heyday of phosphate mining in Cambridgeshire between the years 1851 to *circa* 1910
30 thousands of fossils were discovered and sold to museums around the United Kingdom, and also
31 some museums in continental Europe and the USA (Unwin, 2001). Among this material were some
32 ~2400 isolated pterosaur bones (excluding teeth). This represents one of the largest collections of
33 pterosaur material from a single deposit. Unfortunately, although the material is preserved three -
34 dimensionally, it is very fragmentary and often highly worn, with hard adherent matrix and may be
35 bio encrusted. Nevertheless, in the 1800s, this material provided the first evidence for giant
36 pterosaurs (Owen, 1859b) and some of it became the basis for new taxa of large toothed pterosaur
37 including '*Amblydectes*', *Coloborhynchus*, '*Criorhynchus*', *Ornithocheirus* and *Lonchodectes*. Later
38 some material was identified as *Anhanguera*. Among this material were three pieces of edentulous
39 pterosaur, one piece of which became the holotype of *Ornithostoma sedgwicki* Seeley, 1891

40 At least two major clades of the Pterosauria evolved edentulous beaks: the Pterandontidae, ranging
41 from the Coniacian to the Maastrichtian (Kellner et al., 2016, Longrich et al., 2018) and the
42 Azhdarchoidea, likely ranging from the Upper Jurassic to Maastrichtian (Witton, 2013; Barrett et al.,
43 2008). A third group, the Dsungaripteridae (?Kimmeridgian to Hauterivian) evolved a reduced
44 dentition in the anterior beak, but retained teeth more cranially (Wellnhofer, 1991; Unwin, 2006;
45 Witton, 2013). In some edentulous pterosaurs these beak tips appear to have been preserved

46 preferentially, perhaps related to their often near triangular cross section and
47 thickening/strengthening of bone in the corners (Ibrahim et al., 2010; Martill et al., 2018) making
48 them robust and somewhat resistant to transport damage and compaction. Consequently, many
49 taxa have been erected on the basis of edentulous jaw tips and mid-length fragments (e.g.
50 *Tupuxuara* Kellner and Campos, 1988; *Alanqa* Ibrahim et al., 2010; *Xericeps* Martill et al., 2018,
51 *Aptorhamphus* McPhee, et al., 2020), but in many cases the differences between taxa are
52 extremely subtle and distinguishing between upper and lower jaws challenging.

53

54 1.1. The Cambridge Greensand Member

55 The Cambridge Greensand Member forms the basal 1 to ~2 metres of the Lower Cenomanian aged
56 West Melbury Marly Chalk Formation (Machalski, 2018). The deposit comprises a coccolith marl rich
57 in glauconite and phosphatic clasts derived from the underlying Gault Formation, which is of Upper
58 Albian age in the Cambridge region (Fig. 1). Thus, although the deposit is lower Cenomanian, and
59 contains some autochthonous lower Cenomanian ammonites, notably examples of *Schloenbachia*
60 *varians* (J. Sowerby, 1817), (Machalski, 2018), the vast majority of its fossils are steinkerns in
61 phosphate of upper Albian age (Hart, 1973; Unwin, 2001; Machalski, 2018). Presently there are no
62 permanent exposures of this unit, and little research has taken place on its sedimentology and
63 genesis in Recent times.

64

65 1.2. Historical narrative

66 During the mid-19th century when phosphatic nodule mining for fertiliser to the east of Cambridge,
67 was at its peak, a partial jaw of an edentulous pterosaur was discovered and subsequently figured by
68 Sir Richard Owen (1859a, pl. IV, figs 4-6). That specimen (CAMSM B54485), despite its highly
69 fragmentary nature, proved to have a significant impact on the identification and taxonomic history

70 of later 19th century discoveries of edentulous pterosaurs in North America (Williston 1892, 1893,
71 1895, 1896, 1897a, b). The specimen received only scant attention during the 20th century, largely
72 because it seemed to lack identifying features, and possibly because more spectacular edentulous
73 pterosaur material was being discovered elsewhere (e.g. Lawson, 1975). In the 21st century, a
74 dramatic increase in knowledge of edentulous pterosaurs, based on numerous pterosaur discoveries
75 around the globe (e.g. Lü et al., 2008, Ibrahim et al., 2010; Novas et al., 2012; Kellner and Calvo,
76 2017; Martill et al., 2018) rekindled the relevance of *Ornithostoma*, and works attempting to secure
77 its identity and review its taxonomic history appeared (e.g. Unwin, 2001; Averianov, 2012).
78 Unusually perhaps, at no time in its investigation has a photograph of the *Ornithostoma* type
79 specimen ever been published. See Fig. 2 for a historical timeline of the taxonomy and research of
80 *Ornithostoma*

81

82 1.2.1 *Ornithostoma* according to Richard Owen

83 Richard Owen (1859a) was the only scientist of the 19th century to figure *Ornithostoma* (Owen,
84 1859a Tab. IV, figs 4-5) (Fig. 3 here). (Subsequent authors either reproduced Owen's figure
85 [Averianov 2012, fig. 1] or traced over photographs of the specimen [e.g. Unwin, 2001, fig. 13]).
86 Owen (1859a) identified the specimen (CAMSM B54485) as a partial metacarpal, close to the
87 proximal end of wing finger five (at that time it was assumed that the wing finger of pterosaurs was
88 digit five), and referred it to the genus *Pterodactylus*. More specifically he figured and described it
89 under descriptions of *Pterodactylus sedgwickii* and *Pterodactylus fittoni*, but did not explicitly
90 referred it to either of these taxa. Owen's 'failure' to recognise the fragmentary specimen as a
91 jawbone is a perfectly understandable error given that the concept of a toothless pterosaur was
92 alien at that time (substantial specimens of edentulous pterosaurs would not be described for
93 another 17 years [Marsh 1876]). Owen's figure included a left lateral view (Owen's 'side view' [tab.
94 IV, figs 4]) (Fig. 3B); an occlusal view (Owen's '?back view' [tab. IV, figs 5]) (Fig. 3C) and both anterior

95 and posterior views (Fig 3A, D). It is clear from Owen's figure that the specimen's distal end had
96 been cut to reveal the internal structure by 1859. Likely Owen had requested the specimen be
97 sectioned to expose its internal architecture as he comments on the 'extreme thinness of the
98 compact wall of the bone' (Owen, 1859a, p. 18). It is not known how much had been removed in the
99 cutting process, or if a thin section was made from the cut piece.

100

101 1.2.2. *Ornithostoma according to Seeley*

102 Harry Govier Seeley was first to identify CAMSM B54485 (Cabinet number: case J, comp. c, tablet **28**,
103 specimen **1**) as a partial jaw fragment in his *Index to the fossil remains of Aves, Ornithosauria and*
104 *Reptilia from the secondary strata arranged in the Woodwardian Museum of the University of*
105 *Cambridge* (usually abbreviated to *The Index*), but he was not then confident of its revised identity,
106 listing it as 'a symmetrical bone, either a phalange or a toothless jaw' (Seeley, 1869, p. 7). A year
107 later he stated it was 'probably part of the jaw and not the wing metacarpal' (Seeley, 1870, p. 54).
108 Then the following year Seeley (1871) became more confident of its jaw identity and, in a footnote
109 (reproduced below) named the specimen *Ornithostoma*, but provided no specific epithet.

110 * A new genus appears to be constituted by some (three) pieces of jaws from the
111 Cambridge Greensand. Unfortunately, the extremity is not preserved. They have the
112 ordinary dagger-shaped snout, but appear to be entirely destitute of teeth. I provisionally
113 name the genus *Ornithostoma*. [Seeley, 1871, p. 35].

114 Owen (1859a) had not mentioned any other examples, and perhaps had been unaware of their
115 existence (or they may not have been discovered at that time). Seeley did not describe these
116 additional specimens, nor did he provide registration (cabinet) numbers for them. By 1876 Seeley
117 was confident that the fragment represented a jaw bone, and identified it as a premaxilla, however,

118 he now considered that it may belong to a bird and provided the first detailed description of the
119 specimen:

120 *'It has the base flattened, concave from side to side, marked with blood-vessels, and*
121 *germinating laterally in well-defined ridges gently rounded, which are concave in outline*
122 *from front to back, so as to make the back wider than the front. If the specimen should*
123 *hereafter prove to be a jaw, this would be the palatal surface. It is $2\frac{1}{4}$ inches long, $\frac{3}{4}$ inch wide*
124 *in front, and $1\frac{1}{16}$ inch wide behind. The sides are smooth, finely wrinkled, concave in length,*
125 *convex from above downward, with small oblique vascular foramina near the border, which*
126 *may be alveolar; there are also foramina on the middle of the side. Superiorly the sides*
127 *converge in a rounded ridge. It is $\frac{13}{16}$ inch deep in front, and $1\frac{1}{4}$ inch deep behind.'* [Seeley,
128 1876, p. 499-500].

129

130 Noting the discovery of the toothless pterosaur *Pteranodon* by Marsh that same year, and pointing
131 to the lack of a nasal groove or cavity in *Ornithostoma*, Seeley (1876) suggests that it is probably
132 Pterosaurian. (Seeley's wavering over its pterosaurian identity is understandable, as he had
133 previously described bird cervical vertebrae from the Cambridge Greensand [Seeley 1869]). Notable
134 in Seeley's (1876) description of the *Ornithostoma* holotype is his mention of small foramina on the
135 lateral surfaces. Although he makes little of this, today this feature may to be an apomorphy for
136 Azhdarchoidea. No commentator since Seeley (1876) has mentioned this feature.

137

138 After Marsh (1876) described *Pteranodon*, Seeley (1891), acknowledging the superior nature of the
139 North American material, alluded to the similarities with *Ornithostoma*, and declared *Pteranodon* a
140 junior synonym of the former (Seeley, 1891). In the same paper, Seeley (1891, p. 442) finally
141 provided a specific name for *Ornithostoma*, and thus validated his genus, it becoming *Ornithostoma*

142 *sedgwicki*. For a decade, Williston (1892, 1893, 1895, 1896, 1897, 1902) accepted Seeley's synonymy
143 and referred to *Pteranodon ingens* as *Ornithostoma ingens*, erecting the family Ornithostomatidae
144 Williston, 1893 and subfamily Ornithostomatinae Williston, 1897 for its reception (both ae junior
145 synonyms of Pteranodontidae Marsh, 1876).

146 The synonymy was overturned by Pleininger (1901) on the supposed technicality that *Ornithostoma*
147 was invalid in lacking a species name. Pleininger (1901) also incorrectly stated that *Ornithostoma*
148 had no description or illustration. However, Seeley maintained his opinion that the two were
149 synonymous in his *Dragons of the Air* (Seeley 1901 p. 75), it presumably having been written before
150 publication of Pleininger (1901). Nonetheless, Seeley discusses the postcranial anatomy of
151 *Ornithostoma*, drawing on the anatomy of the North American *Pteranodon* for his analysis, but he
152 did not refer any additional Cambridge Greensand material to *Ornithostoma*. In 1903 Williston
153 reverts to using *Pteranodon* (Williston, 1903), presumably influenced by Pleininger's (1901) analysis,
154 and by this date had met and had discussions with Pleininger.

155

156 1.2.3. *Ornithostoma according to Lydekker*

157

158 Richard Lydekker (1888) first mentioned *Ornithostoma* in his *Catalogue of the reptiles of the BM(NH)*
159 as a mere footnote (Lydekker, 1888, p. 17, footnote 1) where he suggested *Ornithostoma* may
160 belong to Pteranodontia *sensu* Marsh, 1876. Lydekker (1904) further discussed *Ornithostoma* in his
161 review of the vertebrates of Cambridgeshire (Lydekker In Marr and Shipley, 1904), and had clearly
162 been unaware that Seeley (1891) had proposed the specific name *O. sedgwicki* for the holotype
163 specimen. In his ignorance, Lydekker (1904, p. 59) erected the specific name *seeleyi*. The name
164 *Ornithostoma seeleyi* has been used three times in the literature: by Molnar and Thulborn (1980 p.
165 363); in a discussion on *Pteranodon* by Wellnhofer (1980, p. 116), and by Wellnhofer again (1991, p.

166 145) in a list of Cretaceous pterosaurs in the iconic *Encyclopedia of Pterosaurs*. The name *O. seeleyi*
167 appears never to have been used since.

168

169 1.2.4. *Ornithostoma according to Hooley 1914*

170 English vintner and sometime palaeontologist Reginald Walter Hooley undertook the (even then)
171 mammoth challenge of reviewing the genus *Ornithocheirus* and all of the pterosaur material from
172 the Cambridge Greensand held by the Sedgwick Museum in Cambridge (Hooley, 1914). While this
173 was a considerable volume of work, Hooley made many inappropriate assumptions regarding
174 associations of various skeletal elements (see discussions in Unwin, 2001 and Averianov, 2012).
175 Consequently, Hooley referred many cranial and postcranial elements (including ‘all’ fragmentary
176 notaria, scapulocoracoids, type 'B' humeri and ulnae, and group 1 femora) from the CGS to
177 *Ornithostoma*, and considered that much of the hinder parts of the skull of *Ornithostoma* were
178 indeed known among the Cambridge Greensand material. In the light of our knowledge today of
179 Cretaceous edentulous pterosaur diversity, and presence of a second edentulous pterosaur in the
180 CGS (see below) it seems wholly inappropriate to assign any isolated or fragmentary posterior
181 cranium or post cranial material to *Ornithostoma*.

182

183 1.2.5. *Ornithostoma according to Unwin 2001*

184 In his review of Cambridge Greensand Formation pterosaurs, Unwin (2001) discussed the
185 systematics and possible relationships of *Ornithostoma*. He included drawings and was first to
186 provide a ‘dorsal’ view of the specimen, but unfortunately did not provide photographs. In reviewing
187 the practices of previous workers, Unwin concluded that *O. sedgwicki* was a valid taxon, but that
188 referral of non-jaw material to *Ornithostoma* by Hooley (1914) was inappropriate. Of particular note
189 was Unwin’s only cautious acceptance of *Ornithostoma* as a pteranodontid, suggesting that its

190 affinities might lie elsewhere. However, as highlighted by Averianov (2012), Unwin (2001) explicitly
191 excluded *Ornithostoma* from Azhdarchoidea on account of it lacking concave lateral margins, a
192 feature that we now know does not exclude affinities with Azhdarchoidea (see below). Unwin also
193 accepted Seeley's (1871) original identification of the *Ornithostoma* holotype as a
194 maxilla/premaxilla. Unwin (2001, p. 212) mentioned the two other jaw fragments noted by Seeley
195 (1871), but does not describe or figure them. However, in his unpublished PhD thesis (Unwin, 1991)
196 line drawings and photographs of the specimens were included (reproduced here as Fig. 4). A
197 subsequent search of the CAMSM material appears to indicate this unaccessioned material has
198 subsequently been lost.

199

200 1.2.6. *Ornithostoma according to Averianov 2012*

201 Averianov (2012) provided the most detailed and thorough reappraisal of *Ornithostoma*, although he
202 did not provide any new illustrations of the holotype, and missed some features that secure its
203 identity, notably the small elongate foramina on the lateral and occlusal surfaces. Like Hooley (1914)
204 before him, Averianov (2012) assigned additional cranial and post cranial material to *Ornithostoma*
205 on grounds of parsimony. In the light of discovery of further jaw material from the CGS indicating the
206 presence of a second azhdarchoid we reject all of Averianov's referrals to this genus.

207 Averianov (2012) concluded that *Ornithostoma* is an azhdarchoid rather than a pteranodontid, based
208 not on the holotype specimen, but on his referred material (Averianov, 2012, p. 46). Like Unwin
209 (2001), and Seeley (1871), Averianov did not re-evaluate the *Ornithostoma* holotype identity, and
210 continued to regard it as a maxilla/premaxilla.

211 Averianov referred *Ornithostoma* to the Azhdarchoidea Nesson, 1984 on the following grounds: (our
212 commentary in italics)

- 213 1. Teeth absent. (*This is not diagnostic for Azhdarchoidea, edentuly also occurs in*
 214 *Pterodontidae and Nyctosauridae*)
- 215 2. Middle cervicals moderately elongated. (*A feature also found in*
 216 *Ctenochasmatidae*)
- 217 3. Lateral pneumatic foramen on middle cervicals reduced or absent. (*A valid*
 218 *character*)
- 219 4. Pneumatic foramen on ventral side of humerus near the base of humeral
 220 neck. (*Irrelevant*)
- 221 5. Deltopectoral crest of humerus elongated and rounded on distal end, not
 222 warped, with parallel sides. (*Irrelevant*)
- 223 6. Angle of femoral neck to shaft less than 145°. (*Irrelevant*)
- 224 7. A large pneumatic foramen on posterior side of femur between neck and
 225 greater trochanter. (*Irrelevant*)

226 Thus, the only character that is derived from the holotype specimen is the non-diagnostic character
 227 of edentuly. In addition, Averianov (2012) identified a combination of cranial and post cranial
 228 features that exclude *Ornithostoma* from Azhdarchidae, and from such azhdarchoid genera as
 229 *Tapejara*, *Tupandactylus* and *Tupuxuara*, none of which pertain to the holotype.

230 In discussing *Ornithostoma's* azhdarchoid affinities, Averianov notes:

231 “*Actually CAMSM B.54485 is very similar to the rostrum fragments of Azhdarcho lancicollis from the*
 232 *Turonian of Uzbekistan (Averianov, 2010). The only sufficient difference is that no known fragment of*
 233 *Azhdarcho rostrum has such abrupt lateral widening at the posterior end as in Ornithostoma.*”

234 This feature seems to have deterred Averianov from placing *Ornithostoma* in Azhdarchidae, instead,
 235 he draws on comparisons with Chinese chaoyangopterids, but falls shy of referral to this family on
 236 account of the poor state of preservation of the Chinese material, taxonomic issues, and some
 237 problems with possible fabrication of some Chinese specimens (Averianov, 2012, p. 43).

238 Here, we agree entirely with Averianov's (2012) assertion that *Ornithostoma* has azhdarchoid
239 affinities, and we present evidence from the holotype specimen to support this hypothesis.

240 Averianov (2012; p. 41) discusses three specimens described in the 'Index' (Seeley, 1869: xvi)
241 (specimens 1–3 from cabinet J, tablet 16). Averianov (2012) states:

242 *'He [Seeley] identified these specimens as "premaxillary bones" and referred them*
243 *to Ornithocheirus simus (Owen, 1861), establishing a new*
244 *genus Ornithocheirus (Seeley 1869: xvi, 6). In the footnote on page xvi he diagnosed*
245 *the new genus as having "no teeth anterior to the palate". Surprisingly enough,*
246 *Seeley referred to plate 2 in Owen (1861), where the only figured jaw fragment is*
247 *toothed'.*

248 Averianov (2012) then goes on to say *'Seeley's original intention evidently was to*
249 *establish Ornithocheirus for the toothless pterosaur. Later Seeley changed his mind and used*
250 *this name for the species of toothed pterosaurs'.*

251 We disagree with Averianov's interpretation of Seeley's supposed intentions. When Seeley
252 referred to *'no teeth anterior to the palate'*, he was surely discussing the anterior most
253 teeth exhibited by *Coloborhynchus* and examples that would now be called *Anhanguera*,
254 which he later describes as *'peculiar front premaxillary teeth'* Seeley (1881 p.16), which the
255 specimens Seeley (1869) had referred to *Ornithocheirus* did not have. This is, as noted by
256 Averianov, discussed by Hooley (1914), but to different effect. The genus *Ornithocheirus* was
257 originated conceived for 3 'deep club-shaped jaws' of the *'Pterodactylus' simus* type, and
258 the genus *Ptenodactylus* for the spear-shaped jaws of *'Pterodactylus' sedgwicki* type. Seeley
259 became convinced that the type specimen of *'Pterodactylus simus'* was a lower jaw, thus
260 abandoning the genus *Ptenodactylus*, and including all specimens under *Ornithocheirus*. This

261 is presumably why Seeley changed the original character from '*no teeth anterior to*
262 *palate*' to '*the teeth are prolonged anterior to the muzzle*' (Seeley, 1881; Hooley, 1914). This
263 shows that the genus *Ornithocheirus* was never intended for the toothless pterosaur form, and
264 that the specimens listed by Seeley (1869: xvi, 6) were not the edentulous jaw fragments
265 of *Ornithostoma* as supposed by Averianov (2012). This interpretation is further supported
266 by Seeley (1869: p. 7) listing the specimen which would later be the holotype
267 of *Ornithostoma* (CAMSM B54485) as 'a symmetrical bone, either a phalange or a toothless
268 jaw', indicating he was not confident at the time of its identity as an edentulous pterosaur.
269 Therefore, Averianov's (2012) discussion has no relevance to any discussion
270 of *Ornithostoma*.

271

272 1.3. New specimens.

273 During our searches of collections of Cambridge Greensand fossils we encountered three additional
274 edentulous pterosaur fragments. Two examples of anterior jaws of pterosaurs were glued to a card
275 and identified as 'Cestraciontid finrays' (*Paracestracion* sp. fin spines) (CAMSM B40085 and CAMSM
276 B40091), by persons unknown, and which they do superficially resemble (Fig. 5C). Similarly, a card in
277 the Booth Museum, Brighton also had a pterosaur jaw fragment (BMB 019582) included with several
278 fish jaws (Fig. 5B), from which it differs considerably.

279 We identified them as pterosaurian due to the presence of elongate foramina located along the
280 lateral and occlusal margins, features not present on shark fin spines. These misidentifications need
281 putting into context. Shark fin spines and edentulous pterosaur jaw tips are only superficially similar
282 when specimens are of substantial size, but fragments of these can appear remarkably similar.

283 *Paracestracion* fin spines are easily recognised when the enamel sheath is present, but this flakes
284 away in weathered and abraded specimens to reveal a slightly fibrous bone-like material internally

285 that resembles reptilian bone. Furthermore, the posterior margin of the fin spine is flat to slightly
286 sulcate, as is the occlusal surface of the jaws of such edentulous pterosaurs as *Alanqa* and *Xericeps*.
287 Furthermore, the fin spines of *Paracestracion* differ from those of most other elasmobranchs
288 because of their largely hollow nature. Although pulp cavities are present in many shark fin spines
289 (e.g. xenacanthids: Beck et al., 2016), the internal cavity of *Paracestracion* spines is extensive
290 resulting in thin walls to the lateral margins of the spine with thickening in the corners. A very similar
291 pattern of ossification is seen in the jaws of azhdarchid pterosaurs. Thus, using the degree of
292 'hollowness' to identify elements as pterosaurian cannot be employed with *Paracestracion* fin
293 spines, which occur more commonly than edentulous pterosaur jaw fragments in the Cambridge
294 Greensand.

295

296 **2. Material and methods**

297 Institutional abbreviations: **BMB**, Booth Museum of Natural History, Brighton, Sussex, UK; **BMNH**
298 (**NHMUK**), Natural History Museum, London, United Kingdom; **BSP**, Bayerische Staatssammlung für
299 Paläontologie und Geologie, Munich, Germany; **CAMSM**, Sedgwick Museum of Earth Sciences,
300 Cambridge, UK; **FSAC**, Faculté de Sciences Aïn Chock, Laboratoire de Géosciences, Université Hassan
301 II, Casablanca, Morocco; **MMS/VBN**, Musée du Moulin Seigneurial, Velauxe La Bastide Neuve,
302 France; **MN**, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **MTM**,
303 Magyar Természettudományi Múzeum, Budapest, Hungary; **NMSG**, Naturmuseum St. Gallen, St.
304 Gallen Canton, Switzerland; **PSMUBB**, Palaeontology-Stratigraphy Museum, Babeş Bolyai University,
305 Cluj-Napoca, Romania; **SAO**, Collection Urs Oberli, St. Gallen, Switzerland; **SGU**, Saratov State
306 University, Saratov, Russia; **UOP**, University of Portsmouth, School of the Environment, Geography
307 and Geosciences collection, Portsmouth, UK; **YPM**, Peabody Museum of Natural History, Yale
308 University, New Haven, Connecticut, USA.

309 Specimens were examined in the following collections: BMB, Booth Museum of Natural History,
 310 Brighton, Sussex, UK; CAMSM Sedgwick Museum of Earth Sciences, Cambridge. High quality images
 311 of the holotype of *Ornithostoma* are available at [http://www.3d-](http://www.3d-fossils.ac.uk/fossilType.cfm?typSampleId=20004040)
 312 [fossils.ac.uk/fossilType.cfm?typSampleId=20004040](http://www.3d-fossils.ac.uk/fossilType.cfm?typSampleId=20004040).

313 **3. Results**

314 *3.1 Systematic Palaeontology*

315 Pterosauria Kaup, 1834

316 Pterodactyloidea Plieninger, 1901

317 Azhdarchoidea Nesso, 1984 (*sensu* Unwin, 2003)

318 Neoazhdarchia Unwin, 2003

319 ?Chaoyangopteridae Lü, Unwin, Xu, Zhang, 2008

320 *Ornithostoma* Seeley, 1871, validated Seeley, 1891

321 *Type and only valid species. Ornithostoma sedgwicki* Seeley, 1891

322 *Synonymy.*

323 NOTE. All mentions of *Ornithostoma* as *Pteranodon* and '*Ornithostoma orientalis*' are omitted from
 324 this synonymy.

325 1871 *Ornithostoma* SEELEY — Seeley, p. 35 (generic name only).

326 1888 *Ornithostoma* SEELEY — Lydekker, p.17, footnote 1.

327 1901 *Ornithostoma* SEELEY — Seeley, p. 138.

328 1925 *Ornithostoma* (?*Pteranodon*) SEELEY — Williston, p. 298.

329 1971 *Ornithostoma* SEELEY — Miller, p. 4.

330 1978 '*Ornithostoma*' SEELEY — Wellnhofer, p. 63.

- 331 1994 *Ornithostoma* SEELEY — Bennett, p. 17.
 332 2006 *Ornithostoma* SEELEY — Unwin, p. 64.
 333 2010 *Ornithostoma* SEELEY —Myers, p. 1071.
 334 2010 *Ornithostoma* SEELEY — Kellner, p. 1064.

335

336

337

338 *Ornithostoma sedgwicki* Seeley, 1891

339 Holotype. CAMSM B54485, partial jaw fragment (Figs. 3, 5A, 6-7). Referred material. BMB 019582
 340 (Fig. 8), CAMSM B40091 (Fig. 9), CAMSM UNREG 1-2 (Fig. 4).

341 *Diagnosis.* *Ornithostoma sedgwicki* has not previously been formally diagnosed. No certain
 342 autapomorphies have been identified, however it is diagnosed from other edentulous pterosaurs by
 343 a unique combination of synapomorphies. These include a mandible with a rounded triangular cross-
 344 section with convex lateral margins; a shallow sulcate occlusal surface; raised rounded marginal
 345 ridges on the occlusal surface and presence of elongate foramina on the lateral surfaces.

346 *Synonymy.*

347 NOTE. All mentions of *Ornithostoma*, where the citation refers to specimen CAMSM B54485, now
 348 known as *O. sedgwicki*, are included. Mentions of *Ornithostoma* that pertain to material now called
 349 *Pteranodon* from the Niobrara Chalk Formation of Kansas are omitted.

350

- 351 1859a ‘Proximal end of metacarpal of wingfinger of *Pterodactylus*’ — Owen, Tab.
 352 IV, figs 4-5, p. 18.
 353 1869 ‘Symmetrical bone, either a phalange or a toothless jaw’ — Seeley, p. 7.
 354 1870 ‘Probably part of a jaw’ — Seeley, p. 54.

355	1871	<i>Ornithostoma</i> SEELEY — Seeley, p. 35.
356	1876	<i>Ornithostoma</i> SEELEY — Seeley, p. 499-500 (as possible bird).
357	1891	<i>Ornithostoma</i> sp. SEELEY — Woods, p. 174.
358	*1891	<i>Ornithostoma sedgwicki</i> SEELEY — Seeley, p. 441.
359	1897	<i>Ornithostoma</i> sp. SEELEY — Reed, p. 113.
360	1904	<i>Ornithostoma seeleyi</i> LYDEKKER, Lydekker, p. 59.
361	1914	<i>Ornithostoma</i> sp. SEELEY — Hooley, Ser. 8, v. 13, p. 530, 537.
362	1980	<i>Ornithostoma seeleyi</i> , LYDEKKER — Molnar and Thulborn, p. 363.
363	1980	<i>Ornithostoma seeleyi</i> LYDEKKER — Wellnhofer, p. 116.
364	1991	<i>Ornithostoma seeleyi</i> SEELEY — Wellnhofer, p. 145.
365	2001	<i>Ornithostoma sedgwicki</i> SEELEY — Unwin, p. 212, fig. 13.
366	2008	CAMSM B54485 (<i>Ornithostoma</i>) SEELEY — Steel, p. 114.
367	2012	<i>Ornithostoma sedgwicki</i> SEELEY — Averianov, p. 40, fig. 1.
368	2013	<i>Ornithostoma sedgwicki</i> SEELEY — Witton, p. 172.

369

370 *Referred material.* Two jaw fragments from the CGS referred by Seeley (1869 p.7) but not figured
371 (we identify these specimens here as CAMSM UNREG 1 and CAMSM UNREG 2, see Fig. 4). Unwin
372 (2001, p. 212) also mentions two edentulous jaw specimens in the Sedgwick Museum, Cambridge
373 which he assumed were the specimens referred by Seeley (1869), but did not provide their accession
374 number nor did he figure them, and are illustrated here for the first time (Fig. 4). The specimens
375 were not encountered during our searches at Cambridge in January 2020.

376 Specimens BMB 019582 (Fig. 8) and CAMSM B40091 (Fig. 9) are referred to *Ornithostoma* on the
377 basis of a triangular cross-sectional outline with a rounded dorsal margin. The lateral and dorsal
378 angles of both specimens are comparable with the holotype of *Ornithostoma*. These specimens
379 provide additional information on *Ornithostoma* and show that *Ornithostoma* possesses two rows of

380 elongate, slit-like foramina on the lateral surface, one row towards the occlusal margin and one row
381 towards the dorsal margin. They also show *Ornithostoma* has slit-like foramina arranged somewhat
382 randomly on the occlusal surface (measurements are provided in Table 1).

383 *Material.* In total we know of 5 specimens that may be identified as *O. sedgwicki*: these are – the
384 holotype CAMSM B54485, Seeley's lost specimens CAMSM UNREG 1, CAMSM UNREG 2, two
385 specimens referred here, BMB 019582 and CAMSM B40091.

386 The holotype specimen (CAMSM B54485) was identified by Seeley (1876) as a possible premaxillary
387 bones, and Unwin (2001) also listed them as a fragment of rostrum. Averianov (2012) went further
388 supposing the fragment to represent fused maxillae and premaxillae, but none of these authors
389 justified their identification. Here we interpret the holotype specimen as a mandibular symphysis as
390 discussed below.

391 Averianov (2012) also referred material besides the holotype specimen to *O. sedgwicki*. The referred
392 material of Averianov (2012) (CAMSM B54406, posterior skull fragment; CAMSM B54394 and
393 B.54493, cervical vertebrae; CAMSM B54081, right humerus; BMNH 35413, proximal fragment of
394 right humerus; CAMSM B54262, proximal part of right femur) cannot safely be referred to
395 *Ornithostoma*, and we remove them from the paradigm of this taxon. While Averianov (2012)
396 invoked parsimony for the referral, it should be noted that most pterosaur sites with azhdarchoids
397 contain more than one genus (e.g. Crato Formation – Unwin and Martill 2007; Santana Formation –
398 Kellner and Tomida, 2000; Kem Kem Group – Martill et al., 2020a; Moroccan phosphates – Longrich
399 et al., 2018), this seems also true for the CGS in light of the recent discovery of further edentulous
400 jaw fragments. It thus seems more parsimonious to *not* refer the material to *Ornithostoma*.

401 *Description.*

402 The holotype CAMSM B54485 (Fig. 3, 6) was first described in detail by Seeley (1876), and
403 subsequently by Unwin (2001) and Averianov (2012), all of whom identified it as a rostrum. Here we
404 provide a revised diagnosis and description of the specimen as a mandibular symphysis .

405

406 CAMSM B54485 exhibits the typical preservation of the CGS pterosaur material. It is 3-dimensionally
407 preserved with a dark brown brecciated bone surface, with some remnant pale matrix. In Owen's
408 original figure (Owen, 1859a: tab. IV, fig 5) (here Fig. 3C) matrix is clearly visible on the occlusal
409 surface, but this was removed prior to 1891 as indicated by Seeley (1891). The distal end of CAMSM
410 B54485 has been cut twice in the past. Firstly it was cut tangentially by persons unknown prior to
411 illustration by Owen (1859a), but it is not known if any thin section was made from the cut slice or
412 how much material was lost while cutting. Secondly, it was cut again by Steel (2004) and a thin
413 section produced (see Fig. 10). The specimen measured 59.2 mm in length prior to this second
414 cutting and now has a maximum preserved length of 48 mm. It has a rounded triangular cross
415 section with convex lateral margins and a shallow sulcate occlusal surface with raised rounded
416 marginal ridges on this surface. The specimen has a lateral angle of approximately 11° , with a
417 maximum anterior height of 22 mm and posterior height of 33.9 mm. It has a dorsal angle of
418 approximately 5° , with an anterior occlusal width of 18 mm and posterior of 29.4 mm. Posteriorly
419 the specimen begins to widen rapidly as it presumably approached the divergence of the mandibular
420 rami. As first reported by Seeley (1876), there are small, oval (1 x 2 mm) elongate, slit-like foramina
421 on the lateral margins located towards the occlusal margin and spaced approximately 20 mm apart.
422 Seeley (1876) also reported foramina on the 'middle of the side', but these were not observed in this
423 analysis. Foramina cannot be identified on the occlusal surface, possibly due to obscuring matrix and
424 fracturing (see Table 1 for measurements).

425

426 *Remarks.* Bogulobov (1914) erected a new species of pterosaur that he assigned to *Ornithostoma* as

427 '*Ornithostoma orientalis*', based on an isolated posterior cervical vertebra from the
428 Santonian/Campanian of Russia. Subsequent workers considered this species to be an azhdarchid
429 (Nessov and Yarkov, 1989) or a possible azhdarchid (Bakhurina and Unwin, 1995). The former
430 authors erected a new genus for '*O. orientalis*', calling it '*Bogulobovia orientalis*' (Bogulobov, 1914),
431 while the latter regarded '*Bogulobovia orientalis*' as a nomen dubium.

432

433

434 Azhdarchoidea indet.

435 Gen. et sp. indet.

436 *Material.* Partial jaw fragment lacking anterior portion and not including anterior margin
437 nasoantorbital fenestra or divergence of mandibular rami (Fig. 10). Specimen number CAMSM
438 B40085.

439 *Locality and horizon.* From the Cambridge Greensand Member of West Melbury Marly Chalk
440 Formation, Cambridgeshire, United Kingdom

441 *Remark.* Specimen CAMSM B40085 differs from *Ornithostoma* in several respects. The cross-
442 sectional outline of the specimen is more triangular with a sharper dorsal margin. It has a higher
443 lateral angle at 16° as opposed to $11/12^\circ$ in *Ornithostoma*, and a slightly smaller dorsal angle at $\sim 4.5^\circ$
444 as opposed to between 5° and 7° , for the holotype and referred material of *Ornithostoma*. The
445 broken posterior end of the specimen reveals two medially located parallel vertical septa (PVS),
446 which extend from the occlusal margin towards the opposite margin. The Moroccan tapejarid
447 *Afrotapejara zourhrii* Martill et al., 2020a also exhibits these PVS. Presently it is not possible to state
448 if this is a premaxilla or dentary fragment (see Table 1 for measurements).

449

450 **4. Discussion**

451

452 *4.1. CAMSM B54485 as a partial mandibular symphysis*

453 The nature of the holotype specimen of *O. sedgwicki* has been problematic ever since its initial
454 description by Owen in 1859. Problems arose largely because of the specimen's highly fragmentary
455 nature and lack of prominently distinctive features. Owen's (Date) difficulties occurred in part
456 because edentulous pterosaurs were unknown to early 19th century palaeontology. Once it was
457 established that the specimen represented a jaw bone, Seeley (Date) wavered over its affinities with
458 respect to it being a bird or pterosaur, but once it was established as a jaw fragment of a pterosaur,
459 no one appeared to question Seeley's (dates) notion that it represented a premaxilla/maxilla.
460 Subsequent authors all rejected the possibility that it might represent a mandible but without
461 justification.

462 A simplified restoration of the anterior portion of the holotype *Ornithostoma* in both dorsal and
463 lateral views (Fig. 7) assumes the jaw tapered to a straight point, in line with other edentulous
464 pterosaurs including *Chaoyangopterus*, *Nyctosaurus*, *Pteranodon*, *Quetzalcoatlus*, *Tupuxuara* and
465 *Zhejiangopterus*, , but not *Xericeps* which has a upswept jaw (Martill et al., 2018) or *Tapejara* which
466 has a downturned jaw (Kellner, 1989). The restoration was achieved simply by projecting anteriorly
467 the ventral and dorsal borders. The restoration permitted the determination of the lateral and dorsal
468 angles (*sensu* McPhee et al., 2020) as ~11° and ~5° respectively (Fig. 7). The lack of any
469 morphological clues such as the anterior margin of the nasoantorbital fenestra or the divergence of
470 the mandibular rami makes identification as an upper or lower jaw challenging. This is a recurring
471 problem, and applicable (for example) to all of the edentulous pterosaurs described from the Kem
472 Kem Group of Morocco (Ibrahim et al., 2010, Martill et al., 2018, Martill et al., 2020a, McPhee et al.,
473 2020).

474 A lateral angle of 11° for *Ornithostoma* lies within the range for other azhdarchoid jaw tips (see
475 McPhee et al., 2020, table 1.), including premaxillae and mandibles. The range of lateral angles
476 found in azhdarchoid jaws tips measured for premaxillae and mandibles shows some overlap and,
477 while it is frequently the case that mandibles have smaller lateral angles than premaxillae, in some
478 taxa the reverse is true, (e.g. *Bakonydraco galaczi* (9° v 15°); *Chaoyangopterus zhangji* 5° v 9° ;
479 *Pteranodon longiceps* 5° v 8.5°). Thus, the lateral angle is not particularly informative for identifying
480 which bone a jaw fragment represents. It can also be the case that where both upper and lower jaws
481 are known the overall morphology and in particular the cross sectional shape may also be
482 remarkably similar (for example *Quetzalcoatlus* [Kellner and Langston, 1996]).

483 Averianov (2012), in considering the fragment to be a fused maxilla/premaxilla regarded the slight
484 upturn of the posterior non-occluding surface as the commencement of a premaxillary crest. This so-
485 called ‘upturn’ coincides with a slight outward flaring of the lateral margins, a feature seen in the
486 mandible of *Bakonydraco galaczi* from the Santonian Csehbánya Formation of Hungary (Ósi et al.,
487 2005; Ósi et al., 2011). This outward flaring posteriorly of the lateral margins of the occlusal surface,
488 with very little change in the lateral profile (what Averianov [2012] called the ‘dorsal’ surface),
489 indicates that the specimen represents a fragment of mandibular symphysis close to the divergence
490 of the mandibular rami (see Fig. 7E). This is also supported by the lack of any remnant
491 premaxilla/maxilla suture.

492 4.2. Affinities of *Ornithostoma sedgwicki*

493 Comparing *Ornithostoma* with other taxa is challenging due both to its fragmentary nature and the
494 compacted preservation more complete pterosaurs from the Yixian and Jiufotang formations of
495 China, the Crato Formation of Brazil and the Niobrara Chalk Formation of North America.

496 Comparison however can be made with three-dimensional material from deposits such as the Kem
497 Kem Group of Morocco and the Santana Formation of Brazil. In the former pterosaur remains are

498 highly fragmentary, as in the CGS (Martill et al., 2020a), but in the latter they are often 3D
499 articulated partial skeletons (e.g Kellner and Tomida, 2000).

500 Previously, *Ornithostoma* was referred to Pteranodontidae (Seeley, 1891, 1901; Wellnhofer, 1991;
501 Unwin, 2001), due to no other edentulous pterosaur being known and its superficial similarities with
502 the pteranodontid *Pteranodon*, notably, the purported cross-sectional shape and presence of
503 marginal ridges (Unwin, 2001). However, as noted by Bennett (1994) and Unwin (2001) the marginal
504 ridges of *Ornithostoma* which are low and rounded, differ from those of *Pteranodon* which are
505 narrow and tall. Although the cross-sectional outlines superficially look similar (a rounded triangle),
506 the *Pteranodon* cross section is higher exhibiting an isosceles triangle compared to the near
507 equilateral triangle of *Ornithostoma*. The presence of elongate slit-like foramina on *Ornithostoma*,
508 which are seemingly absent on pteranodontids excludes *Ornithostoma* from Pteranodontidae and
509 suggests an azhdarchoid affinity where such foramina are widespread (McPhee et al., 2020; Martill
510 et al., 2020a, b). An affinity with Tapejaridae can be excluded due to the lack of a prominent midline
511 crest, which occurs on both the rostrum and mandible (Unwin, 2001). The cross-sectional outline of
512 *Ornithostoma* is unique amongst azhdarchoids (see Fig. 11). It differs from the chaoyangopterid
513 *Aptorhamphus* (McPhee et al., 2020) and the purported azhdarchids *Xericeps* (Martill et al., 2018);
514 *Aerotitan* (Novas et al., 2012) and *Volgadraco* (Averianov et al., 2008) which all have a more 'U' shaped
515 cross sections, compared to the triangular cross section of *Ornithostoma*. Although the azhdarchids
516 *Albadraco* (Solomon et al., 2020) and *Mistralazhdarcho* (Vullo et al., 2018) both have a triangular cross
517 section, they are more elongate as in *Pteranodon*, whilst *Alanqa* has a triangular cross section with
518 concave lateral margins opposed to convex in *Ornithostoma*.

519 The azhdarchoid *Bakonydraco* has a similar cross-sectional outline to that of *Ornithostoma*. The
520 ventral margin is rounded, the lateral margins are convex and the occlusal surface is concave with
521 raised, rounded margins posteriorly. In *Bakonydraco* these lateral margins become sharper
522 anteriorly ultimately fading away, while the occlusal surface becomes flat and lacks the raised

523 margins (see cross sectional outlines Fig 11). In *Ornithostoma* these margins remain prominent along
524 the entire preserved length.

525 Another significant difference between *Ornithostoma* and *Bakonydraco* is a slight median ridge on
526 the occlusal surface posteriorly in *Bakonydraco*, a feature that cannot be discerned on
527 *Ornithostoma*. Some undescribed specimens of *Bakonydraco* lack this median ridge, and thus its
528 taxonomic utility is of limited value. *Bakonydraco* has considerably thickened bone walls (Fig. 12B),
529 whereas they are thin in *Ornithostoma* (Fig. 12A). The occlusal surface of *Bakonydraco* possesses
530 two parallel rows of prominent foramina along the entire length of the jaw from the raised posterior
531 portion to the tip, but these are seemingly absent on the holotype of *Ornithostoma* (perhaps
532 obscured by fractures).

533 Clearly, there are insufficient similarities for *Ornithostoma* to be synonymous with *Bakonydraco*, but
534 the overall similarity in general structure perhaps hints at a close affinity, and the likelihood that the
535 *Ornithostoma* holotype is a portion of a mandibular symphysis rather than a fused
536 maxilla/premaxilla is supported.

537 The similarities of *Ornithostoma* and *Aptorhamphus*, a ?chaoyangopterid from the mid Cretaceous
538 Kem Kem Group of Morocco are noteworthy. Both have a cross section with a rounded ventral
539 margin. The lateral angle of the holotype rostrum of *Aptorhamphus* is 12 ° with a mandibular lateral
540 angle of 8°. The holotype mandibular symphysis of *Ornithostoma* has a lateral angle only fractionally
541 larger at 11°. Furthermore, the dorsal angles of both *Ornithostoma* and *Aptorhamphus* are the
542 same at approximately 5°. *Aptorhamphus* has a midline row of foramina on the lateral margins and
543 offset pairs of foramina on the occlusal surface. Very few foramina are visible on the holotype of
544 *Ornithostoma* due to damage and hard matrix concealing some of the surface, (these were reported
545 by Seeley [1876], some of which may have been removed when it was thin section by Steel [2004])
546 making direct comparison difficult. The newly referred specimens of *Ornithostoma* from the
547 Cambridge Greensand (BMB 019582 and CAMSM B40091), have two rows of lateral foramina, one

548 towards the dorsal margin and one towards the occlusal margin. Although very few foramina are
549 preserved on the occlusal surface of BMB 019582, several are visible on CAMSM B40091, showing a
550 somewhat more random distribution than those of *Aptorhamphus*. However, foramina distribution
551 may vary within a taxon (McPhee et al., 2020). Although the cross-section outline of *Aptorhamphus*
552 superficially looks similar to that of *Ornithostoma*, it differs in that *Aptorhamphus* has a more
553 inverted 'U' shaped outline anteriorly, becoming somewhat 'tear drop' shaped posteriorly.
554 Contrastingly, *Ornithostoma* has a more equilateral triangular cross section along all of its length.
555 The similarities between *Ornithostoma* and *Aptorhamphus* may hint at a close phylogenetic
556 relationship.

557 Perhaps of some significance are two specimens of edentulous pterosaurs held in private ownership,
558 and figured here (Fig. 13A-C). They were exhibited at the Munich fossil show in 2010, but their
559 present whereabouts is unknown. They are likely from the ?Aptian Crato Formation of Brazil (DMM
560 was provided with an opportunity to examine and photograph these specimens). One specimen (Fig.
561 13A) is a complete skull and mandible preserved in left lateral view and displays a slender rostrum,
562 and skull with strongly concave dorsal surface, similar to some Chaoyangopteridae (Lü et al., 2008;
563 Wu et al., 2017). The mandible of this specimen deepens posteriorly, but is flattened by compaction,
564 and reveals little detailed surface morphology. A second specimen is an isolated mandible in occlusal
565 view with the rami flattened outwards and seen in medial aspect (Fig. 13B). The mandibular
566 symphysis of this specimen (Fig. 13C), although crushed, shows some similarities with *Ornithostoma*
567 *sedgwicki*. Notably, it has a deeply concave occlusal surface, is bordered by rounded ridges, and
568 lacks the small slit-like foramen seen on the occlusal surfaces of Azhdarchidae and *Bakonydraco*. In
569 addition, the lateral margins flare outwards posteriorly in occlusal view.

570 The isolated lower jaw (Fig. 13A, B) would appear to match that of the complete pterosaur skull (Fig.
571 13A). The specimen in figure 13A would appear to be close to Chaoyangopteridae, but it lacks the
572 autapomorphy of having the nasoantorbital fenestra overlapping the orbit (Lü et al., 2008). The

573 lateral profile of *Ornithostoma* is also comparable to other chaoyangopterids including
574 *Shenzhoupterus chaoyangensis* (Lü et al., 2008) (although comparison is difficult due to their
575 compacted preservation). Consequently, we tentatively assign *Ornithostoma sedgwicki* to
576 ?Chaoyangopteridae.

577 The referral of *Ornithostoma* to ?Chaoyangopteridae suggests that Chaoyangopteridae is not
578 restricted to South America and China as previously thought and along with the recently described
579 *Aptorhamphus gyrostega* McPhee et al., 2020 suggests a widespread distribution of the group. It
580 also further highlights similarities between the pterosaur assemblage of the Cambridge Greensand
581 Member and the Kem Kem Group, both of which include the toothed pterosaur genera *Anhanguera*,
582 *Coloborhynchus* and *Ornithocheirus* (Unwin, 2001; Jacobs et al., 2019, 2020) and now a
583 chaoyangopterid and potentially if the affinities of CAMSM B40085 proved to lie with Tapejaridae
584 (see section 4.3) a tapejarid. *Ornithostoma* as a chaoyangopterid removes evidence of a Lower
585 Cretaceous pteranodontid and suggests Pteranodontidae were restricted to the Upper Cretaceous.

586 4.3. Affinities of CAMSM B40085

587 CAMSM B40085 (Fig. 10) is a newly discovered edentulous jaw fragment previously misidentified as
588 a 'Cestraciontid finray'. As previously stated identifying the affinities of small fragmentary jaw
589 material is challenging, but some potentially diagnostic feature including parallel vertical septa (PVS)
590 may be informative. The paired medially located PVS, are a feature seen in *Afrotapejara* a tapejarid
591 from the Kem Kem Group of Morocco (Martill et al., 2020a), which may indicate the specimens'
592 affinities lie within Tapejaridae. However, further investigation is required to indicate whether this
593 feature is exclusive to Tapejaridae. The high lateral angle of the specimen supports this
594 interpretation, being a feature seen in many tapejarids (see Martill et al., 2020a table 3). The
595 specimen has elongate foramina in two rows on the lateral surfaces, one row located near the
596 occlusal margin and the other near to the dorsal margin. Elongate foramina are also present on the

597 occlusal surface in a more random distribution. Due to the fragmentary nature of the specimen and
598 its lack of diagnostic characters, it is assigned to Azhdarchoidea indet.

599 **5. Conclusions**

600 ***Ornithostoma sedgwicki* is a valid, diagnosable taxon.....**

601 Here we identify the holotype of *Ornithostoma sedgwicki* as a portion of mandibular symphysis of an
602 indeterminate azhdarchoid, perhaps with affinities to *Bakonydraco* from the Santonian of Hungary.
603 The position of *Bakonydraco* within Azhdarchoidea has been controversial having been regarded as
604 Azhdarchidae by Ősi et al. (2005) and Ősi et al. (2011), but placed in Tapejaridae by Andres and
605 Myers, 2013) and Longrich et al. (2018). While there are some similarities with chaoyangopterids, as
606 suggested by Averianov (2012), there are no autapomorphies that would confirm such an affinity,
607 we thus place *Ornithostoma* only tentatively with Chaoyangopteridae. Identifying *Ornithostoma* as a
608 chaoyangopterid extends the geographical range of the group and removes evidence of a Lower
609 Cretaceous pteranodontid, restricting the temporal range of Pteranodontidae to the Upper
610 Cretaceous.

611 An additional edentulous taxon distinct from *Ornithostoma* is now recognised for the Cambridge
612 Greensand. The presence of two azhdarchoid taxa adds to the diversity of the Cambridge Greensand
613 pterosaur assemblage, but it also means that isolated cranial and post cranial azhdarchid material
614 cannot automatically be assigned to *Ornithostoma*. The discovery of a new, albeit highly
615 fragmentary pterosaur in the Cambridge Greensand and new material assigned to *Ornithostoma*
616 highlights the importance of re-evaluating old collections and fragmentary material. Of particular
617 note is our discovery of material accessioned as fish remains. Future pterosaur workers might bear
618 this in mind when examining collections.

619

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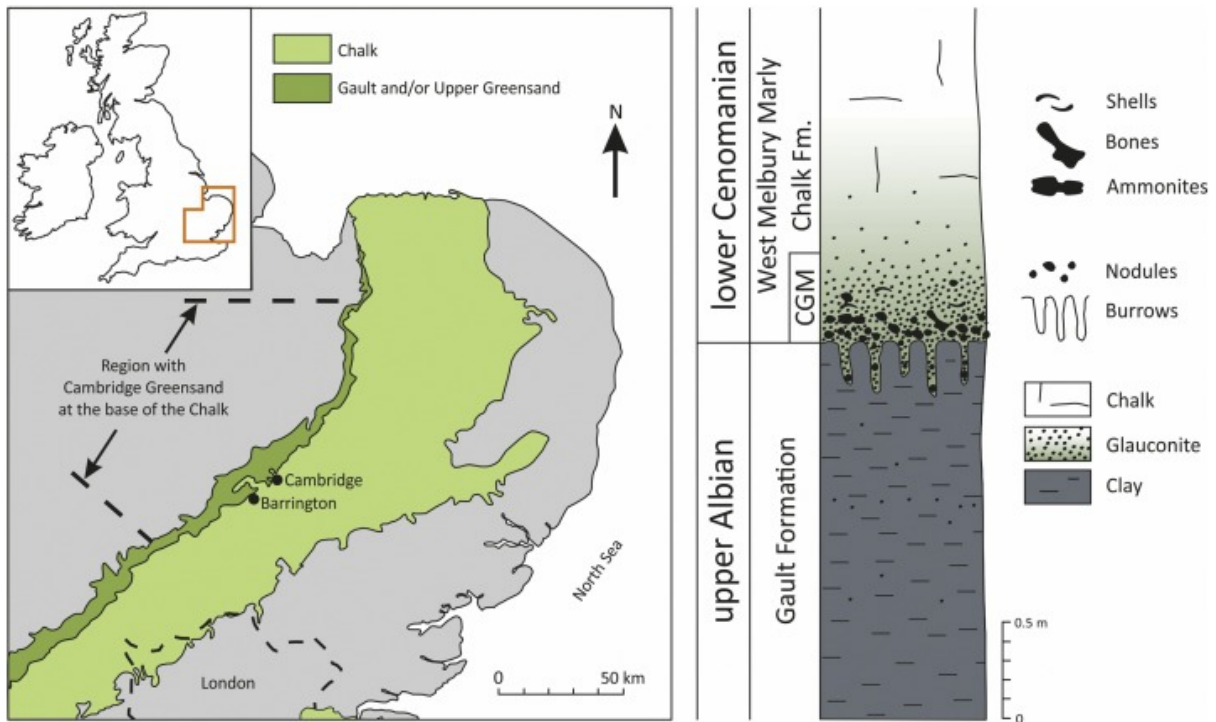
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827

828 **Figures**

829

830



831 **Fig. 1.** A, Map of the Cambridge district with the outcrop of the Cambridge Greensand Member. B,
 832 Simplified stratigraphic column highlighting the Cambridge Greensand Member within the basal part
 833 of the West Melbury Marly Chalk Formation. From Machalski (2018) with minor modification.

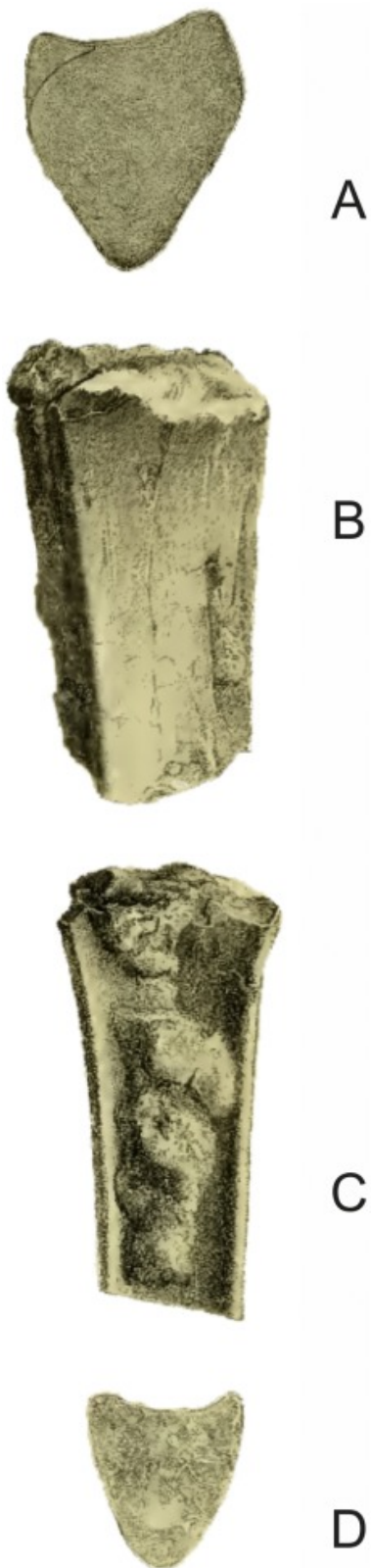
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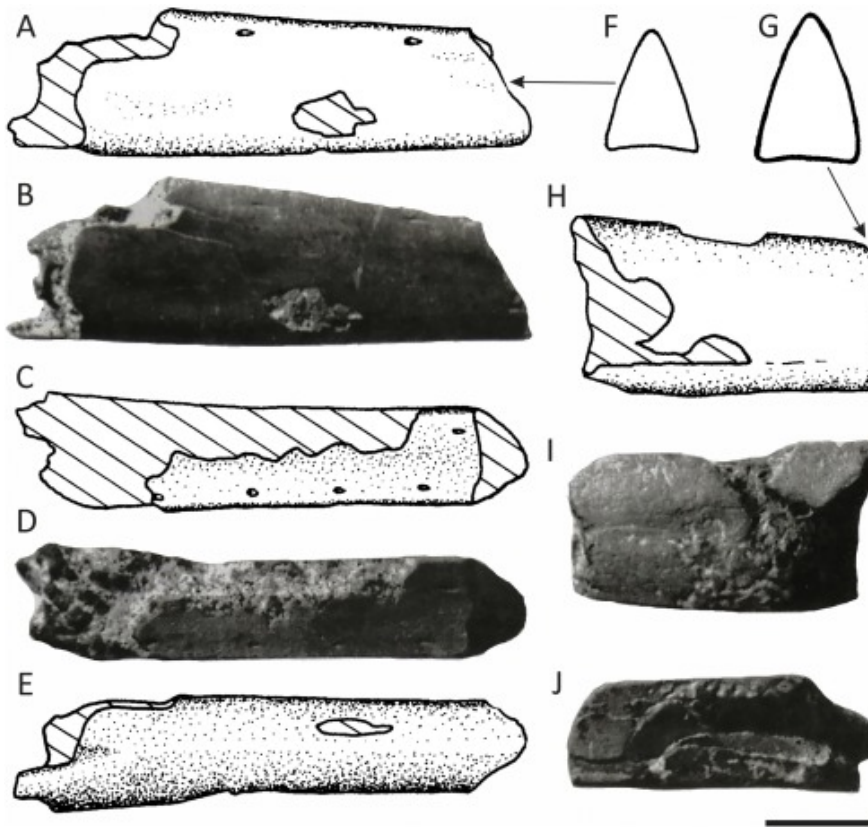
836 **Fig. 2.** A historical timeline of the taxonomy and research of *Ornithostoma*.

837



838

839 **Fig. 3.** Owen's 1959a illustration reproduced here. As Owen considered the specimen to be a wing
840 finger metacarpal he labelled it side view (B in this figure) and 'back' view (C in this figure). Here A
841 and D are the proximal and distal views respectively.



842

843 **Fig. 4.** Illustrations and photographs of the edentulous pterosaur jaw fragments mentioned by
 844 Seeley (1871: p.35) and Unwin (2001, p. 212). Present whereabouts of the specimens are unknown.
 845 A-F CAMSM UNREG 1: A-B, right lateral view; C-D, occlusal view; E, dorsal view; F, anterior cross
 846 section outline. G-J: CAMSM UNREG 2: G, anterior cross section outline; H. right lateral view; I, left
 847 lateral view; J, occlusal view. Scale bar represents 10 mm. Taken from Unwin, 1991.

848



849

850 **Fig. 5.** Edentulous pterosaur specimens on their cards are seen in the museum collections. A. The
 851 holotype of *Ornithostoma sedgwicki* Seeley, 1891 from the Cambridge Greensand Member of the
 852 West Melbury Marly Chalk Formation, Cambridgeshire, with successive citations listed. B. Several
 853 specimens labelled as 'Jaws of Fish' from the Booth Museum, Brighton with the newly identified
 854 edentulous pterosaur specimen (BMB 019582) (red arrow) as found in the collection. C. A card of
 855 'Cestraciontid finray' with two misidentified edentulous pterosaur specimens (CAMSM B40085 and
 856 CAMSM B40091) (red arrows) as found in the Sedgewick Museum collection.

857



858

859 **Fig. 6.** Partial pterosaur symphyseal mandible. Holotype of *Ornithostoma sedgwicki* Seeley, 1891

860 (CAMSM B54485) from the Cambridge Greensand of Cambridgeshire, UK. A, occlusal (dorsal) view.

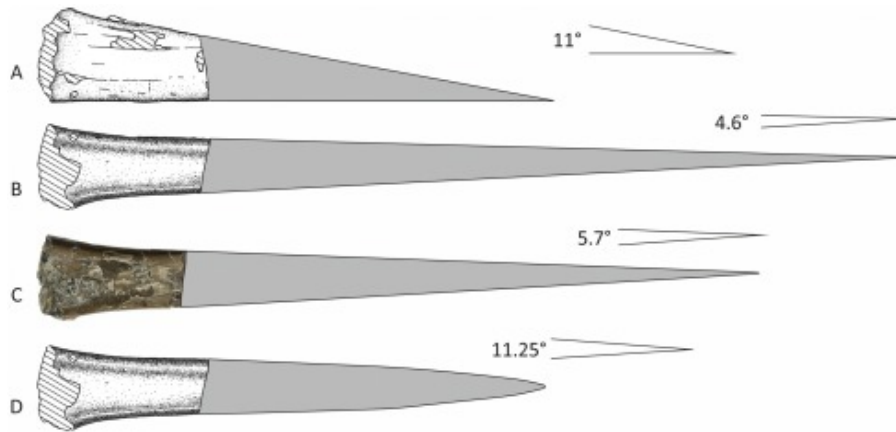
861 B, ventral view. C, right lateral view. D, left lateral view. E, caudal view. F, cranial view of cut surface.

862 G, six small fragments apparently generated during cutting for a thin section have been excluded

863 from this illustration. Images used under Creative Commons protocol, and are attributed © GB3D

864 Type Fossils / Sedgwick Museum, Cambridge, and can be accessed here: <http://www.3d->865 [fossils.ac.uk/fossilType.cfm?typSampleId=20004040](http://www.3d-fossils.ac.uk/fossilType.cfm?typSampleId=20004040). Scale bar represents 10 mm.

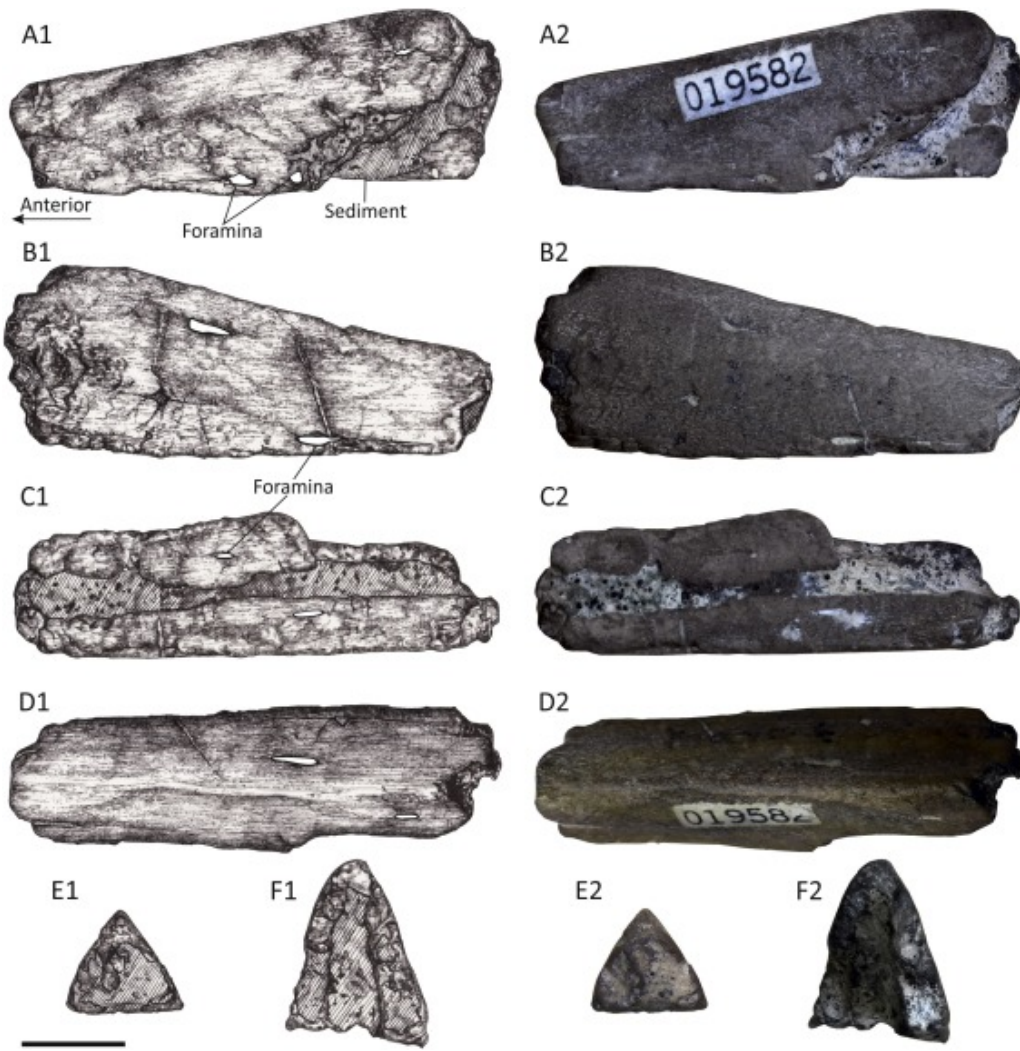
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868 **Fig. 7.** An attempt to restore the missing mandibular tip of the *Ornithostoma* holotype by simple
 869 projections of the ventral and occlusal margins and lateral margins when seen in dorsal and right
 870 lateral views. A, restoration of the lateral aspect based on drawing from Unwin (2001, fig. 13A). B,
 871 restoration of lateral margins using image from Unwin (2001, fig. 13C). C, projection of lateral
 872 margins from photograph of specimen. D, restoration of jaw tip to length of projection based on
 873 lateral margins in A. Lateral and dorsal angles for each restoration are given. E. A schematically
 874 restoration of the mandible of *Ornithostoma* showing its approximate location of the holotype
 875 CAMSM B54485.

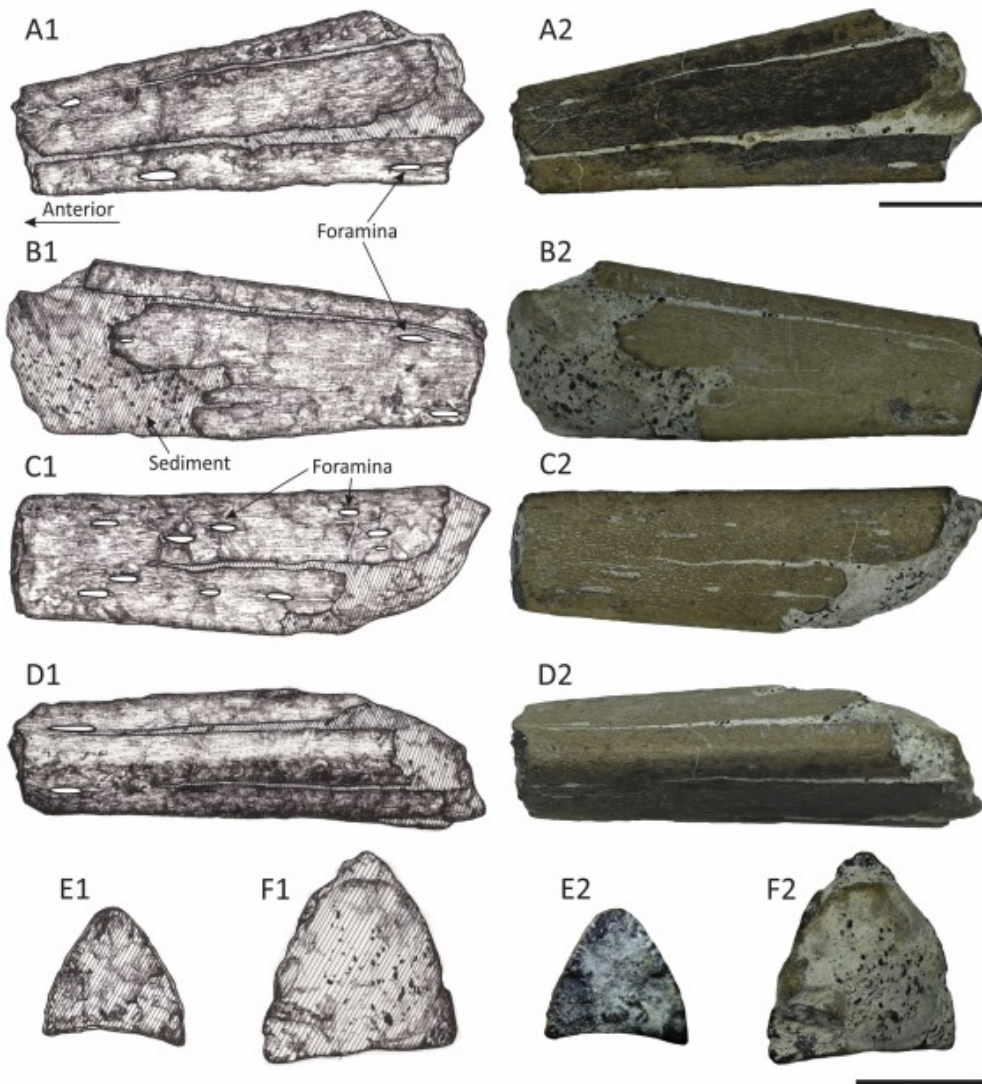
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878 **Fig. 8.** Images of an edentulous jaw fragment (BMB 019582) from the Cambridge Greensand, with
 879 interpretative drawings referred to *Ornithostoma sedgwickii*. A1-A2. Left lateral; B1-B2, right lateral;
 880 C1-C2, occlusal; D1-D2, dorsal, E1-E2, distal end; F1-F2, proximal end. Scale bar represents 5 mm.

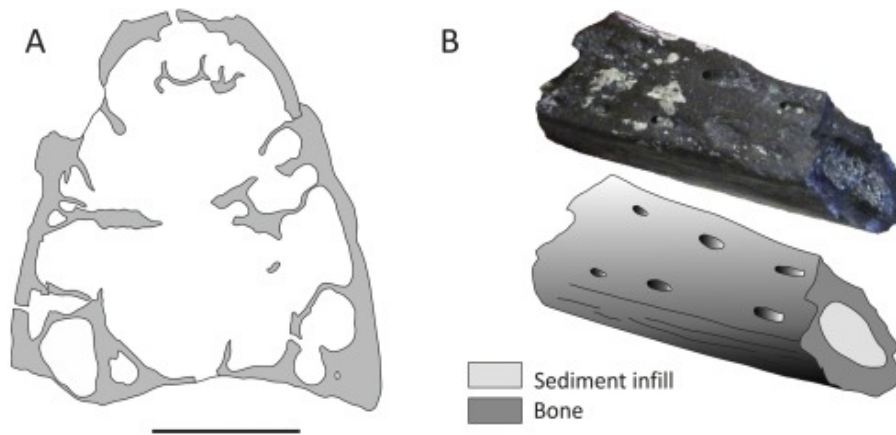
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883 **Fig. 9.** Images of an edentulous jaw fragment (CAMSM B40091) from the Cambridge Greensand,
 884 with interpretative drawings referred to *Ornithostoma sedgwickii*. A1-A2. Left lateral; B1-B2, right
 885 lateral; C1-C2, occlusal; D1-D2, dorsal, E1-E2, distal end; F1-F2, proximal end. Scale bar represents 5
 886 mm.

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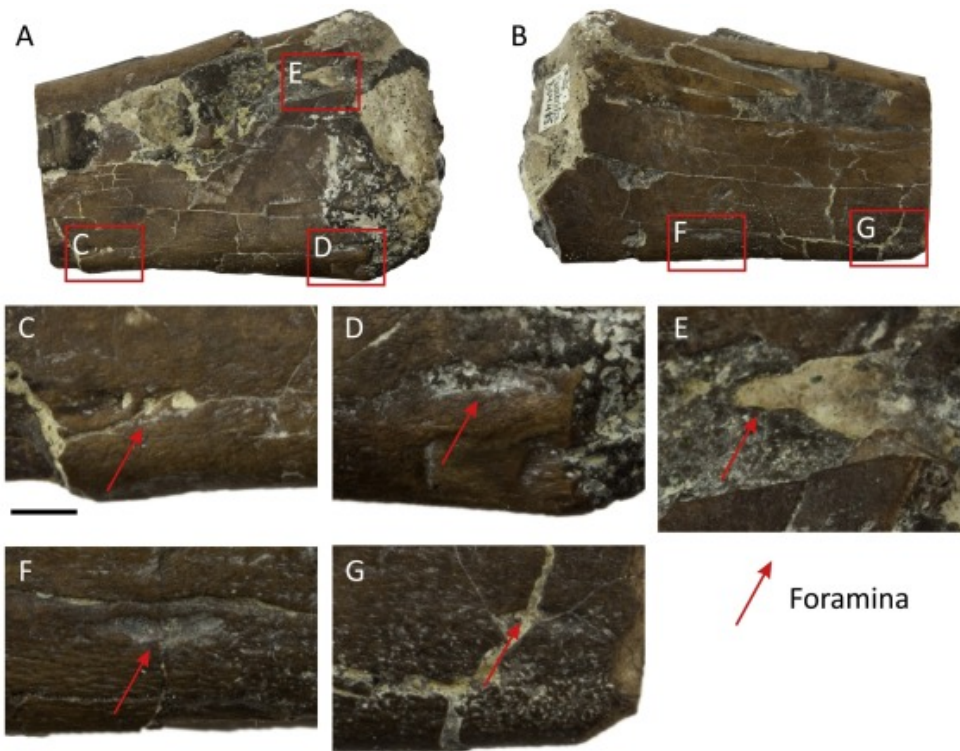


888

889 **Fig. 10.** Images of an edentulous jaw fragment (CAMSM B40085) from the Cambridge Greensand,
 890 with interpretative drawings referred to *Azhdarchoidea* indet. A1-A2. Left lateral; B1-B2, right
 891 lateral; C1-C2, occlusal; D1-D2, dorsal, E1-E2, distal end; F1-F2, proximal end. Scale bar represents 5
 892 mm.

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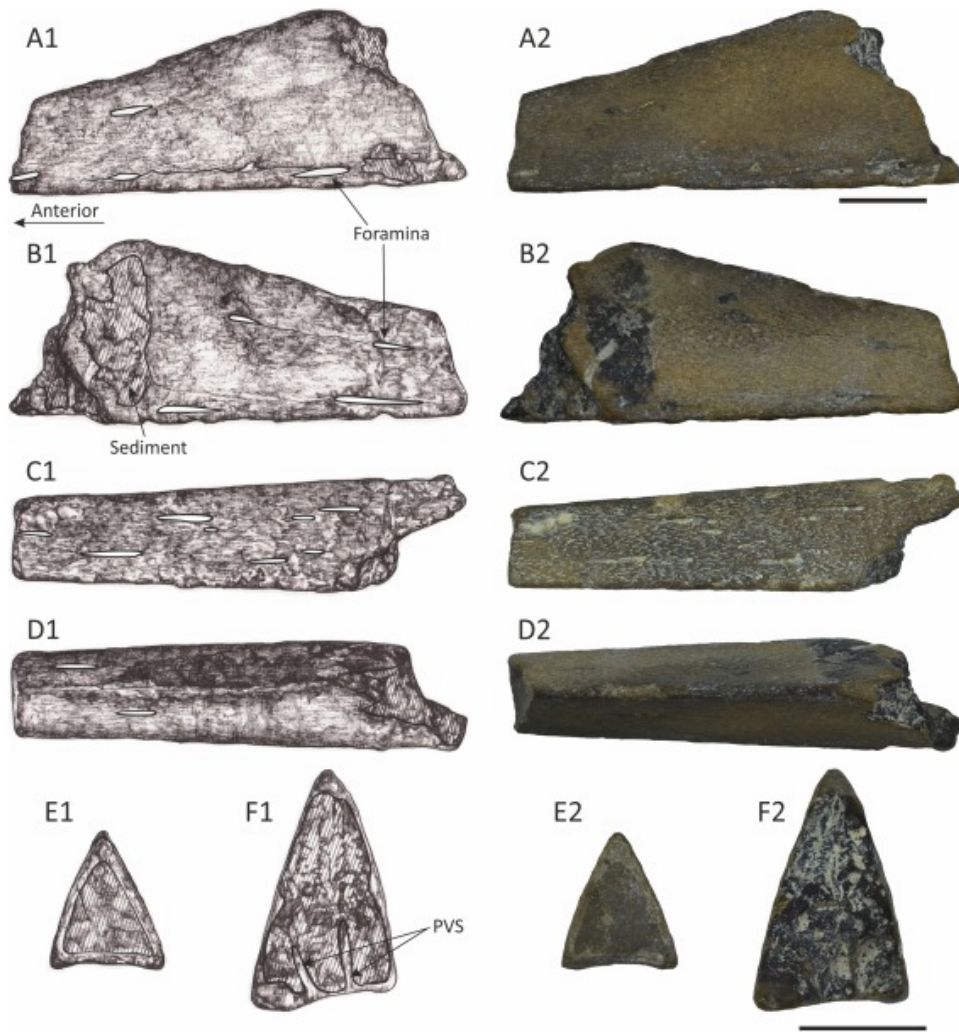
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895

896 **Fig. 11.** Reconstructed cross sections of mandibular symphyses of various azhdarchoid pterosaurs. **A.**
 897 *Ornithostoma sedgwicki* (CAMSM B54485); **B.** *Bakonydraco galaczi* (MTM V 2007.111.1) based on
 898 Prondvai et al. (2014); **C.** *Aptorhamphus gyrostega* (FSAC-KK 5013) from McPhee et al. (2020); **D.**
 899 *Xericeps curvirostris* (FSAC-KK 10700) from Martill et al. (2018); **E.** *Pteranodon* sp. (YPM 2376) from
 900 Bennett (2001); **F.** *Volgadraco bogolubovi* (SGU 46/104a) from Averianov et al. (2008); **G.** c.f.
 901 *Tupuxuara* sp. (UOP-PAL-MS0001) from McPhee et al. (2020); **H.** *Banguela* (= *Thalassodromeus*)
 902 (NMSG SAO 251093) from Headden and Campos (2014); **I.** *Albadraco tharmisensis* (PSMUBB V651b)
 903 from Solomon et al. (2020); **J.** *Mistralazhdarcho maggii* (MMS/VBN.09.C.001a) from Vullo et al.
 904 (2018); **K.** *Alanqa saharica* (FSAC-KK 26) from Ibrahim et al. (2010); **L.** *Aymberedactylus cearensis*,
 905 (MN 7596-V) from Pêgas et al. (2016); **M.** *Afrotapejara zouhrii* (BSP 1997 167) from Wellnhofer and
 906 Buffetaut (1999); Not drawn to scale.

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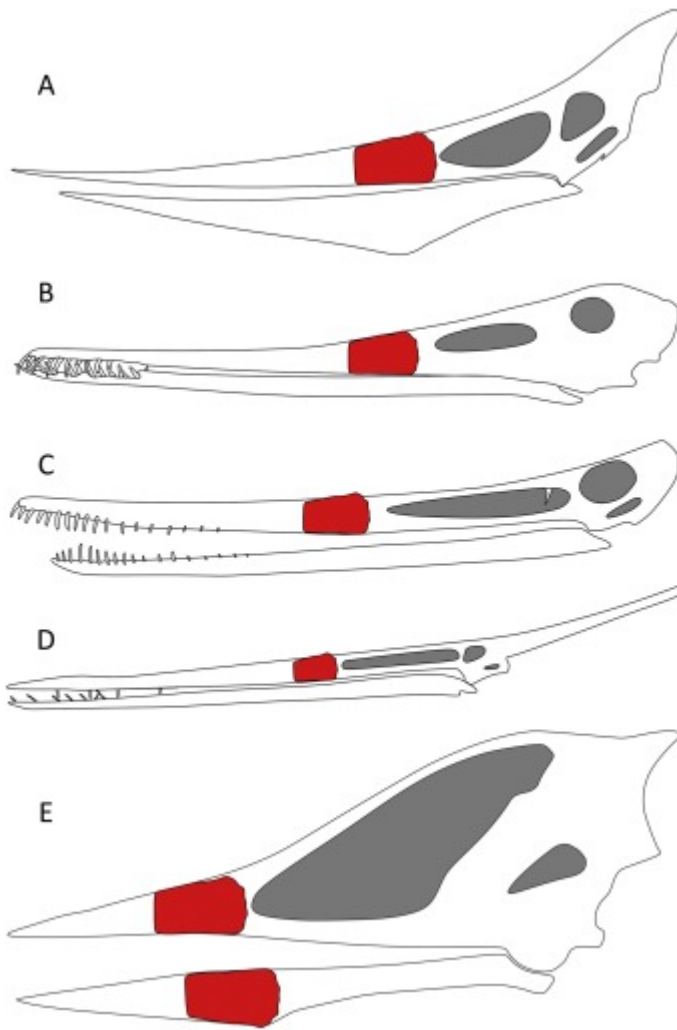
909 **Fig. 12.** A. Diagram of the cut end of the holotype of *Ornithostoma sedgwicki* (CAMBS SM B 54485).

910 Taken from Steel (2004). Photomicrographs of parts of this section are provided by Steel (2004, Figs

911 3.29-3.31). The image has been inverted to conform with its identity as a mandibular symphysis. B,

912 portion of anterior mandible of *Bakonydraco* and interpretive diagram showing thickened bone wall913 and prominent paired foramina on occlusal surface distinguishing it from *Ornithostoma*.

914



915

916 **Fig. 13.** Possible chaoyangopterid from the Crato Formation of Brazil. A, complete skull with
 917 mandible in left lateral view. B, isolated mandible with mandibular rami crushed laterally. C, close up
 918 of mandibular symphysis of B, showing sulcate occlusal surface, rounded margins, lack of neural
 919 foramina and posteriorly flaring lateral margins.

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923 **Tables**

924 **Table 1.** Table of measurements. CAMSM B54485: the holotype of *Ornithostoma sedgwicki*, BMB
 925 019582 and CAMSM B40091: specimens referred to *Ornithostoma*, CAMSM B40085: specimen
 926 referred to *Azhdarchoidea* indet. CAMSM UNREG 1 and CAMSM UNREG 2 lost specimens mentioned
 927 by Seeley (1869: xvi) and Unwin (2001, p. 212) (Measurements from Unwin, 1991). * indicates
 928 specimen length before thin sectioning by Steel (2004).

Specimen	Length	Anterior height	Posterior height	Anterior occlusal width	Posterior occlusal width	Lateral angle	Dorsal angle
CAMSM B54485	48 mm (59.2 mm*)	22 mm (23 mm*)	33.9 mm	18 mm (19.7 mm*)	29.4 mm	~11 °	~5 °
BMB 019582	23.7 mm	5.5 mm	8.8 mm	5.8 mm	7.2 mm	~12 °	~7 °
CAMSM B40091	23.5 mm	5.5 mm	9.5 mm	5.8 mm	7.2 mm	~12 °	~6 °
CAMSM B40085	26.3 mm	5.5 mm	10.4 mm	4.7 mm	6.5 mm	~16 °	~4.5 °
CAMSM UNREG 1	44.5 mm	9.6 mm	12.7 mm	8.4 mm	~10 mm	?~9 °	?~2 °
CAMSM UNREG 2	25.7 mm	11.9 mm	14.4 mm	9.0 mm	9.9 mm	?~7 °	?~2 °

929

930