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PALEONTOLOGY

On the validity of the genus *Amblydectes* Hooley 1914 (Pterodactyloidea, Anhangueridae) and the presence of Tropeognathinae in the Cambridge Greensand

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Abstract: *Amblydectes* is a problematic genus proposed more than a century ago for several pterosaur specimens from the Cambridge Greensand. Its problematic nature is due to the fragmentary preservation of the referred specimens, limited to several rostral tips. In the present work is reassessed the validity of *Amblydectes crassidens* based on new anatomical comparisons and phylogenetic analysis, as well as the description of a new specimen. The results of this work confirm the validity of the species as belonging to the clade Tropeognathinae, a recently proposed group of robust anhanguerids which have only been known so far from Gondwanan landmasses. *Amblydectes* is proposed as a monospecific genus, whilst one the former attributed species is assigned to a new genus, *Draigwenia*, which is proposed as a non-anhanguerian lanceodontian taxon of uncertain placement. The presence of a tropeognathine anhanguerid in the Cambridge Greensand suggests that anhanguerid diversity was really complex both locally and globally.

Key words: Pterosauria, Pterodactyloidea, *Amblydectes*, Cambridge Greensand, Cretaceous.

INTRODUCTION

The Cambridge Greensand is one of the richest pterosaur-yielding geological units in the world, with over two thousand known specimens up to date (e.g., Unwin 2001, Rodrigues & Kellner 2013). Most species from the Cambridge Greensand were tentatively ascribed to the genus *Ornithocheirus* during the last decades of the 19th century (e.g., Seeley 1870, Lydekker 1888, Woods 1891). Such bunching of species within this genus was referred as the *Ornithocheirus* complex: a wastebasket genus for species of uncertain relationships characterised by fragmentary type specimens (Rodrigues & Kellner 2013). One of the first key reviews of the *Ornithocheirus* complex was realised by Hooley (1914). In his reassessment of the *Ornithocheirus* complex, Hooley (1914) provided a revision of the species known up to that time, separating them in several genera based on a certain combination of morphological characters (Hooley 1914, Rodrigues & Kellner 2013). One of such genera established by Hooley (1914) was *Amblydectes*, which was recognised by "*[...] beaks with strong lateral compression forming a dorsal keel, triangular in section, truncated tip, and moderate vertical depth. Dorsal outline rising from the tip at a high angle. Longitudinal ridge on palate as in* Ornithocheirus. *Very large circular teeth, anterior much larger than posterior, none directed forward.*" (Hooley 1914: p. 536).

Later, Kuhn (1967) was the first author to establish *Amblydectes crassidens* as the type species for the genus *Amblydectes* (Kuhn 1967: p. 46, but using the term «genotypus» instead of type species; see also Rodrigues & Kellner 2013). However, Kuhn (1967) considered the genus *Amblydectes* as uncertain and claimed it as synonym of *Ornithocheirus* (Rodrigues & Kellner 2013).

Besides *Amblydectes crassidens*, two other species were originally ascribed by Hooley (1914) within the genus *Amblydectes*: *A.erygnathus* and *A.platystomus*. The latter was originally described as *Ornithocheirus platystomus* by Seeley (1870), being included in the genus *Amblydectes* by Hooley (1914), and many years later to the genus *Lonchodectes* by Unwin (2001). In their extensive review of the *Ornithocheirus* complex, Rodrigues & Kellner (2013) considered "*Ornithocheirus*" *platystomus* out of Lonchodrachonidae due to the absence of both raised alveolar rims and a deep palatal ridge, which results in the lack of a parapet-like palate (characteristic of the "Lonchodectidae" *sensu* Unwin 2001). Furthermore, Rodrigues & Kellner (2013) highlighted in their description of this species "*[...] presents a relatively tall rostrum, whose dorsal margin forms an angle with the ventral one; this angle lies between those in* Ornithocheirus simus *and* Cimoliopterus cuvieri. *The angle (about 27°) is so far unique among the species of the* Ornithocheirus *complex and confirms it as a valid taxon.*" (Rodrigues & Kellner 2013: p. 47).

On the other hand, the type species *Amblydectes crassidens* was originally attributed to the genus *Ornithocheirus* by Seeley (1870), considered "Criorhynchidae *incertae sedis*" [sic] by Wellnhofer (1978), and lately referred as a *Coloborhynchus sedgwickii* specimen by Unwin (2001). Rodrigues & Kellner (2013) deemed as *nomen dubium* due to "*[...] neither a ridge nor a sulcus are evident and thus it is not possible to identify it with certainty*." (Rodrigues & Kellner 2013: p. 59). The third species, *Amblydectes eurygnathus*, had a similar story to the type species: originally attributed to the genus *Ornithocheirus* by Seeley (1870), considered "Criorhynchidae *incertae sedis*" [sic] by Wellnhofer (1978), posteriorly referred as a *Coloborhynchus capito* specimen by Unwin (2001), and finally as *nomen dubium* by Rodrigues & Kellner (2013). In the latter work, the authors tentatively referred the specimen as an upper jaw –*Amblydectes eurygnathus* was originally recognised as a lower jaw by Seeley (1870)–, but stating clear that "*[...] the presence of neither a palatal ridge nor a dentary sulcus could be recognised in the specimen, so it is not possible to identify it as an upper jaw with certainty*." (Rodrigues & Kellner 2013: p. 62).

Recently, in their reassessment of the *Coloborhynchus* complex, Holgado & Pêgas (2020) reconsidered the validity of two species previously attributed to the genus *Amblydectes*: the type species *Amblydectes crassidens* and *Amblydectes*(?) *eurygnathus* "*[...] as potentially valid species of non-coloborhynchine anhanguerids*." (Holgado & Pêgas: p. 13) due to the absence of several synapomorphies that characterised the clade Coloborhynchinae. Furthermore, Holgado & Pêgas (2020) also noted that *Amblydectes crassidens* neither is an anhanguerine anhanguerid "*[...] since they lack an enlarged 4th pair of upper teeth, which is characteristic of the Anhanguerinae (Holgado et al. 2019)*." (Holgado & Pêgas: p.13). Due to a revision of the genus *Amblydectes* was out of the scope in that work, a taxonomic reassessment was pending in order to clarify the taxonomic validity of this former genus.

Here I reassess the validity of the genus *Amblydectes* from a taxonomic and phylogenetic perspective, including the validity of all species previously recognised to this genus and the description of a new specimen that fits in the type species, *Amblydectes crassidens*.

MATERIALS AND METHODS

Phylogenetic Analysis

The phylogenetic analysis performed here is based on a data matrix modified from Holgado & Pêgas (2020), with the inclusion of the scoring of *Amblydectes crassidens* as follows:

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The modifications on the matrix were performed using the software Mesquite 3.6 (Maddison & Maddison 2018). The phylogenetic analysis was performed using the software TNT 1.5 (Goloboff & Catalano 2016). Search for the most parsimonious trees (MPTs) was conducted via Traditional Search (TBR swapping algorithm), 10 000 replicates, random seed, and collapsing trees after search. It was also conducted an analysis via New Technology in order to recover the island with the minimum length trees (MLTs). The parameters used in this analysis were Sectorial Search, ratchet (parameters: 20 substitutions made, or 99% swapping completed, six up-weighting prob., six down-weighting prob., and a total number of iterations of 10), tree fusing, Driven search (15 initial addseqs., 15 times of min. length), random seed, and without collapsing trees after search. Subsequently, the results of the New Technology were analysed via Traditional Search (TBR swapping algorithm), starting trees from RAM, and without collapsing trees after search. The latter search aimed for recovering the maximum trees of the island recovered from the first analysis.

Other Data Analyses

Due to the fragmentary nature of the Cambridge Greensand pterosaur specimens, they were taken several other measurements in order to understand their shape variability. In this sense, the angle of the dorsal margin respect the ventral margin up to the 3rd pair of alveoli as well as two alveoli spacing ratios –(a) the ratio of the half distance between the 2nd pair of alveoli, and the mean value of the spacing of these alveoli between the alveoli pair which immediately precedes (1st pair); and (b) the ratio of the half distance between the 3rd pair of alveoli, and the mean value of the spacing of these alveoli between the alveoli pair which immediately precedes (2nd pair)– were estimated.

A total of 49 different lanceodontian jaw elements –including both upper and lower jaws of those available specimens– were sampled to estimate the margin angle and both alveoli spacing ratios. This sample includes most of the Cambridge Greensand lanceodontian jaws up to the 3rd pair of alveoli (see Rodrigues & Kellner 2013, Holgado & Pêgas 2020), as well as several other three-dimensional preserved lanceodontian from other sites, including most of anhanguerians and targaryendraconians (see Rodrigues & Kellner 2013, Pinheiro & Rodrigues 2017, Pêgas et al. 2019). Measurements for the angle and ratios were taken using free software FIJI (Fiji Is Just ImageJ) for image analysis (Schindelin et al. 2012). For further details on the sample see Table I.

Two different statistical analyses were performed with distinct purpose. First off a boxplot diagram in order to show the variation between the spacing ratios and how those specimens with ambiguous number of alveoli could be related (see Table I and Rodrigues & Kellner 2013 for further details). The latter was a canonical variates analysis (CVA), which was performed to discriminate all sampled

Table I. Sample of lanceodontian jaw elements here analysed, which are listed following its taxonomic attribution, specimen, upper or lower jaw (UJ and LW, respectively), spacing ratios (SR) between the second and first pair of alveoli and between the third and second pair, and values obtained from the canonical axes (CA). Uncertain identifications are preceded by a question mark.

Taxon	Specimen	Bone	SR (2nd–1st)	SR (3rd–2nd)	Angle	CA1	CA2
Amblydectes crassidens	CAMSM B54499	?UJ	4.963	2.174	47	1.326	0.297
	CAMSM B54644	?LJ	2.626	?	46	-	-
	NHMUK PV R546	?LJ	2.854	2.270	52	2.003	0.506
Draigwenia platystomus comb. nov.	CAMSM B54835	?UJ	?	0.983	27	-2.824	-3.897
Tropeognathus mesembrinus	SNSB/BSPG 1987 I 47	UJ	2.546	2.314	69	3.802	0.040
		LJ	2.151	1.937	52	1.409	-0.882
Ferrodraco lentoni	AODF 876	UJ	3.910	2.118	72	3.756	-0.890
Siroccopteryx moroccensis	LINHM FR016	UJ	3.237	2.344	83	5.272	-0.369
Aerodraco sedgwickii	CAMSM B54422	UJ	6.713	2.466	86	5.794	0.024
Coloborhynchus clavirostris	NHMUK PV R1822	UJ	5.199	1.990	90	5.349	-2.110
Nicorhynchus capito	CAMSM B54625	UJ	6.805	2.045	89	5.346	-1.843
	CAMSM B54434	UJ	5.927	2.137	88	5.409	-1.422
Uktenadactylus wadleighi	SMU 73058	UJ	3.050	2.699	87	6.311	0.956
Anhanguera blittersdorffi	MN 4805-V	UJ	2.925	2.340	31	0.003	1.599
Anhanguera piscator	NSM-PV 19892	UJ	2.739	2.210	18	-1.545	1.554
		LJ	2.624	1.870	21	-1.848	0.024
Anhanguera spielbergi	RGM 401 880	UJ	3.070	2.351	35	0.427	1.492
Anhanguera sp.	AMNH FARB 22555	UJ	3.123	2.326	17	-1.439	2.075
	MSNVE 21232	UJ	2.875	2.055	38	0.203	0.145
	NMSG/SAO 200602	LJ	2.693	2.070	29	-0.681	0.551
	SMNK PAL 1136	UJ	2.984	2.283	34	0.205	1.247
	SMNK PAL 2302	LJ	2.711	1.998	33	-0.405	0.099
	SNSB/BSPG 1987 I 47	LJ	2.679	2.028	34	-0.250	0.186

Table I. Continuation.

Brasileodactylus araripensis	MN 4804-V	LJ	2.542	2.332	18	-1.327	2.062
Cearadactylus atrox	MN 7019-V	UJ	2.790	2.361	12	-1.882	2.412
?*Cearadactylus ligabuei*	CCSRL 12692/12713	UJ	2.982	2.453	17	-1.212	2.604
Maaradactylus kellneri	MPSC R 2357	UJ	3.264	2.275	59	2.720	0.260
Caulkicephalus trimicrodon	IWCMS 2002 189.1	UJ	3.032	2.491	22	-0.638	2.571
Hamipterus tianshanensis	IVPP V18936	UJ	3.960	2.237	13	-2.002	1.857
		LJ	2.196	2.018	11	-2.596	1.022
Iberodactylus andreui	MPZ-2014/1	UJ	3.076	1.986	19	-1.843	0.583
Aussiedraco molnari	QM F10613	LJ	1.333	1.258	12	-3.851	-2.180
Barbosania gracilirostris	MNHS 0085	UJ	1.952	1.470	11	-3.574	-1.259
		LJ	1.281	1.810	16	-2.461	-0.035
Targaryendraco wiedenrothi	SMNS 56628	LJ	1.356	1.395	14	-3.404	-1.686
Camposipterus nasutus	CAMSM B54556	UJ	3.375	2.022	12	-2.487	1.001
Cimoliopterus cuvieri	NHMUK PV 39409	UJ	2.708	1.281	15	-3.506	-2.198
Cimoliopterus dunni	SMU 76892	UJ	3.946	1.482	17	-2.945	-1.438
Ornithocheirus simus	CAMSM B54428	UJ	2.037	1.312	77	2.823	-4.436
Ornithocheirus cf. *simus*	FSAC-KK 5025	UJ	2.131	1.562	79	3.4718	-3.472
Lonchodraco giganteus	NHMUK PV 39412	UJ	1.658	0.981	26	-2.928	-3.867
		LJ	?	0.895	25	-3.183	-4.187
"Ornithocheirus" colorhinus	CAMSM B54431	UJ	3.020	2.418	43	1.357	1.466
"Ornithocheirus" denticulatus	?CAMSM B54794	UJ	1.958	1.648	15	-2.851	-0.671
"Ornithocheirus" polyodon	CAMSM B54440	UJ	2.519	2.316	13	-1.861	2.186
"Pterodactylus" daviesii	NHMUK PV 43074	LJ	1.824	1.575	16	-2.880	-1.013
"Ornithocheirus brachyrhinus"	CAMSM B54443	UJ	2.711	1.782	16	-2.511	-0.151
"Ornithocheirus enchorhychus"	CAMSM B54444	UJ	3.018	1.848	14	-2.595	0.200
"Pterodactylus fittoni"	CAMSM B54423	UJ	?	2.053	13	-2.331	1.091

elements within given groups related to known clades: Anhanguerinae, Coloborhynchinae, Hamipteridae, Lonchodraconidae, Tropeognathinae, and Targaryendraconia. The axes are linear combinations of the following variables: the angle of the dorsal margin respect the ventral margin up to the 3rd pair of alveoli, and the spacing ration of the 3rd pair of alveoli. These statistical data analyses were performed under PAST (PAleontological STatistics) version 3.22 (Hammer et al. 2001, Hammer 2018).

Institutional Abbreviations

CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, England; NHMUK, Natural History Museum, London, England; NMSG/SAO, Naturmuseum St. Gallen / Sammlung Urs Oberli, St. Gallen, St. Gallen Canton, Switzerland; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; SNSB/BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns / Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Nomenclatural Acts

This work and the nomenclatural acts it contains were registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The Zoobank Life Science Identifiers (LSIDs) to the prefix http://zoobank.org/. The LSID for this publication is urn:lsid:zoobank.org:pub:9701DD16-DE2D-43A6-84A2-A1E9A9B7D8D4, and the LSID for the new erected genus is urn:lsid:zoobank.org:act:D38F51D4-5F5B-47F5-94C3-E88EE7BCB722 (*Draigwenia*).

The following valid pterosaur genera and species are mentioned in the main text of this study: *Amblydectes crassidens* (Seeley 1870), *Anhanguera piscator* Kellner & Tomida 2000, *Anhanguera spielbergi* (Veldmeijer 2003), *Camposipterus nasutus* (Seeley 1870), *Cimoliopterus cuvieri* (Bowerbank 1851), *Ferrodraco lentoni* Pentland et al. 2019, *Lonchodraco giganteus* (Bowerbank 1846), *Mythunga camara* Molnar & Thulborn 2008, *Ornithocheirus simus* (Owen 1861), *Siroccopteryx moroccensis* Mader & Kellner 1999, and *Tropeognathus mesembrinus* Wellnhofer 1987.

REVIEW OF SPECIES

Amblydectes crassidens as a valid species

The holotype of *Amblydectes crassidens* (CAMSM B54499) is a 45 mm long incomplete anterior portion of the rostral tip (Fig. 1), in which is lacking much of the left side, particularly the lateral and occlusal surfaces. It could be recognised the alveoli from the 1st to the 4th pair of the right teeth, being the last preserved alveolus significantly smaller than in the anterior alveoli.

The anatomical position of CAMSM B54499 as upper or lower jaw was controversial in the literature. Originally, Seeley (1870) tentatively identified it as an upper jaw, but Rodrigues & Kellner (2013) noted that "*[b]ased on its height the holotype seems to be an upper jaw, but neither a ridge nor a sulcus are evident and thus it is not possible to identify it with certainty*." (Rodrigues & Kellner 2013: p. 59). Nevertheless, the placement of the first alveolus with respect to the sagittal axis of the premaxillary crest (Fig. 1e), a feature observed in several anhanguerids (e.g., Wellnhofer 1987: fig. 2a, Kellner & Tomida 2000: figs. 4-6, 10-11, 62, and 66-68, Fastnacht 2001: figs. 2-3, Rodrigues & Kellner: fig. 22b, Holgado & Pêgas 2020: fig. 9), allows to identify CAMSM B54499 as an upper jaw.

Although they have fairly high sagittal crests, "*Ornithocheirus eurygnathus*" (CAMSM B54644) and NHMUK PV R546 could be considered dentary tips due to their placement of the first pair of alveoli and the distance between them (Figs. 2-3), which matches with other anhanguerid dentary

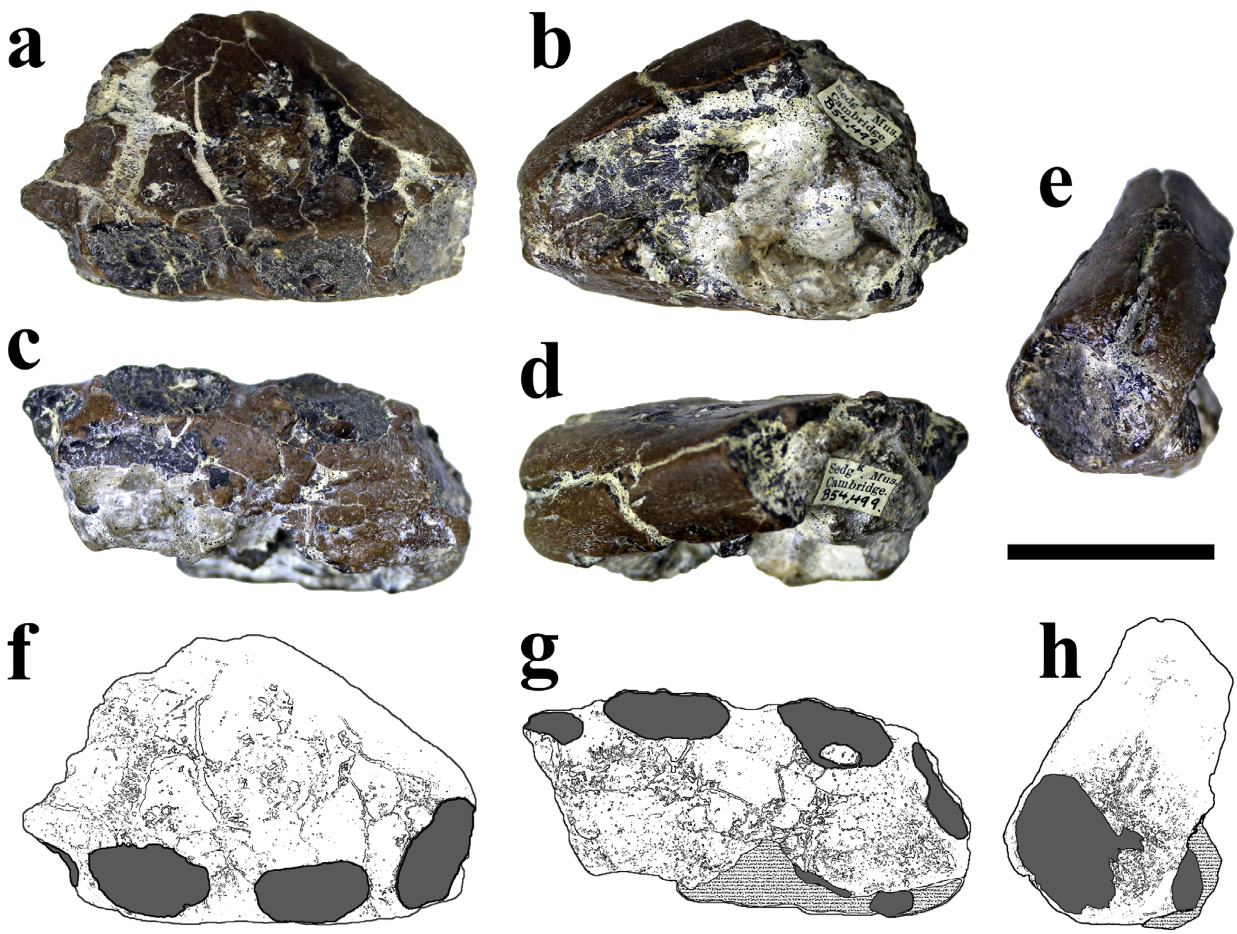

Figure 1. ***Amblydectes crassidens*, holotype CAMSM B54499 (Albian, Cambridge Greensand), anterior part of the rostrum in (a) right lateral, (b) left lateral, (c) palatal, (d) dorsal, and (e) anterior views. Interpretative drawings of the specimen in (f) right lateral, (g) palatal, and (h) anterior views. Scale bar = 20mm.**

tips with high sagittal crests as *Tropeognathus mesembrinus* (e.g., Wellnhofer 1987: fig. 2b, Kellner & Tomida 2000: fig. 67a, Fastnacht 2001: fig. 8) and several dentaries attributed to the genus *Anhanguera* as NMSG/SAO 200602, SNSB/BSPG 1987 I 47, and SMNK PAL 2302 (Wellnhofer 1987: fig. 3, Fastnacht 2001: figs. 4-5, Veldmeijer et al. 2005: figs. 3 and 5; Veldmeijer et al. 2006: fig. 7), including the holotypes of *Anhanguera piscator* (Kellner & Tomida 2000: figs. 4-5 and 10-11, Veldmeijer et al. 2006: fig. 8) and *Anhanguera spielbergi* (Veldmeijer 2003: fig. 4; Veldmeijer 2006: fig. 2.6). Substantial differences between upper and lower jaws of several anhanguerian specimens could be noted at the Table II, which exhibits the ratio of the spacing between the first pair alveoli and the total distance of the element at that line of such specimens.

In the present work are also noted more than a few similarities between both specimens and other tropeognathines, corroborating its assignment within the Tropeognathinae. The holotype of *Amblydectes crassidens* is characterised by a premaxillary sagittal crest reaching rostral tip, a character broadly shared by all tropeognathines (Holgado & Pêgas 2020). The premaxillary sagittal crest present also a relatively broad anterior base, as in in *Tropeognathus mesembrinus* and *Ferrodraco lentoni*, a feature which is roughly distributed

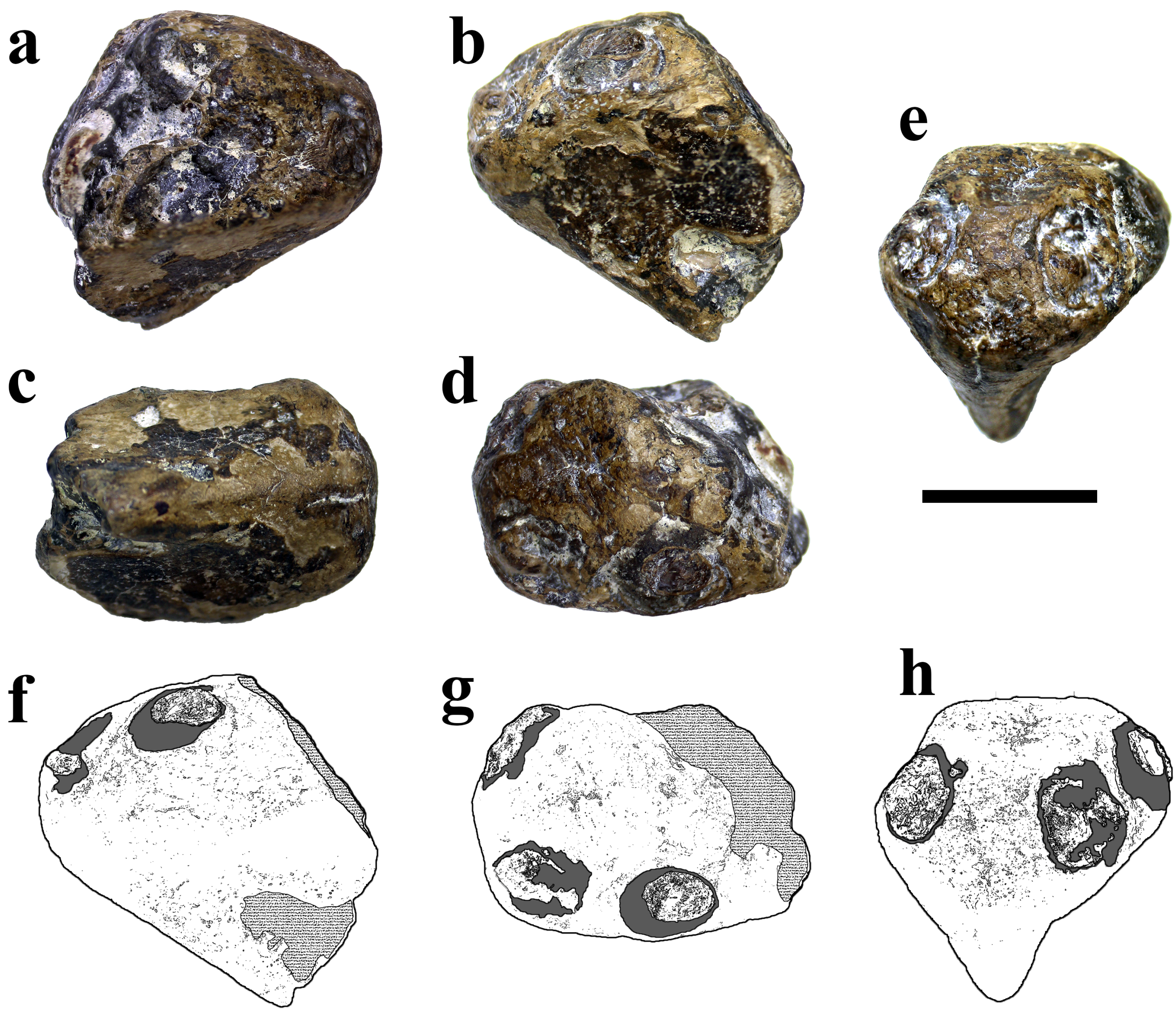

Figure 2. ***Amblydectes crassidens*, referred specimen CAMSM B54644 (Albian, Cambridge Greensand), anterior part of the dentary in (a) right ventrolateral, (b) left lateral, (c) ventral, (d) occlusal, and (e) anterior views. Interpretative drawings of the specimen in (f) right ventrolateral, (g) occlusal, and (h) anterior views. Scale bar = 20mm.**

within Anhangueridae (Holgado & Pêgas 2020). Due to the only 4th preserved alveolus (the right one) is incomplete in the holotype of *Amblydectes crassidens*, at first glance it would not be possible to determine if the 3rd pair of teeth is double the size of the 4th pair (a synapomorphy shared by the coloborhynchines; see Holgado & Pêgas 2020 for further details), but the diameter of the preserved portion of the 4th alveolus is more than 70% of the 3rd right alveolus, differing from such feature shared by the Coloborhynchinae. It is also noteworthy that, even the lack of preservation beyond the fourth alveolus makes extremely difficult to identify with certain whether or not the lateral expansion of the premaxillary tip is reduced as in other tropeognathines (Holgado & Pêgas 2020), when compared with anhanguerines it is recognisable as lesser expansion in *Amblydectes*. In none of the specimens is recognisable a palatal ridge, which led Rodrigues & Kellner (2013) to state both "*Ornithocheirus*" *crassidens* (CAMSM

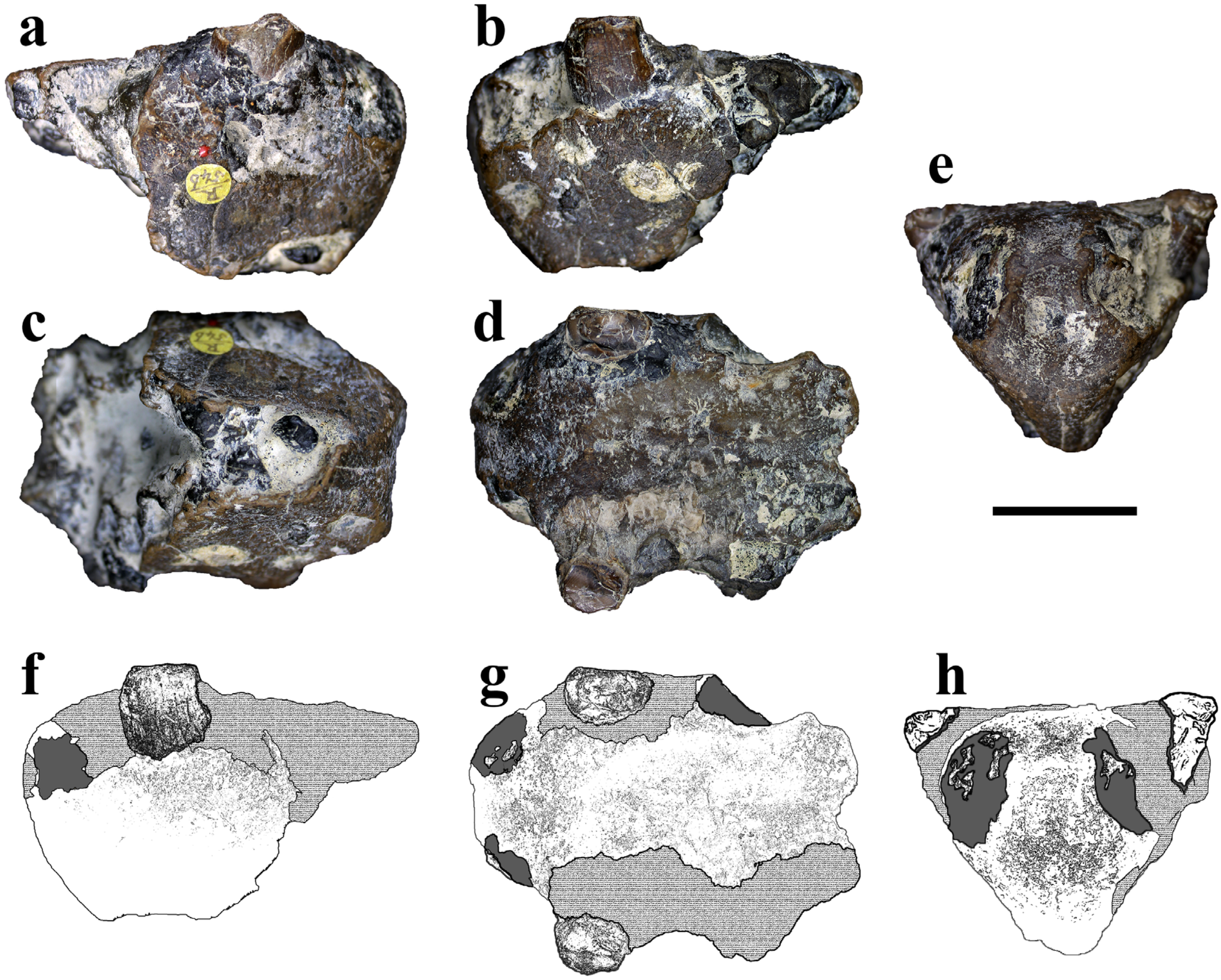

Figure 3. ***Amblydectes crassidens*, referred specimen NHMUK PV R546 (Albian, Cambridge Greensand), anterior part of the dentary in (a) right lateral, (b) left lateral, (c) ventral, (d) occlusal, and (e) anterior views. Interpretative drawings of the specimen in (f) left lateral, (g) occlusal, and (h) anterior views. Scale bar = 20mm.**

B54499) and "*Ornithocheirus eurygnathus*" (CAMSM B54644) as unidentifiable as an upper jaws, and therefore to question their taxonomic validity. However, the absence of a palatal ridge and sagittal sulcus anterior to the fifth tooth position is a feature shared by *Siroccopteryx moroccensis* (just palatal ridge; see Mader & Kellner 1999, Holgado & Pêgas 2020 for further details) and *Tropeognathus mesembrinus* (both ridges of the palate and mandible, respectively; see Wellnhofer 1987, Fastnacht 2001, Veldmeijer 2006 for further details).

Regarding the specimens CAMSM B54644 and NHMUK PV R546 (Figs. 2-3), their nature as dentaries could be alleged on the basis of the placement of the first pair of alveoli, with a distance between them more than twice the width of each alveoli (Figs. 2e and 3e). As pointed out above, this is a frequent feature in anhanguerid dentaries, being observed in several specimens from the Romualdo Formation (Wellnhofer 1987, Kellner & Tomida 2000, Fastnacht 2001, Veldmeijer 2003, 2006). A shallow depression underneath the 1st pair of teeth could be observed in both specimens CAMSM B54644 and NHMUK PV R546

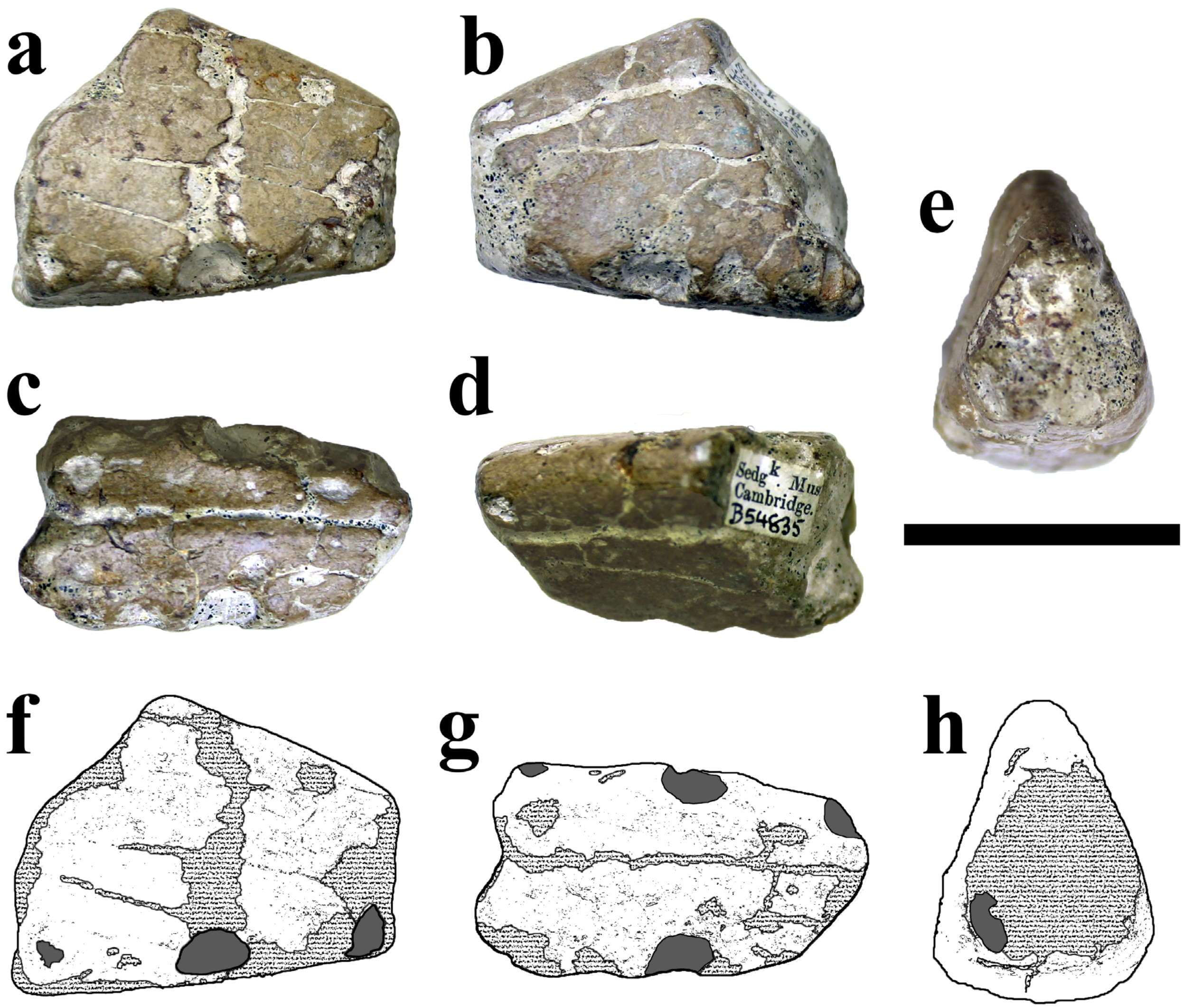

Figure 4. ***Draigwenia platystomus*** **comb. nov., holotype CAMSM B54835 (Albian, Cambridge Greensand), anterior part of the rostrum in (a) right lateral, (b) left lateral, (c) palatal, (d) putative dorsal, and (e) anterior views. Interpretative drawings of the specimen in (f) right lateral, (g) palatal, and (h) anterior views. Scale bar = 20mm.**

(Figs. 2-3). This depression is similar to that of *Tropeognathus*, but it is positioned closer to the alveoli and slightly dorsal due to the shape of the anterior tip in *Amblydectes*. In NHMUK PV R546, the 2nd pair of alveoli bear the broken crowns of both teeth (Fig. 3a). It may be appreciated the curvature of the 2nd right tooth in labial view, mesiodistally hook-shaped and labiolingually slightly compressed. This characteristic shape allows to assert that such tooth is relatively short, a feature clearly distinguishable in other tropeognathines as *Siroccopteryx moroccensis* and *Tropeognathus mesembrinus* (Wellnhofer 1987, Mader & Kellner 1999, Jacobs et al. 2019, Holgado & Pêgas 2020). As noted by Rodrigues & Kellner (2013), the height of the sagittal crest in CAMSM B54644 is fairly high for an anhanguerid dentary, but in *Tropeognathus mesembrinus* and the several specimens formerly associated to *Anhanguera* "*robustus*" –e.g., SNSB/BSPG 1987 I 47 and SMNK PAL 2302– the dentary crest reaches a similar height to that of CAMSM B54644 and NHMUK PV R546 (Wellnhofer 1987, Kellner & Tomida 2000, Pinheiro and Rodrigues

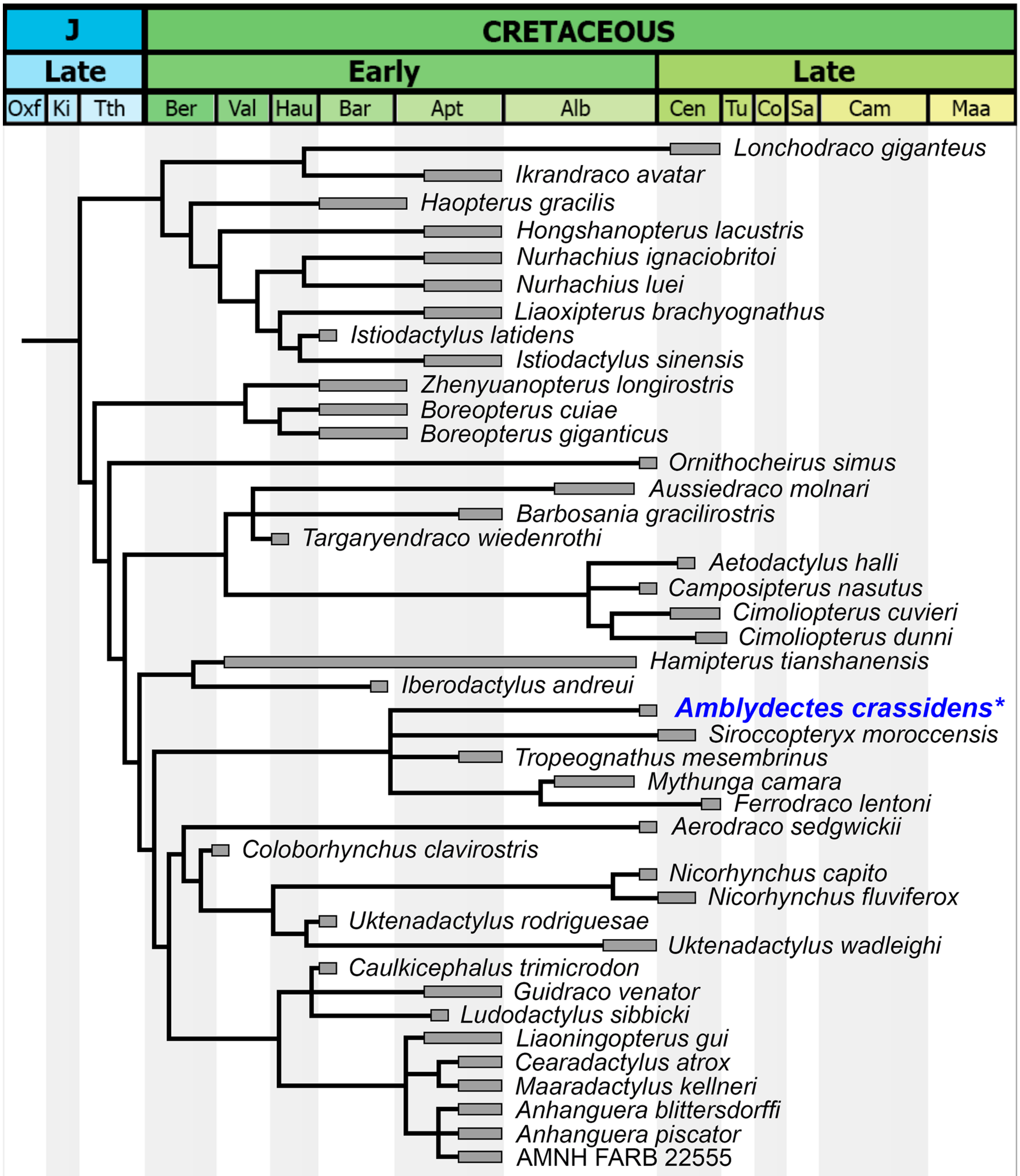

Figure 5. Phylogenetic relationships of *Amblydectes crassidens* within Lanceodontia. Outgroup relationships are not shown (see Holgado & Pêgas 2020 for further details of this data matrix). Intermittent bars show uncertain temporal range. Stratigraphic chart modified from Cohen et al. (2013).

2017). Consequently, the absence of a sagittal sulcus reaching the third pair of teeth is a feature present in *Tropeognathus mesembrinus* dentary but absent in several *Anhanguera* specimens (e.g., SMNK PAL 2302). This could lead us to understand "*Ornithocheirus eurygnathus*" as a tropeognathine dentary and a presumptive junior synonym of *Amblydectes crassidens*.

Table II. Sample of lanceodontian jaw elements here analysed, which are listed following its taxonomic attribution, specimen, upper or lower jaw (UJ and LW, respectively), spacing between the first pair of alveoli (S1PA), total distance of the element at this line (TDEL), and ratios obtained from them. Uncertain identifications are preceded by a question mark.

Taxon	Specimen	Element	S1PA	TDEL	Ratio
Amblydectes crassidens	CAMSM B54644	LJ?	9.23	30.68	0.301
	NHMUK PV R546	LJ?	11.17	39.51	0.283
Anhanguera piscator	NSM PV 19892	UJ	2.48	18.19	0.137
		LJ	10.26	35.23	0.291
Anhanguera spielbergi	RGM 401 880	UJ	5.57	38.03	0.146
		LJ	10.04	35.69	0.281
Anhanguera sp.	AMNH FARB 22555	UJ	3.32	27.58	0.120
	NMSG/SAO 200602	LJ	8.26	29.05	0.284
	SMNK PAL 1136	UJ	2.72	22.94	0.119
	SMNK PAL 2302	LJ	7.45	25.82	0.289
	SNSB/BSPG 1987 I 47	LJ	8.23	26.71	0.308
Brasileodactylus araripensis	MN 4804-V	LJ	5.02	16.99	0.295
Ferrodraco lentoni	AODF 876	UJ	1.66	12.82	0.129
		LJ	2.83	10.12	0.279
Hamipterus tianshanensis	IVPP V18936	UJ	1.91	13.77	0.139
		LJ	4.15	11.54	0.36
Tropeognathus mesembrinus	SNSB/BSPG 1987 I 46	UJ	2.50	35.72	0.07
		LJ	7.54	26.09	0.289

"Ornithocheirus" platystomus as an undefined non-anhanguerian lanceodontian

The monotype of "*Ornithocheirus*" *platystomus* (CAMSM B54835) is a 28 mm long anterior portion of the rostrum, which is broken in its anterior tip (Fig. 4). This is why the first part of alveoli is presumably not preserved, although it is not known categorically whether the first preserved alveoli are the first or the second pair. Unwin (2001) attributed this species to the genus *Lonchodectes*, whilst Rodrigues & Kellner (2013) excluded from the Lonchodraconidae due to the lack of raised alveolar rims and deep palatal ridge. However, these authors retained as a valid taxon because of the featuring angle formed between dorsal and ventral margins of the rostrum. Indeed, this feature is distinctive of all other taxa of the *Ornithocheirus* complex, including the Cimoliopteridae, the Coloborhynchinae, *Amblydectes crassidens* and *Ornithocheirus simus* (see Table I for further details). *Lonchodraco giganteus* shows an angle fairly comparable (Table I), but the layout of the alveoli and palate are significantly different.

Consequently, "*Ornithocheirus*" *platystomus* is unique among all known lanceodontian specimens from the Cambridge Greensand, and it is considered a valid taxon in this work. Nevertheless, due to its patchy preservation and lacking of the anterior tip with apparently the first pair of alveoli, its taxonomic placement remains uncertain. In this sense, it was not included in the data matrix due to it represents an OTU which generates a basal politomy in the clade Lanceodontia. Even so, it is possible to distinguish from the Anhangueria due to the lack of the anterior expansion of the premaxillary tip, which is a synapomorphy of the latter clade.

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup 1834
PTERODACTYLOIDEA Plieninger 1901
ORNITHOCHEIROIDEA Seeley 1870
PTERANODONTOIDEA Marsh 1876 *sensu* Kellner (2003)
LANCEODONTIA Andres et al. 2014
LANCEODONTIA *incertae sedis*
Draigwenia gen. nov.

Etymology: From Welsh *Y Ddraig Wen*, which means 'the white dragon' and it is associated in Welsh mythology with the Anglo-Saxons. This refers to the pale colour of *Draigwenia platystomus* comb. nov. type specimen, together with the usual identification of the extinct pterosaurs with the mythological dragons (e.g., Seeley 1870).

Type species: *Draigwenia platystomus* (Seeley 1870), type by monotypy.

Diagnosis. As for the type species.

Draigwenia platystomus (Seeley 1870)

Holotype. CAMSM B54835, a fragmented anterior portion of the rostral tip (Fig. 4).

Type locality, horizon, and age. Cambridge Greensand, Cambridgeshire, England (Seeley 1870, Unwin 2001, Rodrigues & Kellner 2013). Cenomanian; fossils Albian in age (Unwin 2001, Rodrigues & Kellner 2013).

Revised diagnosis. Lanceodontian pterodactyloid pterosaur characterised by an angle of ~27º between dorsal and ventral margins of the rostrum; small-sized alveoli with a high interdental spacing; and a palatal ridge reaching at least the second pair of alveoli.

ANHANGUERIA Rodrigues & Kellner 2013
ANHANGUERIDAE Campos and Kellner 1985
TROPEOGNATHINAE Holgado & Pêgas 2020
Amblydectes Hooley 1914

Type species: *Amblydectes crassidens* (Seeley 1870), type by monotypy.

Diagnosis. As for the type species.

Amblydectes crassidens (Seeley 1870)

Holotype. CAMSM B54499, a fragmented anterior portion of the rostral tip displaying the alveoli from the 1st to the 4th pair of the right teeth (Fig. 1).

Referred specimens. Holotype of "*Ornithocheirus eurygnathus*" (CAMSM B54644), an anterior fragment of the dentary tip (Fig. 2); and NHMUK PV R546, an anterior portion of the dentary tip displaying the alveoli from the 1st to the 3rd pair, including the 2nd pair of teeth preserved but incisally broken (Fig. 3).

Type locality, horizon, and age. Cambridge Greensand, Cambridgeshire, England (Seeley 1870, Unwin 2001, Rodrigues & Kellner 2013). Cenomanian; fossils Albian in age (Unwin 2001, Rodrigues & Kellner 2013).

Revised diagnosis. Tropeognathine anhanguerian pterosaur characterised by an elevated premaxillary sagittal crest whose tip is arched forming a slight bluntness; a high dentary sagittal crest; and a shallow depression above the 1st pair of dentary alveoli.

PHYLOGENETIC RESULTS

Phylogenetic analysis resulted in 27 most parsimonious trees (MPTs), with 411 steps, a consistency index of 0.637, and a retention index of 0.871. *Amblydectes crassidens* was recovered within the clade Tropeognathinae, in polytomy with *Siroccopteryx moroccensis*, *Tropeognathus mesembrinus*, and *Ferrodraco lentoni* + *Mythunga camara* (Fig. 5). The clade Tropeognathinae is supported by four synapomorphies: premaxillary sagittal crest reaching rostrum tip; premaxillary expansion width reduced (under 130% post-rosette width); teeth relatively short (crown height under 3× diameter); and anterior teeth elongated over twice than wide, but under 4× than wide.

OTHER STATISTICAL RESULTS

The boxplot diagrams displaying the variation with both alveoli spacing ratios of different lanceodontian jaw elements shows that the spacing ratio between the second and first pair of alveoli is slightly higher than the spacing ration between the third and the second (Fig. 6). In the first boxplot (2nd–1st pair), the holotype of *Amblydectes crassidens* is revealed as an upper outlier (though still clearly below of the Coloborhynchinae analysed) whilst the specimen NHMUK PV R546 is placed at the top of the third quartile. In the second boxplot (3rd–2nd pair), both specimens attributed to *Amblydectes crassidens* are placed within the third quartile, whilst *Draigwenia platystomus* is shown as a lower outlier, close to the lower jaw of *Lonchodraco giganteus*.

The canonical variates analysis (CVA) allowed to discriminate all sampled elements within given groups related to known clades (Fig. 7). The two main axes have a 96.67% (78.89% for the Axis 1, with an eigenvalue of 10.932; and 17.78% for the Axis 2, with an eigenvalue of 2.4644). However, the convex hulls of the groups are displayed contiguous in some cases, making their distinctive values feasibly ambiguous. In this sense, whilst some groups as the Coloborhynchinae and the Targaryendraconia are easily distinguishable from the others, the Anhanguerinae, the Hamipteridae, and the Tropeognathinae are found overlapping or next each other, with a large distribution in the Axis 1 in the case of the anhanguerid clades. This is consistent with the results of the holotype of *Amblydectes crassidens* and the specimen NHMUK PV R546, which are placed within the Anhanguerinae convex hull, but very close to the Tropeognathinae one. On the other hand, *Draigwenia platystomus* is placed clearly out of all convex hulls with lower values in both axes.

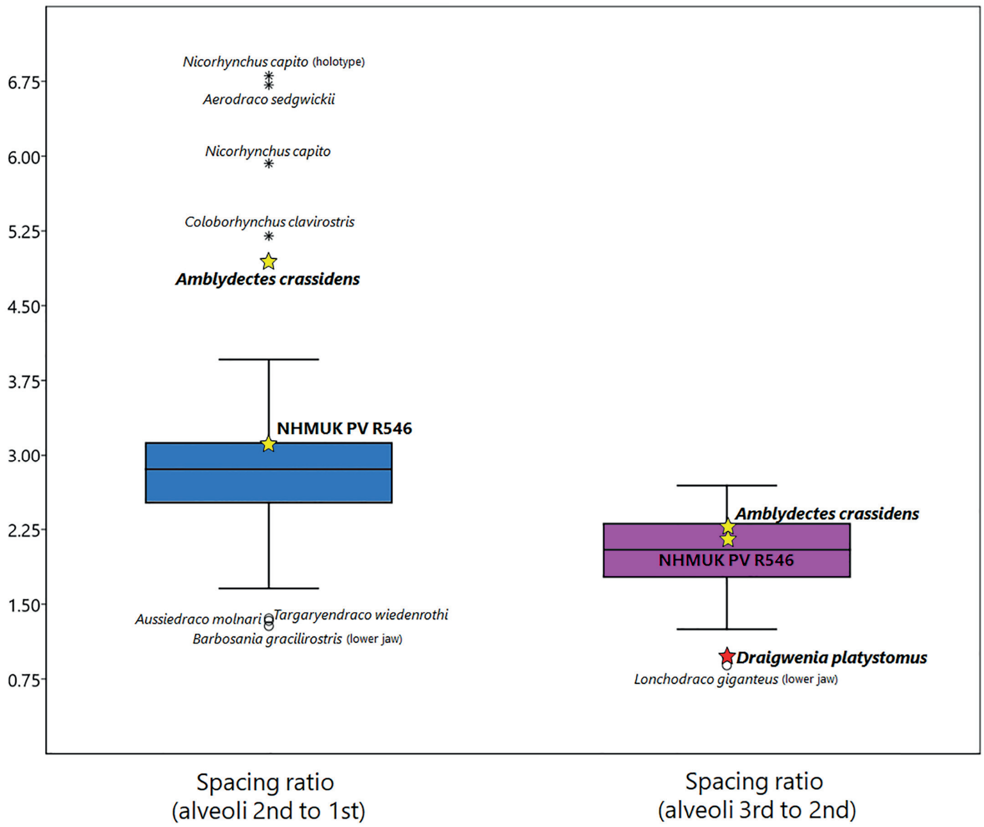

Figure 6. **Boxplot diagrams based on the results obtained from the variation between the spacing ratios (left to the spacing ratio between the 2nd to the 1st alveoli, whilst right to the spacing ratio between the 3rd to the 2nd). Lower outliers are represented by a girth, upper outliers by an asterisk. Case-study specimens are shown by a coloured star (yellow for *Amblydectes*, red for *Draigwenia*).**

Close to *Draigwenia* are place both elements belonging to the holotype of *Lonchodraco giganteus*, with even lower values than *Draigwenia*. *Ornithocheirus* specimens are also placed out of all convex hulls, but with high values in Axis 1 and therefore apart from all others.

DISCUSSION

The characterisation of *Amblydectes crassidens* as a tropeognathine anhanguerid has been extensively supported by several synapomorphies that define this clade (Holgado & Pêgas 2020). However, the several species originally proposed by Hooley (1914) belonging to the genus *Amblydectes* are reconsidered on their validity and allegiance to this genus, being *Amblydectes crassidens* the sole species proposed here.

"*Ornithocheirus eurygnathus*" and NHMUK PV R546 could be identified as dentaries due to the placement of their first pair of alveoli with each other, respectively. Among the entire known pterosaur specimens from the Cambridge Greensand, both specimens exclusively fit with *Amblydectes crassidens*, as well as the depression underneath the first pair of alveoli, the height of the sagittal crest, and the relatively short hook-shaped teeth are features present in the closest relatives of *Amblydectes* (Wellnhofer 1987; Mader & Kellner 1999). But the scarce preservation of both specimens and the lacking of coloborhynchine dentaries left open the question whether or not "*Ornithocheirus eurygnathus*" could only match as an *Amblydectes crassidens* dentary. In addition, both complementary statistical analyses strengthen the hypothesis that all three specimens fall into a same morphological

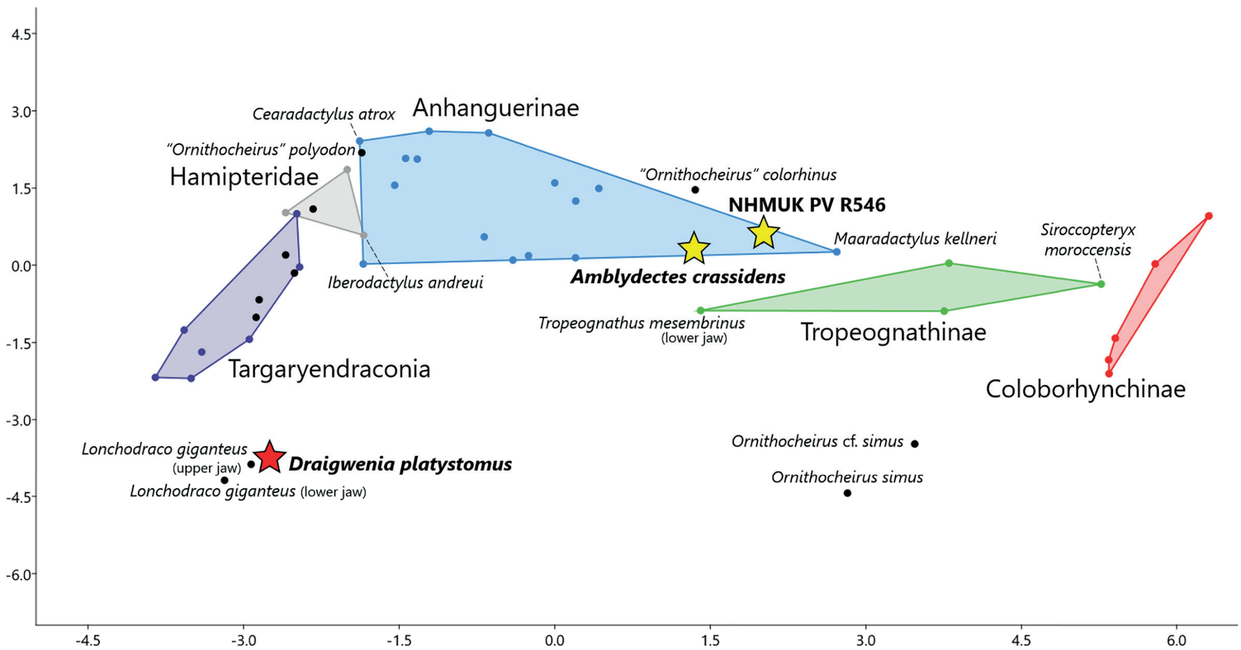

Figure 7. An exploration of the distinction between several ornithocheiraean pterosaur rostra throughout a canonical variates analysis (CVA). Different convex hulls represent each labelled clade, whilst some of the taxa and elements (most of them outliers) are labelled in order to recognise their significance. Case-study specimens are displayed by a coloured star (yellow for *Amblydectes*, red for *Draigwenia*). Percentages are 78.89% for the Axis 1, and 17.78% for the Axis 2. Eigenvalues are 10.932 for the Axis 1, and 2.4644 for the Axis 2. Values obtained from the canonical axes are shown in Table I.

result although they might not be comparable at first glance.

The issue is still more complex with respect to *Draigwenia platystomus*, which is relocated here in a new genus. Even though the validity of the species was previously recognised by Rodrigues & Kellner (2013), these authors considered a species of uncertain placement within Pterodactyloidea which might be relocated in a new genus (Rodrigues & Kellner 2013). The high sagittal crest and suspected sutures between premaxilla and maxillae could be possible to diagnose the monotype *Draigwenia platystomus* as an upper jaw, the only known ornithocheiraean with a similar palatal ridge reaching the tip of the rostrum is the cimoliopterid *Camposipterus nasutus* (Rodrigues & Kellner 2013, Pêgas et al. 2019). Also, a dentary groove extending at the level of the first pair of alveoli was recovered as a synapomorphy of Targaryendraconidae (see Pêgas et al. 2019 for further details), although considering the aforementioned features diagnostic of an upper jaw, this option may not be taken into consideration. Furthermore, Rodrigues & Kellner (2013) considered as an autapomorphy of this taxon the angle of ~27º formed between the putative dorsal margin of the rostrum and its occlusal margin, alleging that this feature is "*[...] so far unique among the species of the* Ornithocheirus *complex and confirms it as a valid taxon.*" (Rodrigues & Kellner: p. 47). The comparative of the lanceodontian rostra from the Cambridge Greensand –and other relative lanceodontians from other localities– shown than this angle is unique among this pterosaur-yielding geological unit, and just *Lonchodectes giganteus* has a similar angle between the two margins. This also matches with both complementary statistical analyses, where

Draigwenia platystomus and *Lonchodraco giganteus* are displayed close to each other. Unwin (2001) considered as a species of the genus *Lonchodectes* and although he noted that sagittal *"[...] crests arise from the anterior tips of the jaws and are rather different in shape and proportions to those of other species of* Lonchodectes." (Unwin 2001: p. 211). Besides these consideration, the most striking point against a lonchodraconid nature was pointed out by Rodrigues & Kellner (2013), showing that *Draigwenia platystomus* "[...] *can be excluded from Lonchodraconidae because it does not have raised alveolar rims and lacks a deep palatal ridge. The absence of these characters results in the lack of a parapet–like palate (which distinguishes Lonchodectidae* sensu *Unwin 2001).*" (Rodrigues & Kellner 2013: p. 47). While I agree with the latter argument for excluding *Draigwenia platystomus* out of Lonchodraconidae and, as aforementioned, the lack of the anterior expansion of the premaxillary tip should excluded it from the clade Anhangueria –and therefore it is out of the genus *Amblydectes*–, its attribution to Cimoliopteridae or any other targaryendraconian and/or non-anhanguerian lanceodontian lineage remains inconclusive due to its fragmented nature. In addition, the broad variability of the Ornithocheirae premaxillary and dentary sagittal crests –both upper and lower jaw and Anhangueria, but just upper jaw in Targaryendraconia is known so far (Pêgas et al. 2019)– should make us think about if this unique angle of ~27º might be addressed with hypothetical changes in ontogeny or to sexual dimorphism (Pinheiro and Rodrigues 2017). Nevertheless, none of the cimoliopterid species known so far presents a premaxillary sagittal crest starting at the tip of the rostrum whilst all known species referred to the genus *Cimoliopterus* have their sagittal crest starting much more posteriorly (Rodrigues & Kellner 2013, Pêgas et al. 2019). Consequently, its taxonomic attribution in a new genus seems to be the most suitable option.

Amblydectes is the first record of a Tropeognathine from the Laurasian landmasses (Fig. 8), which highlights similarities between the English Cambridge Greensand pterosaur fauna with the Romualdo Formation of Brazil and Kem Kem beds of Morocco, among others (e.g., Wellnhofer 1987, Mader & Kellner 1999, Jacobs et al. 2019, Holgado & Pêgas 2020). Nevertheless, similarities between Brazilian and English Cretaceous pterosaurs were realised from the publication of *Tropeognathus mesembrinus* by Wellnhofer (1987), who tentatively interpreted the Brazilian taxon as a close relative of "*Criorhynchus*" *simus* [sic]. Wellnhofer (1987)

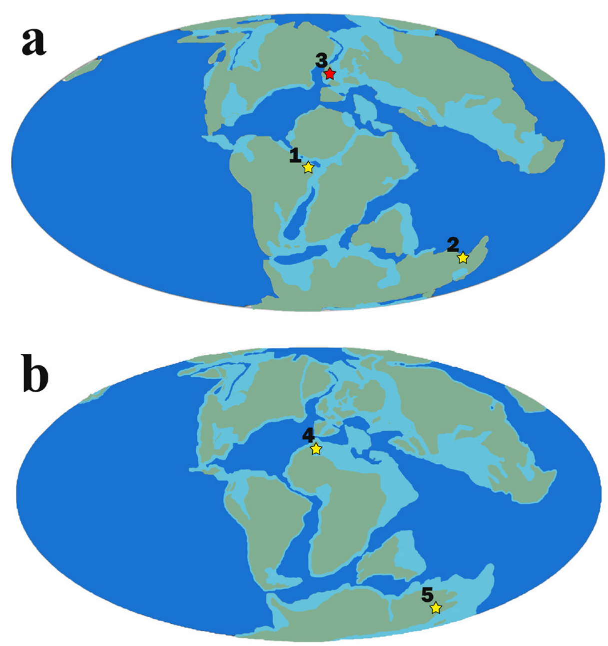

Figure 8. Paleogeographic maps showing distribution of Anhangueridae: (a) Albian – 1. *Tropeognathus mesembrinus* Wellnhofer 1987 from the Romualdo Formation (Araripe Basin, Brazil), 2. *Mythunga camara* Molnar and Thulborn 2008 from the Toolebuc Formation (Queensland, Australia), 3. *Amblydectes crassidens* (Seeley 1870) from the Cambridge Greensand (England); (b) Cenomanian: 4. *Siroccopteryx moroccensis* Mader & Kellner 1999 from the Kem Kem beds (Morocco), and 5. *Ferrodraco lentoni* Pentland et al. 2019 from the Winton Formation (Queensland, Australia).

also stated that "*[...] it is –in my opinion– fairly clear that the high upper jaw of* Criorhynchus *was in fact developed as a premaxillary crest forming the front end of a larger and longer skull similar to* Tropeognathus." (Wellnhofer 1987: p. 184). Such assertion was followed by Fastnacht (2001) and Unwin (2003), who went beyond and considered *Tropeognathus* as a junior synonym of *Ornithocheirus* (the genus "*Criorhynchus*" was widely accepted as a junior synonym of *Ornithocheirus* after Unwin 2001). Several posterior publications followed Unwin's proposal (Unwin 2005, Witton 2013) or even still considered *O. simus* closely related to *Tropeognathus* (Andres et al. 2014, Longrich et al. 2018, Jacobs et al. 2019, 2020). However, in their extensive revision of the *Ornithocheirus* complex, Rodrigues & Kellner (2013) noted that *Ornithocheirus simus* lacks a series of anhanguerian and anhanguerid features, and posteriorly was proposed as a non-anhanguerian lanceodontian by the phylogenetic proposal by Holgado et al. (2019). This view was recently supported by several posterior publications (Kellner et al. 2019a,b, Pêgas et al. 2019, Zhou et al. 2019, Hone et al. 2020, Holgado 2020, Holgado & Pêgas 2020; Buchmann et al. 2021; Cerqueira et al. 2021; Pêgas et al. 2022). Furthermore, the presence of a premaxillary crest is not confirmed for *Ornithocheirus simus* (Rodrigues & Kellner 2013, Holgado & Pêgas 2020). On the contrary, *Amblydectes crassidens* not only presented several anhanguerid synapomorphies as the dorsal deflection of the palate, the expansion of the premaxillary tip and the putative presence of a dentary crest (for further details on Anhangueria and Anhangueridae systematics see Rodrigues & Kellner 2013, and Holgado et al. 2019), but also the presence of several synapomorphies of the clade Tropeognathinae as a premaxillary sagittal crest reaching rostrum tip, a reduced expansion of the premaxillary tip, and teeth relatively short (Holgado & Pêgas 2020). Finally, although the complexity of the anhanguerid diversity seems to show us similarities between the Cambridge Greendsand and Romualdo Formation pterosaur faunas as expected by several authors (e.g., Wellnhofer 1987, Unwin 2003, Longrich et al. 2018), we should be careful not to assume that superficial similarities lead us to think on wrong relatives. In order to avoid this assumptions, it is compulsory to make a pooling among pterosaur researchers to provide a discussion in phylogenetic systematics of the late pterodactyloids –and particularly of the clade Anhangueria (e.g., Rodrigues & Kellner 2013, Holgado et al. 2019, Pêgas et al. 2019, Holgado & Pêgas 2020).

CONCLUSIONS

New anatomical comparisons with other anhanguerid species and the phylogenetic analysis provided in the present work conclude that *Amblydectes crassidens* is a valid species belonging to the clade Tropeognathinae. The validity of *Amblydectes crassidens* highlights that pterodactyloid diversity in the Cambridge Greensand was really complex. The presence of a tropeognathine in the Albian pterosaur fauna of the British Isles shows the first known record of this particular group of anhanguerids from the Laurasian landmasses. Last but not least, *Draigwenia* gen. nov. represents an unique and distinctive taxon with pterosaur fauna from the Cambridge Greensand. Even so its fragmentary nature, which generates large difficulties to recover it in a phylogenetic analysis over a basal politomy in the clade Lanceodontia, *Draigwenia platystomus* could be distinguished from the clades Anhangueria and Lonchodraconidae, remaining as a lanceodontian of uncertain placement.

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