Insights into iguanodontian dental architecture from an Early Cretaceous Chinese basal hadrosauriform maxilla (Ornithischia: Iguanodontia)

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Probactrosaurus maxillae specimens. It is clear though that IVPP V22529 is different from the more advanced Northern Chinese hadrosauriforms *Bactrosaurus* and *Gilmoreosaurus*. The latter lack well-developed maxillary grooves on their medial shelves, unlike IVPP V22529, but all three taxa possess less-developed ones on the medial surfaces of the anteromedial processes of the anterior ramii. Different to IVPP V22529, *Gilmoreosaurus* also has foramina that are more highly-positioned on the lateral surface of its maxilla as well as a row of larger and more circular 'special' foramina on its medial surface. Thus, at this time, IVPP V22529 is identified as a basal hadrosauriform and not as a new genus or as a new species of *Probactrosaurus.*

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Michael Pittman, Xing Xu, Jason R Ali, Rui Pei, Waisum Ma, Jin Meng, Shundong Bi

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also has foramina that are more highly-positioned on the lateral surface of its maxilla as well as a row of larger and more circular 'special' foramina on its medial surface. Thus, at this time, IVPP V22529 is identified as a basal hadrosauriform and not as a new genus or as a new species of *Probactrosaurus.*

1   **Insights into iguanodontian dental architecture from an Early Cretaceous Chinese basal**
2   **hadrosauriform maxilla (Ornithischia: Iguanodontia)**
3
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29   **Abstract**
30   Basal hadrosauriform iguanodontian dinosaurs have been invaluable towards understanding
31   the evolution of the complex and highly efficient advanced hadrosauriform tooth battery
32   dental system. Here we report a new basal hadrosauriform maxilla specimen - IVPP V22529
33   - from the Dashuiguo Formation of Maortu, Nei Mongol, China that preserves a corrugated
34   middle ventrolateral margin that differs from the straight and undulating ventral margins
35   found in most iguandontian and non-iguanodontian dinosaurs. The uniqueness of this
36   ventrolateral margin relates to a new dental structure - cementum 'jackets' that wrap about
37   the labial sides of the teeth. To our knowledge this is the first time that cementum has been
38   described migrated onto the tooth crowns of iguandontians (and other dinosaurs), but this trait
39   is common amongst mammals. This dental morphology - seen in a similar form in the basal
40   hadrosauriform *Equijubus* – therefore broadens our knowledge of iguanodontian maxillary
41   anatomy and shows that the basal hadrosauriform dental system was more morphologically
42   complex than previously thought. IVPP V22529 resembles maxillae specimens of
43   *Probactrosaurus gobiensis*, a contemporaneous taxon known from the same locality in North
44   China, in sharing an inferred subtriangular shape, a relatively flat lateral surface bearing a
45   low row of foramina as well as similar-looking teeth. However, the presence of a unique
46   corrugated middle ventrolateral margin in IVPP V22529, a low row of foramina on its lateral
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49   differences could conceivably be related to ontogenetic and sexual variation, which have not
50   been fully documented in *P. gobiensis*. More detailed comparisons of IVPP V22529 and

51 *Probactrosaurus* are also hampered by the missing posterior portion of IVPP V22529 as well
52 as the missing anterior ramii in *Probactrosaurus* maxillae specimens. It is clear though that
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54 *Bactrosaurus* and *Gilmoreosaurus*. The latter lack well-developed maxillary grooves on their
55 medial shelves, unlike IVPP V22529, but all three taxa possess less-developed ones on the
56 medial surfaces of the anteromedial processes of the anterior ramii. Different to IVPP
57 V22529, *Gilmoreosaurus* also has foramina that are more highly-positioned on the lateral
58 surface of its maxilla as well as a row of larger and more circular 'special' foramina on its
59 medial surface. Thus, at this time, IVPP V22529 is identified as a basal hadrosauriform and
60 not as a new genus or as a new species of *Probactrosaurus*.
61
62
63 **Introduction**
64 Maortu (Chow & Rozhdestvensky, 1960: = Maorty; 毛尔图) is a fossil locality of Early
65 Cretaceous age (Dashuiguo Formation: Barremian to Albian stages (Rozhdestvensky, 1966;
66 Rozhdestvensky, 1974; van Itterbeeck *et al.*, 2001; van Itterbeeck *et al.*, 2004) located
67 approximately half-way along China's northern frontier in Nei Mongol Autonomous Region (
68 内蒙古自治区), ~500km west of the provincial capital Hohhot (呼和浩特市) (Fig. 1).
69

70
71 Figure 1. The basal hadrosauriform maxilla IVPP V22529 was found in the Early Cretaceous
72 Dashuiguo Formation of Maortu, Nei Mongol, China (map produced from a Google Maps
73 image). Maortu is the type locality of the non-euhadrosaurian hadrosauriform
74 *Probactrosaurus gobiensis* (Rozhdestvensky, 1966).
75
76 Maortu is the type locality of three dinosaurs: the non-euhadrosaurian hadrosauriform
77 *Probactrosaurus gobiensis* (Rozhdestvensky, 1966) [this study follows the ornithopod
78 classification of Norman (2015)], the advanced non-carcharodontosaurine
79 carcharodontosaurid *Shaochilong maortuensis* (Brusatte *et al.*, 2009; Brusatte *et al.*, 2010)
80 and the basal non-ankylosaurine ankylosaurid *Gobisaurus domoculus* (Vickaryous *et al.*,
81 2001). It is also the type locality of the trionychine trionychid turtle *Dongania maortuensis*
82 (Hans-Volker, 1999; Yeh, 1965 [See Vitek & Danilov, 2010 for taxonomic discussion]). In
83 the summer of 2014 a team including several of the authors (MP, JRA, JM and SDB) visited
84 Maortu (and its surrounding areas) where they recovered a variety of fragmentary and mostly
85 isolated dinosaur and mammal bones now housed at the Institute of Vertebrate Paleontology

86 and Paleoanthropology (IVPP), Beijing. Amongst the largest of these bones is an isolated,
87 crushed and posteriorly broken right iguanodontian maxilla (~12cm tall and 22cm long; Fig.
88 3).
89
90 Early Cretaceous Asian iguanodontian maxillae are known from nine Chinese taxa
91 (*Bactrosaurus johnsoni* [Prieto-Márquez, 2011], *Bolong yixianensis* [Wu *et al.*, 2010; Zheng
92 *et al.*, 2013], *Equijubus normani* [You *et al.*, 2003c], *Jinzhousaurus yangi* [Wang & Xu,
93 2001], *Lanzhousaurus magnidens* [You *et al.*, 2005], *Probactrosaurus gobiensis* [Norman,
94 2002; Rozhdestvensky, 1966], *P. mazongshanensis* [Lü, 1997; Norman, 2002],
95 *Shuangmiaosaurus gilmorei* [You *et al.*, 2003a] and *Xuwulong yueluni* [You *et al.*, 2011]),
96 two Japanese taxa (*Fukuisaurus tetoriensis* [Kobayashi & Azuma, 2003; Shibata & Azuma,
97 2015] and *Koshisaurus katsuyama* [Shibata & Azuma, 2015]), two Kazak taxa (*Altirhinus
98 kurzanovi* [Norman, 1998] and *Batyrosaurus rozhdestvenskyi* [Godefroit *et al.*, 2012]) and a
99 Thai specimen identified to a higher taxonomic level (*Siamodon nimngami*; Buffetaut &
100 Suteethorn, 2011; *nomen dubium*: Norman, 2015). Comparisons between IVPP V22529 and
101 the aforementioned taxa (Table 1) identifies IVPP V22529 as a non-euhadrosaurian
102 hadrosauriform based on the presence of at least two replacement maxillary crowns and the
103 absence of a single median primary ridge on the teeth (see Description and Comparison and
104 Discussion). The presence of marginal denticles comprising of parallel ledges with single
105 rows of ~6 relatively large mammillae suggests that IVPP V22529 is a basal hadrosauriform.
106

Taxon	Specimen number	Material	References
China			
IVPP V22529	**IVPP V22529 (field number: JLT 20140622-1)**	**Partial right maxilla (posterior ramus missing)**	**This study (Pittman *et al*. 2015)**
Bactrosaurus johnsoni*^	AMNH 6553 (holotype)	Adult/subadult left maxilla	Prieto-Márquez, 2011: Figs. 7, 8
	AMNH 6390-6393, 6514	Juvenile left maxillae (AMNH 6393 is a partial specimen)	Prieto-Márquez, 2011: Figs. 11, 12
	AMNH 6388, 6389, 6583	Juvenile right maxillae	Prieto-Márquez, 2011: Figs. 9, 10
	3 SBDE 1	?	Godefroit *et al.*, 1998
Bolong yixianensis*	YHZ-001	Left maxilla	Wu *et al.*, 2010; Wu & Godefroit, 2012: Figs. 19.2, 19.3
	ZMNH-M8812	Juvenile left and right maxillae	Zheng *et al.*, 2013: Figs. 2, 4-6
Equijubus normani	IVPP V12534 (holotype)	Complete articulated maxilla exposed on both the right and left lateral sides.	You *et al.*, 2003c: Fig. 1
Jinzhousaurus yangi	IVPP V12691 (holotype)	Complete articulated maxilla exposed on its left lateral side; medial side embedded in matrix.	Wang & Xu, 2001: Figs. 1, 2; Barrett *et al.*, 2009: Fig. 1
Lanzhousaurus	GSLTZP01-001	Isolated maxillary	You *et al.*, 2005: Fig.

magnidens*	(holotype)	teeth	2A-H
Probactrosaurus gobiensis	PIN 2232/9-2*	Partial right maxilla (missing anterior ramus)	Norman, 2002: Fig. 5; Rozhdestvensky, 1966
	PIN 2232/10-2*	Partial right maxilla (missing anterior ramus as well as teeth from anterior and posterior aveolar slots)	Norman, 2002: Fig. 5; Rozhdestvensky, 1966
P. mazongshanensis	IVPP V1134.10-15 **	Isolated maxillary teeth	Lü, 1997; Norman, 2002: Fig. 4A
Shuangmiaosaurus gilmorei*#	LPM 0165	Left maxilla	You et al., 2003a: Fig. 1
Xuwulong yueluni*	GSGM-F00001	Both maxillae	You et al., 2011: Figs. 2, 3
Kazakhstan			
Altirhinus kurzanovi*	PIN 3386/7	Both maxillae	Norman, 1998: Fig. 6
Batyrosaurus rozhdestvenskyi*	AEHM 4/1	~30 maxillary teeth	Godefroit et al., 2012: Fig. 20.10C, D
Japan			
Fukuisaurus tetoriensis*	FPDM-V-40-1 (holotype)	Right maxilla	Kobayashi & Azuma, 2003: Fig. 6
	FPDM-V-40-5	Left maxilla	Kobayashi & Azuma, 2003: Fig. 2C-E
	FPDM-V-40-13	Isolated left maxillary tooth	Kobayashi & Azuma, 2003
Koshisaurus katsuyama*	FPDM-V9079	Right maxilla	Shibata & Azuma, 2015: Fig. 3
Thailand			
Siamodon nimngami* (nomen dubium: Norman, 2015	PRC-4	Left maxilla	Buffetaut & Suteethorn, 2011: Fig. 1; Norman, 2015 (nomen dubium)

107

108 *Taxa studied from the literature only; **Specimens absent from host collection; ^Upper
109 Cretaceous taxa that were also found in Nei Mongol; #Suggested to be an Upper Cretaceous
110 taxon by You et al. (2003a) based on biostratigraphic evidence.

111 Table 1. Early Cretaceous Asian iguanodontian dinosaur maxillae studied.
112 List of Early Cretaceous Asian iguanodontian maxillae used to describe IVPP V22529.
113
114
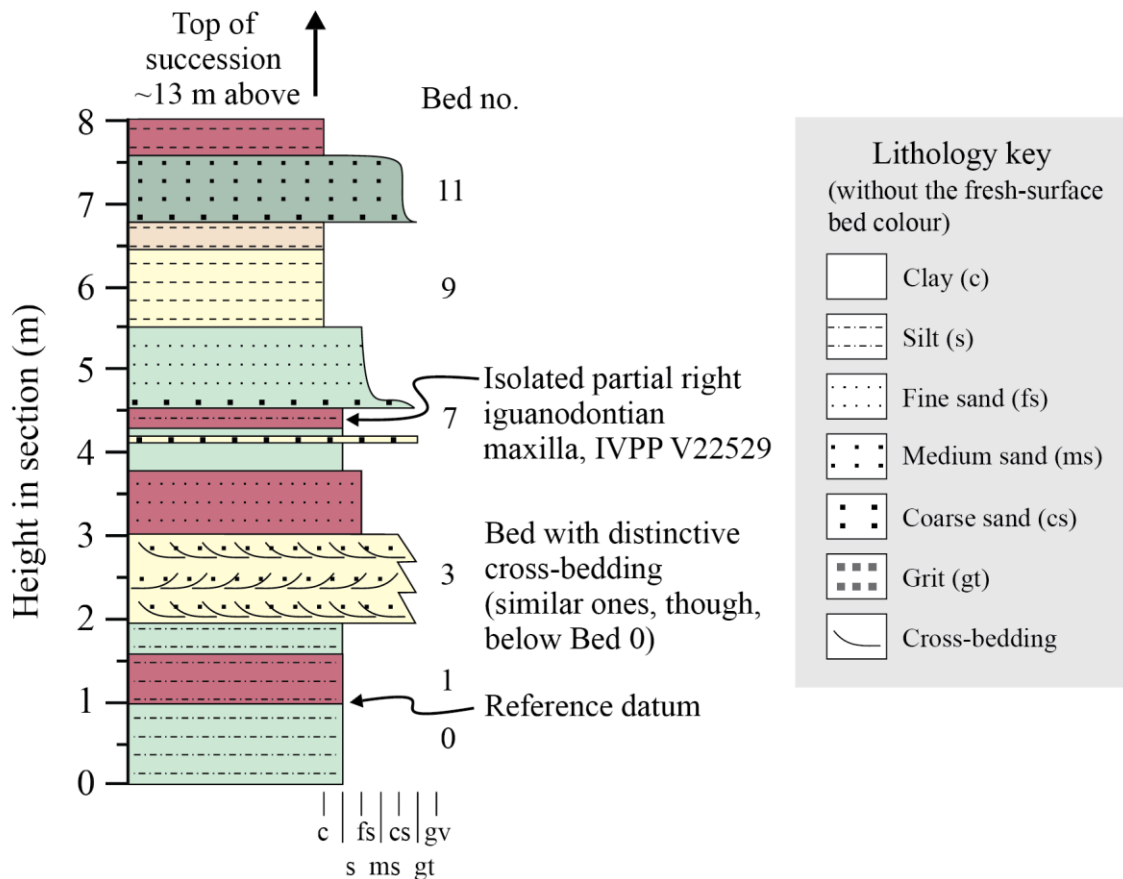
115 **Materials and Methods**
116 IVPP V22529, an isolated partial right iguanodontian maxilla. This specimen was excavated, studied
117 and described using standard palaeontological methods, in accordance with a fossil excavation permit
118 (14-0620-JLT) obtained from the Department of Land and Resources, Nei Mongol, China.
119
120

121 **Locality and Horizon**

122 Maortu (毛尔图), "Women's shoe" (妇女鞋) sublocality (40 12.109' N 105 42.957' E);

123 ~60km north of Jilantai lake (吉兰泰盐湖), Alxa Left Banner, Alashan League, Nei Mongol,

124 China (Figs. 1, 2); Dashuiguo Formation, Barremian to Albian, Early Cretaceous

125 (Rozhdestvensky, 1966; Rozhdestvensky, 1974; van Itterbeeck *et al.*, 2001; van Itterbeeck *et*

126 *al.*, 2004).

127

128
129 Figure 2. Stratigraphic log showing the position of IVPP V22529 in the local rock succession
130 at the "Women's shoe" (妇女鞋) sublocality (40 12.109' N 105 42.957' E). Grain size
131 abbreviations: c, clay; s, silt; fs, fine sand; ms, medium sand; cs, coarse sand; gt, grit; gv,
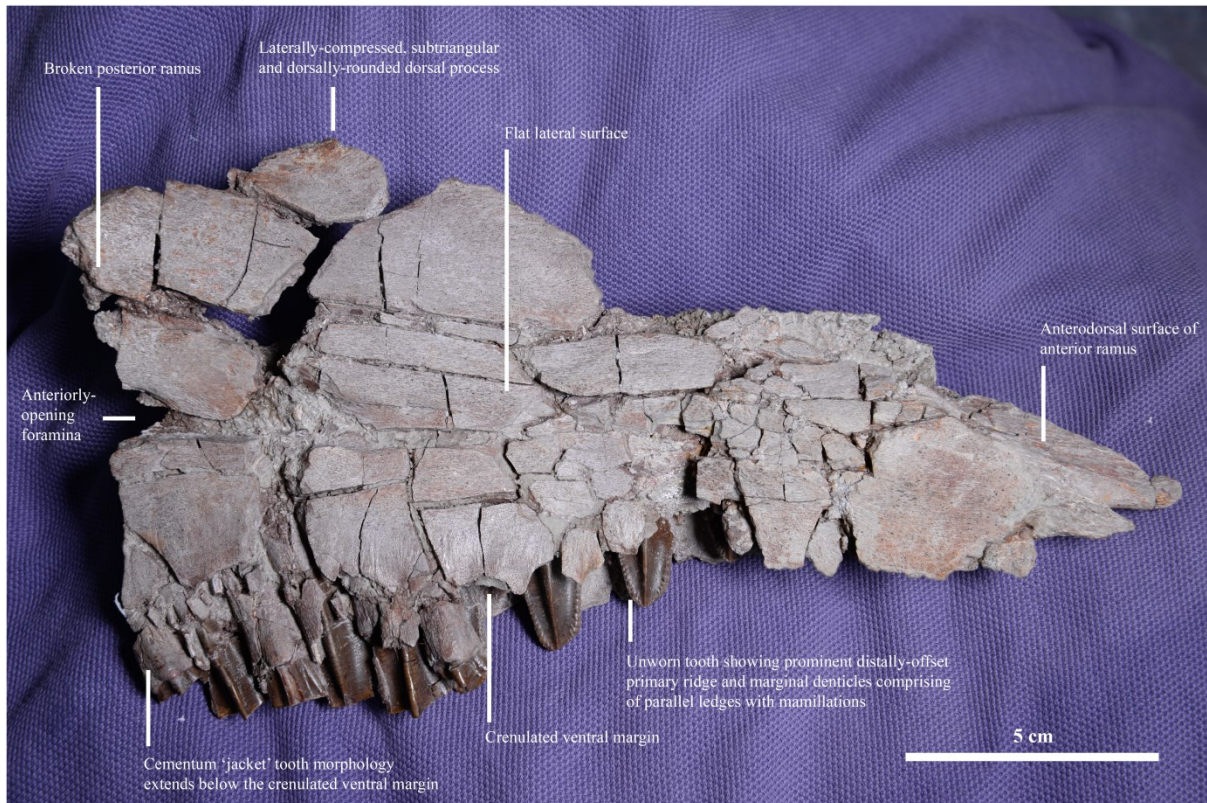132 gravel.

133

134 IVPP V22529 was recovered from the lower part of the exposure at the "Women's shoe"
135 sublocality (Bed 7 in Fig. 2) (40 12.109' N 105 42.957' E) located ~60km north of Jilantai
136 lake in the Alxa Left Banner of the Alashan League of Nei Mongol, China. The specimen
137 was found ~13 metres below where the Early Cretaceous succession is capped by recent
138 gravel washout material. The sediments comprise vari-coloured beds (red-purple, pale green,
139 olive green and cream) that are typically 20–100 cm thick. The grain size is mostly clay or
140 silt, but coarse sands and grits are encountered. Some units show cross-bedding (Bed 3 in Fig.
141 2), but most are devoid of any internal layering, apart from a few that fine upwards. The
142 depositional setting is inferred to be a lake margin, the cross-bedded horizons probably
143 marking a time when a stream or small river, quite probably ephemeral, was discharging into
144 the system.

145
146

Description and Comparison

IVPP V22529 is an isolated right iguanodontian maxilla that is missing its posterior ramus and has a broken anterior one (Fig. 3). This section first describes the specimen's dentition and compares it with other iguanodontians because this portion of the maxilla contains the most diagnostic and unique information in this specimen. Then, the maxillary body will be described and compared with other iguanodontians.

Figure 3. IVPP V22529 in lateral view showing the missing posterior ramus and broken anterior one, the dorsal process and lateral surface, the labial view of the tooth row and the corrugated middle ventrolateral surface formed by an unusual cementum 'jacket' tooth morphology.

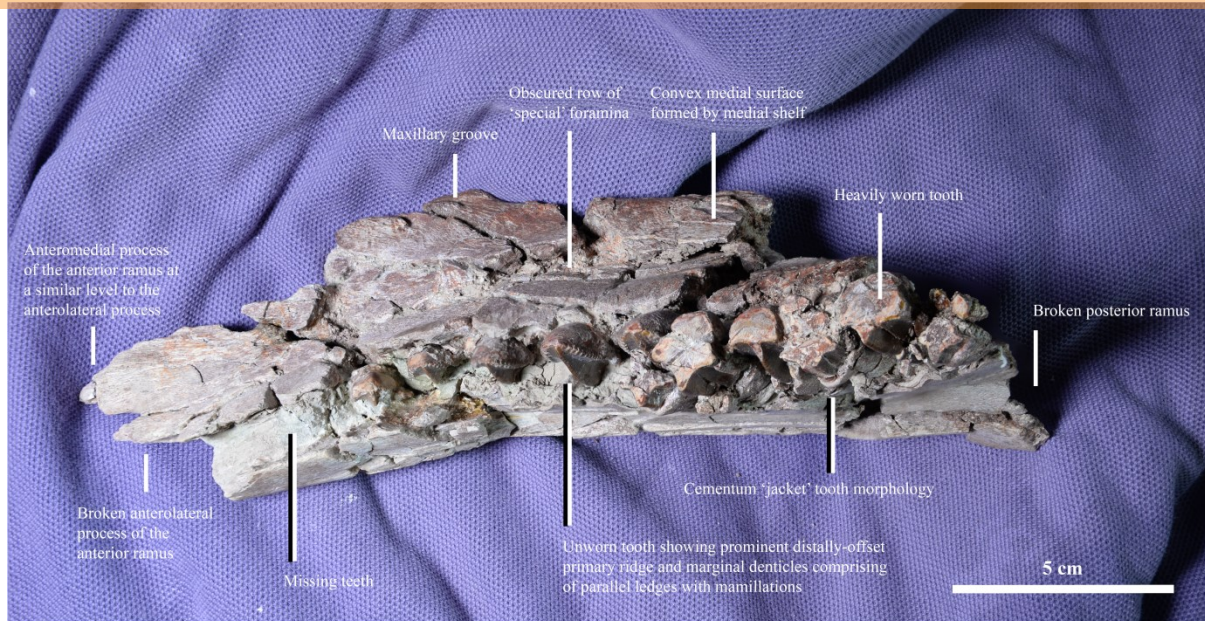*Maxillary Dentition*

Tooth position count
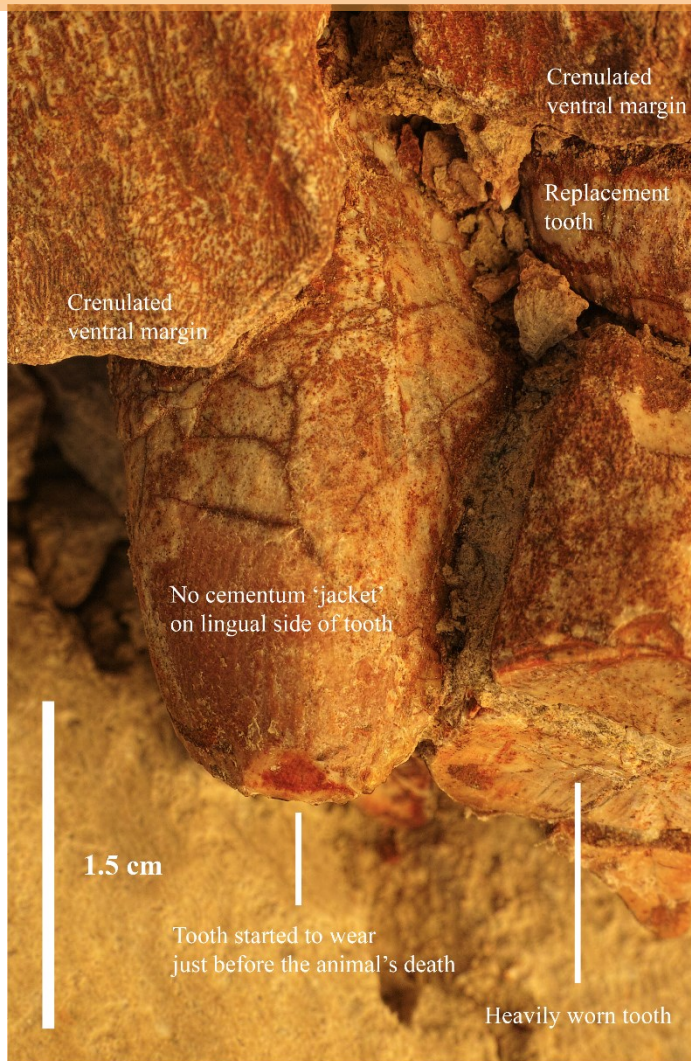
Figure 4. Tooth row in ventral view showing the specimen's partial and heavily worn teeth, its unworn teeth as well as its missing ones.

IVPP V22529 preserves a partial tooth row (Figs. 2, 3) comprising of more than 18 vertical tooth positions, as indicated by 14 *in situ* teeth, an empty aveolar socket and a row of at least three empty parallel aveolar sockets at the anterior end of the maxilla (although the empty sockets may each have accommodated more than one tooth (Norman, 2002)). Without the posterior portion of the maxillary tooth row and no associated complete dentary row to estimate the number of vertical maxillary tooth positions, the latter is uncertain.

Nevertheless, by comparison, the non-euhadrosaurian hadrosauriform *Probactrosaurus* (PIN 2232/9-2, /10-2; Norman, 2002) preserves ~17 vertical maxillary tooth positions out of an estimated total of 22+ positions (22-23 positions estimated by Norman (2002); 23 or more total positions estimated by Rozhdestvensky (1966)). The 'iguanodontoid' styracosternan *Jinzhousaurus* is estimated to have fewer maxillary teeth than *Probactrosaurus* with only ~15-16 teeth [IVPP V12691, Barrett *et al.*, 2009: Fig. 3C]), as in the hadrosauriform *Koshisaurus* which has 19 vertical tooth positions [FPDM-V907, Shibata & Azuma, 2015: Figs. 3, 8]. The basal non-euhadrosaurian hadrosauriform *Altirhinus* may have had a slightly higher vertical tooth position count than *Probactrosaurus* as Norman (1998) estimated 26 positions on the basis of the 24 positions present in its dentary (PIN 3386/7, Norman, 1998: Fig. 16). However, *Altirhinus* only preserves direct evidence of 21 vertical maxillary tooth positions (right maxilla of PIN 3386/7; Norman, 1998: Fig. 6). Given the uncertain tooth position count in IVPP V22529 it might even be possible that it has a high tooth position count as in the basal non-euhadrosaurian hadrosauriform *Eolambia* (32 positions in the left maxilla of CEUM 9758; Kirkland, 1998: Fig. 4A-C). Amongst iguanodontians the number of maxillary teeth appears to increase during ontogeny (Horner *et al.*, 2004; Hübner & Rauhut, 2010; Zheng *et al.*, 2013), but the relatively large size of the maxilla fragment suggests that IVPP V22529 probably has close to its maximum number of vertical tooth positions.
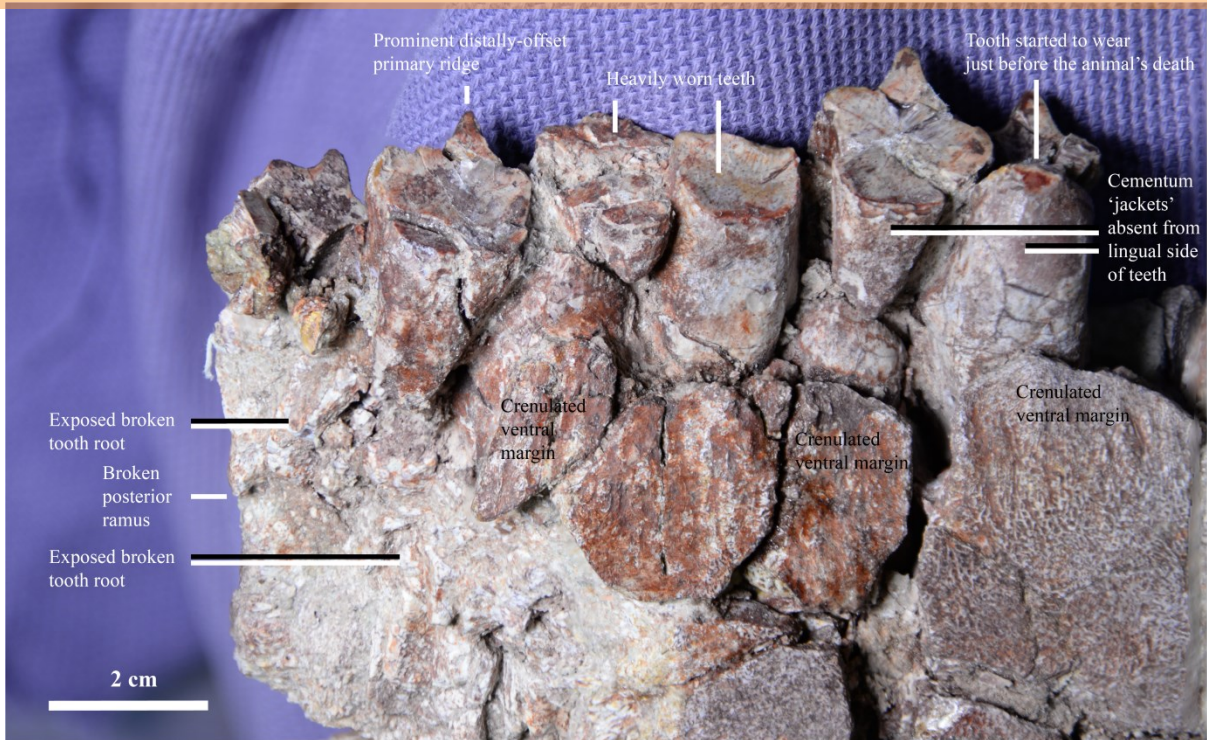
Replacement crowns

Figure 5. IVPP V22529 appears to be a hadrosauriform iguandontian because it has at least two replacement teeth (Norman, 2015). This is indicated by a heavily worn tooth (right) that is supported by a replacement tooth, which is adjacent to a tooth that had just started to wear before the animal died.

One replacement crown is observed in five positions along the tooth row (Fig. 4), but the preservation of the socket walls prevents the total number of replacement crowns from being determined e.g. two replacement crowns are revealed by the broken posterior portion of the right medial wall of *Altirhinus* PIN 3386/7 (Norman, 1998: Fig. 6). However, there appears to be indirect evidence of at least two replacement teeth in IVPP V22529 because one heavily worn tooth is supported by a replacement tooth and anterior to it there is a taller erupted tooth that had only just started to be worn prior to the animal's death (Fig. 5). The presence of at least two replacement crowns implies that IVPP V22529 is a hadrosauriform iguandontian (Norman, 2015: character 54, state 1) - non-hadrosauriform iguanodontians have one functional crown supported by only one replacement crown (Norman, 2015: character 54, state 0)).

Denticles

Figure 6. Six heavily worn teeth in IVPP V22529 shown in ventromedial view.

Figure 7. The teeth of IVPP V22529 are dominated by a well-developed distally-offset primary ridge and lack any subsidiary (accessory) ridges. The unworn teeth of IVPP V22529 show marginal denticles comprising of parallel ledges with single rows of ~6 relatively large mammillae. The latter suggests that IVPP V22529 is a basal hadrosauriform.

224   Six of the teeth preserved in IVPP V22529 have well-developed wear facets (Fig. 6) that are
225   up to 2cm shorter vertically than the tallest of the three teeth with slightly worn tips (the latter
226   are presumed to have erupted not long before the animal's death). There is a small fragment
227   of a seventh worn tooth located in the most posteriorly preserved position along the tooth row
228   (Fig. 6). One of the extensively worn teeth as well as all of the slightly worn or non-worn
229   teeth have marginal denticles comprising of parallel ledges with single rows of ~6 mammillae
230   (Fig. 7). Styracosternan iguanodontians have marginal denticles on both their maxillary and
231   dentary teeth that form ledges with mammillations (Norman, 2015: character 58, state 2), but
232   in IVPP V22529 the mammillae are comparatively large suggesting that it is a basal
233   hadrosauriform as more advanced hadrosauriforms have smaller mammillae.
234
235   Primary and subsidiary (accessory) ridges
236   In labial view, the enamelled surface of the crown is narrow and appears lozenge-like
237   (elongated and asymmetrically diamond-shaped), as in *Probactrosaurus* (Norman, 2002),
238   *Altirhinus* (Norman, 1998) and *Iguanodon* (Norman *et al.*, 1987) [Fig. 7]. The crown's
239   asymmetry is indicated by the distal offset of an enlarged primary ridge relative to the tooth's
240   mid-line (a feature diagnostic of Iguanodontia (Norman, 2015: character 68, state 1) which
241   includes *Probactrosaurus*, *Altirhinus* and *Jinzhousaurus* (Norman, 1998; Norman, 2002;
242   Wang & Xu, 2001)) and the anterior position of the shoulder of the crown margin (as in
243   *Altirhinus* (PIN 3386/7, Norman, 1998: Fig. 21B) and *Jinzhousaurus* (IVPP V12691, Wang
244   & Xu, 2001) [Fig. 7]. The absence of a single median primary ridge indicates that IVPP
245   V22529 is not a euhadrosaurian iguanodontian (Norman, 2015: character 68, state 3). As in
246   *Probactrosaurus*, there appears to be little evidence of subsidiary ridges (Norman, 2002)
247   [Fig. 7], unlike in *Altirhinus* (Norman, 1998: Fig. 21B) and *Jinzhousaurus* (IVPP V12691,
248   Wang & Xu, 2001) where there is one anterior to the primary ridge and unlike in the
249   styracosternan iguanodontian *Lanzhousaurus* (GSLTZP01-001; You *et al.*, 2005: Fig. 2A)
250   where the primary ridge is flanked by several subsidiary ones. There is no lingual ridge on
251   the maxillary tooth crowns of IVPP V22529, so this ridge still appears to be an autapomorphy
252   of *Koshisaurus* (FPDM-V907, Shibata & Azuma, 2015: Figs. 3C, 8B, 9B]). It is worth
253   mentioning that the two isolated near-complete maxillary teeth (IVPP V1134.10) of
254   *Probactrosaurus mazongshanensis* Lü, 1997 - not a junior synonym of *Probactrosaurus*
255   *gobiensis* (Norman, 2002) - could not be located at the IVPP in May 2015 for direct
256   comparison with IVPP V22529. However, Lü (1997) noted that these teeth have a large
257   highly-developed primary ridge and his figure of one of them (his Figure 4) shows very
258   similar morphological traits to the maxillary teeth of IVPP V22529.
259
260   Tooth root morphology
261   Relatively straight but poorly preserved tooth roots are exposed on the broken posteromedial
262   surface of IVPP V22529. One portion of an exposed tooth root appears to be longitudinally
263   grooved (a synapomorphy of Iguanodontia (Norman, 2015: character 59, state 1 –
264   DELTRAN)), but this observation is equivocal owing to the root's poor preservation.
265   Hadrosauromorpha is characterised by highly angular-sided roots (hexagonally prismatic)
266   that relate to close packing of the teeth in a functionally integrated multi-tooth magazine
267   (Norman, 2015: character 59, state 2). Given the poor state of tooth root preservation in IVPP
268   V22529, the presence of the latter in the specimen cannot be excluded at present.
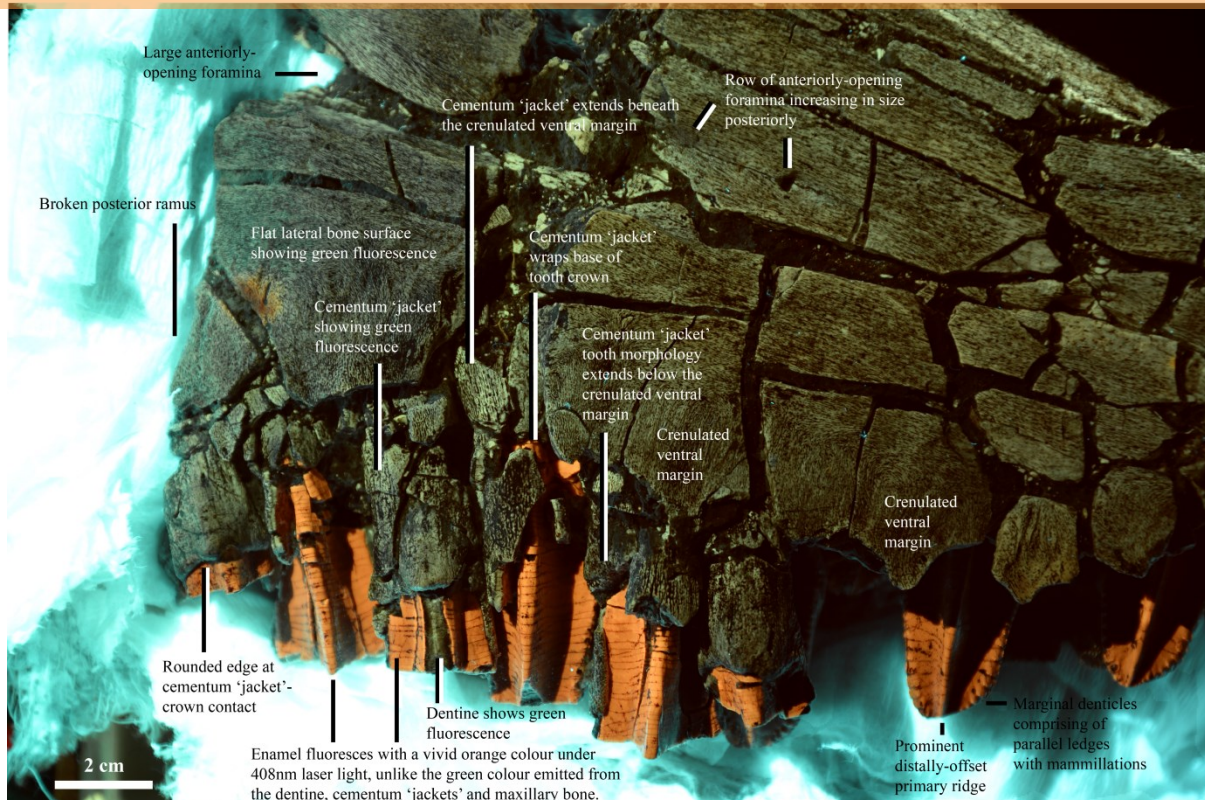269

Figure 8. In labial view, the five middle maxillary crowns preserve a bone-like sheath over their base. This appears to be cementum owing to its rugose texture and the absence of the fibres expected in ossified periodontal ligaments. This cementum 'jacket' morphology - which is the first to be described amongst dinosaurs to our knowledge – originates within the tooth socket and extends below the crenulated ventral margin of the maxilla to form a corrugated ventrolateral surface created by the grooves that separate each 'jacket'.

Below the five middle maxillary crowns at the broken posterior end of the specimen, the labial side of each tooth appears to be tightly enveloped by smooth to a slightly rugose material (Fig. 8). These bone-like sheaths do not form a continuous surface and appear separate from the walls of the tooth socket. They extend beyond the crenulated ventral margin of the lateral surface, but begin beneath the socket walls themselves as revealed through a broken portion of the wall (Fig. 8). The separation of this structure from the tooth socket walls and its non-uniform roughened texture suggests that it is cementum (Fig. 8). Cementum with similar textural characteristics has been identified in *Probactrosaurus* (Norman, 2002) and other iguanodontians; this texture is presumably associated with ligamentous scarring on the tooth root. However, the unknown structure could conceivably be ossified periodontal ligaments as these bind the tooth root to its socket. However, this hypothesis is poorly supported as no structures resembling ligamental fibres were observed in IVPP V22529. If these fibres were observed they should also show differences in orientation along the length of the ligament. The lack of pathologies on the 'jackets' suggests that tooth eruption was probably relatively smooth and unhindered.
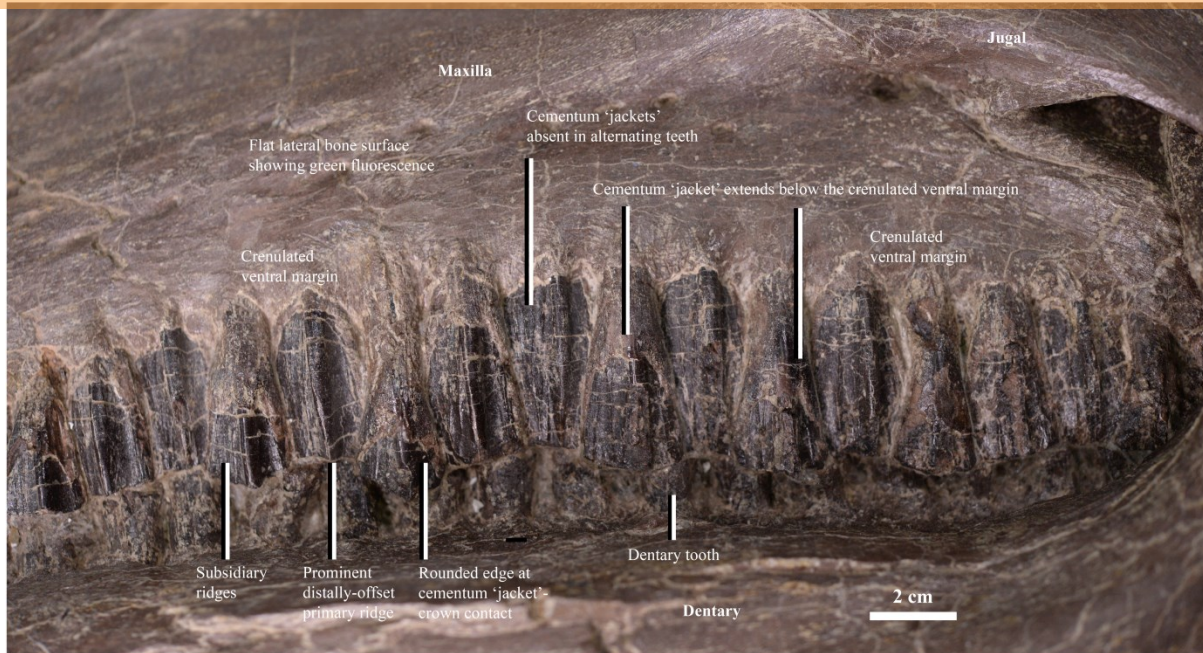
294
295 Figure 9. Laser-stimulated fluorescence imaging (LSF; Kaye *et al.*, 2015) of IVPP V22529
296 shows that the unknown structure has similar green fluorescence colours to dentine and
297 maxillary bone. However, this does not help to constrain the identification of the unknown
298 structure because cementum and ossified periodontal ligaments would probably fluoresce
299 with similar colours since these materials are both made of fossilised hydroxylapatite. In the
300 LSF image enamel reacts differently to the laser light even though it is also made of fossilised
301 hydroxylapatite. Clearly, the mineralogy of the fossilised enamel is sufficiently different to
302 the other parts of the fossil to give such a vividly different orange fluorescence colour.
303
304 Unfortunately, laser-stimulated fluorescence (LSF) analysis (using a 408nm violet laser;
305 Kaye *et al.*, 2015) was unable to support either the cementum 'jacket' or ossified ligament
306 identifications. The LSF image (Fig. 9) shows similar greeny fluorescence colours for the
307 unknown structure, dentine and maxillary bone, but a vivid orange colour for the enamel.
308 This is interesting because all of these materials are varieties of fossilised hydroxylapatite
309 (the ligaments are expected to have been ossified prior to fossilisation), but clearly there is a
310 marked mineralogical difference between the fossilised enamel and the other fossilised
311 materials that is probably related to mineral density. Thus, the unknown structures are
312 proposed as cementum 'jackets' given the current evidence available.
313
314 To our knowledge these cementum 'jackets' have not been described amongst
315 iguanodontians and other dinosaurs, but this derived root attachment tissue is commonly
316 found in mammals where it also migrates onto the crowns (Erickson *et al.*, 2012). Studies of
317 existing iguanodontian specimens in person and from the literature revealed their presence in
318 *Equijubus normani* (IVPP 12534, You *et al.*, 2003c: Fig. 1E). Unlike IVPP V22529, these
319 'jackets' are found on alternating teeth rather than on each one.

Figure 10. A cementum 'jacket' tooth morphology is also present in the basal hadrosauriform *Equijubus normani* (IVPP 12534, You *et al.*, 2003c: Fig. 1E), but unlike IVPP V22529 this is observed in alternating teeth rather than on each tooth.
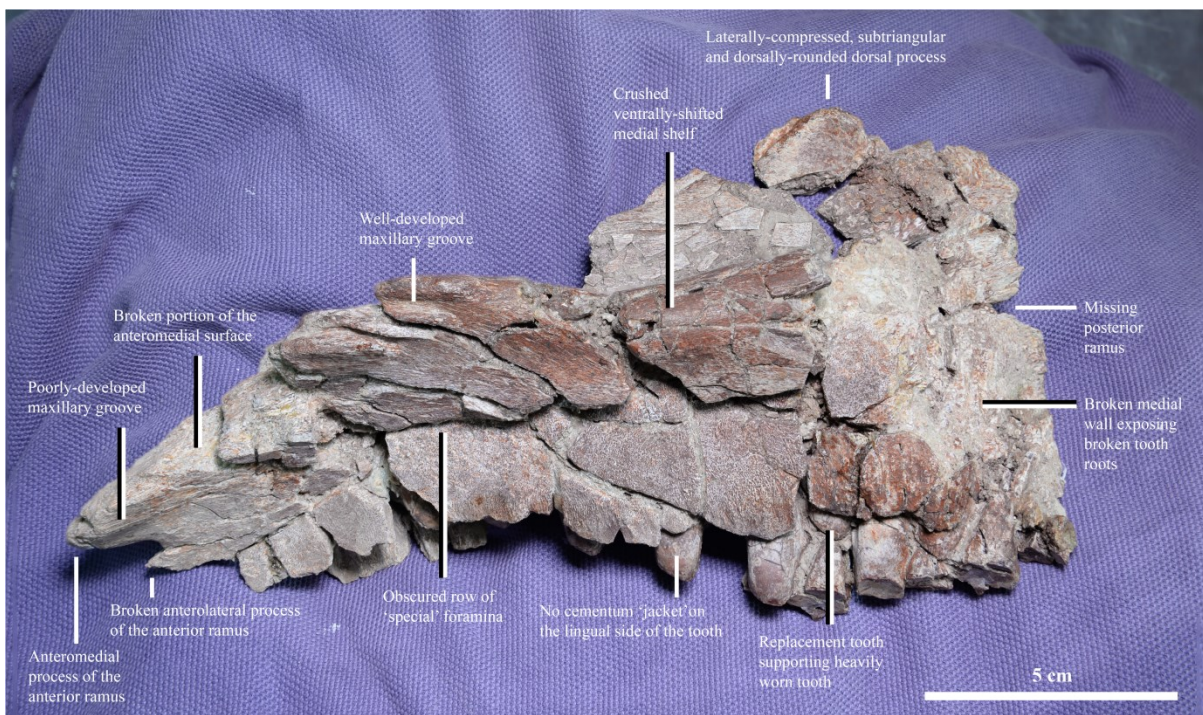
Tooth orientation

The maxillary tooth row follows a laterally concave path (Fig. 4). The slightly worn and unworn teeth appear to be posteriorly inclined whilst the heavily worn teeth are anteriorly inclined, but the latter appears to be an artefact of the fragmentation of the bone sockets holding them in place (Fig. 3). Thus, the specimen's tooth orientation is considered to be consistent with that of *P. gobiensis* (Norman, 2002) – posteriorly inclined.
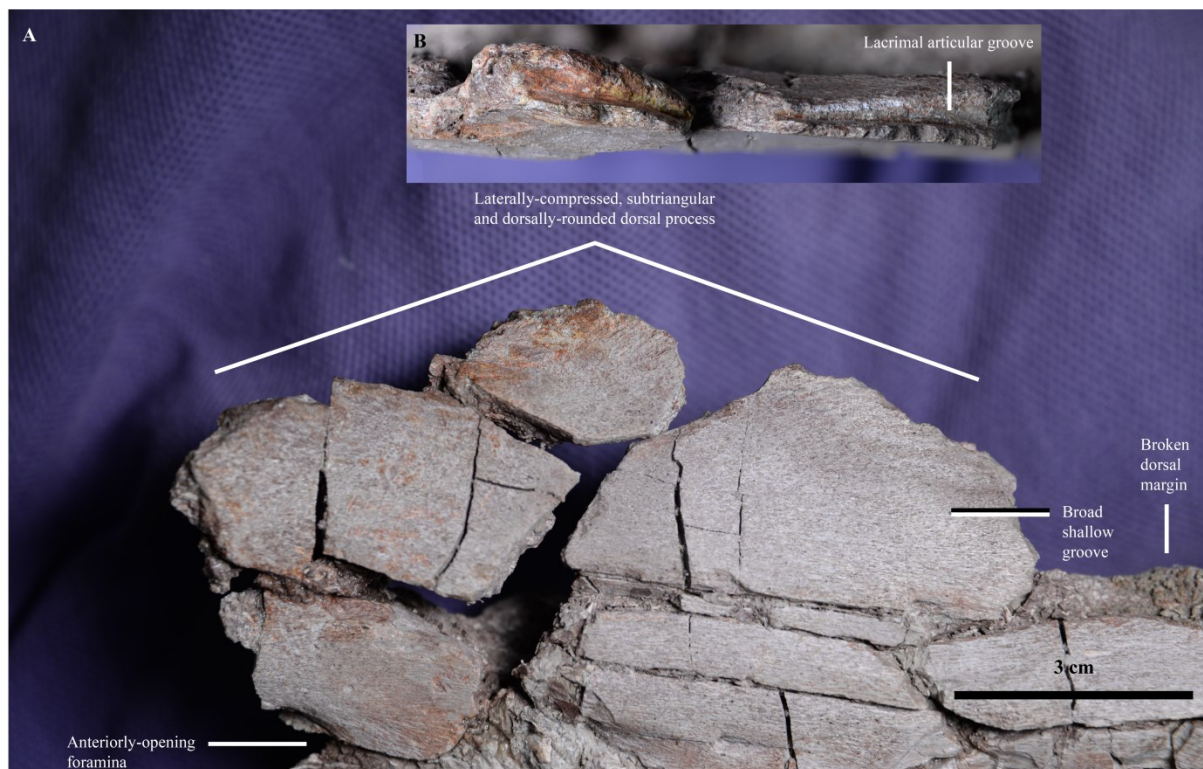
Maxillary body

335   Figure 11. Maxilla in medial view showing the broken anterior ramus and missing posterior
336   ramus as well as the maxillary grooves, medial shelf, dorsal process, lingual view of the tooth
337   row and the broken posteromedial surface that exposes several fragmentary tooth roots.

338

339   The medial shelf (Fig. 11) has been artificially shifted ventrally partially obscuring the row of
340   'special' foramina such that their exact number and shapes are unclear; they are located
341   relatively low on the medial surface, as in other basal hadrosauriforms such as *Altirhinus*
342   (PIN 3386/7; right maxilla [Norman, 2002]). In *Altirhinus* (PIN 3386/7; Norman, 1998) an
343   incomplete row of 14 regularly spaced foramina is preserved subparallel to the ventral margin
344   of the maxilla (the missing posterior portion of the maxilla truncates this row of foramina). In
345   *Bactrosaurus* their appearance varies between individuals of similar and different ages
346   (adult/subadult: AMNH 6553, Fig. 7 Prieto-Márquez, 2011; juvenile: AMNH 6389, 6390,
347   Figs. 9, 11 Prieto-Márquez, 2011). In *Gilmoreosaurus* there are at least 17 large, evenly-
348   spaced and circular 'special' foramina (AMNH FARB 30653; Prieto-Márquez & Norell,
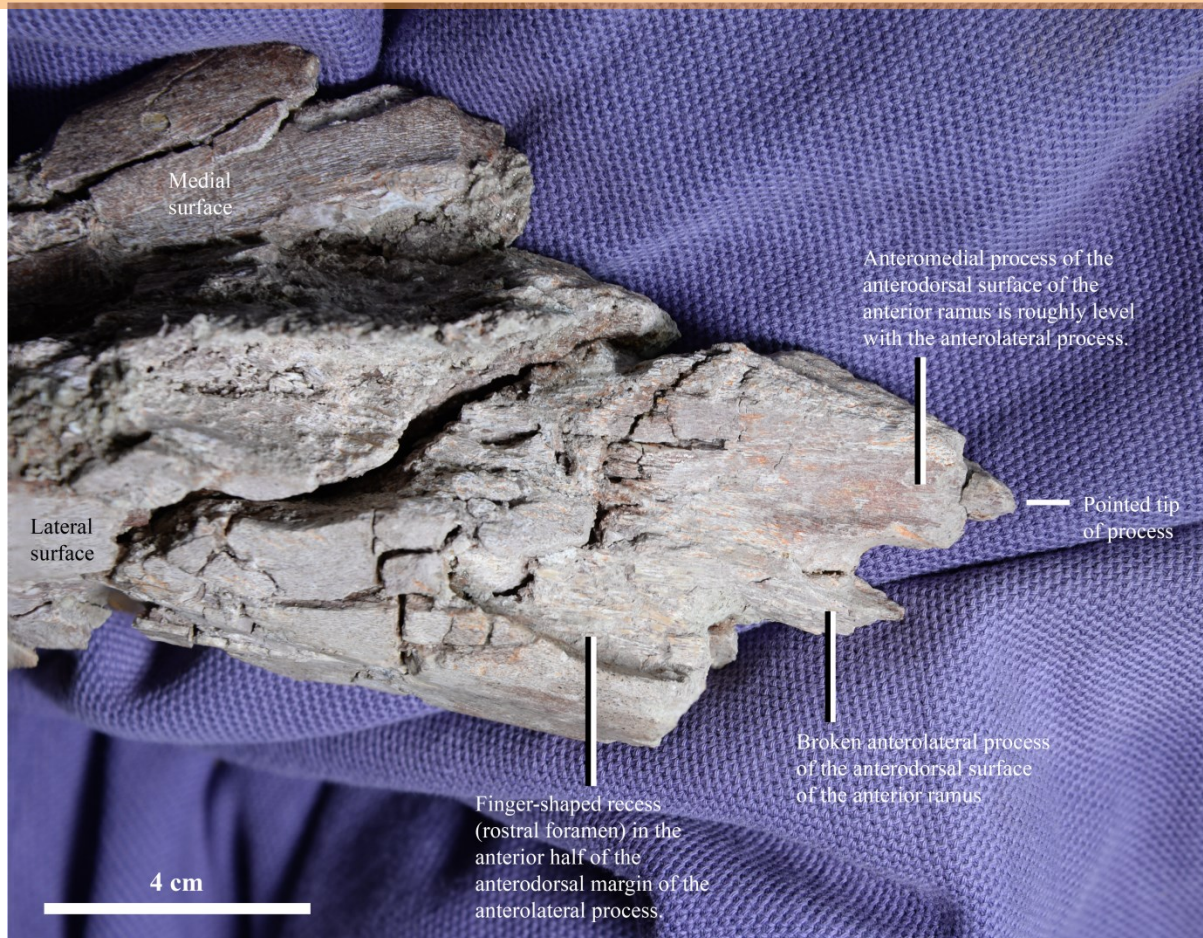349   2010).

350

351

352   Figure 12. The dorsal process of IVPP V22529 is laterally-compressed, subtriangular and
353   dorsally-rounded similar to the ones present in *Altirhinus* (PIN 3386/7; Norman, 2002: Fig. 6)
354   and *Bactrosaurus* (AMNH 6389, 6390; Prieto-Márquez, 2011: Figs. 9, 11). Dorsal process in,
355   A, lateral view; B, in dorsal view showing the lacrimal articular groove that is also present in
356   *Koshisaurus* and *Fukuisaurus* [Shibata & Azuma, 2015: Fig. 8C].

357

358   A relatively straight portion of the dorsal margin is preserved occupying around three-
359   quarters of the specimen's preserved anteroposterior length (Figs. 2, 11). This makes an ~30°
360   angle with the ventral margin of the maxilla and is grooved (as observed in *Koshisaurus* and
361   *Fukuisaurus* [Shibata & Azuma, 2015: Fig. 8C]), presumably for articulation with the
362   lacrimal (Fig. 12). The highest point of this section of preserved dorsal margin appears to
363   preserve a laterally-compressed, subtriangular and dorsally-rounded dorsal (ascending)
364   process similar to the ones present in *Altirhinus* (PIN 3386/7; Norman, 2002: Fig. 6) and

365 *Bactrosaurus* (AMNH 6389, 6390; Prieto-Márquez, 2011: Figs. 9, 11). Norman (2015)
366 characterises this process shape as a 'laterally flattened subtriangular plate' (Character 17,
367 state 2) (Figs. 2, 11, 12). This process shape does not have a well-defined distribution
368 amongst iguanodontians unlike the 'narrow' and 'finger-like' dorsal process morphologies
369 that Norman (2015) recovered as synapomorphies of Iguanodontia and Ankylopollexia
370 respectively (state 0 of character 17 respectively under ACCTRAN [='narrow, figure-like
371 process']). The dorsal process of IVPP V22529 possesses a shallow subcircular depression on
372 its lateral surface beneath its tip (Figs. 2, 11, 12) which is not observed in *Bactrosaurus* and
373 *Altirhinus*. A comparison with the condition in *Probactrosaurus* is not possible as the dorsal
374 region is not preserved e.g. in PIN 2232/9-2 and /10-2 (Norman, 2002) [coded as a '?' in
375 Norman, 2015]. IVPP V22529 is not sufficiently well-preserved to confidently characterise
376 the presence or absence of an antorbital fenestra, a feature that is used to diagnose clypeodont
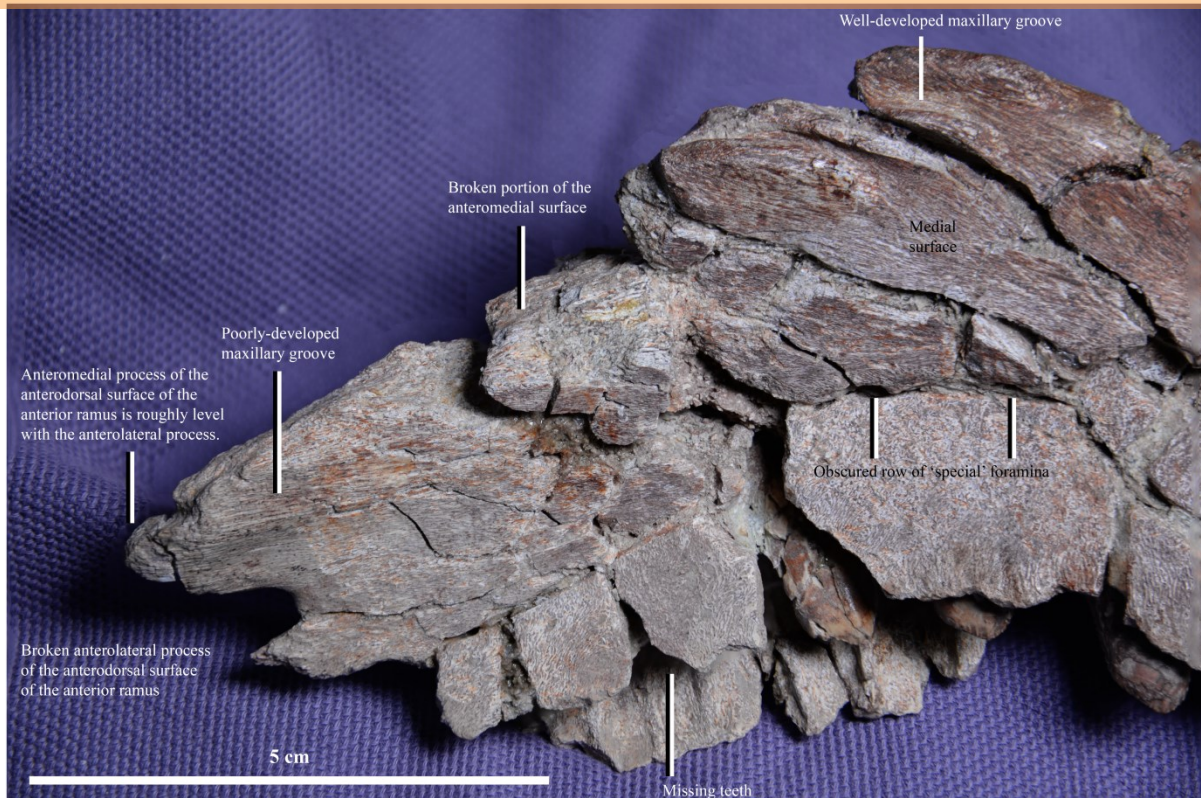377 ornithischians and their subclades (Norman, 2015).
378
379 The anterior portion of the maxilla appears to be subtriangular (Figs. 2, 11, 13), as in most
380 iguanodontians including *Altirhinus* (PIN 3386/7; Norman, 1998: Fig. 6B), *Bactrosaurus*
381 (AMNH 6553; Prieto-Márquez, 2011) and *Probactrosaurus* (PIN 2232/9-2; Norman, 2002).
382 The anterior maxillary ramus of IVPP V22529 is forked into a pointed anteromedial process
383 at around the same level as the incompletely preserved anterolateral process (Figs. 2, 11, 13).
384 Owing to the incomplete preservation of the latter process (Figs. 2, 11, 13), the relative length
385 and size of these processes cannot be determined. Processes of different sizes are found in the
386 'iguanodontoid' styracosternan *Iguandon* (Weishamphel *et al.*, 1993), *Protohadros* (Head,
387 1998: Fig. 3C, D), *Bactrosaurus* (AMNH 6553, 6389, 6390; Prieto-Márquez, 2011: Figs. 7-
388 12) and *Koshisaurus* (Shibata & Azuma, 2015: Figs. 3A, C; 8A, B, E), but in the latter the
389 anterior processes are actually of similar rather than different lengths (Shibata & Azuma,
390 2015: Fig. 3A). Bifurcated anterior processes are actually diagnostic of Iguanodontia
391 (Norman, 2015: character 15, state 1; ACCTRAN), but in the left maxilla of
392 *Shuangmiaosaurus* the anterolateral process appears to have become particularly enlarged
393 with a dorsally placed nubbin at its base potentially being the remnants of the anteromedial
394 process (LPM0165; You *et al.*, 2003b: Fig. 1A). Teeth are present right up to base of the
395 anteromedial process, as in *Protohadros* (Head, 1998: Fig. 3C, D). The anterior half of the
396 anterodorsal margin of the anterolateral process of IVPP V22529 has a finger-shaped recess
397 (rostral foramen) (Fig. 13), as in non-hadrosaurid iguandontians.
398

400 Figure 13. Dorsal view of the anterodorsal process of IVPP V22529 showing the bifurcating
401 anterior processes at roughly the same level. Only the pointed anteromedial process is
402 complete. This is a finger-shaped recess (rostral foramen) in the anterior half of the
403 anterodorsal margin of the anterolateral process.
404
405 Halfway up the medial side of the maxilla there is a well-developed medially projecting shelf
406 that originates from the dorsomedial portion of the anterior ramus (Fig. 11). Subhorizontal
407 ridges along the medial side of the anteromedial process and the medial shelf become
408 increasingly well-developed dorsoposteriorly (although a portion of the intervening area is
409 broken). These ridges demark the boundaries of the maxillary grooves. Unlike IVPP V22529,
410 the maxillary grooves of *Koshisaurus* (Shibata & Azuma, 2015: Figs. 3C; 8B, E) are all
411 poorly-developed where there are all well-developed in *Protohadros* (SMU 74582; Head,
412 1998: Fig. 3D) and *Fukuisaurus* (FPDM-V40-1; Shibata & Azuma, 2015: Fig. 8B, E; three
413 and five grooves respectively). Maxillary grooves presumably relate to the attachment of soft
414 tissues in the roof of the mouth, but these seems to be absent in the most derived
415 iguanodontians - the distribution of this feature is unclear across Iguanodontia. The evolution
416 of maxillary grooves is therefore of interest in further understanding iguanodontian feeding
417 and as a potential source of phylogenetic information.
418

Figure 14. The maxillary grooves in IVPP V22529 become better-developed along the medial surface of the anteromedial process and the medial shelf, unlike in *Protohadros* (SMU 74582; Head, 1998: Fig. 3D), *Fukuisaurus* (FPDM-V40-1; Shibata & Azuma, 2015: Fig. 8B, E) and *Koshisaurus* (Shibata & Azuma, 2015: Figs. 3C; 8B, E) where the grooves in each specimen are of similar sizes. However, the phylogenetic significance of maxillary groove morphologies is not understood.

The mediolateral width of the medial shelf is affected by dorsoventral diagenetic compression, as evident from bone fragments that are thrusted upon each other (Fig. 11). However, the exact extent of this diagenetic artefact is unclear because a compression-corrected bone reconstruction is beyond the scope of this paper to produce. *Bactrosaurus* has a comparatively less developed shelf in both adult (AMNH 6553; Prieto-Márquez, 2011: Fig. 7) and juvenile specimens (AMNH 6389, 6390; Prieto-Márquez, 2011: Figs. 9, 11) as well as *Altirhinus* (PIN 3386/7; Norman, 1998: Fig. 6B) [but the degree of lesser development is unknown for the aforementioned reason]. In these specimens and in IVPP V22529 the shelf is angled slightly dorsoposteriorly (Fig. 11). In contrast, *Probactrosaurus* was described by Norman (2002) as having a vertical and planar medial wall.

The entire posterior portion of IVPP V22529 is missing so the morphology of the jugal-maxilla suture is unknown (Figs. 2, 11). In *Altirhinus* (PIN 3386/7; Norman, 1998: Fig. 6A) the jugal sutural surface is a finger-like process that fits into a slot in the anterior ramus of the jugal, a feature that unites styracosternan iguanodontians (Norman, 2015: character 20, state 1). The missing anterodorsal margin makes it impossible to infer the morphology of the jugal's ventral margin which is sinusoidal in ankylopollexian iguanodontians (Norman, 2015: character 21, state 1). The missing posterior ramus means it is unclear if this is dorsoventrally tall with a rounded but slightly irregular tip, as in *Probactrosaurus* (PIN 2232/9-2,10-2; Norman, 2002: Fig. 5), or if it is more 'finger-like', as in *Altirhinus* (PIN 3386/7; Norman, 2002, Fig. 6A, B).

448

Figure 15. Close-up of the relatively flat lateral surface of IVPP V25529 showing a row of
anteriorly-opening foramina that increase in size posteriorly.

The lateral surface of the maxilla is relatively flat, a trait that is undoubtedly influenced by
the fragmentation of the specimen (Figs. 2, 15). Ventral to the dorsal process is a broad
shallow groove (Figs. 2, 12). There is a low scattered row of five anteriorly-opening
neurovascular foramina on the lateral surface that increase in size posteriorly (Fig. 15). These
observations appear to be generally consistent with *Probactrosaurus*, notably the right
maxilla of PIN 2232-10-2 (Norman, 2002, Fig. 5A), except that the foramina in the latter do
not increase in size posteriorly. However, these arguments are weakened by the absence of
foramina in the larger left maxilla *Probactrosaurus* PIN 2232-9-2 (Norman, 2002, Fig. 5B)
suggesting that these foramina are not consistently expressed on the sides of the skull and/or
they may undergo changes with age or be different between sexes.

Discussion

Taxonomic status of IVPP V22529

A basal hadrosauriform based on tooth anatomy
IVPP V22529 matches the maxillary teeth characteristics in the diagnosis of *Probactrosaurus*
(Norman, 2002): 'maxillary teeth narrow with prominent primary ridge and no subsidiary
ridges; tall and interlocking teeth that form a high, posteriorly inclined battery; marginal
denticles are mammillate.' However, these characteristics are not used to refer IVPP V22529
to *Probactrosaurus* (Norman, 2002) as the aforementioned characteristics are now
understood to have a wider distribution amongst iguanodontians than previously appreciated
(Norman, 2015). The tooth anatomy of IVPP V22529 identifies it as a non-euhadrosaurian

477 hadrosauriform: two or more replacement crowns are a hadrosauriform iguandontian feature
478 (Norman, 2015: character 54, state 1) whilst the absence of a single median primary ridge is a
479 non-euhadrosaurian iguanodontian feature (Norman, 2015: character 68, state 3). The
480 marginal denticles of IVPP V22529 comprise of parallel ledges with single rows of ~6
481 relatively large mammillae, a feature that further constrains the specimen as a basal
482 hadrosauriform.
483
484 *IVPP V22529 compared to* Probactrosaurus
485 IVPP V22529 has a number of noteworthy differences with *Probactrosaurus* maxillae,
486 despite the former missing its posterior portion and the latter missing anterior ramii. Firstly,
487 Norman (2002) noted that *Probactrosaurus gobiensis* has a vertical and planar medial wall
488 whereas in IVPP V22529 this in non-planar owing to its well-developed medial shelf (Fig.
489 11). However, a small proportion of the latter is ascribed to specimen deformation. Secondly,
490 there is a low scattered row of five anteriorly-opening foramina on the lateral surface of IVPP
491 V22529 that increase in size posteriorly, but in *Probactrosaurus* PIN 2232-10-2 (Norman,
492 2002, Fig. 5A) these foramina do not increase in size posteriorly and are even absent in
493 specimen PIN 2232-9-2 (Norman, 2002, Fig. 5B). In *Probactrosaurus* (and iguanodontians
494 more generally) there is incomplete knowledge of how maxillary foramina change with age
495 and how they can be different between sexes or individuals. Thus, further work is needed to
496 evaluate these types of variability so that the phylogenetic utility of maxillary foramina can
497 be established. Therefore, erring on the side of caution, the foraminal differences between
498 IVPP V22529 and *Probactrosaurus* should be considered tentatively as differences with
499 taxonomic value, and certainly warrant lesser value than the aforementioned medial shelf
500 difference. The presence and absence of the unique cementum 'jackets' in IVPP V22529 and
501 *Probactrosaurus* respectively could be strong evidence for differentiating them. However,
502 given the areas of uncertainty in the identification and formation mechanism of this structure
503 as well as its presence in at least one iguanodontian, it would be inappropriate to place
504 phylogenetic value on this structure until it is more extensively investigated. The teeth of
505 IVPP V22529 and *Probactrosaurus* are very similar and their maxillae are both
506 subtriangular.
507
508 *IVPP V22529 compared to* Bactrosaurus *and* Gilmoreosaurus
509 The expression of neurovasucular foramina on the lateral surface of the maxilla is variably
510 expressed in *Bactrosaurus*, which has a row of different-sized ones in juvenile specimen
511 AMNH 6389 (Prieto-Márquez, 2011: Fig. 9) but more random arranged one in juvenile
512 specimen AMNH 6390 (Prieto-Márquez, 2011: Fig. 11). However, as in IVPP V22529 these
513 foramina appear low on the lateral surface. In contrast, the maxillary foramina of
514 *Gilmoreosaurus* AMNH FARB 30653 (Prieto-Márquez & Norell, 2010) are more randomly
515 distributed but appear high as well as low on the lateral surface. On the medial surface of the
516 latter specimen the 'special foramina' are larger and more circular than those in IVPP
517 V22529 (although these are partially obscured by the displaced medial shelf) and
518 *Bactrosaurus* (AMNH 6553, 6389, 6390; Prieto-Márquez, 2011: Figs. 8, 10, 12).
519 *Gilmoreosaurus* AMNH FARB 30653 (Prieto-Márquez & Norell, 2010) and *Bactrosaurus*
520 (AMNH 6553, 6389, 6390; Prieto-Márquez, 2011: Figs. 8, 10, 12) lack maxillary grooves
521 that become increasingly developed along the medial surface of the anteromedial process and
522 the medial shelf, as in IVPP V22529 (Fig. 11). However, *Gilmoreosaurus* AMNH FARB
523 30653 (Prieto-Márquez & Norell, 2010) has less-developed maxillary grooves restricted to
524 the medial surface of the anteromedial process and so are less extensive than those of
525 *Koshisaurus* (Shibata & Azuma, 2015: Figs. 3C; 8B, E). *Bactrosaurus* AMNH 6389 (Prieto-

526   Márquez, 2011: Fig. 10) also appears to share this characteristic with *Gilmoreosaurus*, but
527   this needs to be confirmed by first-hand study of this specimen.
528
529   Cementum 'jackets'
530   Cementum 'jackets' are a dental structure presumably related to feeding style, but how it is
531   related to this is not yet obvious. The restriction of these 'jackets' to the labial side of the
532   tooth appears to be genuine and suggests this side was well-anchored to the tooth socket. The
533   latter trait may have been important in allowing the 'jackets' to help resist lateral components
534   of bite forces, a force regime that is evident from the medially-directed slope of the wear
535   facets of the teeth. The 'jackets' probably reduced stress on the brittle tooth crests more
536   generally as well by transmitting loads amongst the tissues of the teeth (Erickson *et al.*,
537   2012). However, if these structures did have these roles then the alternating occurrence of the
538   'jackets' in *Equijubus* implies that not all taxa benefitted from this hypothesised function
539   equally. Histological analysis will no doubt be invaluable in testing the cementum 'jacket'
540   hypothesis at the microscopic level and should help to clarify both the composition and
541   morphology of these structures. Unfortunately, such work is beyond the scope of the current
542   study, but it should be a priority for future studies of IVPP V22529. Future opportunities to
543   compare feeding biomechanics in IVPP V22529 (and other basal hadrosauriformes) with
544   more derived hadrosauriforms (Erickson *et al.*, 2012) will also be worthwhile to determine
545   how important these cementum 'jackets' were in iguandontian dental system evolution.
546
547
548   **Conclusions**
549   IVPP V22529 is an isolated Early Cretaceous partial right iguanodontian maxilla that
550   possesses tooth characteristics identifying it as a basal hadrosauriform. However, other parts
551   of this bone fail to convincingly support a referral to a new or existing taxon, including to a
552   new or existing species of *Probactrosaurus*, a contemporaneous genus known from the same
553   locality in North China. Further work may better constrain the taxonomic status of this
554   specimen if characteristics differing from *Probactrosaurus* can be validated, namely: a
555   unique corrugated middle ventrolateral margin, a row of foramina on its lateral surface that
556   open anteriorly and increasing in size posteriorly as well as a prominent medial shelf. Despite
557   its coarse level of identification, IVPP V22529 has important implications for our
558   understanding of iguanodontian (and dinosaurian) dental architecture. In labial view, five
559   middle maxillary crowns each preserve a rugose cementum sheath over their basal portions
560   that are separate from the tooth socket but actually originate within them and extend ventrally
561   below the crenulated ventral margin of the maxilla. This arrangement forms a corrugated
562   ventrolateral surface as grooves separate the sides of these sheaths. This structure - which we
563   propose to call a cementum 'jacket' structure - appears to be present in the basal
564   hadrosauriform *Equijubus* as well, but this differs from IVPP V22529 in being present in
565   every other tooth rather than on each tooth. To our knowledge this structure has not been
566   described in other dinosaurs, but cementum commonly migrates onto the tooth crowns of
567   mammals (Erickson *et al.*, 2012). The wider distribution of cementum 'jackets' amongst
568   iguanodontians (and dinosaurs more generally) warrants further attention as their morphology
569   could carry important phylogenetic information. The restriction of these 'jackets' to the labial
570   face of the teeth might indicate a structural role in resisting the lateral component of bite
571   forces and/or the stress on the brittle tooth crests, but these hypotheses and confirmation of
572   'jacket' composition and morphology would greatly benefit from future histological analysis
573   and biomechanical studies that were beyond the scope of this study. Despite, the further work
574   required, IVPP V22529 provides important new insights into the dental architecture of basal

575 hadrosauriforms that deepens our understanding of the morphological diversity that preceded
576 the revolutionary advanced hadrosauriform dental battery system (Erickson *et al.*, 2012).
577
578

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584
585

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592
593

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