

1 Morphology and function of the palatal dentition in Choristodera

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8

9 **Abstract**

10 Choristoderes are a group of extinct freshwater reptiles that were distributed throughout Laurasia
11 from the Middle Jurassic to the Miocene. They are inferred to have had a lifestyle similar to that
12 of extant gavialid crocodiles, but they differed from crocodiles in retaining an extensive palatal
13 dentition. All choristoderes had teeth on the vomers, palatines, and pterygoids, and teeth are
14 rarely present on the parasphenoid. Palatal teeth are conical, as in the marginal dentition, and
15 form longitudinal and transverse rows. Detailed examination of different genera shows that the
16 orientation of the palatal tooth crowns changes with their position on the palate, supporting the
17 view that they are involved in intra-oral food transportation, presumably in combination with a
18 fleshy tongue. Moreover, observed variation in palatal tooth shape and the width of palatal tooth
19 batteries may provide additional clues about diet. The European *Simoedosaurus lemoinei* has
20 sharper palatal teeth than its North American counterpart, *S. dakotensis*, suggesting a
21 preference for softer prey - a conclusion consistent with the more gracile teeth and narrower
22 snout.

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24

25 **Keywords**

26 *Champsosaurus*, *Simoedosaurus*, Palatal dentition, Function, Morphology, subthecondont

27

28 **Introduction**

29 Choristodera is an extinct (Middle Jurassic to Miocene) group of aquatic diapsid
30 reptiles that typically occurred as part of a mesic Laurasian vertebrate assemblage (including
31 fish, frogs, salamanders, turtles and crocodiles) in relatively warm, temperate climates
32 (occasionally sub-tropical areas: Matsumoto & Evans, 2010). The group is characterized by a
33 unique combination of characters including a dorsoventrally depressed cordiform skull and

34 conical subtheodont teeth.

35 Choristoderes are represented by three morphotypes (short-necked longirostrine,
36 short-necked brevirostrine, and long-necked brevirostrine). The short-necked longirostrine taxa
37 form a monophyletic clade named Neochoristodera (sensu Evans & Hecht, 1993). The other
38 morphotypes (short-necked brevirostrine and long-necked brevirostrine) fall into a paraphyletic
39 set, informally named non-neochoristoderes, the earliest of which is *Cteniogenys*, a small
40 lizard-like reptile known from the Middle–Late Jurassic of Euramerica (Britain, Portugal, USA:
41 Evans, 1989, 1990, 1991; Chure & Evans, 1998). ~~Of the other non-neochoristoderan taxa, three~~
42 ~~are long-necked and three are short-necked.~~ The long-necked taxa are all from the Early
43 Cretaceous of Asia: *Hyphalosaur* (*H. lingyuanensis*; *H. bitaigouensis*, China: Gao et al. 1999;
44 Ji et al. 2004), *Shokawa ikoi* (Japan: Evans & Manabe, 1999), and probably *Khurendukhosaurus*
45 *orlovi* (Mongolia and Russia: Sigogneau-Russell & Efimov 1984; Efimov & Storrs, 2000;
46 Skutchas, 2008). *Hyphalosaur* is represented by nearly complete skulls, but many of these are
47 dorsoventrally compressed and are rarely preserved in ventral view (Gao & Ksepka, 2008). The
48 Japanese long-necked *Shokawa* is known from an articulated postcranial specimen and a few
49 attributed jaw elements (Evans & Manabe, 1999). *Khurendukhosaurus* is known only from
50 disarticulated postcranial elements and a few skull bones (basioccipital, exoccipital, maxilla,
51 dentary) (Skutchas, 2008). The short-necked brevirostrine morphotype has a wider geographical
52 and chronological range: *Monjurosuchus splendens* (Gao et al. 2000; Gao & Li, 2007;
53 Matsumoto et al. 2007) and *Philydrosaurus proseilus* (Gao & Fox, 2005; Gao et al. 2007; Gao et
54 al. 2013) are from the Early Cretaceous of Asia (China and Japan), whereas the European
55 *Lazarussuchus* (*L. inexpectatus* Hecht, 1992; *L. dvoraki* (Evans & Klembara, 2005) is recorded
56 from the Late Paleocene (France; Matsumoto et al. 2013) to Early Miocene (France, Czech
57 Republic, Germany) (Hecht, 1992; Evans & Klembara, 2005; Böhme, 2008). Neochoristodera
58 (short-necked longirostrine type) is comprised of four genera of similar morphology - the Early
59 Cretaceous *Tchoiria* (*T. namsarai*; *T. klauseni*: Efimov, 1975; Ksepka et al. 2005) and
60 *Ikechosaurus* (*I. magnus*; *I. sunailinae*; *I. gaoi*; *I. pijiagouensis*: Efimov, 1979; Sigogneau-Russell,
61 1981; Liu, 2004; Brinkman & Dong, 1993; Lü et al. 1999) from Asia (China, Mongolia), and the
62 Late Cretaceous to Paleogene *Champsosaurus* (*C. laramiensis*, *C. ambulator*, *C. natator*, *C.*
63 *lindoei*, *C. albertensis*; *C. dolloi*, *C. gigas*, *C. tenuis*: Erickson, 1972; Gao & Fox, 1998;
64 Matsumoto, 2011) and *Simoedosaurus* (*S. lemoinei* and *S. dakotensis*: Gervais, 1877;
65 Sigogneau-Russell, 1985; Erickson, 1987) from Europe and North America (e.g., Brown, 1905;
66 Sigogneau-Russell & Russell, 1978).

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68 The phylogenetic position of Choristodera within Reptilia remains problematic (e.g.
69 Matsumoto et al. 2007, 2013), although many authors have placed the group somewhere on the
70 diapsid stem (e.g. Evans, 1988; Gao & Fox, 1998; Modesto & Sues, 2004; Rieppel & Reisz,
71 1999). As with many phylogenetically problematic groups, they show a mixture of specialized
72 and primitive traits. Among the latter is the presence of an extensive palatal dentition
73 (Sigogneau-Russell, 1979, 1985), a feature generally considered plesiomorphic within amniotes
74 where all major lineages show a crownward trend toward reduction or loss. Gao et al. (2007)
75 recently presented a brief overview of palatal morphology in Choristodera, prompted by new
76 specimens from the Early Cretaceous of China. They concluded that the choristoderan palate
77 was uniquely modified from the basal diapsid condition in features such as the elongated vomers,
78 posteriorly relocated choana, and reduction of the interpterygoid vacuity, features probably linked
79 to the aquatic lifestyle. However details of palatal tooth morphology, replacement, and function
80 remain poorly understood, despite the recovery of many new specimens of both
81 neochoristoderes and non-neochoristoderes. Our aim in this review is to provide a detailed
82 comparative study of the choristoderan palatal dentition and to relate it, where possible, to diet
83 and/or feeding strategy.

84

85 **Material and Methods**

86 Of the eleven known choristodere genera, palatal elements are preserved in nine.
87 Representatives of each were examined (Table 1) by stereomicroscopy, digital photographs,
88 and/or SEM, with some supplementary data taken from the literature. *Champsosaurus lindoei*
89 (NMC 8920) was subjected to micro-computed tomography (CT) at the National Museum of
90 Nature and Science, Tokyo, Japan, using TESCO, Microfocus CT TXS 320-ACTIS. The software
91 Avizo 8.0 was used to visualize 3D images of the CT data. Palatal tooth pattern of choristoderes
92 were plotted on a phylogenetic tree (Fig. 1) is based on the bootstrap consensus tree of
93 Matsumoto et al. (2013).

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95

96 **Abbreviations**

97 ***Institutional:*** **AMNH**, American Museum Natural History, New York, USA; **BMNH**, The Natural
98 History Museum, London, UK; **IGM**, Geological Institute of the Mongolian Academy of Sciences,
99 Ulan Bataar, Mongolia; **IRSNB**, Institut Royal des Sciences naturelles de Belgique, Bruxelles,

100 Belgium; **IVPP V**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China;
101 **LPMC**, Liaoning Paleontological Museum of China; **MNHN**, Muséum National d'Histoire
102 Naturelle, Paris, France; **NMC**, Canadian Museum of Nature, Ottawa, Canada; **PIN**,
103 Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **RTMP**, Royal Tyrrell
104 Museum of Palaeontology, Drumheller, Canada; **SMNS** Staatliches Museum für Naturkunde,
105 Stuttgart, Germany; **SMM**, The Science Museum Minnesota, St. Paul, Minnesota, USA.

106

107 *Anatomical*: ch, choana; D, dentary; Ept, ectopterygoid; F, frontal; Hy, hyoid; ip-v, interpterygoid
108 vacuity; J, jugal; Mx, maxilla; P, parietal; Pal, palatine; Psh, parasphenoid; Pt, pterygoid; pt f,
109 pterygoid foramen; pl f, palatal foramen; Po, postorbital; Prf, prefrontal; rtp, replacement tooth
110 pit; sbt f, subtemporal fenestra; Sp, splenial; Vo, vomer.

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112

113 **Description**

114 **Structure of marginal dentition in choristoderes**

115 The marginal teeth of choristoderes are essentially homodont in both upper and lower
116 jaws, and the implantation is subthecodont. Teeth are replaced by the erosion of a pit in the
117 lingual surface of the old tooth base. However, there are minor differences between
118 non-neochoristoderes and neochoristoderes in marginal tooth morphology. Teeth of
119 non-neochoristoderes are relatively simple, and striated enamel covers the tooth crown but not
120 the base (Fig. 2A-B). Furthermore, the crown is straight, allowing the teeth to be closely packed
121 along the tooth row. In contrast, teeth of neochoristoderes are completely covered by striated
122 enamel and there is enamel infolding at the base. In some neochoristoderes, such as
123 *Simoedosaurus* and *Champsosaurus*, the anterior teeth are sharper and more slender than the
124 posterior ones (Fig. 2D-E). The crown is labiolingually compressed and there are keels on each
125 side of the tooth. The sharp tooth apex is curved either posteriorly or medially depending on
126 tooth position (anterior-posterior, upper-lower jaws) and taxon. *Ikechosaurus* is unique among
127 neochoristoderes in having straight tooth crowns and a lack of enamel over the tooth base, as in
128 non-neochoristoderes, but it shows the basal dentine infolding of neochoristoderes (Matsumoto
129 et al. 2014).

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131

132 **General structure of the palatal dentition in choristoderes**

133 Non-neochoristoderes: the palatal dentition of neochoristoderes is relatively well
134 known due to many specimens with nearly complete palatal elements, but this region is less
135 known for non-neochoristoderes, due to poor preservation or a lack of relevant elements (Table
136 1). In many cases, description of the palatal dentition is based on, at most, a few specimens (e.g.
137 *Hyphalosaurus*). The teeth are arranged as a series of longitudinal rows on the vomer, palatine
138 and pterygoid, a pattern inherited from that of basal amniotes (Matsumoto & Evans, work in
139 progress). Although choristoderes were all essentially aquatic, there is no obvious aquatic
140 specialization in the palatal dentition of basal taxa. The presence of a pterygoid flange tooth row
141 is confirmed in neochoristoderes and *Cteniogenys* (Fig. 1, 3), but it remains uncertain in most
142 non-neochoristoderes (e.g. Fig. 1, 4, 5: *Monjurosuchus*, *Philydrosaurus*, *Hyphalosaurus* and
143 *Lazarussuchus*). In *Monjurosuchus* and *Philydrosaurus*, pterygoid flange teeth are obscured by
144 poor preservation (Fig. 1, 5; Gao et al. 2007; RM personal observation). Gao et al. (2013)
145 reported the pterygoid flange teeth to be absent in *Philydrosaurus*, based on a newly discovered
146 juvenile specimen, but the flange is damaged. As in most diapsids, non-neochoristoderes
147 generally lack parasphenoid and ectopterygoid teeth

148 Neochoristoderes: some species are represented by multiple specimens and
149 examination has shown that palatal features are consistent within species. As in
150 non-neochoristoderes, neochoristoderes generally lack parasphenoid and ectopterygoid teeth,
151 the exception being the Early Cretaceous *Ikechosaurus sunailinae* (Fig. 6: IVPP V9611-3;
152 10596.1), which has parasphenoid teeth. However, these were probably secondarily acquired as
153 has been reported in Lepidosauromorpha (e.g., Kuehneosauridae; Evans, 2009). Lateral and
154 medial tooth rows run longitudinally over the palate. The lateral row arises on the palatine,
155 posterior to the choana, and runs onto the lateral side of the pterygoid, extending posterior to the
156 end of the marginal tooth row. The row is generally continuous, but in some species it is
157 interrupted by a gap at the palatine-ptyerygoid suture (e.g., *Tchoiria klauseni*; Ksepka et al. 2005).
158 The medial row, on the other hand, begins on the vomer, anterior to the choana, runs along the
159 medial side of the pterygoid, and terminates posterior to the interptyerygoid vacuity. There is
160 usually a toothless gap around the vomer-ptyerygoid suture. Both lateral and medial rows are
161 generally single, except in a few *Champsosaurus* species (e.g., *C. gigas* and *C. dolloi*) where the
162 pterygoid bears several rows (Fig. 7). However, the width of the tooth rows varies between
163 species and between genera. In most species the longitudinal rows are fewer than ten tooth
164 positions across and the pterygoid flange tooth row has 1–3 tooth positions. However, in
165 *Simoedosaurus* (Fig. 8-9) and *Ikechosaurus* (Fig. 6) the longitudinal rows are generally more

166 than ten teeth across and the pterygoid flange tooth row may be 4–19 teeth across. These wide
167 tooth batteries are a characteristic feature of *Simoedosaurus* and *Ikechosaurus*, so that the teeth
168 cover most of the palatal surface (Fig. 6, 8-9).

169 Naso-palatal trough: the medial and lateral longitudinal rows in neochoristoderes are
170 separated by a distinct groove, the naso-palatal trough. Erickson (1985) suggested that this
171 might be the functional equivalent of the secondary palate (by extending the nasal groove
172 posteriorly). This structure is less obvious in non-neochoristoderes, but a newly discovered
173 specimen of *Philydrosaurus* from the Early Cretaceous of China (Gao et al. 2007) appears to
174 show some development of a trough extending posteriorly from the choana. However, due to the
175 poor preservation of palatal elements in most non-neochoristoderes, the distribution and
176 evolutionary history of the nasopalatal trough among non-neochoristoderes remains uncertain.

177

178 Palatal tooth replacement

179 The marginal tooth replacement pattern is almost mirrored in the palatal dentition.
180 Marginal tooth replacement has been described in *Cteniogenys* (Evans, 1990). Initially, the new
181 tooth grows at the lingual side of the old tooth base. The new tooth attaches weakly to the base
182 and erodes a pit in it (Fig. 2C, G). A similar replacement pattern can be recognized on one of the
183 pterygoid teeth in *Cteniogenys*. The tooth shows an erosion pit made by a new tooth on the
184 lingual side of the old tooth base. In contrast, in *Champsosaurus* (RTMP 92.36.270) the eroding
185 pit straddles two old teeth (Fig. 2H), suggesting two original teeth were being replaced by a
186 single larger tooth. A matching replacement pattern for marginal and palatal teeth was also
187 reported in living squamates (e.g. Mahler & Kearney, 2005), although there is some variation in
188 the position of the replacement (e.g. *Iguana* shows both lingual and labial replacement in
189 different tooth rows: Mahler and Kearney, 2005).

190

191 Palatal tooth platforms

192 Although there are differences of degree between species, the palatal tooth batteries
193 of neochoristoderes sit on a bony platform that raises them above the level of the palatal surface.
194 These platforms are particularly strongly developed anteriorly in *Champsosaurus* and
195 *Simoedosaurus*, so that the palatine tooth bases lie almost level with, or even ventral to, the
196 maxillary tooth bases (Fig. 10). Among non-neochoristoderes, a tooth platform is, at most,
197 weakly developed in *Cteniogenys* (clearly recognized only in the longitudinal pterygoid row) and
198 *Monjurosuchus*.

199 Tooth platforms may also be present along the posterior margin of the pterygoid
200 flange, but in this case, the orientation of the tooth row also depends on that of the flange itself.
201 The pterygoid flange is always angled forward in choristoderes, but the angulation is least in
202 Neochoristodera (10–30 degrees; e.g., *Ikechosaurus*, IVPP V9611-3) and greatest in
203 *Cteniogenys* (45 degrees; e.g., BMNH 11759) and *Monjurosuchus* (40 degrees; e.g., IVPP
204 14261), with *Philydrosaurus* midway between the two extremes (35 degrees; Gao et al.
205 2007)(Supplementary information). In *Champsosaurus* and *Simoedosaurus*, the pterygoid flange
206 also extends ventrally, due to the ectopterygoid contribution, and leans slightly anteroventrally,
207 so that the pterygoid flange tooth tips face anteriorly (Fig. 9F-H, 11H). Despite the uncertain
208 relationship of the ectopterygoid and pterygoid, *Ikechosaurus* has an anteriorly facing pterygoid
209 flange tooth platform (uncertain in *Tchoiria*). This is absent in *Cteniogenys* and *Monjurosuchus*
210 (Fig. 1, 3C, 5B), but unknown in other non-neochoristoderes.

211

212 **Palatal tooth morphology, size and direction of tooth crowns**

213 Individual palatal teeth (neochoristodere and non-neochoristodere) show the same
214 morphology as the marginal teeth of non-neochoristoderes: they are conical, with enamel only
215 partially covering the crown, and weakly developed ridges on the enamel surface (Fig. 2). All
216 palatal teeth sit in shallow circular alveoli and lack basal enamel infolding.

217 In neochoristoderes the palatal teeth gradually become smaller from anterior to
218 posterior ends of the longitudinal rows. In addition, the teeth on the lateral row are larger than
219 those on the medial row. In the pterygoid flange row, teeth decrease in size from lateral to medial,
220 but where the row is wide (*Simoedosaurus* and *Ikechosaurus*), the reduction is from anterolateral
221 to posteromedial. This pattern differs in non-neochoristoderes. *Monjurosuchus* sp. (IVPP
222 V14261) shows a reverse pattern on the pterygoid (longitudinal row), with the largest teeth in the
223 medial row, and at its posterior end. In *Cteniogenys*, there is no significant size difference along
224 either the longitudinal pterygoid row or the pterygoid flange row.

225 Kordikova (2002) reviewed palatal tooth morphology in choristoderes based on
226 *Simoedosaurus* and *Champsosaurus* and stated that the tooth crowns point sharply backward.
227 However detailed examination in several species of neochoristoderes, mainly *Champsosaurus*
228 and *Simoedosaurus*, shows that the orientation of palatal tooth crowns changes with the position
229 on the palate. In *Simoedosaurus*, the European (Paleocene) *S. lemoinei* has anterior vomerine
230 and palatine teeth that are blunt (Fig. 8C, F), with more posterior teeth becoming sharper and
231 more backward pointed (Fig. 8E, G, I). In contrast, the shorter-snouted North American *S.*

232 *dakotensis* is characterized by blunt palatal tooth crowns throughout the tooth row, with the
233 crowns oriented vertically on the vomer and palatine, but varying posteriorly from straight to
234 recurved (Fig. 9). SMM P76.10.1 is the only specimen of *S. dakotensis* that preserves a
235 complete skull and palatal dentition. However, the marginal teeth are preserved in position with
236 no trace of wear of the tooth crowns. It is therefore unlikely that the shape of the palatal tooth
237 crowns is due to wear. The pterygoid flange tooth crowns curve medially in both species but in *S.*
238 *dakotensis* the teeth along the edge of the subtemporal fenestra point anteriorly.

239 Among the eight valid species of *Champsosaurus*, there is variation in the number
240 and width of the longitudinal palatal tooth rows, and in the orientation of the tooth crowns. For
241 example, although the Late Cretaceous *C. albertensis* (Fig. 12; RTMP86.12.11) and the
242 Paleocene *C. gigas* (Fig. 11; SMM P77.33.24) have similar sized skulls, the palatal dentition is
243 different. *C. albertensis* has either straight or randomly oriented crowns anteroposteriorly (Fig.
244 12), whereas in *C. gigas*, the crowns are straight on anterior teeth (vomer and palatine) but curve
245 sharply posteriorly in the pterygoid part of the rows (Fig. 11). In addition, *C. albertensis* has a
246 relatively small number of large teeth in the longitudinal pterygoid row, whereas *C. gigas* has a
247 larger number of small teeth. This seems to be a general difference between the Late
248 Cretaceous (e.g., *C. lindoei*; *C. natotor*) and Paleocene species (e.g., *C. tenuis*; *C. dolloi*). Minor
249 ontogenetic variation is also recognized in *Champsosaurus lindoei*, in which the width of
250 longitudinal palatal tooth row seems to increase slightly through ontogeny, from a single tooth
251 wide in smaller individuals (Fig. 7B, 12: RTMP 94.163.01: inner biquadrate width 50 mm) to
252 double that in a larger individual (Fig. 7A: RTMP 87.36.41: inner biquadrates width 86 mm).
253 However, *Champsosaurus* species are more consistent in the morphology of the pterygoid
254 flange rows, which are usually 1-2 tooth positions wide with vertical tooth crowns (Fig. 7).

255 In the wide longitudinal tooth rows of the Early Cretaceous *Ikechosaurus*, the anterior
256 (vomer and palatine) crowns are straight or point backward, but those on the pterygoid are first
257 directed posteriorly and then gradually turn medially (Fig. 6A). The expansion of the palatal tooth
258 row is essentially similar to that of the Paleocene species *Simoedosaurus lemoinei* and *S.*
259 *dakotensis*. However unlike these *Simoedosaurus*, several well-preserved palatal teeth of
260 *Ikechosaurus* show distinctive ridges on the sides (Fig. 6D). Interestingly within the extensive
261 pterygoid tooth and pterygoid flange tooth rows, the teeth form antero-posteriorly and
262 mediolaterally radiating lines, instead of having a random distribution as in *Simoedosaurus*.
263 Furthermore the parasphenoid tooth crowns incline posteriorly and, uniquely, the pterygoid
264 flange teeth incline medially.

265 There is less available data on crown-orientation in non-neochoristoderes due to poor
266 palatal preservation (e.g., *Hyphalosaurus*, Fig. 4). The teeth of the anterior longitudinal row
267 (vomer, palatine) are generally straight (*Hyphalosaurus*, *Monjurosuchus*, *Cteniogenys* [vomer
268 unknown in *Cteniogenys*]), but the posterior teeth show some variation. In *Cteniogenys*, some
269 worn teeth are retained in the sockets, stripped of their enamel and with the tips smooth and flat
270 (Fig. 3G). Originally, they were presumably conical and covered by enamel as shown in Fig. 3E-F.
271 The tooth tips incline in random directions in the posterior part of the tooth row (pterygoid), but
272 some terminal teeth are inclined posteriorly. In *Monjurosuchus*, the conical tooth tips are
273 randomly oriented, posterior, anterior or vertical (Fig. 5). This orientation is recognized in at least
274 two specimens (IVPP V 13761, 14261), so is unlikely to be due simply to deformation.

275

276 **Discussion**

277 **Evolutionary history of the palatal dentition in Choristodera**

278 Tracing the evolutionary history of the choristoderan palatal dentition is complicated
279 by a paucity of information on the palate of many non-neochoristoderes (poor preservation,
280 specimen orientation), the absence of Triassic representatives (ghost lineage), and a lack of
281 consensus on the interrelationship of non-neochoristoderes. However, a review of amniote
282 palate morphology (Matsumoto & Evans work in progress) suggests that the primitive diapsid
283 pattern consisted of longitudinal tooth rows on the vomer, palatine and pterygoid; a pterygoid
284 flange row; and, probably, a tooth patch on the parasphenoid. This pattern would have been
285 inherited by the common ancestor of all choristoderes and is broadly retained in the Jurassic
286 *Cteniogenys* (Evans, 1990), albeit with an increase in width of the pterygoid tooth row and loss of
287 the parasphenoid teeth. There was also a tendency to develop bony palatal ridges/platforms on
288 the vomer, palatine and pterygoid to which the palatal teeth attached and which contribute to the
289 formation of a nasopalatal trough. The latter feature is most obvious in *Champsosaurus* and
290 *Simoedosaurus* (Figs 8-12) where it separates wide tooth batteries, and was thought to be a
291 neochoristodere character. However, a weakly developed nasopalatal trough was recently
292 reported in the non-neochoristodere *Philydrosaurus* (Gao et al. 2007). It is not present in
293 *Cteniogenys* nor is it evident in a juvenile *Monjurosuchus* sp. (IVPP 14261) for which the palate
294 is known. Additional specimens are required to understand the evolutionary history of the
295 nasopalatal trough in choristoderes.

296

297 **The function of the palatal dentition**

298 Although there is variation in the choristoderan palatal dentition, the basic pattern can
299 be summarized as follows. Medial and lateral longitudinal tooth rows, of variable width, run from
300 the vomers to the pterygoids, supplemented by transverse pterygoid flange rows. The palatal
301 tooth crowns on the vomer and palatine point straight down while the more posterior (pterygoid)
302 teeth point backward and/or medially (e.g., *Ikechosaurus*), often with a reduction in size. The
303 pterygoid flange teeth are straight or medially directed. This is especially clear in ~~the extensively~~
304 ~~toothed~~ neochoristoderes *Ikechosaurus*, *Simoedosaurus*, and *Champsosaurus* (*C. gigas*,
305 juvenile *C. lindoei*). The anterior limit of the palatal dentition corresponds to the posterior limit of
306 the lower jaw symphysis. Non-neochoristoderes have a shorter symphysis and their anterior
307 palatal teeth extend close to the premaxilla (unknown in *Cteniogenys*), whereas in the
308 long-snouted neochoristoderes, with long symphyses, the palatal dentition begins further
309 posteriorly. A mobile fleshy tongue, with both intrinsic and extrinsic musculature, is inferred to
310 have been primitive for amniotes (Iwasaki, 2002), and seems to be correlated with the retention
311 of a palatal dentition (lizards), or its replacement with analogous keratinized tubercles or ridges
312 in the oral epithelium (crocodiles, turtles, mammals, birds). As suggested by Erickson (1985),
313 therefore, a fleshy tongue probably worked with the palatal dentition in choristoderes during
314 intra-oral transport of prey (Fig. 10). The positional changes of palatal tooth orientation may
315 correspond to the feeding stages categorized by Schwenk (2000): 1) prey capture; 2) ingestion;
316 3) intraoral transport; 4) swallowing.

- 317 1) Prey capture: mainly involves the anterior marginal teeth, the crowns of which are directed
318 medially in neochoristoderes, but are generally straight in non-neochoristoderes.
- 319 2) Ingestion: the straight anterior palatal teeth (on vomer and palatine) might have had a role in
320 holding and reorienting the prey in combination with a fleshy tongue. In addition, in
321 neochoristoderes, the ridges formed by the combination of raised palatal platforms and
322 embedded teeth form a crest on the palatine medial to the marginal tooth row. This may help
323 to hold prey where the larger marginal teeth are located (Fig. 13).
- 324 3) Intraoral transport: the prey is manipulated by the tongue and pushed towards the back of
325 the mouth with the posteriorly directed pterygoid teeth minimizing resistance against the
326 tongue but preventing the prey from moving or sliding forward (Fig. 13).
- 327 4) Swallowing: At the back of the mouth, the tooth crowns of the transverse pterygoid tooth row
328 point medially. This may have helped to hold prey and avoid forward slippage while the
329 tongue pushes food into the pharynx (pharyngeal packing). These pterygoid teeth are also
330 level with the point at which the marginal tooth size is reduced. However, the posterior

331 palatal teeth in some *Champsosaurus* (e.g., *C. albertensis*) are oriented randomly, perhaps
332 to resist moving prey.

333 In the absence of muscular pharyngeal walls in reptiles (Schwenk, 2000), the pharynx
334 itself then needs to be compressed externally (by neck muscles or neck flexion) in order to
335 finally push the food item into the esophagus to initiate swallowing. With external
336 constriction, there is a danger of the prey being squeezed back into the mouth instead of
337 into the esophagus (Schwenk, 2000), and the posterior pterygoid teeth may help to resist
338 this. The parasphenoid teeth in *Ikechosaurus* may have a similar function as the
339 parasphenoid lies in the roof of the pharyngeal region. Their inferred redevelopment
340 suggests that something has changed with respect to feeding strategy – in prey size, oral
341 soft tissues or neck muscles – so that a firmer grip is required here.

342 Observed variation in palatal tooth shape and the width of palatal tooth batteries may also
343 provide clues about diet. A study of the extant fish (*Cichlasoma*) found a correspondence
344 between pharyngeal tooth morphology and diet: fish with pointed pharyngeal teeth showed a
345 greater preference for soft prey than those with more robust rounded teeth (Trapani, 2003;
346 Trapani et al. 2005). Relating this to choristoderes, the European *Simoedosaurus lemoinei* has
347 sharper palatal teeth than its North American counterpart, *S. dakotensis*, suggesting a
348 preference for softer prey - a conclusion consistent with the more gracile marginal teeth and
349 narrower snout. Moreover, some *Champsosaurus* species, before and after the K/Pg boundary,
350 are differentiated by their palatal tooth morphology and arrangement. As noted above, the
351 Cretaceous species *C. albertensis*, *C. lindoei*, *C. natator* tend to have fewer, larger pterygoid
352 teeth than the Paleocene species *C. gigas* and *C. dolloi*. There are also differences in the snout
353 length of these species. Paleocene species have slightly longer snouts and therefore higher
354 marginal tooth count (59 in *C. dolloi*; 50 in *C. gigas*) than Cretaceous species (e.g., ~40 in *C.*
355 *laramiensis*; 43 in *C. albertensis*). These differences could correlate with dietary change across
356 the K/Pg boundary, reflecting the faunal and floral transformation associated with the major
357 extinction event, as reported in mammals (Archibald and Bryant, 1990), birds (Longrich et al.
358 2011), insects (Labandeira et al. 2002), plants (Nichols & Johnson, 2008) and squamates
359 (Longrich et al. 2012). Moreover, *Champsosaurus* and *Simoedosaurus*, having survived the
360 extinction, seem to have co-occurred at some Paleocene localities (e.g., Mont-Berru, France;
361 Fort Union Formation). They may have avoided competition by taking different prey, the long
362 slender-snouted *Champsosaurus* feeding on schools of fish, like the extant *Gavialis*, and the
363 wider-snouted *Simoedosaurus* taking single prey items as in broad-snouted modern crocodiles

364 (Evans and Hecht, 1993; Matsumoto et al. work in progress on neck anatomy). The morphology
365 of the marginal teeth and their size (diameter and height) relative to the skull width (inner
366 biquadrate width), are similar in both genera (Matsumoto, 2011), but *Simoedosaurus* has wider
367 longitudinal and transverse palatal tooth rows, corresponding to the greater snout width. These
368 shagreen teeth may have provided a more efficient gripping surface to hold large prey. The Early
369 Cretaceous species *Ikechosaurus* is unique in having elongated snout as in *Champsosaurus*
370 (Matsumoto and Evans, 2010; Fig. 7) with broad palatal tooth row as in *Simoedosaurus*.
371 Remarkably, marginal dentition represents non-neochoristoderan character, and exposed area
372 of marginal dentition might be short due to soft-tissue cover at the tooth base (Matsumoto et al.
373 2014). One of hypothesis is suggested that wider gripping surface on the palate might be
374 necessary to support marginal dentition.
375 Thus differences in the palatal dentition suggest that the neochoristoderan diet may have varied
376 interspecifically. However, the evolutionary history of the palatal dentition remains incomplete,
377 because palatal morphology as a whole is known only in a limited number of
378 non-neochoristoderan genera. ~~As always, further specimens are required.~~ Moreover, the question
379 of diet and feeding strategy in this enigmatic group of reptiles needs to be approached from other
380 perspectives, such as whole skull morphology and the structure of the marginal dentition.

381

382 **Conclusions**

- 383 • Choristodera show a modification of the primitive diapsid tooth arrangement, with one or
384 two longitudinal rows and a transverse pterygoid row.
- 385 • Individual palatal teeth of neochoristoderes resemble the marginal teeth of
386 non-neochoristoderes in being conical with striations on the enamel and in having a
387 similar mode of tooth replacement.
- 388 • The width of the palatal tooth row, the sharpness of individual teeth, and the orientation
389 of the tooth tips, show interspecific variation in *Champsosaurus* and *Simoedosaurus*.
- 390 • The sharpness of the palatal teeth differs between species and may reflect prey
391 preference: sharp teeth for soft prey; blunt teeth for harder prey.
- 392 • Although the Late Cretaceous *C. albertensis* (RTMP86.12.11) and Paleocene *C. gigas*
393 (SMM P77.33.24) have similar-sized skulls, they differ in the pattern of their palatal
394 dentition. *C. albertensis* has fewer, larger palatal teeth, an arrangement that may be
395 correlated with prey size and preference.
- 396 • The European *Simoedosaurus lemoini* has sharper palatal teeth than its North

397 American counterpart, *S. dakotensis*, a difference also reflected in the marginal
398 dentition.
399 • The orientation of the palatal tooth tips changes antero-posteriorly across the palate in a
400 manner consistent with the major stages of feeding: prey capture, ingestion, intraoral
401 transport and swallowing.

402

403 Acknowledgements

404 Thanks are due to Mark Turmaine (UCL) for help with SEM: for access to specimens, Drs Don
405 Brinkman and Don Henderson (Royal Tyrrell Museum, Canada); Dr Bruce Erickson and Ms
406 Jackie Hoff (Science Museum Minnesota, USA); Drs Bernard Battail, Virginie Bouetel, and Hervé
407 Lelièvre (Muséum National d'Histoire Naturelle, Paris); Dr Denise Sigogneau-Russell (Paris); Dr
408 Rainer Schoch (Staatliches Museum für Naturkunde, Germany); Dr Annelise Folie (Institut Royal
409 des Sciences Naturelles de Belgique); Dr Yuan Wang, Dr Zhijie Jack Tseng, Ms Fang Zheng, Mr
410 Binghe Geng, and Ms Shuqin Duan (Institute of Vertebrate Paleontology and Paleoanthropology,
411 Beijing), Dr X-C. Wu and M. Feuerstack (Canadian Museum of Nature, Ottawa, Canada), Dr
412 Tamaki Sato (Tokyo Gakugei University); for access to μ CT scanner, Dr Makoto Manabe and Ms
413 Chisako Sakata (National Museum of Nature and Science). This research was supported by an
414 Estes Memorial Award, Society of Vertebrate Paleontology; the Sasakawa Scientific Research
415 Grant, Japan Society; and the Japan Society for the Promotion of Science Scholarship (JSPS)
416 for the Postdoctoral Fellowship and the Scientific Research Grant for Young Scientists B.

417

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613
614
615

616 **Table**
617 Table 1: List of specimens examined
618
619

620 **Figure captions**
621

622 **Fig. 1** Choristoderan phylogenetic tree with palatal tooth arrangement; phylogenetic tree based
623 on Matsumoto et al. (2013). Dentition on each palatal element marked in a different color; red,
624 vomerine teeth; yellow, palatine teeth; green, longitudinal pterygoid tooth row; blue, pterygoid
625 flange tooth row.
626

627 **Fig. 2** Palatal tooth replacement: A) juvenile *Monjurosuchus* sp. (IVPP V14261) dentary teeth in

628 medial view; B) *Cteniogenys* sp. dentary (UCL uncatalogued) in lateral view, scanning electron
629 micrograph; C) *Champsosaurus gigas* (SMM P77.33.24) left dentary teeth in lateral view; D-E)
630 *Champsosaurus gigas* (SMM P77.33.24) right maxillary teeth in lateral view, image reflected for
631 ease of comparison; F) *Simoedosaurus lemoinei* (MNHN BR1935) replacement maxillary teeth
632 in medial view; G) *Cteniogenys* sp. (BMNH R11759), right pterygoid tooth; H) *Champsosaurus*
633 sp. isolated right palatine teeth (RTMP 92.36.270) in medial view. Tooth position is uncertain in B,
634 G, H due to incompleteness of specimens.

635

636 **Fig. 3** Pterygoid teeth in *Cteniogenys* sp. (BMNH R11759) from the Middle Jurassic of Kirtlington,
637 Oxfordshire, UK; A) reconstructed skull in palatal view (Evans, 1990); colour coding of the
638 different regions of the palatal dentition are the same as in Fig. 2; B) anterior longitudinal tooth
639 row; C) posterior pterygoid teeth; D) isolated pterygoid from UCL uncatalogued specimens
640 (magnification X50); E) enlarged image of B, worn tooth crown from the longitudinal pterygoid
641 tooth row in medial view; F) enlarged image of D, complete crown on the longitudinal pterygoid
642 tooth row in medial view (magnification X500); G) enlarged image of D, posterior pterygoid tooth
643 (magnification X500).

644

645 **Fig. 4** *Hyphalosaurus lingyuanensis* holotype from the Early Cretaceous of the Yixian Formation
646 of China (IVPP V11075): A) photograph of the skull in palatal view; B) line drawing of A; colour
647 coding of the different regions of the palatal dentition are the same as in Fig. 2.

648

649 **Fig. 5** A) *Monjurosuchus* sp. (IVPP V14261) from the Early Cretaceous of China, skull in palatal
650 view; B) photographs of the skull, enlarged view of palatal tooth area in A; C) line drawing of B;
651 colour coding of the different regions of the palatal dentition are the same as in Fig. 2.

652

653 **Fig. 6** *Ikechosaurus sunailinae* from the Early Cretaceous Chabu-Sumu locality, Inner Mongolia
654 (IVPP V9611-3), skull in palatal view: A) photograph and line drawing of the skull in ventral view.
655 Black circles indicate alveoli of palatal teeth; white circles showing presence of the teeth; colour
656 coding of the different regions of the palatal dentition are the same as in Fig. 2; grey zone
657 indicating nasopalatal trough; arrows on tooth row showing orientation of tooth crowns. B)
658 enlarged image of pterygoid and parasphenoid regions; C) enlarged image of the longitudinal
659 pterygoid tooth row (posterior); D) pterygoid flange teeth in occipital view (image Inverted for
660 comparison).

661

662 **Fig. 7** Comparison of the palatal dentition in *Champsosaurus*; A-D from the Late Cretaceous;
663 E-F from Late Cretaceous and Paleocene; G-I from the Paleocene. A) semi-adult *C. lindoei*
664 (RTMP 87.36.41); B) juvenile *C. lindoei* (RTMP 94.163.01); C) *C. albertensis* (RTMP 86.12.11),
665 pterygoid flange teeth incomplete; D) *C. natator* (NMC8919) pterygoid flange teeth incomplete;
666 E) *C. ambulator* (modified from Sigogneau-Russell, 1979); F) *C. laramiensis* (redrawn based on
667 Brown, 1905 and Sigogneau-Russell, 1979); G) *C. gigas* (SMM P77.33.24); H) *C. dolloi* (IRSNB
668 R21) pterygoid flange teeth incomplete; I) *C. tenuis* (SMM P79.14.1) pterygoid flange teeth and
669 pterygoid longitudinal tooth rows are incomplete. Scale bars are 50 mm, but scale is unknown in
670 7E. Blue coloured area marks the distribution of the palatal dentition, and grey coloured area
671 marks nasopalatal trough extending from the choana.

672

673 **Fig. 8** Palatal dentition of *Simoedosaurus* sp. (SMNS 59026) (A-E) and *S. lemoinei* (F-I) from
674 Mont Berru Reims, France: A) photograph and line drawing of the skull (SMNS 59026) in palatal
675 view; colour coding of the different regions of the palatal dentition is the same as in Fig. 2; B)
676 lateral view of the snout A; C) enlarged image of anterior vomerine teeth of B; D) enlarged image
677 of anterior palatine teeth of B; E) enlarged image of pterygoid teeth of B (reflected image); F)
678 isolated left vomer with teeth in lateral view, image inverted (MNHN BL9947); G) isolated left
679 palatine, image inverted (MNHN BR728); H) posterior palatine dentition (MNHN BR 1935;
680 neotype of *S. lemoinei*); I) enlarged image of H.

681

682 **Fig. 9** *Simoedosaurus dakotensis* (SMM P76.10.1) from the Paleocene of western North Dakota
683 (near top of Slope Formation), USA: A) skull in palatal view, digital image above and line drawing
684 below (the letters B-H correspond to the following close-up images below); colour coding of the
685 different regions of the palatal dentition is the same as in Fig. 2; B, anterior vomerine teeth; C)
686 anterior palatine teeth; D) posterior pterygoid, lateral tooth row; E) posterior pterygoid, medial
687 tooth row; F) pterygoid flange in lateral view; G) pterygoid flange in posterior view; H) pterygoid
688 flange teeth in lateral view.

689

690 **Fig. 10** A) CT image of *Champsosaurus lindoei* (NMC 8920) without scale; the numbers on the
691 skull corresponding to slice images 1-4. Red arrows showing nasopalatal trough. B) diagram of
692 skull and lower jaw in anterior section (*Champsosaurus* as the model), the palatine teeth lie on
693 the ridge, soft tissues are drawn in dashed-lines.

694

695 **Fig. 11** *Champsosaurus gigas* (SMM P77.33.24) from the Paleocene of western North Dakota:
696 A) skull in lateral view; B) line drawing and photograph of palatal dentition; C) anterior vomerine
697 teeth (reflected image); D) palatine tooth row (reflected image); E) anterior palatal dentition; F)
698 pterygoid, lateral tooth row; G) pterygoid, medial tooth row; H) pterygoid flange tooth row in
699 lateral view. Black circles indicate alveoli of palatal teeth; colour coding of the different regions of
700 the palatal dentition is the same as in Fig. 2.

701

702 **Fig. 12** Late Cretaceous *Champsosaurus*; A-C) *C. albertensis* (RTMP 86.12.11) from the
703 Horseshoe Canyon Formation at Drumheller, Canada; A) photo and line drawing of *C.*
704 *albertensis* in palatal view; B) right vomerine teeth in lateral view; C) right palatine teeth in medial
705 view, reflected image. D-F) *C. lindoei* (RTMP 94.163.01) from the Oldman Formation Alberta,
706 Canada; D) photo and line drawing of *C. lindoei* in palatal view; E) right vomerine teeth in lateral
707 view; F) right anterior palatine teeth in lateral view. Black circles indicate alveoli of palatal teeth;
708 colour coding of the different regions of the palatal dentition is the same as in Fig. 2.

709

710 **Fig. 13** Summary of the morphological variation in the palatal dentition of neochoristoderes
711 corresponding to feeding stages; colour coding of the different regions of the palatal dentition is
712 the same as in Fig. 2.

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715 **Supplementary information**

716 Summary of the palatal dentition in choristoderes.

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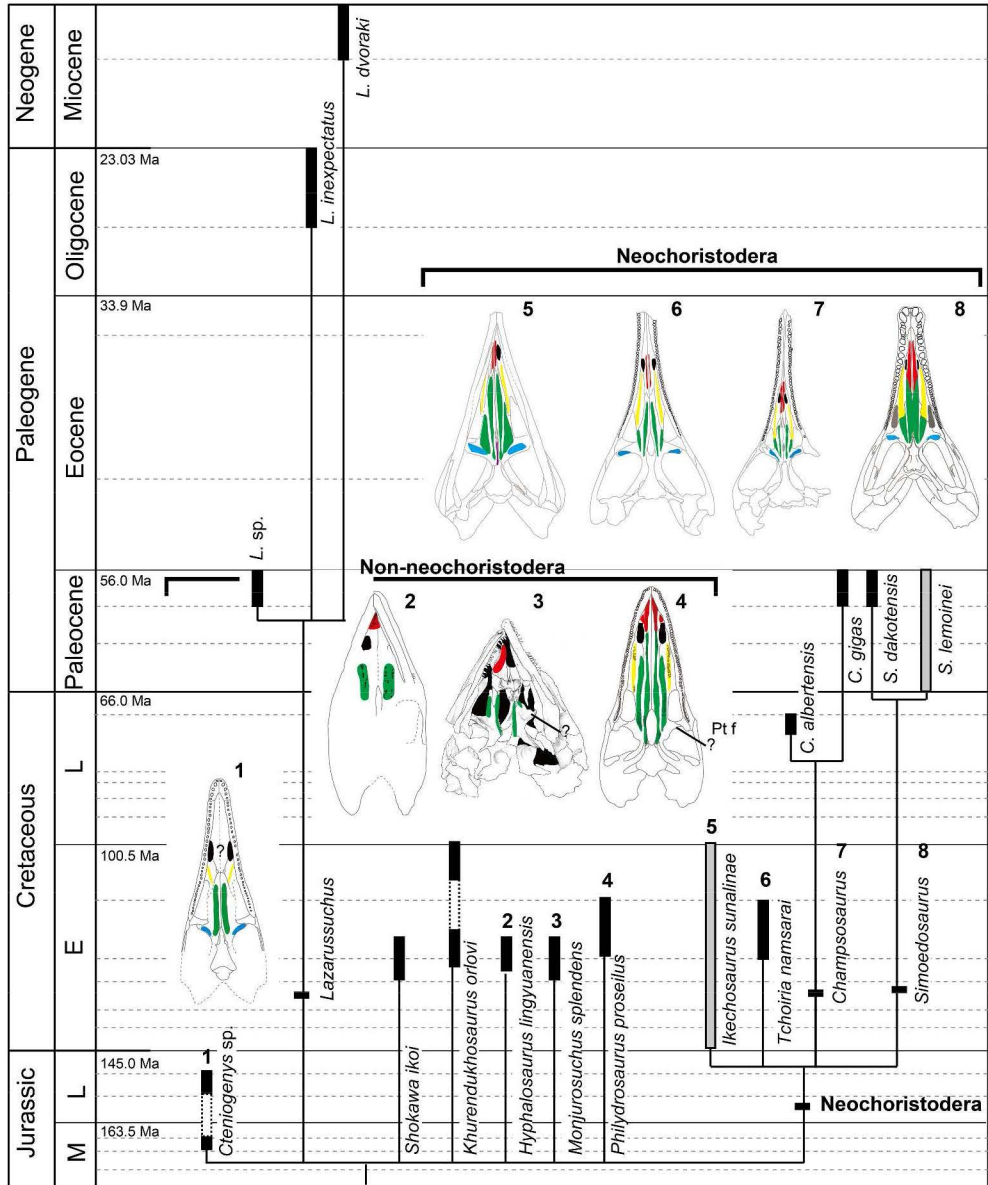


Fig. 1 Choristoderan phylogenetic tree with palatal tooth arrangement; phylogenetic tree based on Matsumoto et al. (2013). Dentition on each palatal element marked in a different color; red, vomerine teeth; yellow, palatine teeth; green, longitudinal pterygoid tooth row; blue, pterygoid flange tooth row. 206x246mm (600 x 600 DPI)

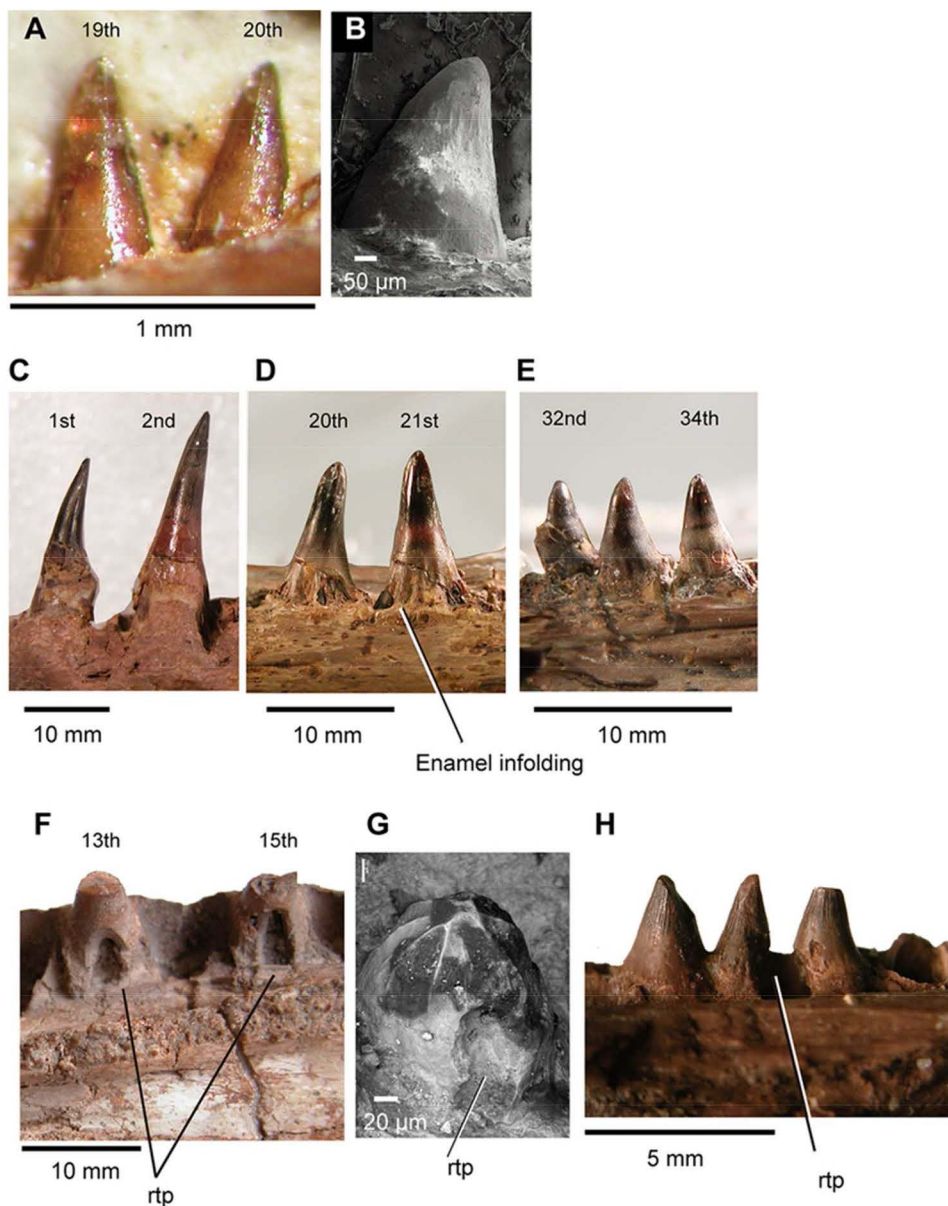


Fig. 2 Palatal tooth replacement: A) juvenile *Monjurosuchus* sp. (IVPP V14261) dentary teeth in medial view; B) *Cteniogenys* sp. dentary (UCL uncatalogued) in lateral view, scanning electron micrograph; C) *Champsosaurus gigas* (SMM P77.33.24) left dentary teeth in lateral view; D-E) *Champsosaurus gigas* (SMM P77.33.24) right maxillary teeth in lateral view, image reflected for ease of comparison; F) *Simoedosaurus lemoinei* (MNH BR1935) replacement maxillary teeth in medial view; G) *Cteniogenys* sp. (BMNH R11759), right pterygoid tooth; H) *Champsosaurus* sp. isolated right palatine teeth (RTMP 92.36.270) in medial view. Tooth position is uncertain in B, G, H due to incompleteness of specimens.
66x81mm (300 x 300 DPI)

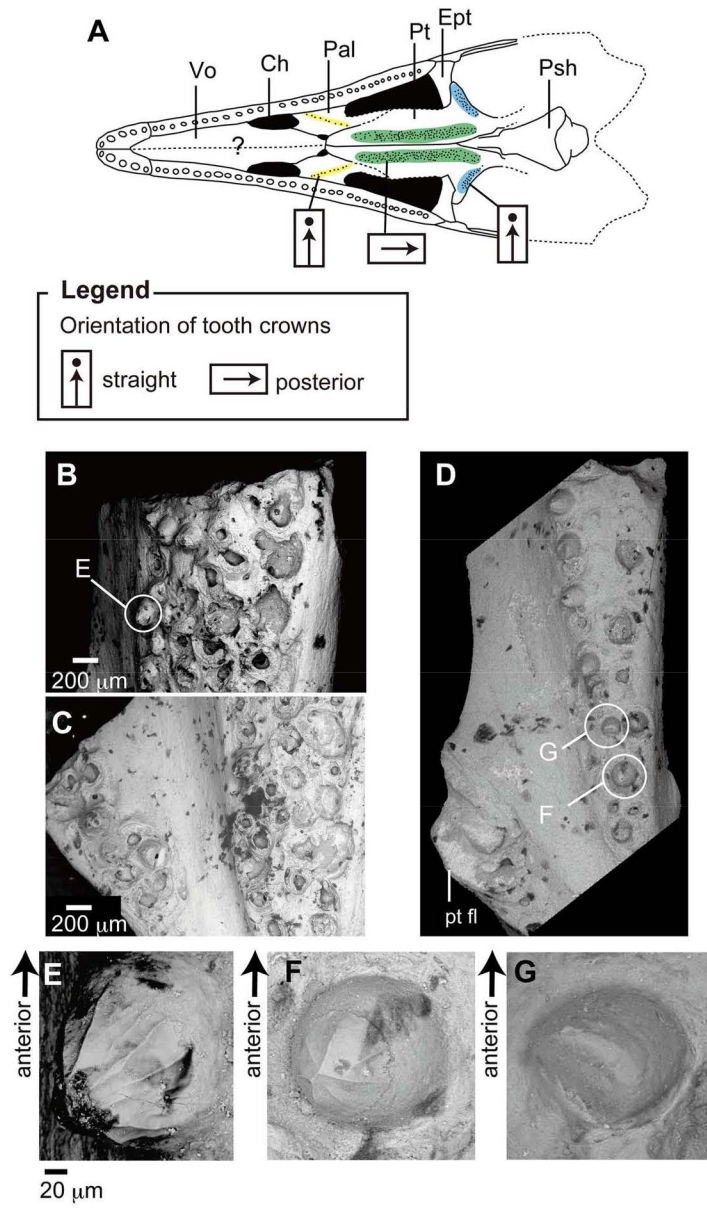


Fig. 3 Pterygoid teeth in *Cteniogenys* sp. (BMNH R11759) from the Middle Jurassic of Kirtlington, Oxfordshire, UK; A) reconstructed skull in palatal view (Evans, 1990); colour coding of the different regions of the palatal dentition are the same as in Fig. 2; B) anterior longitudinal tooth row; C) posterior pterygoid teeth; D) isolated pterygoid from UCL uncatalogued specimens (magnification X50); E) enlarged image of B, worn tooth crown from the longitudinal pterygoid tooth row in medial view; F) enlarged image of D, complete crown on the longitudinal pterygoid tooth row in medial view (magnification X500); G) enlarged image of D, posterior pterygoid tooth (magnification X500).
117x194mm (300 x 300 DPI)

A



10 mm

B

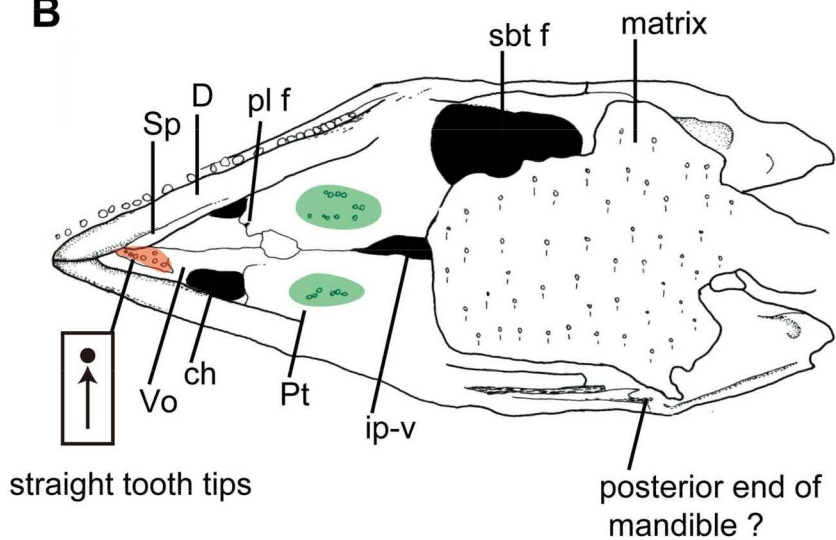


Fig. 4 *Hyphalosaurus lingyuanensis* holotype from the Early Cretaceous of the Yixian Formation of China (IVPP V11075): A) photograph of the skull in palatal view; B) line drawing of A; colour coding of the different regions of the palatal dentition are the same as in Fig. 2.
119x165mm (300 x 300 DPI)

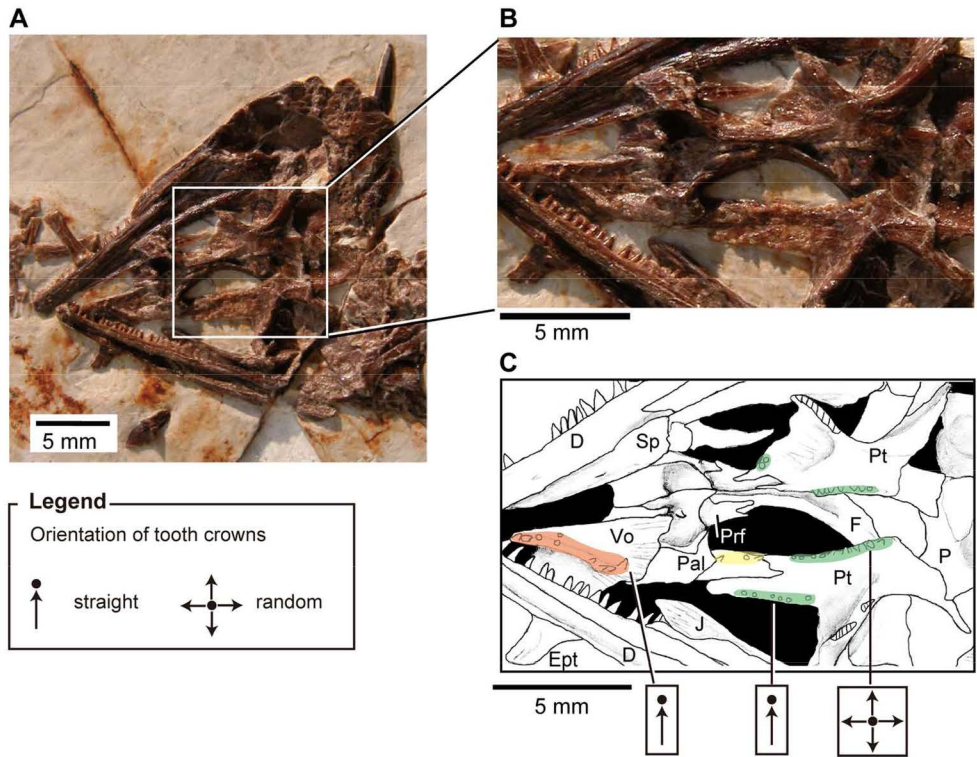


Fig. 5 A) *Monjurosuchus* sp. (IVPP V14261) from the Early Cretaceous of China, skull in palatal view: B) photographs of the skull, enlarged view of palatal tooth area in A; C) line drawing of B; colour coding of the different regions of the palatal dentition are the same as in Fig. 2.

123x94mm (300 x 300 DPI)

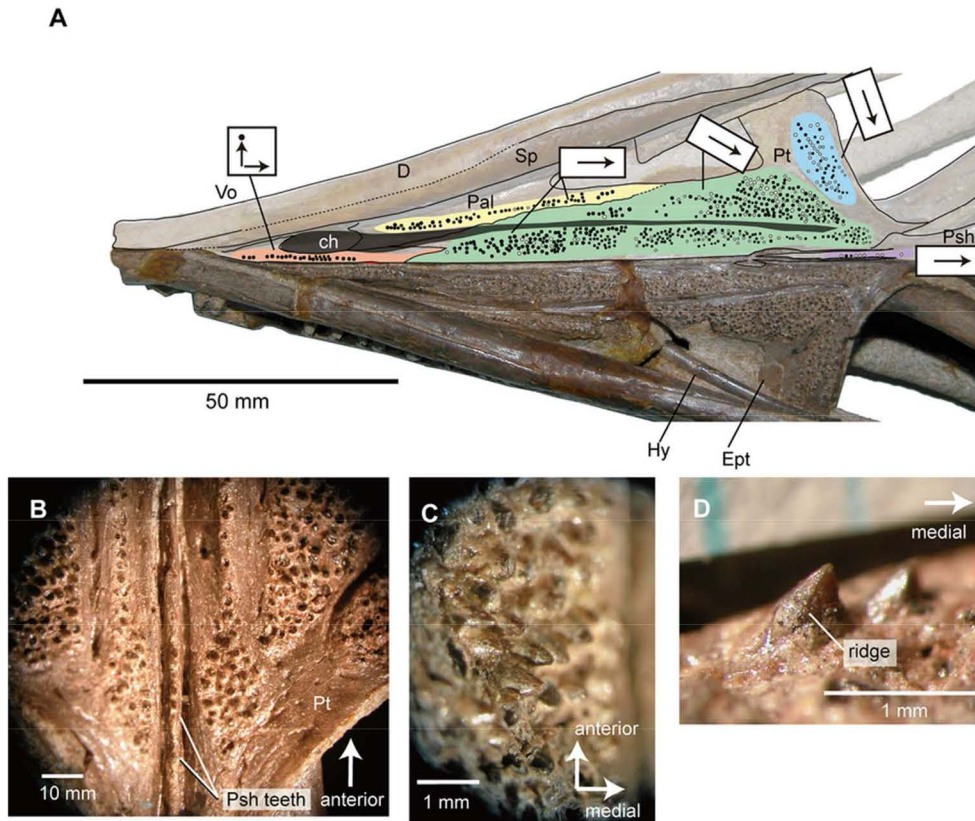


Fig. 6 *Ikechosaurus sunailinae* from the Early Cretaceous Chabu-Sumu locality, Inner Mongolia (IVPP V9611-3), skull in palatal view: A) photograph and line drawing of the skull in ventral view. Black circles indicate alveoli of palatal teeth; white circles showing presence of the teeth; colour coding of the different regions of the palatal dentition are the same as in Fig. 2; grey zone indicating nasopalatal trough; arrows on tooth row showing orientation of tooth crowns. B) enlarged image of pterygoid and parasphenoid regions; C) enlarged image of the longitudinal pterygoid tooth row (posterior); D) pterygoid flange teeth in occipital view (image Inverted for comparison).
78x65mm (300 x 300 DPI)

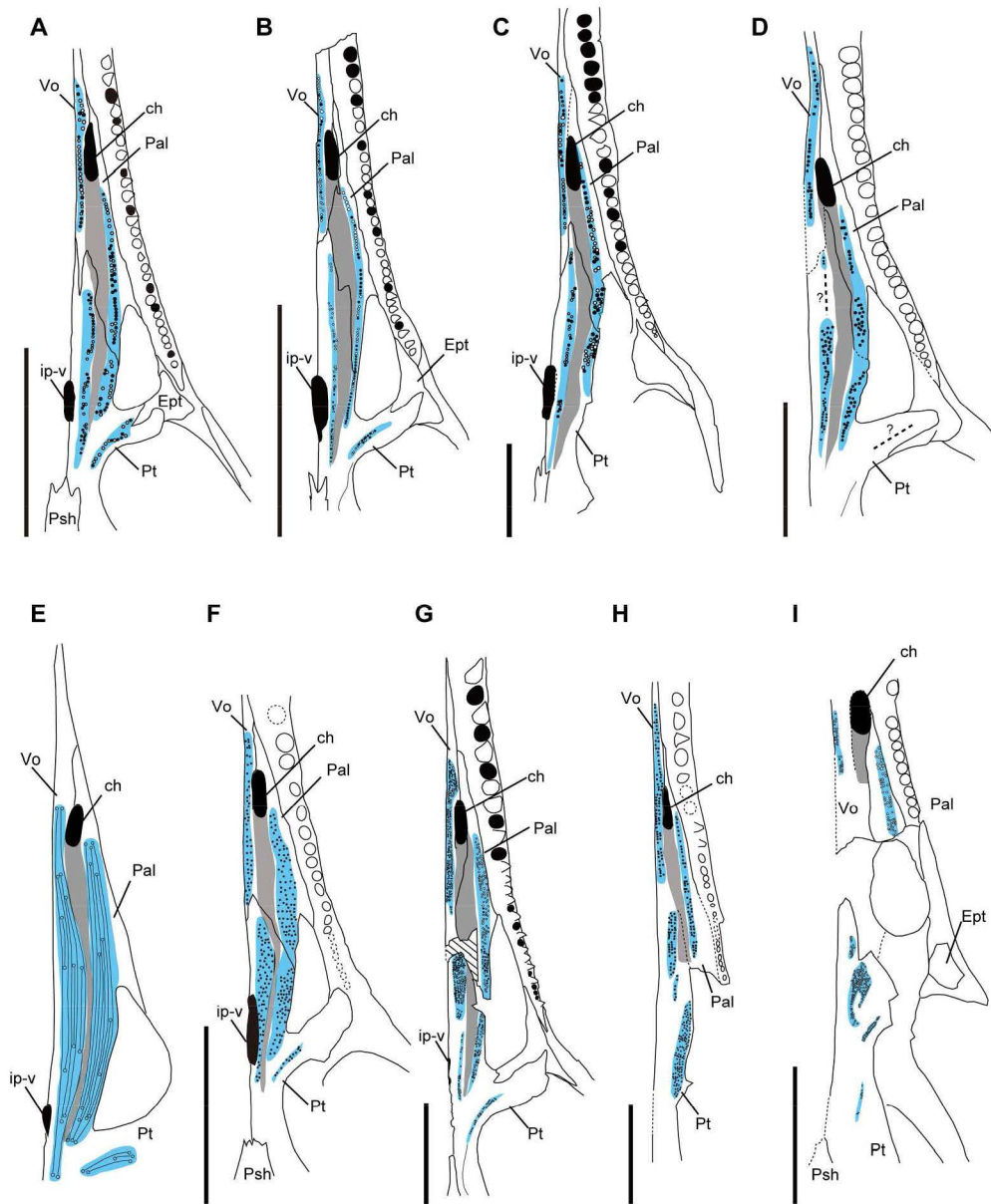


Fig. 7 Comparison of the palatal dentition in Champososaurus; A-D from the Late Cretaceous; E-F from Late Cretaceous and Paleocene; G-I from the Paleocene. A) semi-adult *C. lindoei* (RTMP 87.36.41); B) juvenile *C. lindoei* (RTMP 94.163.01); C) *C. albertensis* (RTMP 86.12.11), pterygoid flange teeth incomplete; D) *C. natator* (NMC8919) pterygoid flange teeth incomplete; E) *C. ambulator* (modified from Sigogneau-Russell, 1979); F) *C. laramiensi* (redrawn based on Brown, 1905 and Sigogneau-Russell, 1979); G) *C. gigas* (SMM P77.33.24); H) *C. dolloi* (IRSNB R21) pterygoid flange teeth incomplete; I) *C. tenuis* (SMM P79.14.1) pterygoid flange teeth and pterygoid longitudinal tooth rows are incomplete. Scale bars are 50 mm, but scale is unknown in 7E. Blue coloured area marks the distribution of the palatal dentition, and grey coloured area marks nasopalatal trough extending from the choana.

205x250mm (300 x 300 DPI)

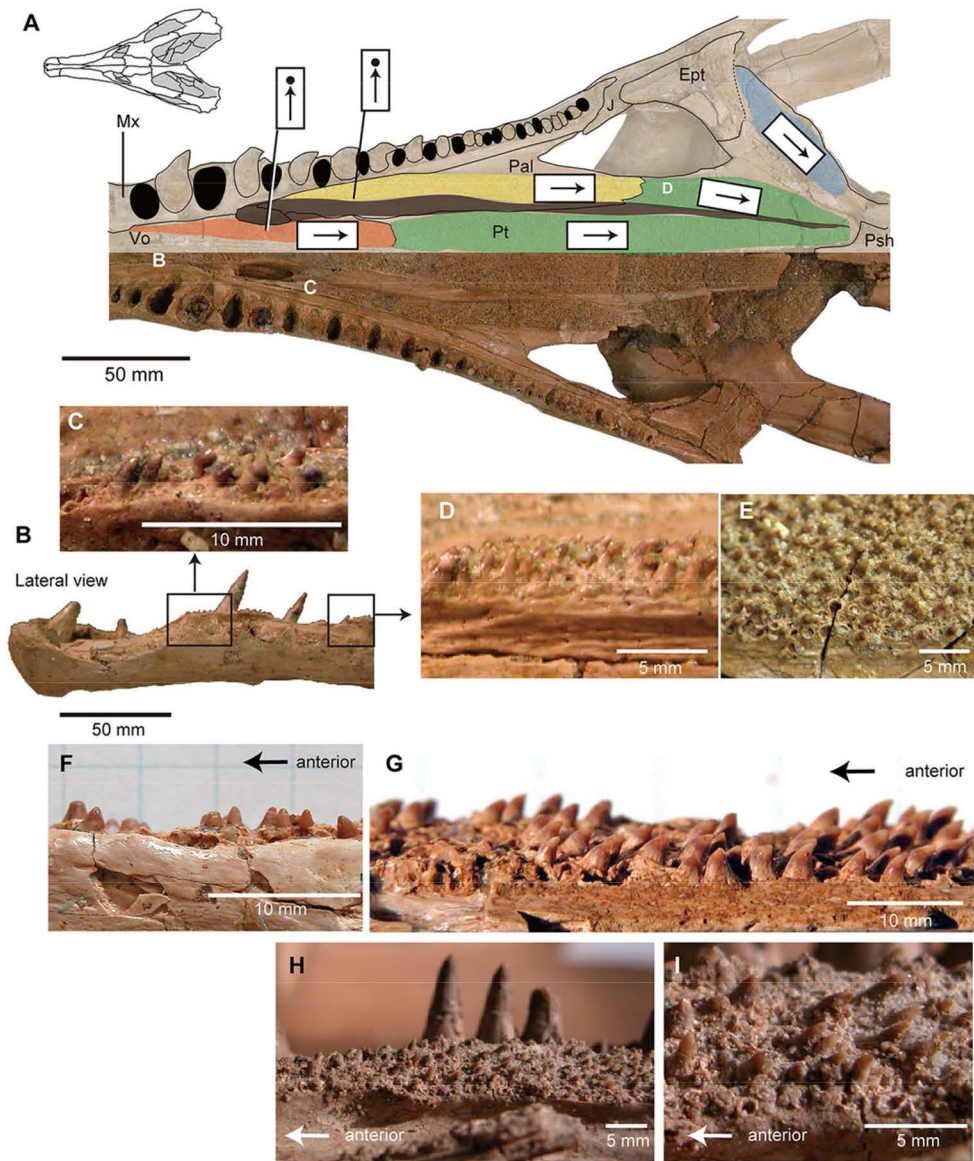


Fig. 8 Palatal dentition of *Simoedosaurus* sp. (SMNS 59026) (A-E) and *S. lemoinei* (F-I) from Mont Berru Reims, France: A) photograph and line drawing of the skull (SMNS 59026) in palatal view; colour coding of the different regions of the palatal dentition is the same as in Fig. 2; B) lateral view of the snout A; C) enlarged image of anterior vomerine teeth of B; D) enlarged image of anterior palatine teeth of B; E) enlarged image of pterygoid teeth of B (reflected image); F) isolated left vomer with teeth in lateral view, image inverted (MNHN BL9947); G) isolated left palatine, image inverted (MNHN BR728); H) posterior palatine dentition (MNHN BR 1935; neotype of *S. lemoinei*); I) enlarged image of H. 88x106mm (300 x 300 DPI)

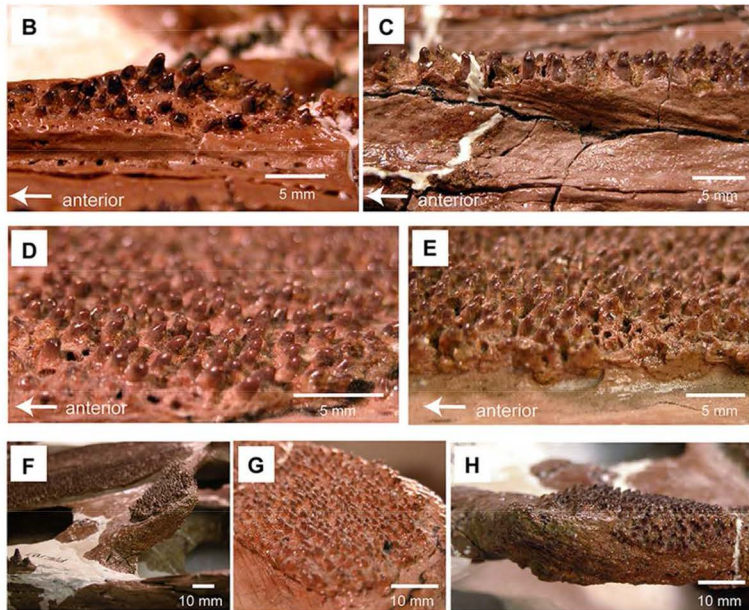
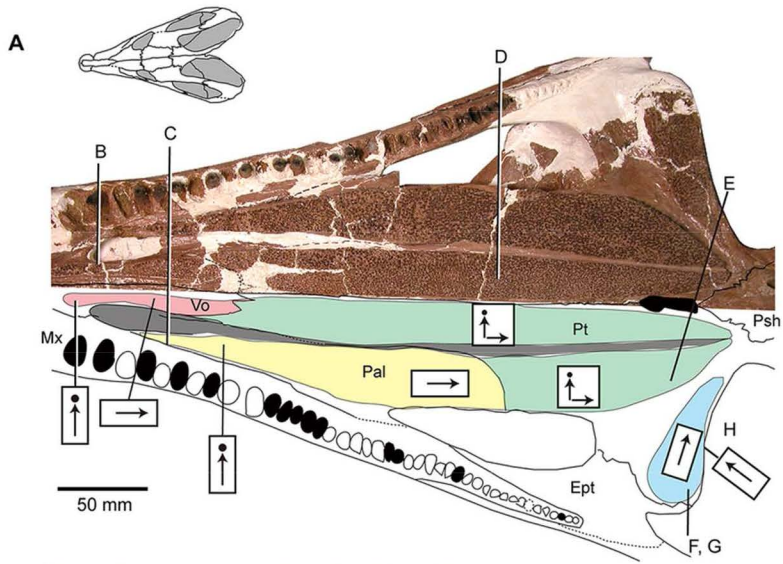


Fig. 9 *Simoedosaurus dakotensis* (SMM P76.10.1) from the Paleocene of western North Dakota (near top of Slope Formation), USA: A) skull in palatal view, digital image above and line drawing below (the letters B-H correspond to the following close-up images below); colour coding of the different regions of the palatal dentition is the same as in Fig. 2; B, anterior vomerine teeth; C) anterior palatine teeth; D) posterior pterygoid, lateral tooth row; E) posterior pterygoid, medial tooth row; F) pterygoid flange in lateral view; G) pterygoid flange in posterior view; H) pterygoid flange teeth in lateral view.
72x105mm (300 x 300 DPI)

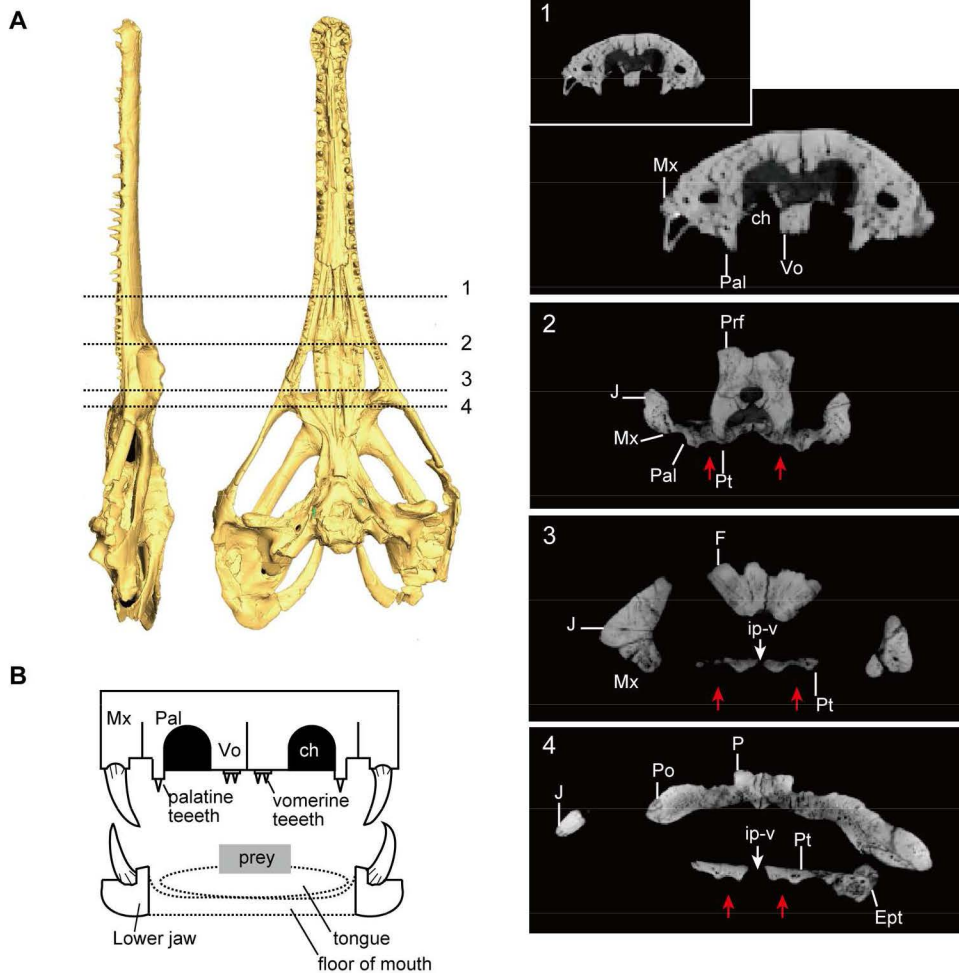


Fig. 10 A) CT image of *Champsosaurus lindoei* (NMC 8920) without scale; the numbers on the skull corresponding to slice images 1-4. Red arrows showing nasopalatal trough. B) diagram of skull and lower jaw in anterior section (*Champsosaurus* as the model), the palatine teeth lie on the ridge, soft tissues are drawn in dashed-lines.

177x184mm (300 x 300 DPI)

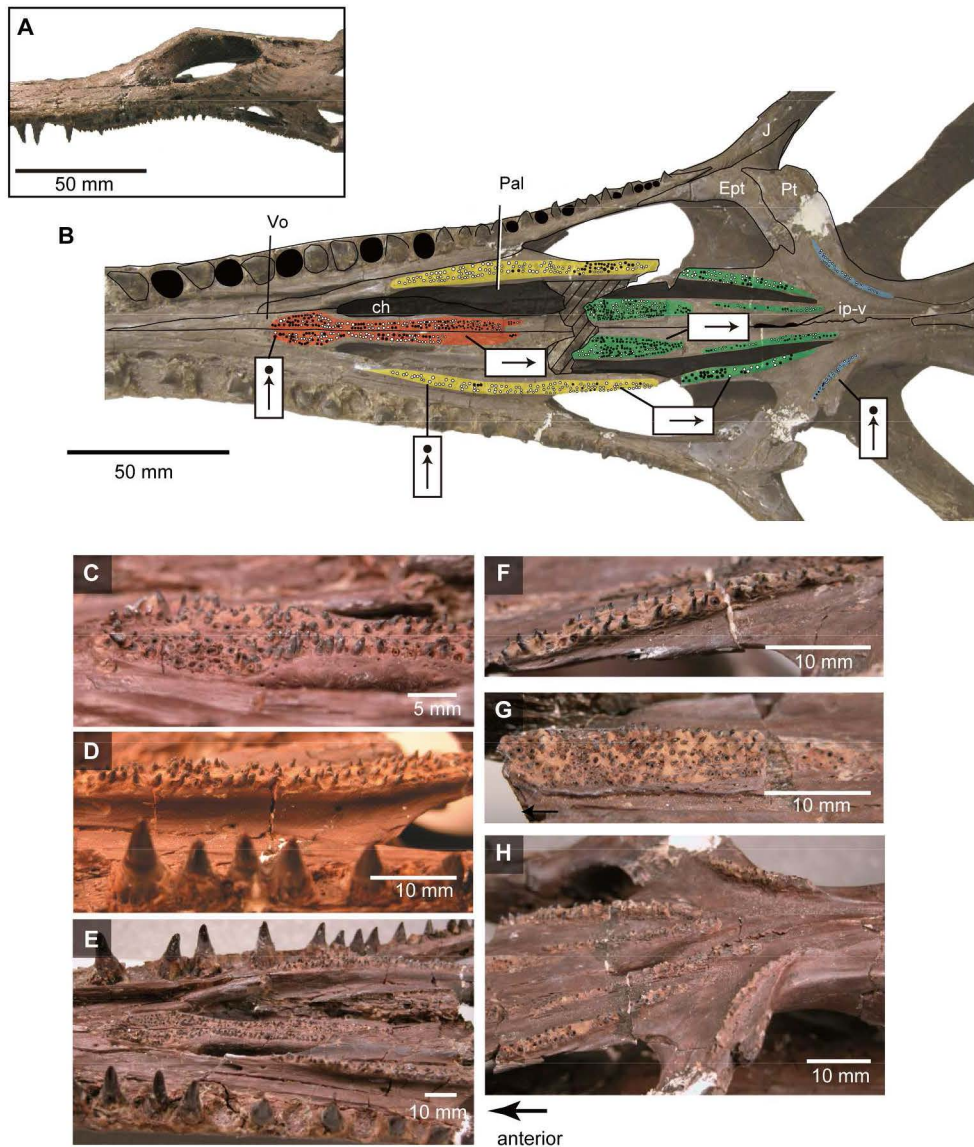


Fig. 11 *Champososaurus gigas* (SMM P77.33.24) from the Paleocene of western North Dakota: A) skull in lateral view; B) line drawing and photograph of palatal dentition; C) anterior vomerine teeth (reflected image); D) palatine tooth row (reflected image); E) anterior palatal dentition; F) pterygoid, lateral tooth row; G) pterygoid, medial tooth row; H) pterygoid flange tooth row in lateral view. Black circles indicate alveoli of palatal teeth; colour coding of the different regions of the palatal dentition is the same as in Fig. 2. 214x251mm (300 x 300 DPI)

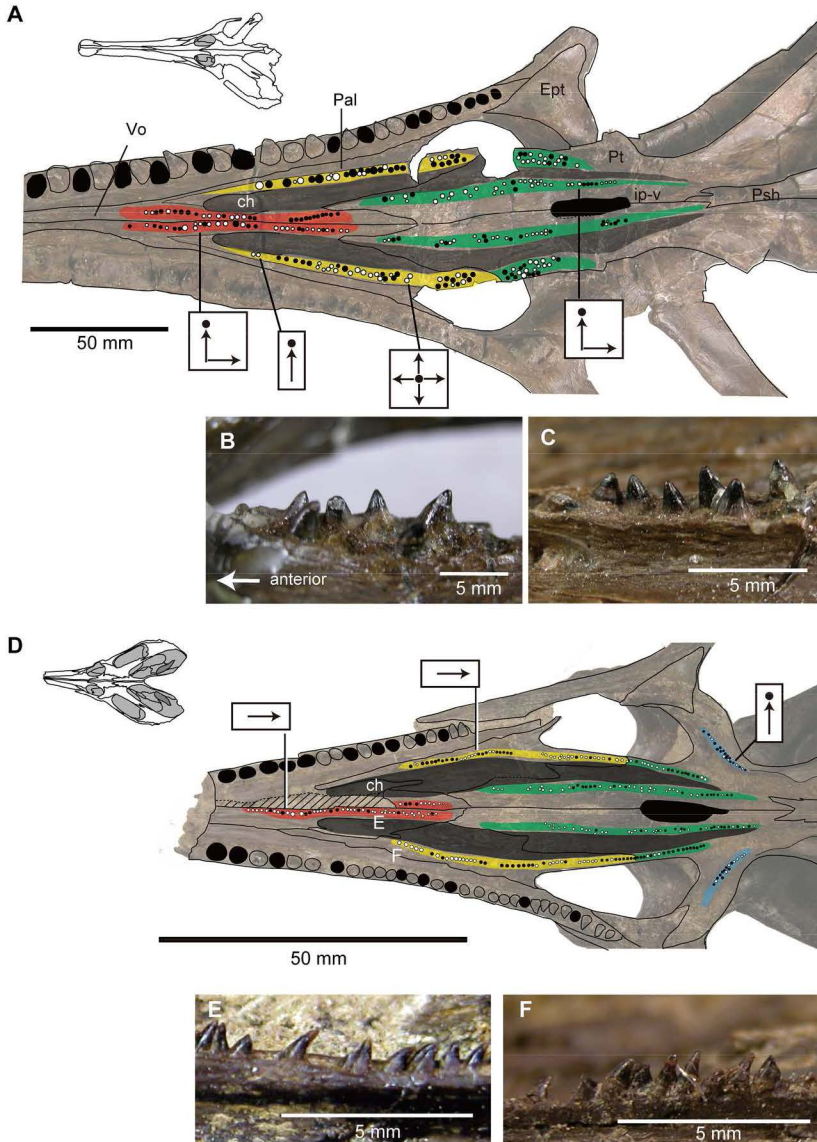


Fig. 12 Late Cretaceous *Champsosaurus*; A-C) *C. albertensis* (RTMP 86.12.11) from the Horseshoe Canyon Formation at Drumheller, Canada; A) photo and line drawing of *C. albertensis* in palatal view; B) right vomerine teeth in lateral view; C) right palatine teeth in medial view, reflected image. D-F) *C. lindoei* (RTMP 94.163.01) from the Oldman Formation Alberta, Canada; D) photo and line drawing of *C. lindoei* in palatal view; E) right vomerine teeth in lateral view; F) right anterior palatine teeth in lateral view. Black circles indicate alveoli of palatal teeth; colour coding of the different regions of the palatal dentition is the same as in Fig. 2.

159x222mm (300 x 300 DPI)

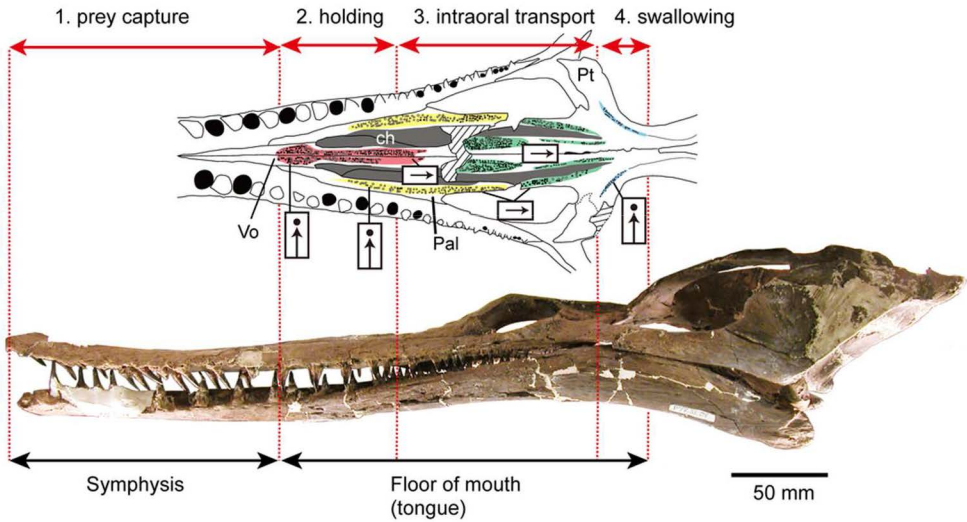


Fig. 13 Summary of the morphological variation in the palatal dentition of neochoristoderes corresponding to feeding stages; colour coding of the different regions of the palatal dentition is the same as in Fig. 2.

91x47mm (300 x 300 DPI)

Specimens examined

Genus	Species	Specimen number	Element	Reference
<i>Cteniogenys</i>	sp.	BMNH R11756–11758 uncataloged UCL specimens	Isolated palatine	Evans, 1990; personal observation
	sp.	BMNH R11759	Isolated pterygoid.	
<i>Lazarussuchus</i>	<i>inexpectatus</i>	Re 437	Preserves posterior palatine and anterior pterygoid tooth rows	Hecht, 1992
<i>Monjurosuchus</i>	sp. <i>splendens</i>	IVPP V14261 IVPP V13761	Juvenile, complete palate Adult, partial pterygoid	Personal observation; Xiaolin et al., 2005
<i>Philydrosaurus</i>	<i>proseilus</i>	LPMC 021	Nearly complete palate pterygoid flange tooth row missing	Gao et al. 2007
<i>Hyphalosaurus</i>	<i>lingyuanensis</i>	IVPP V11075	Mostly covered by matrix	Gao et al. 1999; personal observation
	<i>baitaigouensis</i>	LPMC no number	Nearly complete palatine and pterygoid	Gao and Ksepka, 2008
<i>Ikechosaurus</i>	<i>sunailinae</i>	IVPP V2774	Palatine	Sigogneau-Russell, 1981
	<i>sunailinae</i>	IVPP V9611-3	Complete palate	Brinkman and Dong, 1993; personal observation
	sp.	IVPP V10596.1; IVPP V9611-2	Isolated parasphenoid; partial palatine and vomer;	
<i>Tchoiria</i>	<i>namsarai</i>	PIN3386/1	Complete palate	Efimov, 1975; Efimov and Storrs, 2000
	<i>namsarai</i>	HMNS 96720	Pterygoid flange missing	Personal observation
	<i>klauseni</i>	IGM 1/8	Pterygoid flange missing	Ksepka et al., 2005
<i>Champsosaurus</i>	<i>lindoei</i>	RTMP 87.36.41; RTMP 94.163.01; NMC 8920	Complete palate, juvenile and subadult	Gao and Fox, 1998; personal observation
	<i>albertensis</i>	RTMP 86.12.11	Pterygoid flange missing	Gao and Fox, 1998; personal observation
	<i>laramiensis</i> ,	AMNH 982; 981	Complete palate	Brown, 1905 personal observation
	<i>ambulator</i>	AMNH 983	Complete palate	Brown, 1905
	<i>natator</i>	NMC 8919	Pterygoid flange tooth row missing	Russell, 1956; and personal photographs
	<i>dolloi</i>	IRSNB R21; IRSNB R 1568; IRSNB R 3662 MNHN BR 2020	Pterygoid flange missing Isolated vomer	Sigogneau-Russell, 1979; personal observation
	<i>gigas</i>	SMMP 77.33.34	Complete palate	Erickson, 1985; personal observation
	<i>tenuis</i>	SMMP 79.14.1	Vomer, partial palatine	Erickson, 1981; personal observation
	sp.	MNHN BR-9-P; RTMP 92.36.270; RTMP 91.50.104; RTMP 89.36.332	Complete palate; isolated palatine; isolated palatine; isolated vomer	Personal observation
<i>Simoedosaurus</i>	<i>lemoinei</i>	MNHN BR1935; MNHN BR728; MNHN BR9947; MNHN BR1-Gi-13	Pterygoid flange missing; Isolated palatine; isolated vomer; isolated pterygoid	Sigogneau-Russell and Russell, 1978; personal observation
	<i>dakotensis</i>	SMMP 76.10.1	Complete palate	Erickson, 1987; personal observation
	sp.	SMNS 59026	Complete palate	Personal observation