

1 **The palatal dentition of tetrapods and its functional significance**

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11

12 **Abstract**

13 The presence of a palatal dentition is generally considered to be the primitive condition in
14 amniotes, with each major lineage showing a tendency toward reduction. This study
15 highlights the variation in palatal tooth arrangements and reveals clear trends within the
16 evolutionary history of tetrapods. Major changes occurred in the transition between early
17 tetrapods and amphibians on the one hand, and stem amniotes on the other. These changes
18 reflect the function of the palatal dentition, which can play an important role in holding and,
19 manipulating food during feeding. Differences in the arrangement of palatal teeth, and in their
20 pattern of loss, likely reflect differences in feeding strategy but also changes in the
21 arrangement of cranial soft tissues, as the palatal dentition works best with a well-developed
22 mobile tongue. It is difficult to explain the loss of palatal teeth in terms of any single factor, but
23 palatal tooth patterns have the potential to provide new information on diet and feeding
24 strategy in extinct taxa.

25

26 **Keywords:** Palatal dentition; Function; Feeding behavior; Cranial soft anatomy; Tetrapoda;
27 Amniota; Evolution.

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30

31 **Introduction**

32 Any consideration of feeding in vertebrates will include detailed discussion of the marginal
33 dentition. Far less attention has been paid to the palatal dentition, although characters of the
34 palatal dentition are used in phylogenetic analysis (early tetrapods, Sigurdson & Bolt, 2010;
35 Diapsida, Benton, 1985; Evans, 1988; Archosauria, e.g. Sereno, 1991; Lepidosauromorpha,
36 e.g. Evans, 1991; Parareptilia, Tsuji, 2006; Rhynchosauria, Dilkes, 1998; Synapsida, Sidor,
37 2003; Abdala et al. 2008; Campione & Reisz, 2010; and Choristodera (Evans, 1990;
38 Matsumoto, 2011)). There is a general acceptance that an extensive palatal dentition is
39 plesiomorphic for amniotes. However, the evolutionary history of this dentition is poorly
40 understood, and detailed studies of its structure and function in either extant or extinct
41 tetrapods are rare (e.g. Regal, 1966; Kordikova, 2002; Mahler & Kearney, 2006; Diedrich,
42 2010). During feeding, the jaws, tongue, and palate cooperate in food prehension, intra-oral
43 transport, and swallowing, thus changes in the palatal dentition should reflect changes in
44 feeding behaviour and/or changes in the anatomy of the oral soft tissues. Potentially,
45 therefore, a better understanding of the functional morphology of the palatal dentition may
46 provide an additional source of information on the biology of extinct tetrapods. Here we
47 review the main trends in the evolutionary history of the tetrapod palatal dentition and then
48 discuss them in relation to changes in the anatomy of the skull and oral soft tissues.

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50

51 **Material and Methods**

52 Palatal tooth arrangements were mapped onto phylogenetic trees for the tetrapodomorph
53 *Eusthenopteron*, early tetrapods, and basal Amniota (Ruta et al. 2003; Ruta & Coates, 2007;
54 Snitting, 2008); Synapsida (Sidor, 2001); Parareptilia (Tsuji & Müller, 2009; Tsuji et al. 2012);
55 and Diapsida (DeBraga & Rieppel, 1997; Rieppel & Reisz, 1999; Brusatte et al. 2010; Borsuk
56 –Białynicka & Evans, 2009a; Dilkes & Sues, 2009). The data on palatal tooth arrangement
57 patterns for each taxon were collected from descriptions in the literature or data matrices for
58 phylogenetic analysis. For some synapsids and early diapsids, the palatal tooth arrangement
59 has not been described, and specimens were examined first hand (see Appendix 1-7).

60

61 **Evolutionary patterns in the palatal dentition of early tetrapods and**
62 **amphibians**

63 Early tetrapods (e.g. *Acanthostega*, Clack, 1994; *Ichthyostega*, Clack, 2012; *Pederpes*, Clack
64 & Finney, 2005; *Crassigyrinus*, Clack, 2012; *Greererpeton*, Smithson, 1982; *Megalocephalus*,
65 Beaumont, 1977) inherited the basic pattern of the palatal dentition (vomer, palatine, and
66 ectopterygoid) from that of ancestral sarcopterygians (e.g. *Eusthenopteron*, Clack, 2012).
67 There was a single lateral palatal tooth row on each side, running parallel to the jaw margin
68 and with teeth of similar size (and/or larger) to those of the marginal dentition. In
69 *Eusthenopteron*, the parasphenoid intervened between the vomers and the pterygoids in the
70 midline, with the latter element expanded posterior to the marginal tooth row. Small teeth
71 were randomly and widely distributed across the parasphenoid and pterygoid, forming a
72 shagreen dentition. Early tetrapods retained shagreen teeth on the pterygoid (e.g.
73 *Ichthyostega*, *Acanthostega*; Fig. 1), with parasphenoid teeth in a more limited area (e.g.
74 *Acanthostega*, Clack, 1994; *Pederpes*, Clack & Finney, 2005; *Greererpeton*, Smithson, 1982;
75 Fig. 1). This primitive arrangement was conserved in many Temnospondyli (e.g.
76 *Phonerpeton*, Dilkes, 1990; *Doleserpeton*, Sigurdson & Bolt, 2010), Anthracosauria
77 (*Silvanerpeton*, Ruta & Clack, 2006; *Proterogyrinus*, Holmes, 1984; *Pholiderpeton*, Clack,
78 1987) and Seymouriamorpha (*Seymouria*, Klembara et al., 2005; *Discosauriscus*, Klembara,
79 1997; *Utegenia*, Laurin, 1996), with a tooth shagreen on all palatal elements but a reduction
80 in the number of large lateral palatal teeth (Fig. 1). However, in temnospondyls enlargement
81 of the interpterygoid vacuity separated the pterygoids with loss of their anterior midline
82 contact (Fig. 1). As a result, the shagreen teeth on the pterygoid became more laterally
83 restricted. In addition, the ventral surface of the interpterygoid vacuity was sometimes
84 covered by a bony plate bearing patches of loosely set denticles (Schoch & Milner, 2000).

85 Many lepospondyls retained the primitive arrangement with a lateral palatal tooth row
86 parallel to the jaw margin, but there is more variation in the presence and/or arrangement of
87 the shagreen teeth on the palate and the parasphenoid (Fig. 1: e.g. *Odonterpeton*;
88 *Tambachia*, Sumida et al. 1998). *Pantylus* (Romer, 1969) had teeth scattered across the
89 palate (various sizes distributed randomly), *Brachydectes* (Wellstead, 1991) possessed
90 longitudinally aligned midline vomerine tooth rows, and some derived taxa (e.g.

91 *Cardiocephalus*, *Ptyonius*, Carroll et al. 1998) had reduced or lost the shagreen teeth
92 completely (Fig. 1). Further variations are listed in Appendix 1.

93 Living lissamphibians (Gymnophiona, Caudata, and Anura) have reduced shagreen teeth,
94 and palatal teeth are usually restricted to the vomer and parasphenoid, although some
95 species also bear teeth on a palatine/pterygopalatine (e.g. the caudates *Siren* and *Necturus*)
96 or maxillopalatine (e.g. the gymnophionan *Dermophis*, Trueb, 1993). Gymnophiona generally
97 have a single lateral vomerine tooth row parallel to the jaw margin (e.g. *Epicrionops*,
98 Nussbaum, 1977) whereas in frogs (Anura) there is more often a transverse tooth row lying
99 parallel, or nearly parallel, to the anterior part of the marginal tooth row (e.g. *Pelobates*,
100 Roček, 1981; the hylid *Triprion*, Trueb, 1993) (see Appendix 1). The pattern in caudates is
101 much more variable and ranges from a transverse anterior vomerine row (e.g. *Ambystoma*;
102 the plethodontid *Desmognathus*, Trueb, 1993), a medial longitudinal row (e.g. the
103 salamandrids *Notophthalmus* and *Taricha*, Trueb, 1993, Duellman & Trueb, 1994), a roughly
104 “T” shaped combination row (e.g. the plethodontids *Pseudotriton* and *Stereochilus*, Regal,
105 1966, Wake, 1966), an anterior row parallel to the marginal tooth row (e.g. *Necturus*, Trueb,
106 1993; *Cryptobranchus*, Elwood & Cundall, 1994)(Fig. 2A), or a tooth platform in either the
107 anterior (*Siren*, Trueb, 1993) or posterior part of the mouth in combination with a transverse
108 anterior vomerine row (e.g. the plethodontids *Bolitoglossa* and *Plethodon*, Wake, 1966).

109

110 **Evolutionary patterns in the palatal dentition of amniotes**

111 A dramatic change occurred in the palatal dentition of Diadectomorpha, the sister taxon of the
112 Amniota (e.g. Ruta et al. 2003; Ruta & Coates, 2007). They lost the early tetrapod pattern (a
113 lateral palatal row and median tooth shagreen) and replaced it with an arrangement of
114 longitudinally oriented rows of conical teeth on the anterior palatal elements (e.g. *Diadectes*,
115 Olson, 1947; Berman et al. 1998; *Orobates*, Berman et al. 2004) and/or a transverse posterior
116 row on the pterygoid flange (*Limnoscelis*, Williston, 1911, Berman et al. 2010; *Tseajaia*,
117 Moss, 1972). This palatal morphology would have been inherited by early members of both
118 Synapsida (mammals and stem-mammals) and Reptilia (Parareptilia+Eureptilia) when these
119 two major clades diverged in the Late Carboniferous.

120

121 **Synapsida**

122 Recent phylogenetic analyses place either Caseidae or Ophiacodontidae + Varanopidae as
123 the basal synapsid clade (Benson, 2012). In members of the Caseidae (e.g. *Cotylorhynchus*,
124 Reisz & Sues, 2000; *Ennatosaurus*, Maddin et al. 2008) and Varanopidae (*Mesenosaurus*,
125 Reisz & Berman, 2001, detailed information shown in Appendix 2), there were palatal teeth
126 on the vomer, palatine, pterygoid, and, in some cases, the parasphenoid (Caseidae) and
127 ectopterygoid (e.g. *Edaphosaurus*, Modesto, 1995). However, there was a general trend
128 towards simplification and reduction of the longitudinal palatal tooth rows, while retaining the
129 transverse pterygoid flange tooth row, which was usually located posterior to the marginal
130 tooth row (Fig. 3). The vomerine tooth row tended to become narrower as the choanae
131 elongated anteroposteriorly, and it was lost in Sphenacodontidae (e.g. *Dimetrodon*, Case,
132 1904; *Secodontosaurus*, Reisz et al. 1992; *Tetraceratops*, Laurin & Reisz, 1996). The
133 posterior elongation of the choanae also had the effect of restricting the longitudinal palatine
134 and pterygoid tooth rows to the back of the mouth (Fig. 3). In these non-therapsid synapsids,
135 particularly in the carnivorous *Haptodus* (Laurin, 1993), *Dimetrodon* (Case, 1904)(Fig. 2B),
136 and *Tetraceratops* (Laurin & Reisz, 1996), the pterygoid flange teeth were often larger than
137 those of the longitudinal tooth rows (vomer, palatine, pterygoid). By contrast, the herbivorous
138 *Edaphosaurus* lacked pterygoid flange teeth but developed a large plate of closely packed
139 palatine and pterygoid teeth level with the posterior teeth of the marginal row (Fig. 3).

140 Further reductions occurred within the clade Therapsida (including Biarmosuchia,
141 Dinocephalia, Anomodontia, and Theriodontia). Although some Biarmosuchia and
142 Dinocephalia retained the transverse pterygoid flange tooth row, they lost vomerine teeth (the
143 dinocephalian *Estemmenosuchus* is an exception, King, 1988) (Fig. 3). The longitudinal tooth
144 rows were rearranged into either circular patches (e.g. the biarmosuchian *Lycaenodon*,
145 Sigogneau-Russell, 1989 and the dinocephalian *Syodon*, King, 1988), or a predominantly
146 transverse, M-shaped anterior tooth row (e.g. *Biarmosuchus*, Ivakhnenko, 1999, and the
147 dinocephalian *Titanophoneus*, King, 1988).

148 Loss of the palatal dentition occurred independently within Anomodontia (except the basal
149 *Biseridens*, Liu et al. 2009) and Theriodontia (Modesto et al. 1999). In the latter group, a
150 palatal dentition was retained in Gorgonopsidae and some Therocephalia (Fig. 4). The palatal

151 dentition of gorgonopsids was similar to that in non-therapsids (e.g. Biarmosuchia), with
152 posteriorly located circular tooth patches on the palatine and pterygoids (Fig. 4). The
153 presence of a pterygoid flange row varied, even between species (e.g. *Cyonosaurus*, see
154 Appendix 2). In Therocephalia, the medial palatal teeth were further restricted to a small area
155 well posterior to the marginal tooth row (e.g. *Regisaurus*, Mendrez, 1972; Fourier & Rubidge,
156 2007; *Theriognathus*, Brink, 1956; *Viatkosuchus*, Tatarinov, 1995), or were lost completely
157 (e.g. *Bauria*, Kemp, 1982; *Moschorhinus*, Battail & Surkov, 2000). Palatal teeth were absent
158 in Cynodontia (the lineage leading to mammals).

159

160 **Reptilia (Parareptilia+Eureptilia)**

161 In contrast to Synapsida, many basal members of both Parareptilia and Eureptilia retained
162 longitudinal palatal tooth rows, in conjunction with those on the pterygoid flange (Fig. 5–7;
163 Appendix 3–4).

164

165 *Parareptilia*. Most parareptiles had the same palatal tooth arrangement as diadectidomorphs
166 and basal amniotes, but shagreen teeth were generally absent (the Permian *Macroleter* was
167 an exception, Tsuji, 2006). Several early parareptiles had teeth on the parasphenoid and/or
168 ectopteryoid (e.g. *Millerosaurus*, Carroll, 1988 and *Lanthanosuchus*, Efremov, 1946;
169 *Nyctiphruetus*, Tsuji et al. 2012), but whether as a retention of the primitive condition or a
170 redevelopment is unclear. Most parareptiles retained a tooth row on the pterygoid flange (e.g.
171 *Lanthanosuchus*, Efremov, 1946; *Nycteroleter*, Tverdokhlebova & Ivakhnenko, 1984),
172 although this is absent in Procolophoniodea (including *Procolophon*, Carroll & Lindsay, 1985;
173 Cisneros, 2008; *Barasaurus*, Piveteau, 1955; *Owenetta*, Reisz & Scott, 2002) and
174 *Mesosaurus* (Modesto, 2006). Where present, the orientation of the flange row also varies
175 from clearly transverse (most taxa) to more oblique (~ 45° to the transverse axis in
176 *Scutosaurus* [Tsuji et al. 2012] and *Pareiasuchus* [Lee et al. 1997]) (Fig. 5). The longitudinal
177 tooth rows are generally straight, but there was some variation within procolophonids. In
178 *Procolophon*, the palatine and pterygoid tooth rows form a “w” shape (Carroll and Lindsay,
179 1985; Cisneros, 2008); *Owenetta* shows a triangular arrangement composed of vomer,

180 palatine and pterygoid rows (Fig. 5); and *Bashkyroleter mesensis* had an additional row
181 running parallel to the marginal dentition (Ivakhnenko, 1997).

182 Members of the Permian Bolosauridae (e.g. *Bolosaurus*, *Eudibamus*) generally lacked
183 palatal teeth (Watson, 1954; Berman et al. 2000). This includes *Belebey maximi* and *B.*
184 *chengi* (Ivakhnenko & Tverdochlebova, 1987; Müller et al. 2008), but pterygoid flange rows
185 were present in *B. vegrandis* (Müller et al. 2008).

186

187 *Eureptilia* and stem *Diapsida*. Eureptilia also inherited the primitive amniote pattern of
188 longitudinal and transverse palatal tooth rows, as shown by *Captorhinus* which had teeth on
189 the palatine, pterygoid, and, variably, the parasphenoid (Warren, 1961; Modesto, 1998), but
190 not the ectopterygoid. Warren (1961) recorded sporadic vomerine teeth in *Captorhinus* sp.,
191 but other authors recorded them as absent (Fox & Bowman, 1966). Perhaps they were
192 variable like those of the parasphenoid, although *Labidosaurus* had lost both sets (Modesto et
193 al. 2007). Parasphenoid teeth were present in several other stem eureptilian taxa and stem
194 diapsids (e.g. *Paleothyris*, Carroll, 1969; *Petrolacosaurus*, Reisz, 1981; *Orovenator*, Reisz et
195 al. 2011), but ectopterygoid teeth were rare (e.g. *Araeoscelis*, Vaughn, 1955)(Fig. 6).

196 *Claudiosaurus* appears to have been exceptional in replacing the discrete tooth rows with a
197 shagreen of small teeth across all but the ectopterygoid bones (Carroll, 1981)(Fig. 6).

198 The stem diapsid pattern was inherited by members of some descendant clades (e.g.
199 *Youngina*, Gow, 1975) but parasphenoid and ectopterygoid teeth were generally absent.
200 Subsequently, members of the two major crown diapsid clades, Archosauromorpha and
201 Lepidosauromorpha, showed parallel patterns of reduction from the primitive palatal pattern
202 (Fig. 6–7).

203 Basal archosauromorphs, like *Protorosaurus* (Late Permian, Seeley, 1887) and *Czatkowiella*
204 (Early Triassic, Borsuk-Białynicka & Evans, 2009a), retained longitudinal tooth rows on the
205 vomer, palatine and pterygoid, but lacked teeth on either the pterygoid flange or
206 parasphenoid (ectopterygoid teeth unknown; Fig. 7). In contrast, Choristodera (if these are
207 archosauromorphs, e.g. Evans, 1988, 1990; Gauthier et al. 1988) generally retained the
208 pterygoid flange row and expanded the longitudinal pterygoid row into a broad tooth battery.
209 Most choristoderes, including the earliest (Middle - Late Jurassic *Cteniogenys*; Evans, 1990),

210 lacked parasphenoid teeth, so their presence in the Early Cretaceous neochoristodere
211 *Ikechosaurus* (Brinkman & Dong, 1993) was probably a reacquisition (Fig. 2C). The broad-
212 snouted Paleocene choristodere *Simoedosaurus* (e.g. Sigogneau-Russell & Russell, 1978) is
213 characterized by shagreen teeth covering the palate, and there may be a relationship
214 between snout width and palatal tooth row width in this group (Matsumoto & Evans, 2015).

215 Members of some early archosauromorph clades (e.g. Rhynchosauridae, Langer &
216 Schultz, 2000; Trilophosauria, Spielmann et al. 2008) independently lost the palatal dentition,
217 possibly in association with the evolution of a specialized marginal dentition, but the primitive
218 arrangement was retained in archosauriform stem taxa (*Tanystropheus* being unusual in
219 having vomerine teeth running parallel to the marginal tooth row [Wild, 1973])(Fig. 7).

220 Most crown-group archosaurs lacked palatal teeth (Dilkes & Sues, 2009), but a
221 longitudinal row persisted on the palatal ramus of the pterygoid in a few taxa, including the
222 early pterosaur *Eudimorphodon* (Wild, 1978), the basal non-avian dinosaur, *Eodromaes*,
223 and the basal sauropodomorph *Eoraptor* (Martinez et al. 2011; Sereno et al. 2012).

224 Marginal and palatal teeth were both present in the oldest recorded chelonian, the late
225 Triassic aquatic *Odontocheilus* (Li et al. 2008), which had longitudinal tooth rows on the
226 vomer, palatine and pterygoid, but not the pterygoid flange. A similar palatal tooth
227 arrangement was present in the terrestrial *Proganochelys* (Gaffney, 1990; Kordikova,
228 2002)(Fig. 7), but teeth were absent in all known later testudine taxa.

229 Within the aquatic Sauropterygia, Placodontia is exceptional in the possession of plate-like
230 crushing palatal teeth that were larger than those of the marginal dentition (Neenan et al.,
231 2013)(Fig. 6). However, the palatal dentition was lost at an early stage in the Eosauropterygia
232 (e.g. *Nothosaurus*, Albers & Rieppel, 2003; *Simosaurus*, Rieppel, 1994) and Ichthyopterygia
233 (Motani, 1999). A single individual of the basal ichthyosaur *Utatsusaurus hataii* reportedly had
234 teeth on the pterygoid, but some re-examination is needed (Motani, 1999, and personal
235 communication to RM, 2007).

236 In Lepidosauromorpha, the longitudinal rows remained extensive in stem lepidosaurs like
237 the kuehneosaurs and in early rhynchocephalians (e.g. *Gephyrosaurus*, Evans, 1980), but the
238 pterygoid flange row was lost in most taxa (Fig. 6). The palate of early squamates remains
239 unknown but was probably like that of stem-lepidosaurs. Crown rhynchocephalians lost the

240 pterygoid teeth but preserved and enlarged the lateral palatine row (e.g. *Palaeopleurosaurus*,
241 Carroll & Wild, 1994; *Priosphenodon*, Apesteguia & Novas, 2003; *Sphenodon*, Jones et al.
242 2012), which was realigned so as to lie parallel to the maxillary tooth row. This arrangement
243 allows the specialized shearing mechanism that characterizes Rhynchocephalia (Jones et al.
244 2012), whereby the teeth of the dentary bite between the maxillary and palatine tooth rows.
245 Squamates only rarely have palatine teeth (e.g. polychrotines, *Lanthanotus*, *Heloderma*) but
246 pterygoid teeth are more common (Mahler & Kearney, 2006; Evans, 2008), usually along the
247 margins of the interpterygoid vacuity (Fig. 6). Without well-preserved early members of major
248 lineages, it is difficult to determine whether palatine teeth were lost multiple times, or have
249 occasionally been regained as has been suggested for the vomerine teeth of the anguid
250 *Ophisaurus apodus* (Evans, 2008)(Fig. 6). In snakes, the small-mouthed scolecophidians,
251 anomochilids, and uropeltids lack any palatal teeth (Cundall & Irish, 2008), but this is likely to
252 be a specialization rather than the primitive condition. 'Primitive' alethinophidian snakes (e.g.
253 cylindrophiids, aniliids, xenopeltids) have a row of teeth on both the palatine and pterygoid,
254 and this arrangement is retained in macrostomatan snakes, where enlarged palatal teeth play
255 an important role in gripping prey as it is drawn into the mouth (Mahler & Kearney, 2006;
256 Cundall & Irish, 2008). Again, the palatine teeth, at least, may have been regained (Cundall &
257 Greene, 2000). The palate is incompletely known in basal fossil snakes like the Cretaceous
258 *Najash* (Zaher et al. 2009) and *Dinilysia* (Zaher & Scanferla, 2012), but the marine
259 simoliophids (e.g. *Haasiophis*, Tchernov et al. 2000) already show the macrostomatan
260 configuration.

261

262 **Discussion**

263 The review presented above highlights the variation in palatal tooth morphology that exists
264 across tetrapods, but also show some clear trends, summarized in Figure 8. The first is a
265 major difference between early tetrapods and Temnospondyli ('amphibians'), on the one
266 hand, and early amniotes on the other. Early amniotes are characterized by a rearrangement
267 of the palatal dentition to produce a series of distinct longitudinal and/or transverse tooth
268 rows. This arrangement was retained in early representatives of both Synapsida and Reptilia,
269 but there followed a similar, but independent, pattern of reduction in both lineages, starting

270 with the teeth on the parasphenoid and ectopterygoid, and then the vomer and/or pterygoid
271 flange. Within synapsids, all remaining palatal teeth were lost in the ancestors of cynodonts,
272 concomitant with the evolution of the secondary palate. However, as most Reptilia have only
273 a primary palate, palatal teeth persisted somewhat longer, especially in parareptiles and early
274 members of both Archosauromorpha and Lepidosauromorpha. Palatal teeth were lost
275 completely in the ancestors of crown-group crocodiles and turtles, and in early non-avian
276 dinosaurs. In contrast, lepidosaurs tended to retain (or regain) at least some palatal teeth,
277 most often on the posterior part of the pterygoid plate. Regain would also help to explain the
278 presence of parasphenoid teeth in some derived members of Choristodera and
279 *Kuehneosaurus*, despite their absence in more primitive members of the same lineages. It
280 seems likely the developmental mechanism for generating palatal teeth was suppressed
281 rather than lost in some lineages, a phenomenon that has been reported for the marginal
282 dentition in, for example, birds and frogs (Harris et al. 2006; Wiens, 2011).

283 These trends in the arrangement and subsequent reduction of the palatal dentition raise
284 questions about the role of palatal teeth generally and of different patterns (e.g. tooth
285 shagreen versus distinct rows) or groups (e.g. transverse pterygoid flange teeth versus
286 longitudinal rows) of palatal teeth. Like the marginal dentition, the palatal dentition would be
287 expected to reflect diet and feeding strategy to some degree, but diet alone is less likely to
288 explain major trends. Palate morphology should also be correlated with structures in the floor
289 of the mouth, notably the tongue, the hyobranchial apparatus, and the pharynx, as well as jaw
290 muscles like the pterygoideus that have palatal attachments, and with other aspects of
291 feeding strategy including skull kinesis and jaw movements.

292 Based on studies of living taxa (as referenced below), Figure 9 presents a summary of
293 some major changes that are thought to have occurred in the soft tissues and/or feeding
294 mechanics of major tetrapod groups. Some of these changes may be correlated with changes
295 in the palatal dentition. However, developing functional hypotheses to explain palatal tooth
296 distribution in extinct taxa is complicated by the fact that, with the exception of snakes (which
297 are highly specialized), most living amniotes have either significantly reduced the palatal
298 dentition (lizards, rhynchocephalians) or lost it completely (chelonians, archosaurs,
299 mammals). Moreover, examination of the palatal surface in a bony skull provides an

300 incomplete understanding of its original structure, much of which relies on the presence of
301 overlying soft tissues. Thus, for example, an apparently smooth bone surface may have been
302 covered in life by keratinized oral epithelium that was itself ridged or papillate (Fig. 10).

303 One of the major challenges faced by early land animals was food acquisition (e.g. Lauder
304 & Gillis, 1997). Although aquatic animals often rely on suction feeding to ingest prey and
305 transport it through the mouth toward the pharynx (e.g. Lauder & Shaffer, 1993; Deban &
306 Wake, 2000; Iwasaki, 2002), terrestrial animals must move food physically into the mouth,
307 pass it towards the back of the oral cavity (intra-oral transport, e.g. Smith, 1993; Schwenk,
308 2000a), and finally push into the pharynx prior to swallowing. The palatal dentition, lying
309 between the teeth of the upper jaws, is positioned to assist the tongue and jaws primarily in
310 intra-oral transport. Very small or thin prey may be moved by the tongue alone (due to
311 surface adhesion) but the development of a palatal gripping surface would have made it
312 easier to manipulate (and perhaps subjugate) larger, potentially resistant, food items. The
313 longitudinal palatal rows of adult terrestrial salamanders have also been correlated with the
314 possession of a mobile tongue (Regal, 1966; Wake & Deban, 2000), the two working together
315 to hold and transport food. However, the absence of intrinsic muscles in most amphibian
316 tongues (Schwenk, 2000a) may limit their mobility and power within the oral cavity.

317 A muscular tongue with both extrinsic and intrinsic muscles is found in many amniotes and
318 probably evolved in stem members of that group, followed by keratinization of the epithelial
319 surface (Iwasaki, 2002). This type of tongue is well adapted to work against the roof of the
320 mouth during intra-oral transport and also to help to roll the food into a bolus at the back of
321 the oral cavity (Schwenk, 2000a). It may therefore be significant that the inferred evolution of
322 this type of tongue (stem-amniotes) was coincident with the change in the pattern of palatal
323 teeth into an ordered arrangement of distinct longitudinal rows. In the absence of a muscular
324 pharynx, a muscular tongue is also used to push the food bolus into the entrance of the
325 pharynx, a process known as pharyngeal packing (Schwenk, 2000a). Teeth on the posterior
326 part of the palate (parasphenoid and pterygoid flanges) may originally have been important in
327 holding the food bolus in place at the entrance to the pharynx, but perhaps became less so as
328 food positioning and swallowing became more efficient (e.g. by expansion of posterior lobes
329 on the tongue, or by kinetic movements of the jaws and palate, Schwenk 2000a).

330 Reacquisition of parasphenoid teeth (as in the Late Triassic kuehneosaurs and the
331 neochoristodere *Ikechosaurus*) may therefore indicate a change in skull biomechanics or
332 feeding strategy whereby an extra gripping surface at the entrance to the pharynx was
333 beneficial. In kuehneosaurs, at least, this may have been correlated with a potential for the
334 quadrates (and attached pterygoids) to splay out laterally to increase pharyngeal width (SE
335 unpublished). Moreover, a subsequent increase in size of the pterygoideus muscle in later
336 lineages, parts of which attach to the pterygoid flange, may have resulted in loss of the
337 pterygoid flange tooth row (e.g. King et al. 1989; Maier et al. 1996).

338 The dichotomy in the fate of the palatal dentition between archosauromorphs and
339 lepidosauromorphs may, in part, reflect changes in the archosaurian tongue. Both crocodiles
340 and birds, and thus potentially their common archosaurian ancestor, have lost much of the
341 intrinsic tongue musculature (Schwenk, 2000a). Instead of using the tongue for prehension
342 and transport, they mainly use jaw prehension, inertial feeding, and gravity (Schwenk,
343 2000a). Loss of the palatal dentition would be consistent with this, as would the development
344 of a secondary palate in derived crocodiles. However, some extant archosaurs (birds,
345 crocodiles) and chelonians (e.g. the sea turtles *Dermochelys coriacea*, *Chelonia mydas*) have
346 keratinized epithelium forming corny papillae and/or rugae on the palate and/or on the tongue
347 (e.g. Shimada et al. 1990; Kobayashi et al. 1998; Iwasaki, 2002) (Fig. 10). These may have a
348 role analogous to that of the original palatal dentition, especially in turtles where a muscular
349 tongue is retained. In some birds, palatal papillae run transversally across the back of the oral
350 cavity, an arrangement similar to that of a pterygoid flange tooth row. Harrison (1964)
351 suggested that this arrangement, which can also occur across the back of the tongue,
352 facilitates positioning of prey prior to swallowing, a role that we also infer for the pterygoid
353 flange and parasphenoid teeth of more primitive amniote taxa.

354 Most lepidosaurs have a mobile muscular tongue with a papillose surface (Schwenk,
355 2000b). Although many non-iguanian lizards used jaw prehension to bring food into the
356 mouth, aided by varying levels of kinesis, most lizards still use the tongue for intraoral
357 transport and pharyngeal packing, with the latter aided in most taxa by enlarged posterior
358 lobes on the tongue (chameleons, varanids and some teiids lack these). The retention of
359 clusters or lines of teeth on the posterior part of the pterygoid plate, close to the opening of

360 the pharynx (Mahler & Kearney, 2006) may help in positioning/restraining the food bolus
361 during packing. Pharyngeal packing is followed by pharyngeal compression, in which external
362 neck muscles (constrictor colli) contract to squeeze the bolus into the muscular esophagus for
363 swallowing (Schwenk, 2000a). However, the bolus needs to be pushed posterior to the main
364 body of the hyoid before compression begins, to ensure it does not move back up into the
365 mouth instead. In derived anguimorphs and snakes, together or independently depending on
366 the phylogenetic hypothesis, the anterior part of the tongue is bifid and slender, with a purely
367 chemosensory role. In *Varanus*, this change in tongue function is compensated for by the
368 adoption of inertial feeding whereby food items are effectively thrown to the back of the mouth
369 (Schwenk, 2000b). Snakes employ a different strategy, using kinetic jaws and, especially in
370 macrostomatans, enlarged palatine and pterygoid teeth, to draw prey to the back of the
371 mouth for swallowing. As noted above, these may be a secondary development, given that
372 both tongue action and inertial feeding are precluded in snakes.

373 The fossil record of synapsids is generally good, permitting many stages in the evolution of
374 the mammalian feeding apparatus, such as heterodonty, reduction of the accessory jaw
375 bones, and formation of a bony secondary palate, to be followed. Coincident changes in oral
376 soft anatomy must also have occurred (Fig. 9), although these are more difficult to pinpoint in
377 time. They include formation of a soft tissue secondary palate prior to the bony one (choanal
378 folds), extension of the bony secondary palate by a muscular soft palate to improve the
379 separation of food and air streams, and muscularization of the pharynx so that the food bolus
380 can be formed within the oropharynx rather than in the mouth, and then swallowed rapidly
381 (e.g. Maier et al. 1996; Schwenk, 2000a). This would have reduced the need for
382 parasphenoid or pterygoid flange teeth. The mammalian tongue remained large and
383 muscular, and reduction of the hyoid apparatus gave it greater mobility for intraoral transport,
384 aided by the development of muscular cheeks. Although palatal teeth were lost, many
385 terrestrial mammals (like birds and turtles) have developed transverse palatal rugae to help to
386 grip food. These rugae are generally reduced in aquatic mammals that feed under water (e.g.
387 suction feeders) where a gripping palatal surface is less useful (Werth, 2000), although
388 Beaked Whales are an exception to this, in developing papillose rugosities to hold their
389 slippery prey (Heyning & Mead, 1996).

390

391 **Conclusions**

392 Palatal teeth clearly had an important role in holding and manipulating food within the mouth
393 (although they may occasionally have contributed to food reduction), and it is reasonable to
394 conclude that an extensive palatal dentition was correlated with a well-developed mobile
395 tongue (although the obverse is not necessarily true). The more anterior palatal teeth (vomer,
396 palatine, anterior pterygoid) were probably used mainly during intraoral transport, whereas
397 posterior palatal teeth, notably those on the pterygoid flange and parasphenoid, may have
398 had a greater role in positioning and stabilizing the food bolus at the entrance to the pharynx.
399 Subsequent loss/reduction of the palatal dentition in derived members of most major tetrapod
400 lineages was probably linked to anatomical and functional changes that rendered a palatal
401 gripping surface less important or effective. These include

- 402 1. reduction of the tongue (e.g. archosaurs, varanid lizards).
- 403 2. functional replacement of the palatal dentition with palatal or lingual rugosities (e.g.
404 some turtles, mammals), or with keratinized papillae (e.g. birds).
- 405 3. skull or jaw adaptations that improved food holding (e.g. cranial kinesis)
- 406 4. changes in feeding strategy (e.g. the adoption of inertial feeding, *Varanus*, crocodiles)
- 407 5. invasion of the ventral palatal surface by pterygoid musculature
- 408 6. development of an extensive hard and soft palate (e.g. mammals).

409 No single factor can be invoked to explain the loss (or reacquisition) of palatal teeth in any
410 one taxon, and many aspects remain poorly understood (e.g. the relationship between
411 skeletal and soft tissue anatomy in the palate; the developmental biology of the palatal
412 dentition). Nonetheless, palatal tooth patterns have the potential to provide additional
413 information on diet and feeding strategy in extinct taxa and would benefit from further more
414 detailed study.

415

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428

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911 **Figure captions**

- 912 **Fig. 1** Phylogenetic tree for early tetrapods and amphibians showing arrangement of palatal
913 dentition. Colour coding of the palatal figures is consistent in all figures (tree modified from
914 Ruta & Coates, 2007). Palatal figures as follows: 1, *Eusthenopteron*; 2, *Acanthostega*; 3,
915 *Pederpes*; 4, *Crassigyrinus*; 5, *Greerepeton*; 6, *Edops*; 7, *Balanerpeton* (original image
916 reflected); 8, *Phonerpeton*; 9, *Doleserpeton*; 10, *Dermophis mexicanus*, Gymnophiona; 11,
917 *Stereochilus marginatum*, Caudata; 12, *Gastrotheca walker*, Anura; 13, *Silvanerpeton*; 14,
918 *Proterogyrinus*; 15, *Seymouria*; 16, *Odonterpeton*; 17, *Rhynchonkos*; 18, *Cardiocephalus*
919 (original image reflected); 19, *Pantylus*; 20, *Brachydectes*; 21, *Batrachiderpeton*; 22,
920 *Ptyonius*; 23, *Diadectes*. Image sources: 1,2,4, Clack, 2012; 3, Clack & Finney, 2005; 5,
921 Smithson, 1982; 6, Romer & Witter, 1942; 7, Holmes 2000; 8, Dilkes, 1990; 9, Sigurdson &
922 Bolt, 2010; 10-12, Duellman & Trueb, 1994; 13, Ruta & Clack, 2006; 14, Holmes, 1984; 15,

923 Klembara et al. 2005; 16-22, Carroll et al. 1998; 23, Reisz & Sues, 2000 ; 1, 10-13, 20
924 original without scale. Abbreviations: ANTH, Anthracosauria; LISS, Lissamphibia; SEY,
925 Seymouriamorpha.
926
927 Fig. 2 Photographs of the palatal tooth arrangement in various lineages: A, *Andrias japonicus*
928 (Lissamphibia; NSM-PO-H-447); B, *Dimetrodon limbatus* (Synapsida; AMNH FR 4001); C,
929 *Ikechosaurus sunailinae* (Choristodera, Diapsida; IVPP V9611-3), grey coloured area marks
930 nasopalatal trough and blue coloured area marks the distribution of the palatal dentition.
931 Institutional abbreviations: American Museum Natural History (AMNH); IVPP Institute of
932 Vertebrate Paleontology and Paleoanthropology, Beijing, China (IVPP); National Museum of
933 Nature and Science, Tokyo (NSM). Anatomical abbreviations: d, dentary; ept, ectopterygoid;
934 hy, hyoid; pal, palatine; psh, parasphenoid; pt, pterygoid; pt fl, pterygoid flange; v, vomer.
935
936 **Fig. 3** Skulls of synapsids in palatal view (phylogeny based on Sidor, 2001): 1
937 *Cotylorhynchus*; 2, *Ennatosaurus*; 3, *Mesenosaurus*; 4, *Varanosaurus*; 5, *Edaphosaurus*; 6,
938 *Haptodus*; 7, *Secodontosaurus*; 8, *Tetraceratops*; 9, *Biarmosuchus*; 10, *Lycaenodon*; 11,
939 *Herpetoskylax*; 12, *Titanophoneus*; 13, *Syodon*; 14, *Styracocephalus* (original without scale);
940 15, *Estemmenosuchus*; 16, *Struthiocephalus*. Image sources: 1, Reisz & Sues, 2000; 2,
941 Maddin et al. 2008; 3, Reisz & Berman, 2001; 4, Berman et al. 1995; 5, Modesto, 1995; 6,
942 Laurin, 1993; 7, Reisz et al. 1992; 8, Laurin & Reisz, 1996; 9, Ivakhnenko, 1999; 10-11,
943 Sigogneau-Russell, 1989; 12-13, 15, King 1988; 14, Rubidge & van den Heever, 1997; 16,
944 Rubidge, 1991. Abbreviations: BIAR, Biarmosuchia; CASE, Caseasauria; DINO,
945 Dinocephalia; OPHI, Ophiacodontidae; SPHE, Sphenacodontidae; VARA, Varanopidae.
946
947 **Fig. 4** Skulls of synapsids in palatal view (phylogeny based on Sidor, 2001), continued from
948 Figure 4: 1, *Aelurosaurus*; 2, *Arctognathus*; 3, *Leontocephalus*; 4, *Scylacops*; 5, *Aloposaurus*;
949 6, *Gorgonops*; 7, *Arctops*; 8, *Prorubidgea*; 9, *Dinogorgon*; 10, *Rubidgea* (original without
950 scale); 11, *Theriognathus*; 12 *Viatkosuchus* (original without scale); 13 *Regisaurus*. Image
951 sources: 1-10, Sigogneau-Russell, 1989; 11,13, Kemp, 1982; 12, Tatarinov, 1995.
952

953 **Fig. 5** Skulls of parareptiles in palatal view (phylogeny based on Tsuji et al., 2012). 1,
954 *Mesosaurus*; 2, *Millerosaurus*; 3, *Acleistorhinus*; 4, *Nyctiphruetus*; 5, *Procolophon* (original
955 without scale); 6, *Owenetta*; 7, *Scutosaurus*; 8, *Pareiasuchus*; 9, *Macroleter*; 10, *Nycteroleter*;
956 11, *Bashkyroleter mesensis*. Image sources: 1, Modesto, 2006; 2, 4,7, Carroll, 1988; 3,
957 DeBraga & Reisz, 1996; 5, Carroll & Lindsay, 1985; 6, Reisz & Scott, 2002; 8, Lee et al.
958 1997; 9, Tsuji, 2006; 10, Tverdokhlebov & Ivakhnenko, 1984; 11, Ivakhnenko, 1997.
959 Abbreviations: LANT, Lanthanosuchidae; BOL, Bolosauridae; PROCOL, Procolophonoidea;
960 PAREIA, Pareiasauria.

961
962 **Fig. 6** Skulls of Eureptilia and Diapsida, Sauropterygia, Ichthyopterygia, and
963 Lepidosauromorpha in palatal view (phylogeny based on DeBraga & Rieppel, 1997; Pyron et
964 al. 2013; Rieppel & Reisz, 1999; Wiens et al. 2010) 1, *Captorhinus*; 2, *Paleothyris*; 3,
965 *Petrolacosaurus*; 4, *Araeoscelis*; 5, *Claudiosaurus*; 6, *Youngina*; 7, *Placodus*; 8,
966 *Kuehneosaurus*; 9, *Marmoretta*; 10, *Gephyrosaurus*; 11, *Clevosaurus*; 12, *Sphenodon*; 13,
967 *Lacerta*; 14, *Ctenosaura* (original without scale); 15, *Ophisaurus*; 16 *Heloderma*; 17,
968 *Shinisaurus*; 18, *Platecarpus* (original without scale); 19, *Anilius*. Image sources: 1, Reisz &
969 Sues, 2000; 2, Benton, 2000; 3, Reisz, 1981; 4, Vaughn, 1955; 5-7, Carroll, 1988; 8,
970 Robinson, 1962; 9, Evans, 1991; 10-11, Jones, 2006; 12,18, Romer, 1956; 13-17, Evans,
971 2008; 19, Cundall & Irish, 2008. Abbreviation: Rhyncho, Rhynchocephalia.

972
973 **Fig. 7** Skulls of Archosauromorph in palatal view (phylogeny based on Brusatte et al. 2010;
974 Borsuk-Białynicka & Evans, 2009a; Dilkes & Sues, 2009): 1, *Czatkowiella*; 2, *Cteniogenys*; 3,
975 *Proganochelys*; 4, *Mesosuchus*; 5, *Tanystropheus*; 6, *Proterosuchus*; 7, *Osmolskina*; 8,
976 *Euparkeria*; 9, *Doswellia*; 10, *Proterochampsa*. Image sources: 1, Borsuk-Białynicka &
977 Evans, 2009a; 2, Evans, 1990; 3,6, Carroll, 1988; 4, Dilkes, 1998; 5, Wild, 1987; 7,
978 Borsuk-Białynicka & Evans, 2009b; 8, Ewer, 1965; 9, Weems, 1980; 10, Sill, 1967.

979

980

981 **Fig. 8** Summary of evolutionary patterns in the palatal dentition of tetrapods.

982

983 **Fig. 9** Summary of evolutionary history of soft tissues related to feeding through tetrapod
984 evolution (see text for detail and references).

985

986 **Fig. 10** Keratinized oral epithelium in extant taxa; A, *Anas platyrhynchos* (Mallard; KPM-NF
987 2002622, floor of mouth (left) and palate (right); B, *Spheniscus demersus* (African Penguin;
988 KPM-NF 2002403), dissection photographs and CT image of a sagittal section; C,
989 *Osteolaemus tetraspis* (Dwarf Crocodile; Ueno Zoo, Tokyo Japan, no number), palatal
990 surface; D, *Chelonia agassizii* (Galápagos Green Turtle; KPM-NFR 389), palatal surface with
991 keratinized keels and serrations. Institutional abbreviation: Kanegawa Prefectural Museum of
992 Natural History (KPM-NF).

993

994 Appendices 1–4

995 1. Early tetrapods and amphibians, arrangement of the palatal dentition

996 2. Synapsida, arrangement of the palatal dentition

997 3. Parareptilia, arrangement of the palatal dentition

998 4. Diapsida, arrangement of the palatal dentition

999

1000 **Supplementary information**

1001 **Sup-Fig. 1.** Skulls of early tetrapods in palatal view. A, *Eusthenopteron* (original without
1002 scale); B, *Acanthostega*; C, *Pederpes*; D, *Crassigyrinus*; E, *Greerepeton*; F, *Edops*; G,
1003 *Balanerpeton*; H, *Phonerpeton*; I, *Doleserpeton*; J, *Silvanerpeton*; K, *Proterogyrinus*; L,
1004 *Pholiderpeton*; M, *Seymouria*; N, *Odonterpeton*; O, *Microbrachis*; P, *Hapsidopareion*; Q,
1005 *Rhynchonkos*; R, *Cardiocephalus* (original image reflected); S, *Pantylus*; T, *Brachydectes*
1006 (original without scale); U, *Batrachiderpeton*; V, *Ptyonius*; W, *Diadectes*; X, *Dermophis*
1007 *mexicanus* (Gymnophiona); Y, *Stereochilus marginatum* (Caudata); Z, *Gastrotheca walker*
1008 (Anura), original without scale. Image sources: A, B,D, Clack, 2012; C, Clack & Finney, 2005;
1009 E, Smithson, 1982; F, Romer & Witter, 1942; G, Holmes, 2000 (original image reflected); H,
1010 Dilkes, 1990; I, Sigurdson & Bolt, 2010; J, Ruta & Clack, 2006; K, Holmes, 1984; L, Clack,
1011 1987; M, Klembara et al. 2005; N, P-T, Carroll et al. 1998; O, Vallian & Laurin, 2004; U-V,

1012 Carroll et al. 1998; W, Reisz & Sues, 2000; X-Z, Duellman & Trueb, 1994 . Colour coding on
1013 the palate same as text Figures 1–7.

1014

1015 **Sup-Fig. 2** Skulls of synapsids in palatal view, Part 1: A, *Cotylorhynchus* (Caseasauria); B,
1016 *Ennatosaurus* (Caseasauria); C, *Mesenosaurus* (Varanopidae); D, *Varanosaurus*
1017 (Ophiacodontidae); E, *Edaphosaurus*; F, *Haptodus*; G, *Secodontosaurus*
1018 (Sphenacodontidae); H, *Tetraceratops*; I, *Biarmosuchus*; J, *Lycaenodon* (Biarmosuchia); K,
1019 *Titanophoneus* (Dinocephalia); L, *Syodon* (Dinocephalia); M, *Styracocephalus* (Dinocephalia,
1020 original without scale bar); N, *Estemmenosuchus* (Dinocephalia); O, *Struthiocephalus*
1021 (Dinocephalia); P, *Ulemosaurus* (Dinocephalia). Image sources: A, Reisz & Sues, 2000; B,
1022 Maddin et al. 2008; C, Reisz & Berman, 2001; D, Berman et al. 1995; E, Modesto, 1995; F,
1023 Laurin, 1993; G, Reisz et al. 1992; H, Laurin & Reisz, 1996; I, Ivakhnenko, 1999; J,
1024 Sigogneau-Russell, 1989; K-L, N-P, King, 1988; M, Rubidge & van den Heever, 1997.

1025

1026 **Sup-Fig. 3** Skulls of synapsids in palatal view, Part 2: A, *Otsheria* (Anomodontia, original
1027 without scale); B, *Aelurosaurus* (Gorgonopsidae); C, *Arctognathus* (Gorgonopsidae); D,
1028 *Leontocephalus* (Gorgonopsidae); E, *Scylacops* (Gorgonopsidae) ; F, *Arctops*
1029 (Gorgonopsidae); G, *Prorubidgea* (Gorgonopsidae) ; H, *Dinogorgon* (Gorgonopsidae) ; I,
1030 *Rubidgea* (Gorgonopsidae); J, *Moschorhinus* (Therocephalia); K, *Theriognathus*
1031 (Therocephalia); L, *Viatkosuchus* (Therocephalia, original without scale bar); M, *Regisaurus*
1032 (Therocephalia); N, *Bauria* (Therocephalia, original without scale); O, *Dvinia* (Cynodontia,
1033 original without scale). Image sources: A, K, M-N, Kemp, 1982; B-I, Sigogneau-Russell, 1989;
1034 J, Mendrez, 1974a; L, Tatarinov, 1995; O, Tatarinov, 1968.

1035

1036 **Sup-Fig. 4** Skulls of Parareptilia in palatal view. A, *Mesosaurus*; B, *Millerosaurus*; C,
1037 *Lanthanosuchus*; D, *Acleistorhinus* (Lanthanosuchidae); E, *Belebey* (Bolosauridae); F,
1038 *Nyctiphruetus*; G, *Procolophon* (Procolophonoidea, original without scale); H, *Owenetta*
1039 (Procolophonoidea); I, *Scutosaurus* (Pareiasauria); J, *Pareiasuchus* (Pareiasauria); K,
1040 *Macroleter* ('nycteroleter'); L, *Nycteroleter*; M, *Bashkyroleter mesensis* ('nycteroleter', original
1041 without scale). Image sources: A, Modesto, 2006; B,F,I, Carroll, 1988; C,D, DeBraga &

1042 Reisz, 1996; E, Ivakhnenko & Tverdochlebova, 1987; G, Carroll & Lindsay, 1985; H, Reisz &
1043 Scott, 2002; J, Lee et al. 1997; K, Tsuji, 2006; L, Tverdokhlebov & Ivakhnenko, 1984; M,
1044 Ivakhnenko, 1997.

1045

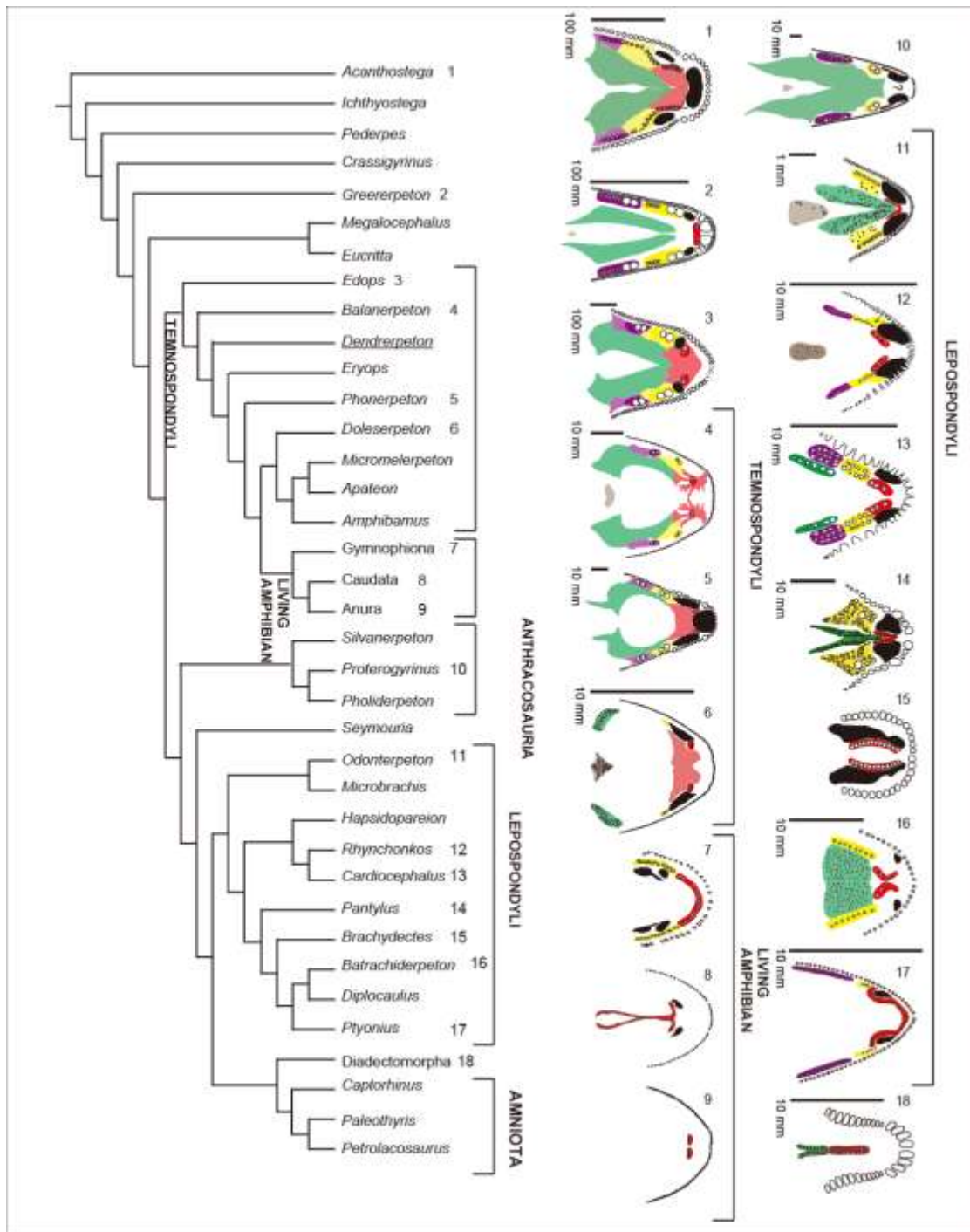
1046 **Sup-Fig. 5** Skulls of eureptiles and basal diapsids (A-F), Sauropterygia (G–H),
1047 Ichthyopterygia (I), and Lepidosauromorpha (J–Z) in palatal view: A, *Captorhinus*; B,
1048 *Paleothyris*; C, *Petrolacosaurus*; D, *Araeoscelis*; E, *Claudiosaurus*; F, *Youngina*; G, *Placodus*;
1049 H, *Simosaurus*; I, *Ichthyosaurus* (original without scale); J, *Kuehneosaurus*; K, *Marmoretta*; L,
1050 *Gephyrosaurus* (Rhynchocephalia); M, *Clevosaurus* (Rhynchocephalia) ; N, *Sphenodon*
1051 (Rhynchocephalia); O, *Hemitheconyx* (Squamata, Gekkota); P, *Tropidophorus* (Squamata,
1052 Scincoidea); Q, *Lacerta* (Squamata, Lacertoidea); R, *Uromastyx* (Squamata, Iguania); S,
1053 *Ctenosaura* (Squamata, Iguania: original without scale); T, *Xenosaurus* (Squamata,
1054 Anguimorpha); U, *Ophisaurus* (Squamata, Anguimorpha); V, *Heloderma* (Squamata,
1055 Anguimorpha); W, *Shinisaurus* (Squamata, Anguimorpha) ; X, *Varanus* (Squamata,
1056 Anguimorpha) ; Y, *Platecarpus* (Squamata, Mosasauria: original without scale); Z, *Anilius*,
1057 Squamata, Serpentes). Image sources: A, Reisz & Sues, 2000; B, Benton, 2000; C, Reisz,
1058 1981; D, Vaughn, 1955; E-G, Carroll, 1988; H, Rieppel, 1994; I,N,Y, Romer, 1956; J,
1059 Robinson, 1962; K, Evans, 1991; L-M, Jones, 2006; O-X, Evans, 2008; Z, Cundall & Irish,
1060 2008.

1061

1062 **Sup-Fig. 6** Skulls of Archosauromorpha in palatal views: A, *Czatkowiella*; B, *Cteniogenys*
1063 (Choristodera); C, *Proganochelys* (Testudines); D, *Mesosuchus* (Rhynchosauria); E,
1064 *Trilophosaurus*; F, *Paradapedon* (Rhynchosauria); G, *Tanystropheus*; H, *Proterosuchus*; I,
1065 *Euparkeria*; J, *Doswellia*; K, *Proterochampsa*; L, *Rutiodon* (Phytosauria); M, *Stagonolepis*
1066 (Aetosauria); N, *Sphenosuchus* (Crocodylomorpha); O, *Ornithosuchus*. Image sources: A,
1067 Borsuk-Białynicka & Evans, 2009a; B, Evans, 1990; C, E, F, H, Carroll, 1988; D, Dilkes,
1068 1998; G, Wild, 1987; I, Ewer, 1965; J, Weems, 1980; K, Sill, 1967; L-M, O, Kuhn, 1976; N,
1069 Walker, 1990.

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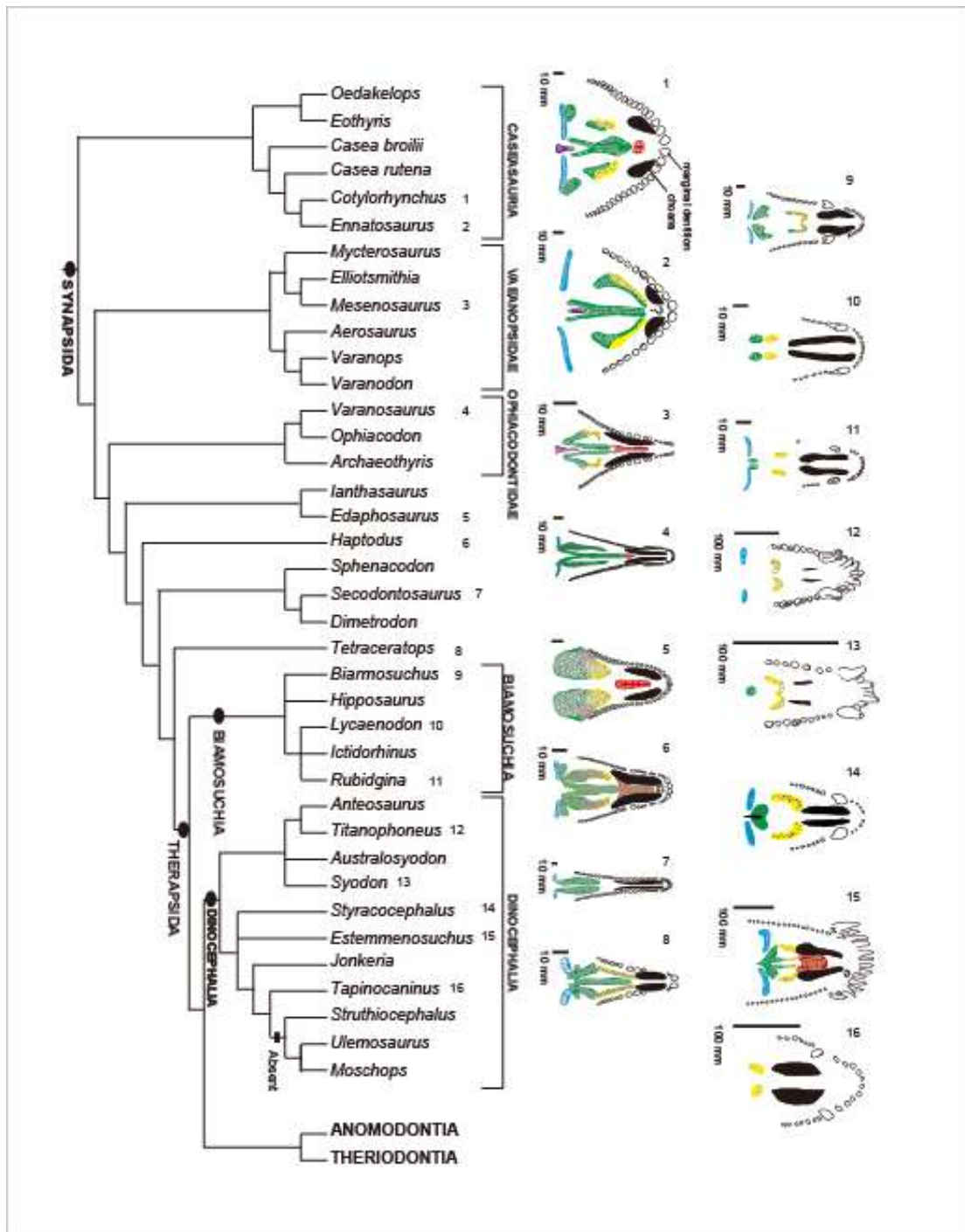
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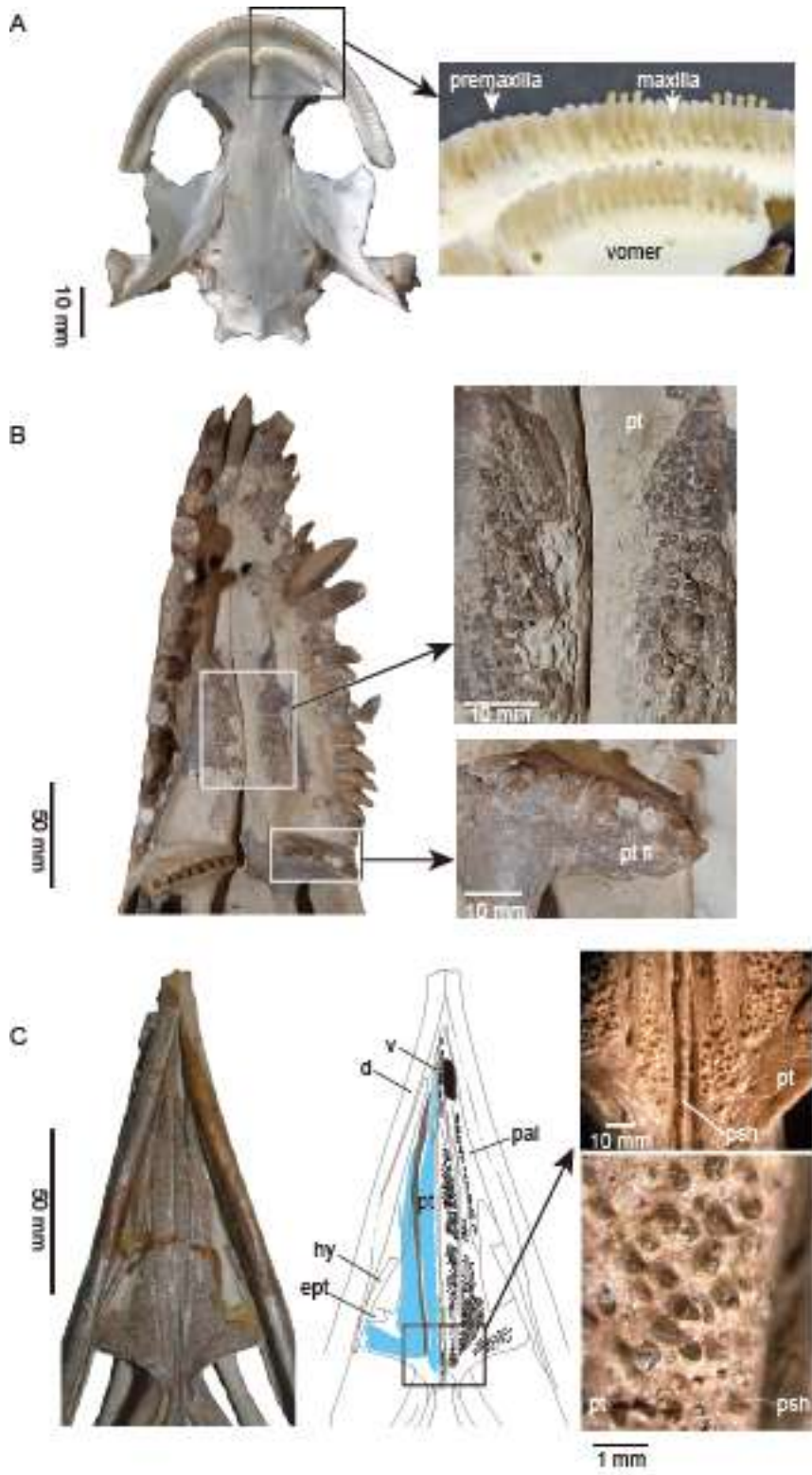
1073 Fig.1

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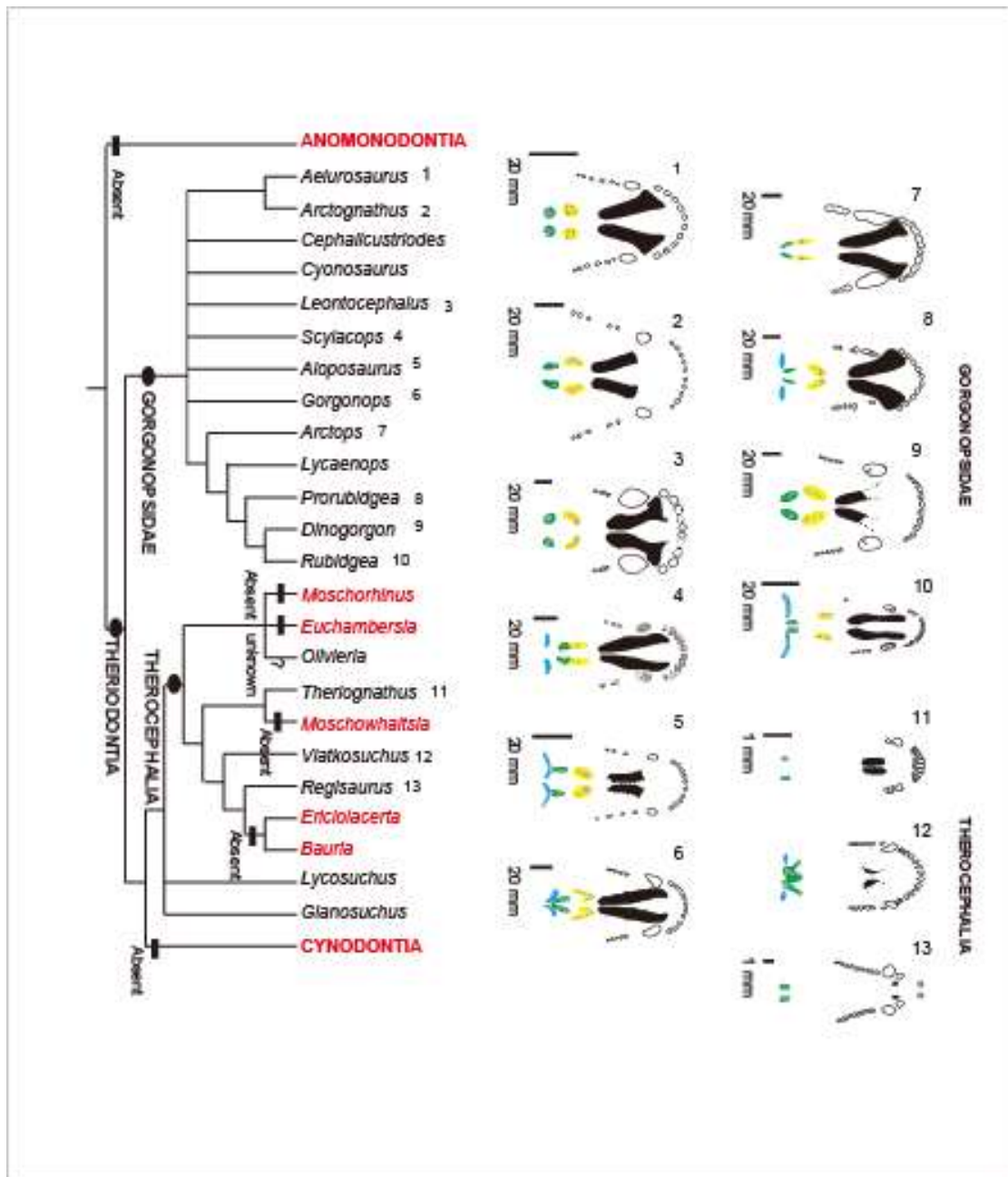
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1076 Figure 2



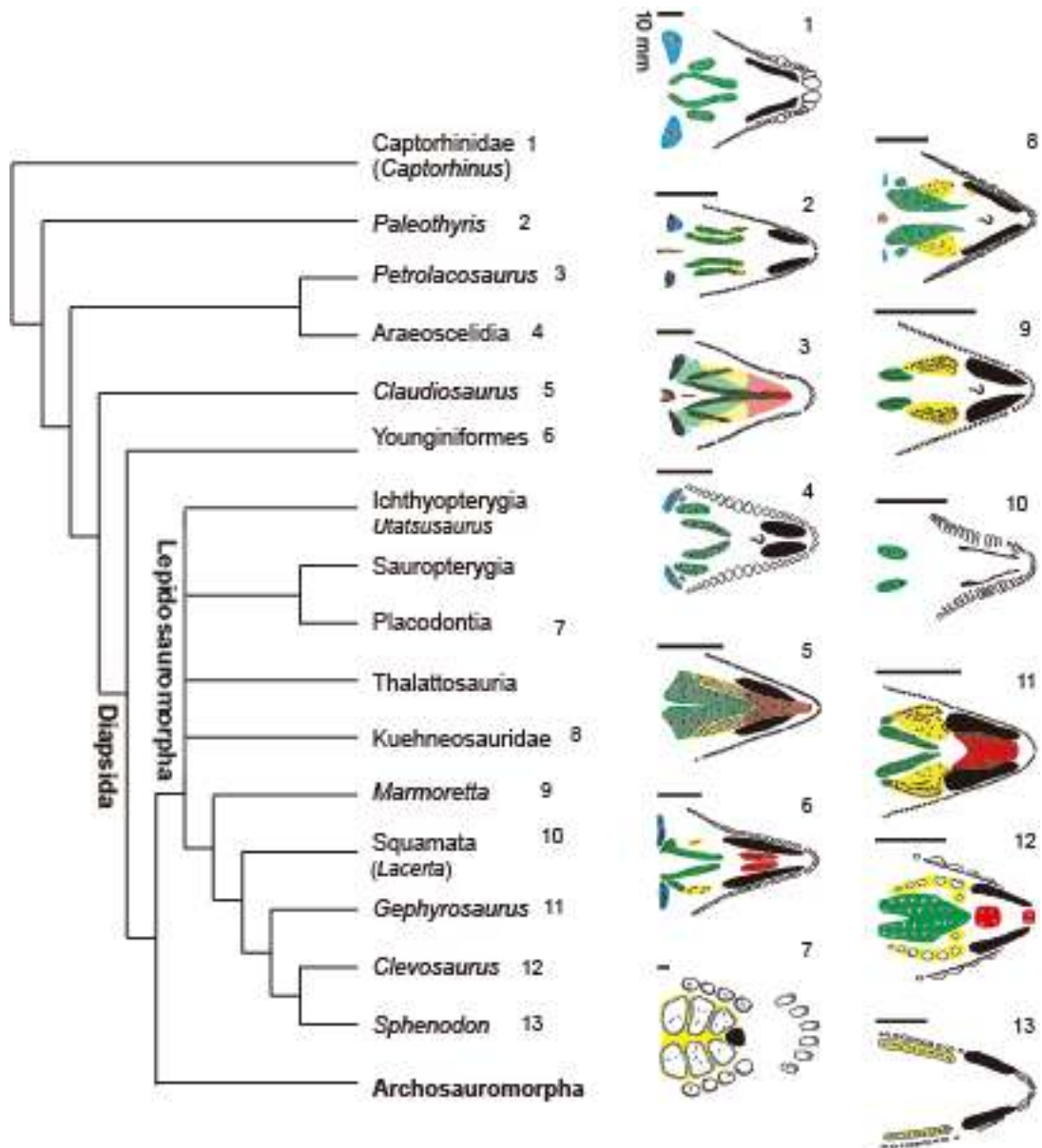
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1078 Figure 3



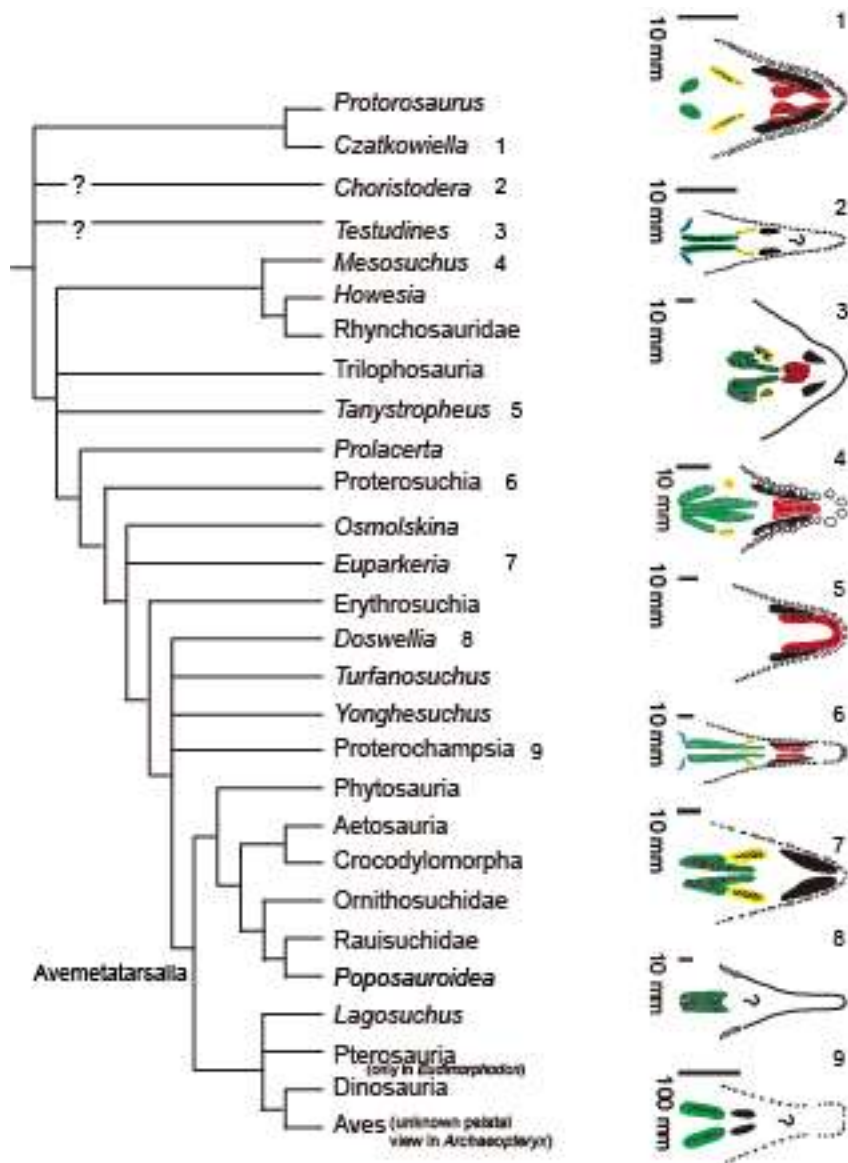
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1080 Figure 4



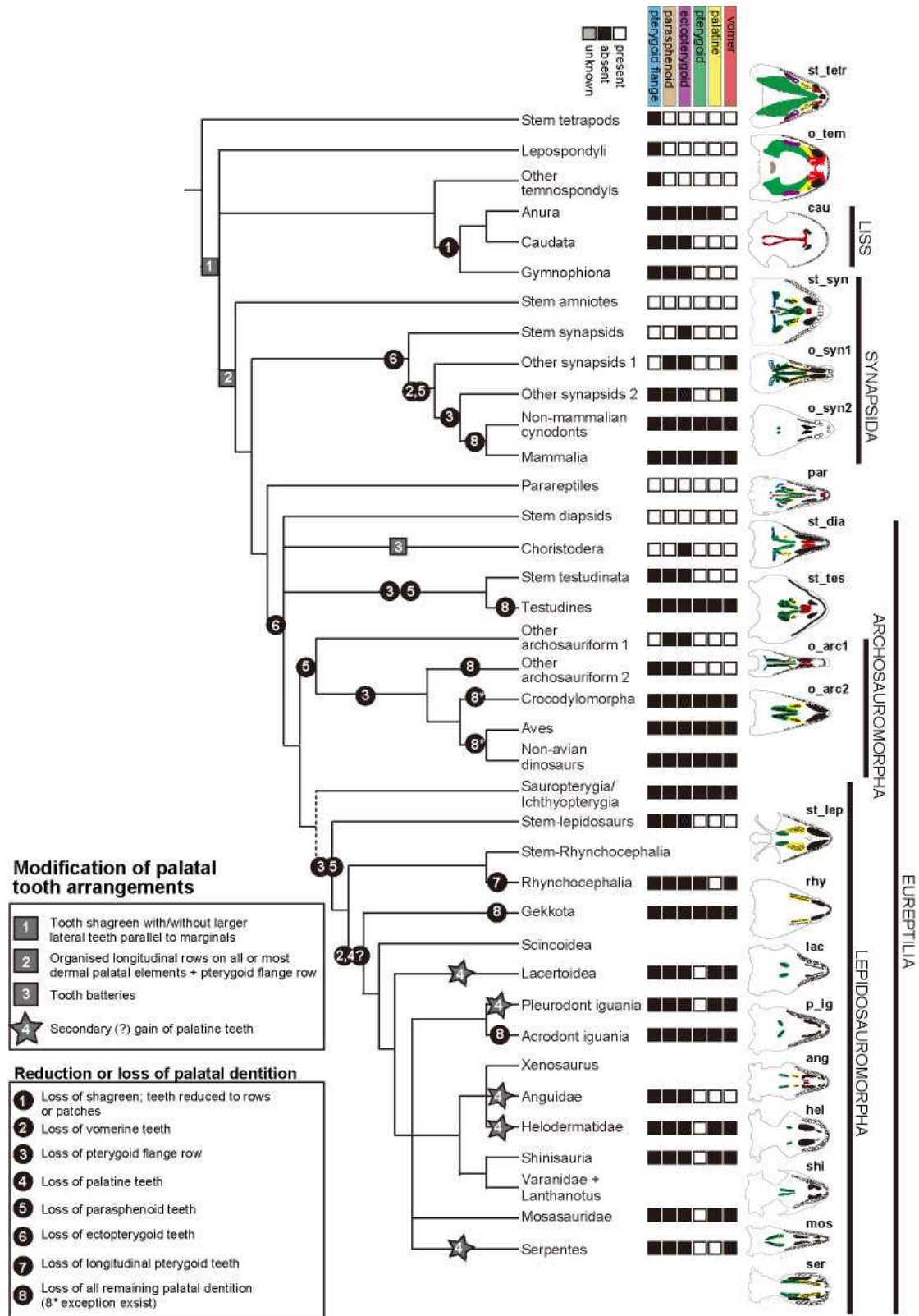
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1084 Figure 6



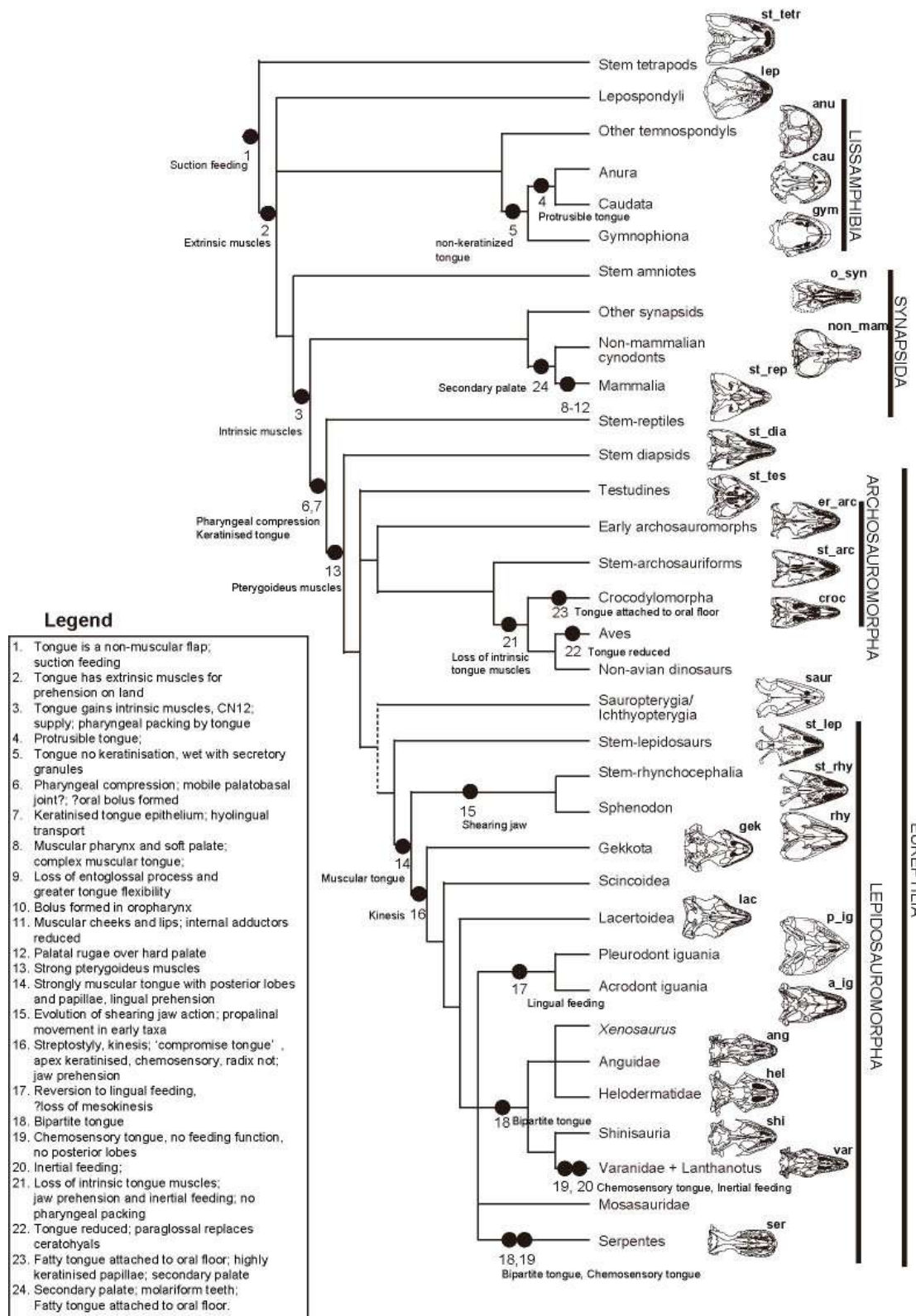
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1086 Figure 7



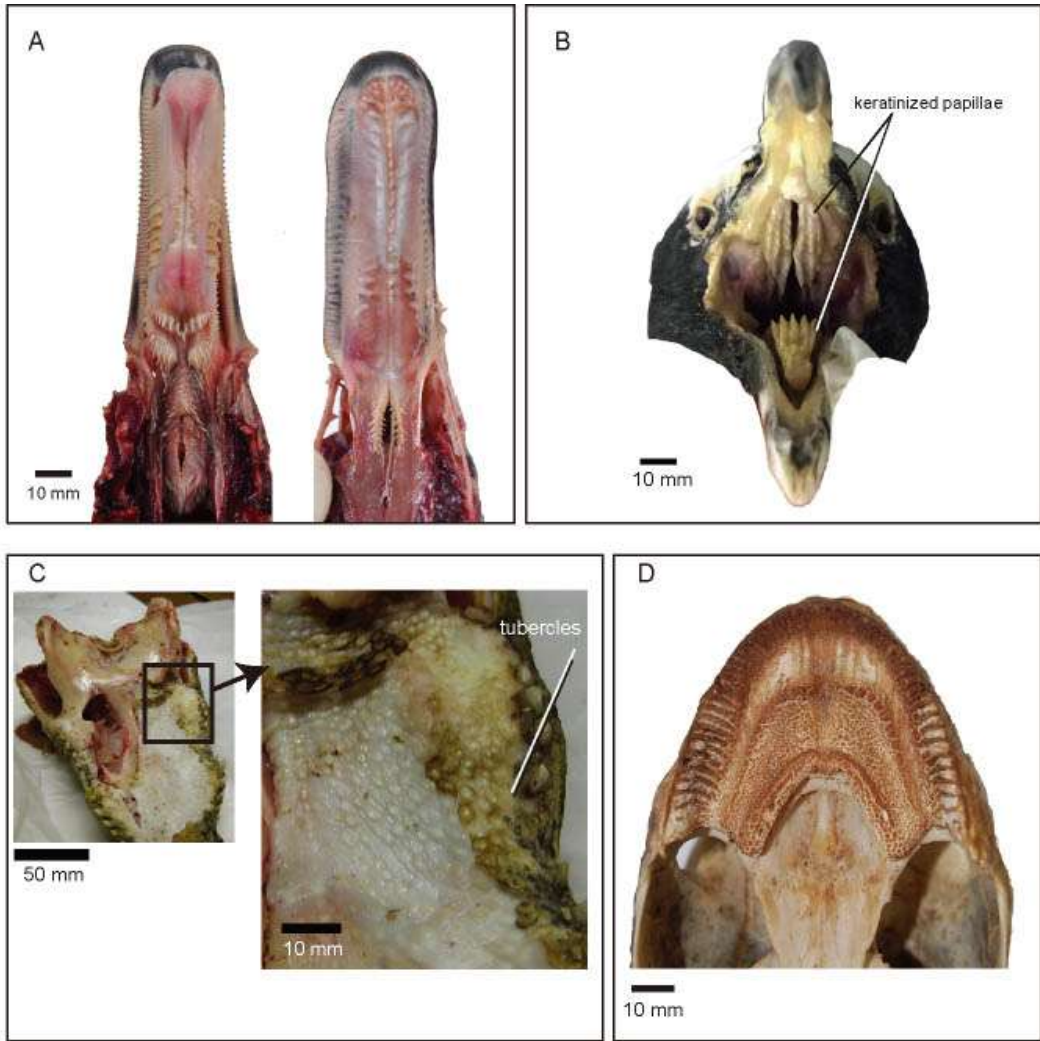
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1088 Figure 8



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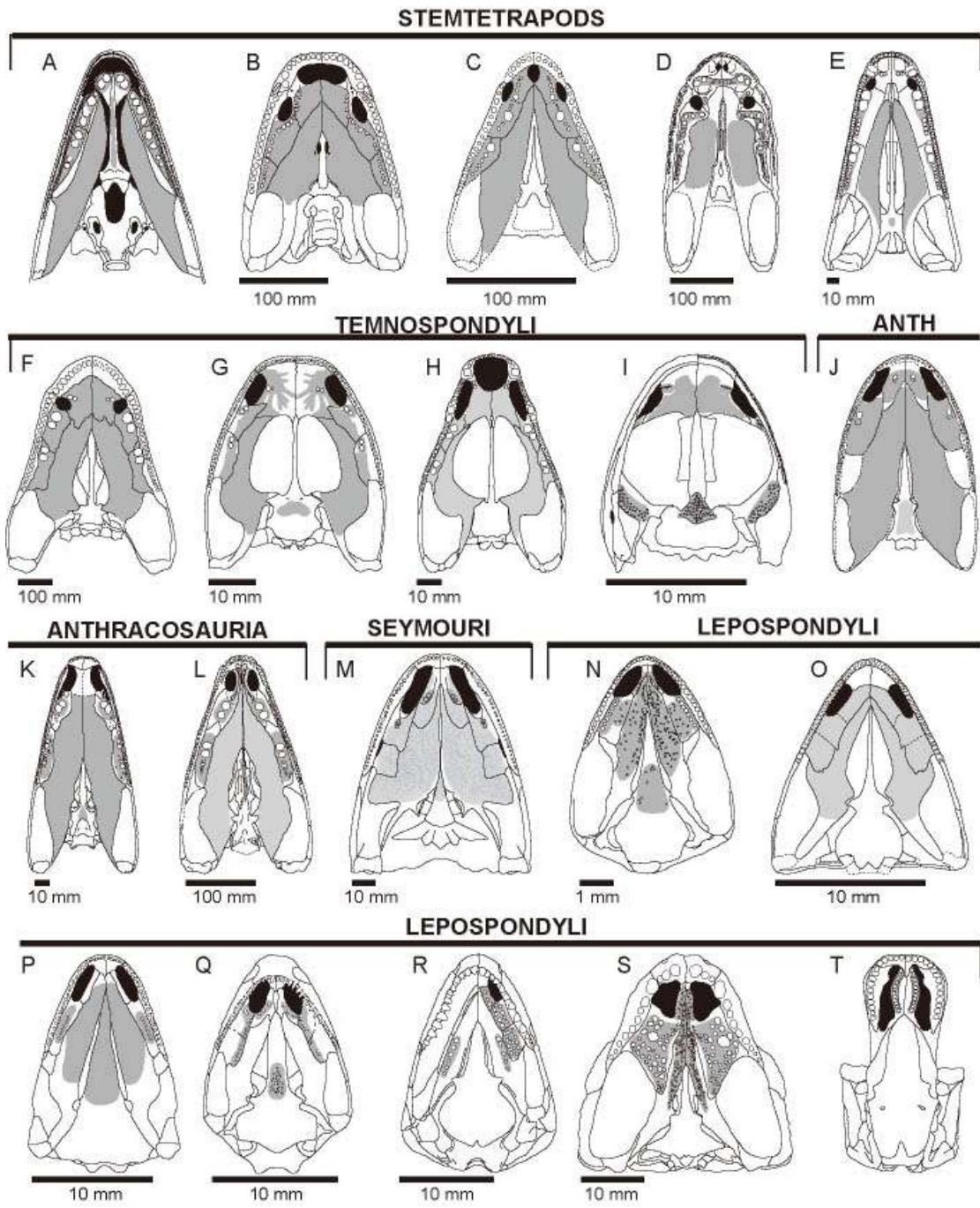
1090 Figure 9



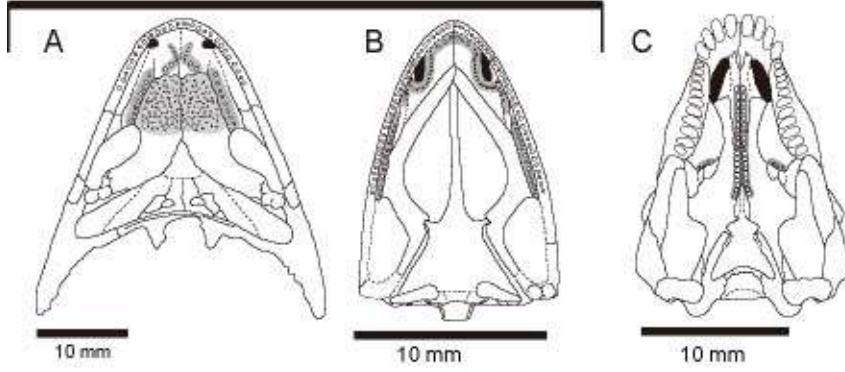
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1092 Figure 10

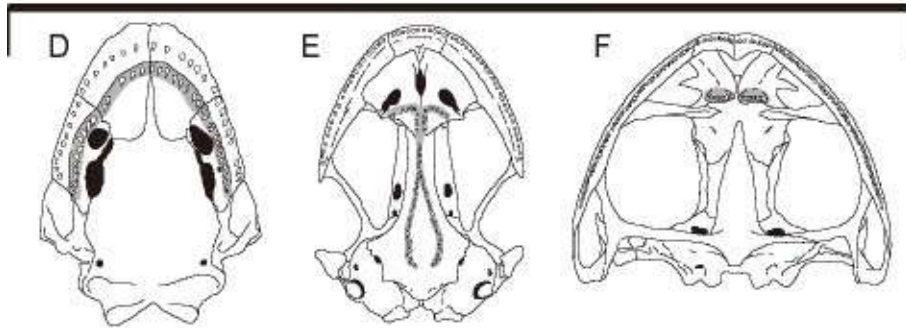
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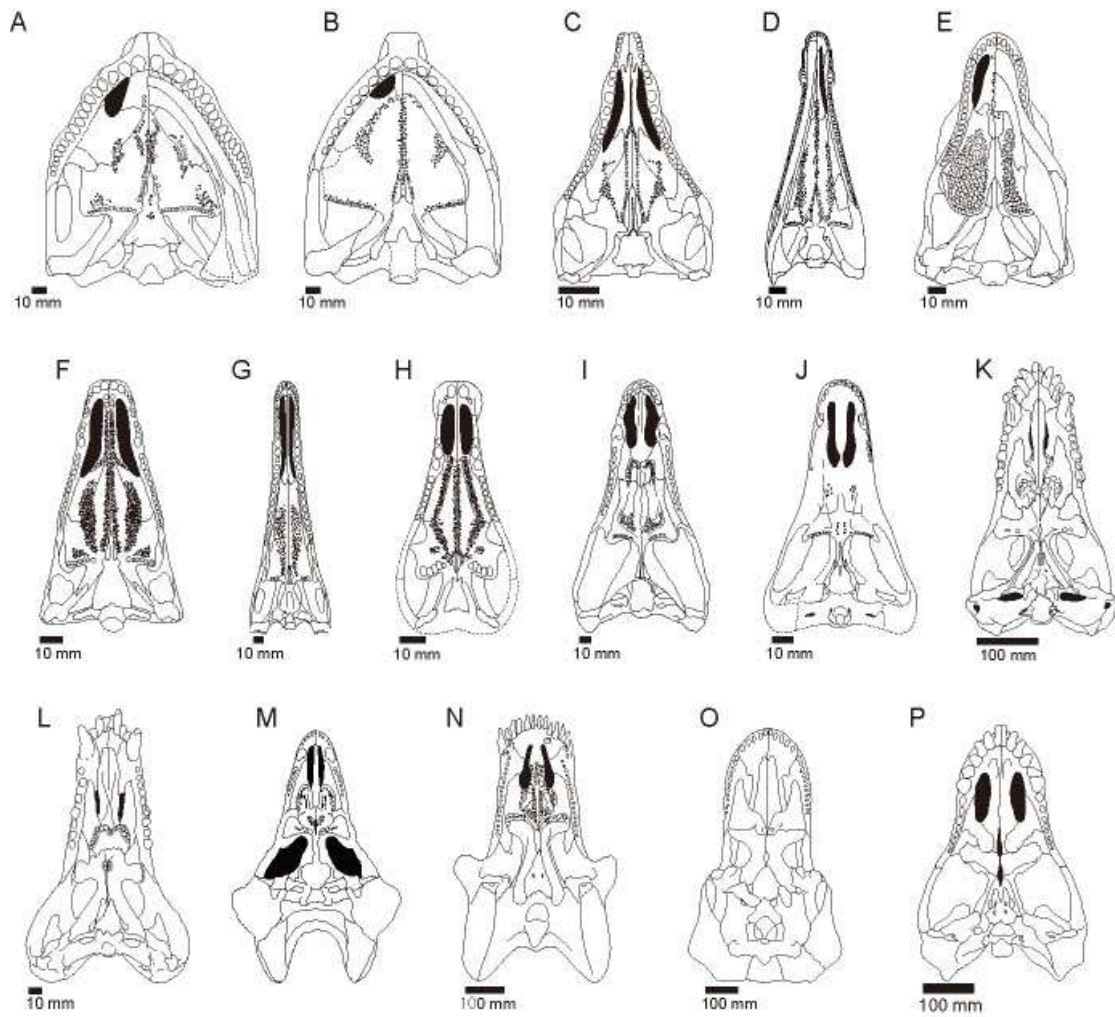
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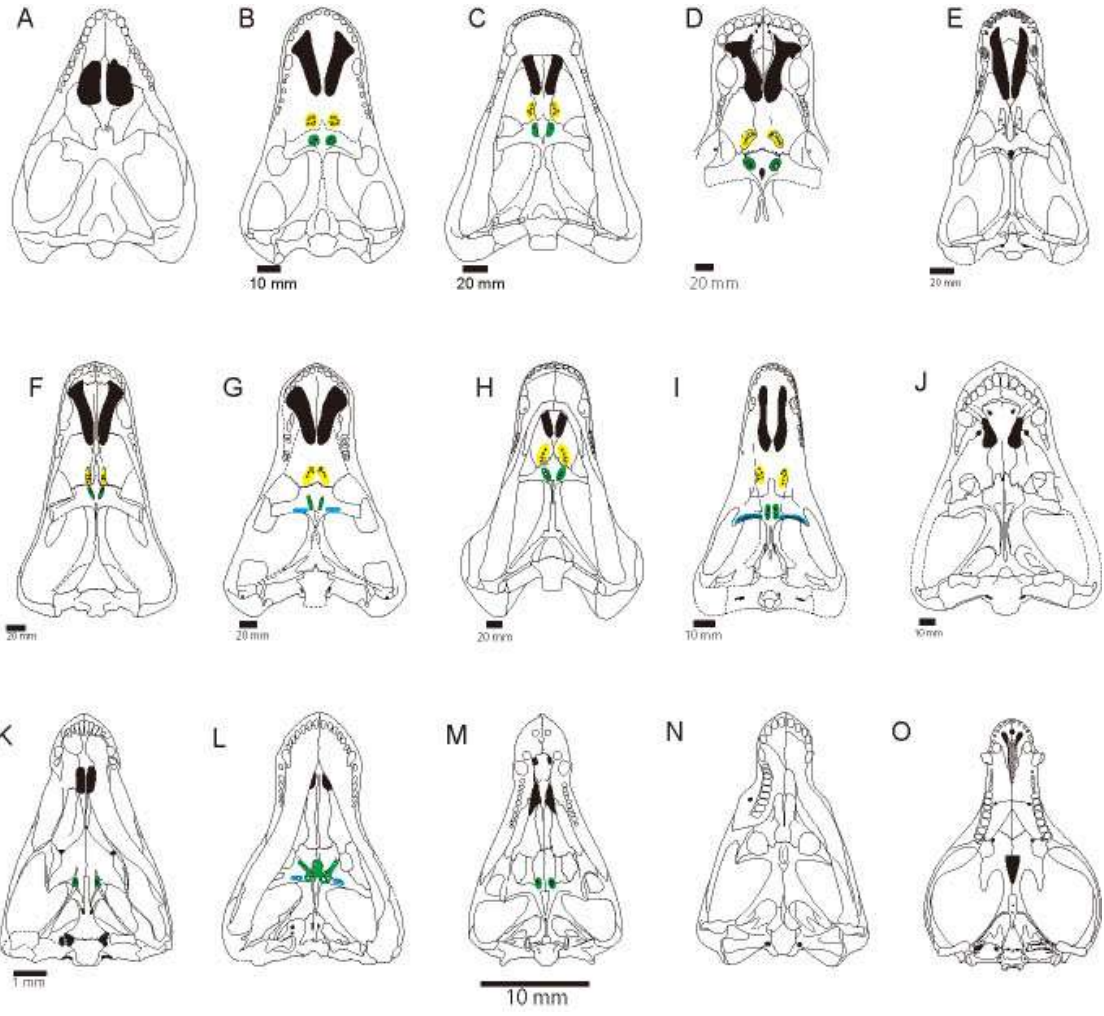
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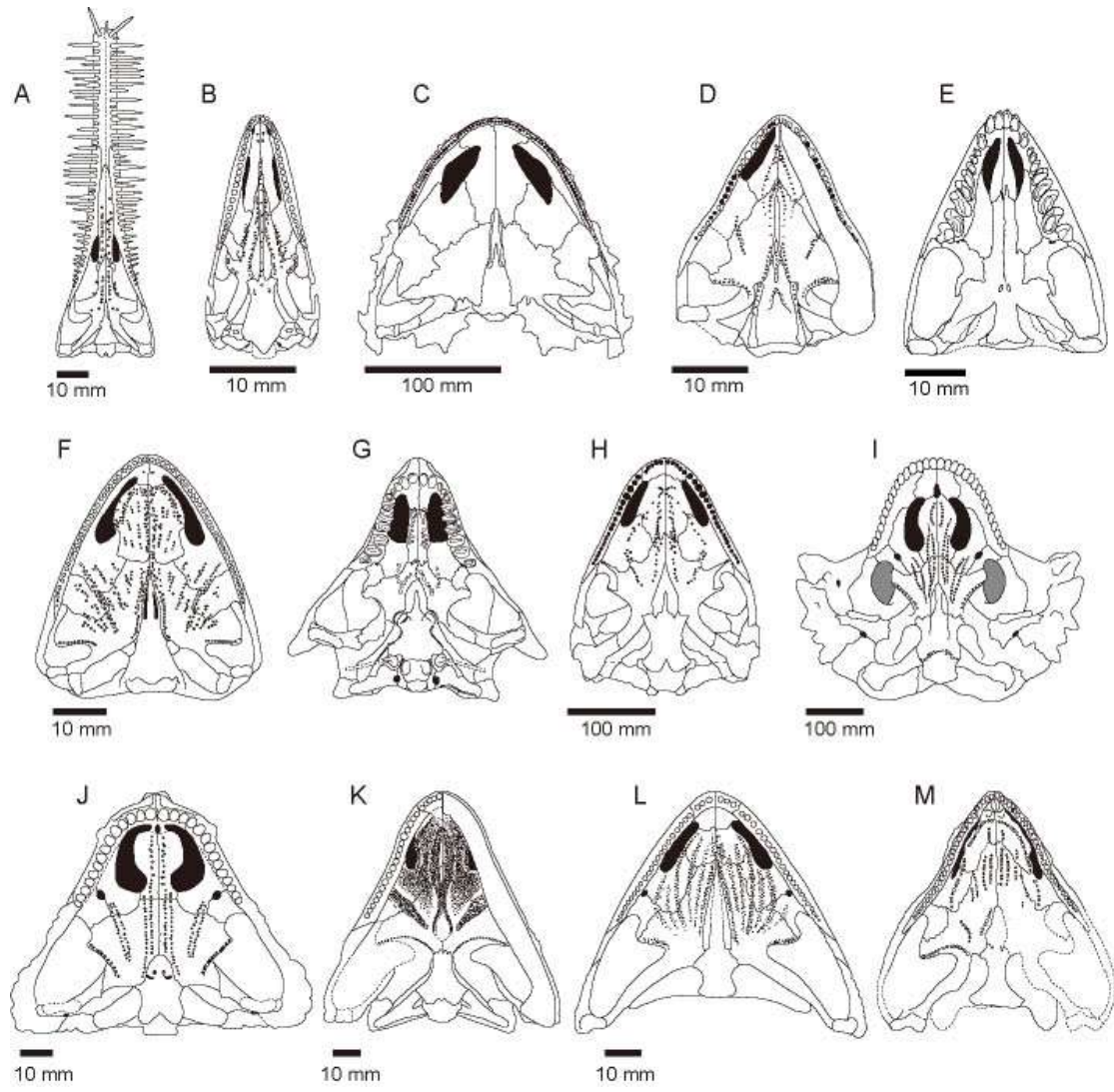
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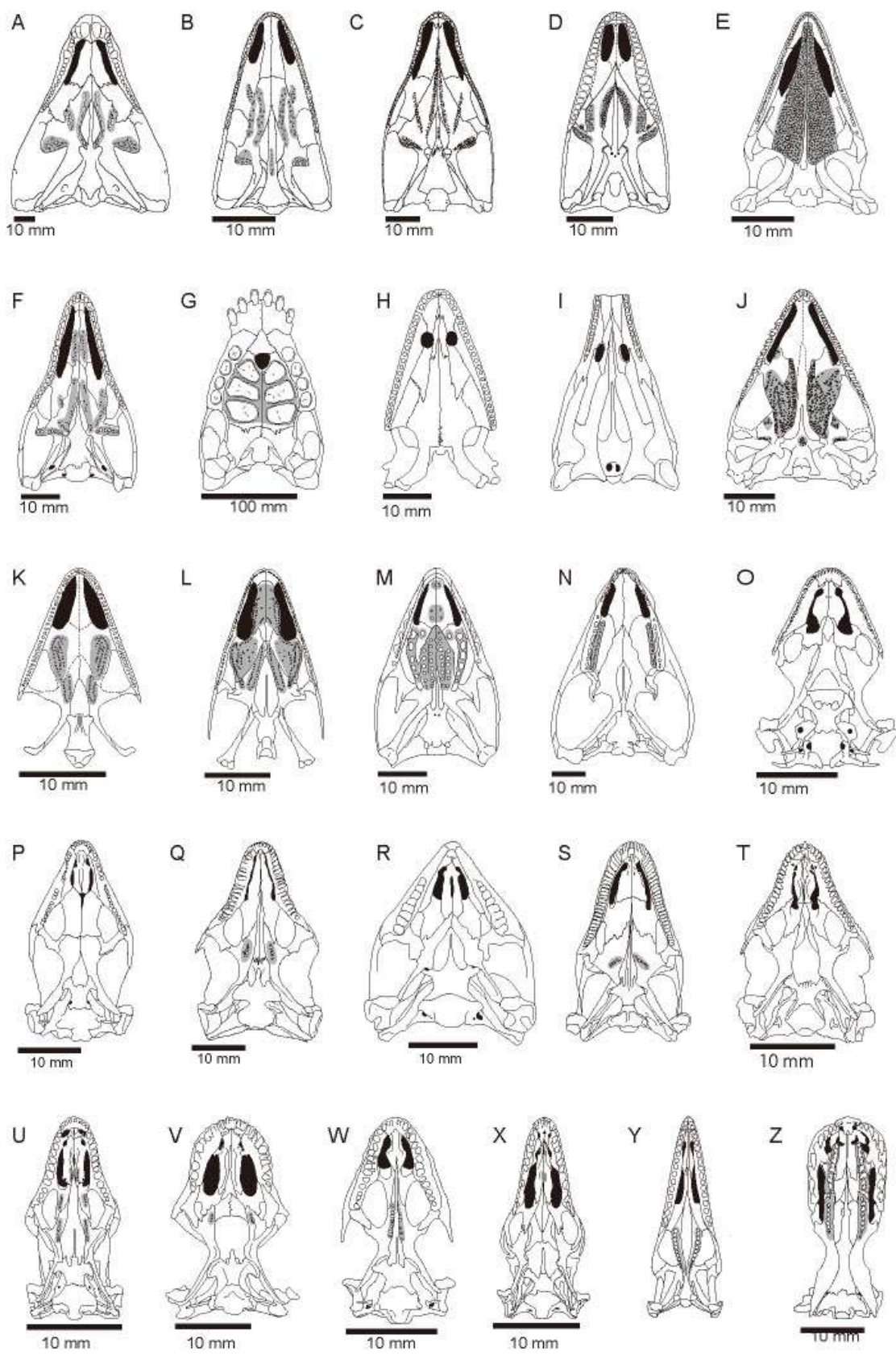
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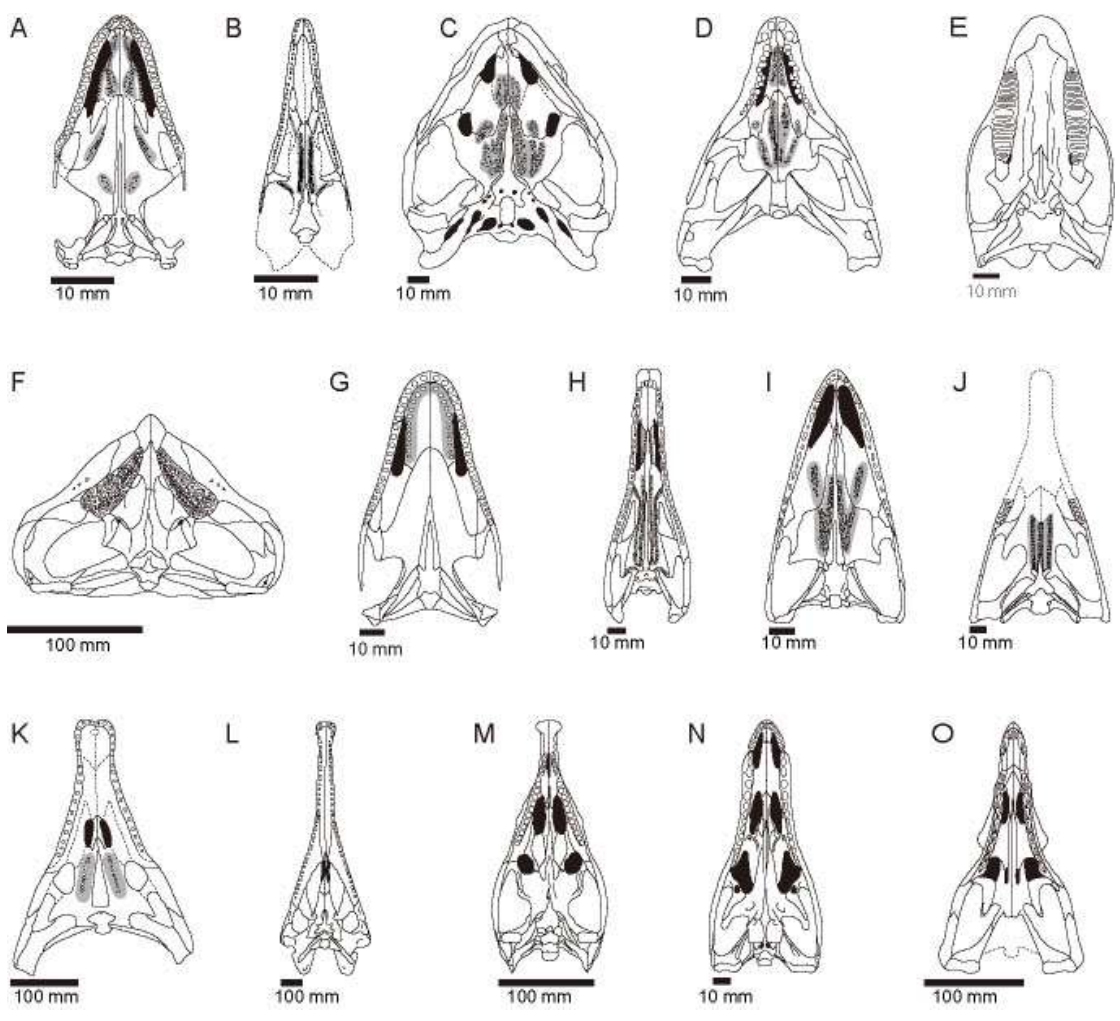
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