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Cranial Elements and Ontogeny in *Tropidolaemus wagleri*

1 Description of Cranial Elements and Ontogenetic Change within *Tropidolaemus wagleri*

2 (Serpentes: Crotalinae)

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21 **Abstract**

22 *Tropidolaemus wagleri* is a species of Asian pitviper with a geographic range including
23 Thailand, Vietnam, Malaysia, Singapore, Bruniei, parts of Indonesia, and the Philippines.
24 *Tropidolaemus* is a member of the Crotalinae subfamily, within Viperidae. The genus
25 *Tropidolaemus* includes five species, and was once included within the genus *Trimeresurus*.
26 While some osteologic characteristics have been noted a comprehensive description of cranial
27 elements has not been produced for *T. wagleri*. An in-depth description of the cranial skeleton of
28 *Tropidolaemus wagleri* lays the foundation for future projects to compare and contrast other taxa
29 within Crotalinae and Viperidae. The chosen reference specimen was compared to the presumed
30 younger specimens to note any variation in ontogeny. The study here provides a comprehensive
31 description of isolated cranial elements as well as a description of ontogenetic change within the
32 specimens observed. This study contributes to the knowledge of osteological characters in *T.*
33 *wagleri* and provides a foundation for a long term project to identify isolated elements in the
34 fossil record.

35
36 **Key words:** Crotalinae; Viperidae; Pitviper; *Tropidolaemus*; Skull morphology; Wagler's Palm
37 Viper, Wagler's Pitviper

38 **Abbreviations:** AR = Age Rank; APPSU = Appalachian State University; ASU = Appalachian
39 State University; ETVP = East Tennessee State University Vertebrate Paleontology Collections;
40 SVL = snout-vent length.

41

42 In order to best understand and evaluate the relationship between snake genera one must
43 first understand the morphological variation observed within a single species. The in-depth
44 description here of select cranial bones of *Tropidoleamus wagleri* (Wagler’s Palm Viper,
45 Wagler’s Pitviper) is intended to act as a foundation to be used to compare and contrast other
46 related species along with possibly identifying fossils recorded in Southeast Asia deposits. After
47 this ‘base’ was created, ontogenetic change within *Tropidoleamus wagleri* was noted using
48 morphological characteristics of the skull.

49 *Tropidolaemus* is a member of the Crotalinae subfamily within the family Viperidae
50 (Reptilia: Squamata). Members of the Crotalinae possess a heat sensitive pit between the eye and
51 the naris located on each side of the head (“pitvipers”). *Tropidolaemus wagleri* specimens often
52 show laterally compressed bodies, slender in males while thick and stout in females. The
53 laterally compressed body is a specialization for their arboreal lifestyle. *Tropidolaemus wagleri*
54 has a geographic range including Southern Thailand, West Malaysia, Sumatra, Nias, Mentawai
55 Archipelago, and Bangka Island (but not Belitung) [1]. They are typically found in wet, low
56 elevation forests on lower branches of trees, and are viviparous [2]. The head shows a distinct
57 triangular shape. Females display a black and yellow “speckled” coloration, their body is a
58 glossy black with 25-30 irregular bright yellow vertical crossbars [1]. Males display a bright or
59 deep green color with dorsolateral dots ranging from red at the anterior to white at the posterior
60 [3]. *Tropidolaemus* exhibits dramatic ontogenetic color change and dramatic sexual dimorphism,
61 further complicating the arrangement of species and possible subspecies [3].

62 *Tropidolaemus wagleri* possesses a complex taxonomic background. The genus is
63 attributed to Wagler in 1830 according to McDiarmid et al. [4], Gumprecht et al. [5], and Vogel
64 et al. [1]. There has been a long running discussion as to whom the name *T. wagleri* should be

65 attributed to; H. Boie in 1826 (not seen), F. Boie in 1827 (not seen), or Schlegel in 1826 or 1827.
66 Schlegel [6, 7] cited the name to H. Boie, whose manuscript contained descriptions, but was
67 unpublished and therefore not considered valid. Schlegel [6, 7] did not include a description for
68 the name, thus he cannot be correctly credited with the species name [1, 4, 5]. In most recent
69 literature the species has been attributed to Boie 1827 (not seen), where he listed it under the
70 genus *Cophias* [1, 4, 5]. While Boie did not provide a description, he did reference a previous
71 description and definition in Seba [8], allowing for a description via indication [1, 4]. In 1830
72 Wagler reassigned the species to the genus *Tropidolaemus*, and then Brattstrom [9] regarded
73 *Tropidolaemus* as a subgenus of *Trimeresurus*. After many synonyms and reassignments, Burger
74 [10] resurrected the genus based on morphological characteristics and it has since been
75 considered valid and supported by molecular studies [11, 12, 13.]. Hoser [14] suggested that a
76 separate subfamily, Tropidolaemusiinae and a tribe Tropidolaemusini be created. Because these
77 levels do not seem to be well founded, his taxonomy will not be followed in this paper.
78 *Tropidolaemus* was initially accepted as monotypic, with the only species being *T. wagleri* until
79 1998 when *Trimeresurus huttoni* was shown to be a member of the genus [David and Vogel in
80 Vogel et al. 1]. Vogel et al. [1] selected a neotype of *Tropidolaemus wagleri* and identified three
81 additional species within the genus, for a current total of five species: *T. wagleri*, *T. huttoni*, *T.*
82 *laticinctus*, *T. subannulatus*, and *T. philippensis*.
83 *Tropidolaemus spp.* are characterized by: “absence of a nasal pore, upper surfaces of the snout
84 and head covered with distinctly keeled small scales, strongly keeled gular scales, second
85 supralabial not bordering the anterior margin of the loreal pit and topped by a prefoveal, and a
86 green coloration in juveniles which may or may not change with growth” [1 p2].
87 Following Vogel et al. [1 p2] *Tropidolaemus wagleri* is characterized by:

- 88 • Internasal scales always touching
- 89 • Background body color with clear ontogenetic variation: black (never green) in adult
- 90 females, whereas males and juveniles retain a vividly green background color
- 91 • Pattern with clear ontogenetic variation: yellow crossbands around the body in adult
- 92 females, white spots in adult and juvenile males, and white crossbars in juvenile females
- 93 • Postocular stripe with ontogenetic variation: black stripe in adult females whereas males
- 94 and juveniles of both sexes exhibit a white and red stripe
- 95 • Belly pattern: banded in adult females while uniform in males and juveniles
- 96 • Number and keeling of dorsal scale rows at midbody: feebly keeled with 21–23 in males
- 97 and distinctly keeled with 23–27 in females
- 98 • Ventral plates: 143–152 in males and 134–147 in females
- 99 • Subcaudal plates: 50–55 in males and 45–54 in females

100 Descriptions of the cranial skeletal elements of select taxa within Viperidae have
101 previously been constructed by many authors. Dullenmeijer [15] described the head of the
102 common viper (*Vipera berus*, Viperinae), with functional morphology aspects. Brattstrom [9]
103 looked at pitviper osteology to better understand the evolution of the group. He described
104 multiple species with hand-drawn illustrations of the various bones, and described the
105 importance of certain osteologic characters of *Tropidolaemus wagleri*. Burger [10] looked at
106 multiple pitviper genera and their characteristics. Lombard [16] looked at the shape of the
107 ectopterygoid of Colubroidea using morphometrics. Guo et al. [17] compared skull morphology
108 of Crotalinae species. Guo and Zhao [18] aimed to identify diagnostic characters for some of the
109 genera within *Trimeresurus* (sensu lato). A number of characters were found to be important in
110 distinguishing species and genera such as the size of the ectopterygoid anterior lateral process,

111 the shape of the palatine, and the shape of the frontal. Cundall and Irish [19] described
112 characteristics of several different families of snakes. Guo et al. [20] examined the systematic
113 value of using skull morphology to distinguish between members in the *Trimeresurus* radiation.
114 Different characters exhibited various success within the different pitvipers studied, leading them
115 to conclude that “skull morphology can contribute to an overall understanding of pitviper
116 taxonomy, but that it would be unwise to rely on skull characteristics alone” [20 p378]. Guo et
117 al. [21] observed the evolution of 12 osteological characters in 31 species of Asian pitvipers in
118 order to form a phylogenetic perspective.

119 Due to *T. wagleri* being one of the first Asian pitvipers described, and its substantial
120 sexual dimorphism and geographic and ontogenetic variation, many specimens were initially
121 identified as other species [1, 11]. Within tropical Asia pitvipers of the genus *Tropidolaemus* are
122 the most widespread and commonly encountered venomous snakes in many islands of the Malay
123 Archipelago [1]. The wide geographic distribution and prevalence of human interaction
124 demonstrate the importance of understanding *T. wagleri*. The descriptions in this study have the
125 potential to contribute to many future projects spanning a variation of emphases.

126

127 **Methods and results**

128 Multiple specimens of the same age were located to begin the description of
129 *Tropidoleamus wagleri*. Specimens were compared to ensure the characteristics are consistent
130 within each specimen of *T. wagleri*. Twelve cranial elements were studied: quadrate,
131 ectopterygoid, pterygoid, palatine, maxilla, parietal, prefrontal, premaxilla, dentary, angular,
132 splenial, and compound bone. Elements chosen were expected to show the most ontogenetic
133 variation, and are often distinct between snake taxa. Among previous works on pitviper cranial

134 osteology, Guo and Zhao [18] presented diagnostic characters for nine Asian pitvipers (not
135 including *Tropidolaemus*); their characters include the shape of the palatine, shape of the frontal,
136 presence or absence of a projection on the border of the pit cavity, and the size of the
137 ectopterygoid anterior lateral process. These and other characters were recorded for *T. wagleri*
138 specimens in the study presented here. All distinct characters are described in detail allowing for
139 future in-depth comparisons to other species. After the descriptions were produced, the skeletal
140 elements were then compared to those in other *T. wagleri* specimens of different ages. The
141 distinct characters used to describe *T. wagleri* were used as a reference for any changes through
142 ontogeny.

143 Twelve specimens were used for this study, 11 from the East Tennessee State University
144 Vertebrate Paleontology Collections (ETVP) and one from Appalachian State University (ASU).
145 In addition, an articulated specimen from Appalachian State University (APPSU 25497) was
146 used as a guide to an articulated skull but not used for descriptions (Figs. 1-3). Of the 12
147 specimens, only one (ASU 19452) had a recorded snout-vent length (SVL). Burger [10] reported
148 a total length of 700mm while Kuch et al. [3] gave a range of 350–1000mm for total length. One
149 study reported a maximum SVL of 770mm for a female and 435mm for a male [1]. This study
150 functions under the assumption that greater size is equivalent to greater age. In order to
151 determine the relative age of the remaining 11 specimens the SVL had to be calculated. Length
152 of the quadrate was used as a proxy to estimate a snout-vent length. Using quadrate length to
153 estimate SVL, the 12 specimens were then arranged by size and categorized into an age rank
154 (AR) series based on estimated SVL; where 1 is the youngest (neonate) and 12 is the oldest.
155 Quadrates were measured along the ventral side, creating a greatest anteroposterior length.

156

157 **Fig. 1.— Skull of *Tropidolaemus wagleri* (APPSU 25497) in dorsal view.** Anterior is to the
158 right. Scale bar = 10 mm. Abbreviations: ecp = ectopterygoid; p = parietal; pfr = prefrontal; pmx
159 = premaxilla; pt = pterygoid; q = quadrate.

160 **Fig. 2.— Skull of *Tropidolaemus wagleri* (APPSU 25797) in right lateral view.** Anterior is to
161 the right. Scale bar = 10 mm. Abbreviations: ecp = ectopterygoid; cp = compound bone; d =
162 dentary; mx = maxilla; pfr = prefrontal; pt = pterygoid.

163 **Fig. 3.— Lower left jaw of *Tropidolaemus wagleri* (APPSU 25797) in medial view.** Anterior
164 is to the right. Scale bar = 10 mm. Abbreviations: an = angular; sp = splenial.

165 The quadrate of specimen ASU 19452 was measured, and the quadrate-to-SVL ratio was
166 then used to calculate the SVL for the rest of the specimens (Table 1). A total of 12 elements
167 were studied and described, only using the right of paired elements, following the terminology
168 used in Cundall and Irish [19] and Evans [24]. Abbreviations from Cundall and Irish [19] were
169 followed. When not available in Cundall and Irish (19) abbreviations from Evans [24] were
170 followed. When neither were available abbreviations were created. The chosen reference
171 specimen (ETVP 3295) was then compared to other age ranks in order to record any ontogenetic
172 changes. Reference specimen was chosen due to it being the largest specimen and therefore, the
173 presumed most mature.

174 ASU 19452 $\rightarrow \frac{541}{14} = 38.6$ $(4.3 \times 38.6) = x$

175 ETVP 3306 $\rightarrow \frac{x}{4.3} = 38.6$ $x = 165.98$

176 **Table 1. Calculated SVL (mm) and Age Ranks (AR) using quadrate length (mm).** Reference
177 specimen is indicated by asterisk*

Age Rank	Specimen ID	Quadrate length (mm)	Calculated SVL
1	ETVP 3306	4.3	166
2	ETVP 3290	13.0	502
2	ETVP 3293	13.0	502
3	ETVP 3298	13.5	521
4	ASU 19452	14.0	541
5	ETVP 3296	14.3	552
6	ETVP 3292	15.0	579
7	ETVP 3300	15.3	591
8	ETVP 3301	18.0	695
9	ETVP 3297	18.5	714
10	ETVP 3294	19.0	734
11	ETVP 3299	19.5	753
12	ETVP 3295*	20.0	772

178

179 **Descriptions**

180 **Quadrate**— The anterior end of the quadrate overlaps the posterior of the supratemporal.
181 Posterior end forms a mandibular condyle that interlocks with the articular of the compound
182 bone. The posteromedial end adjoins the posterior of the pterygoid.

183 **Dorsal-** Anterior end is slightly curved with a flat edge. The conch is also located at the
184 anterior end, is concave, and spans half the length of the bone. The tips of the mandibular
185 condyle gently flare medially. Distally it has a large curve forming a process that curves into the
186 mandibular condyle (Fig 4).

187 **Ventral-** Anterior end is the widest part of the bone. It is moderately curved with a flat
188 edge. No conch is present. Less than half way down the shaft, the articular process of the
189 quadrate is present. This articular process is distal in ventral view on the right quadrate, and

190 has a flat surface. It articulates with the columellar cartilage. Posterior end shows a larger part of
191 the mandibular condyle. Medial side curves outward significantly. Distal end appears to extend
192 slightly past the articulation surface. The articulation surface appears grainy compared to the
193 smooth bone of the shaft. There appears to be a small fossa close to the distal end

194 **Ontogeny-** Anterior, spatulate end has a rough, textured edge in AR1; in AR2 the edge
195 is smoother, but still more rough than in AR12. The anterior end is more flared and widens
196 quickly in AR1, while the widening occurs more gradually in AR2, much like in AR12. Articular
197 process on the ventral side protrudes more and is slightly more elongate in AR2. Lateral process
198 of the mandibular condyle is more rounded and protrudes greater in AR1. The notch is also not
199 completely formed in AR1, medial side of the lateral process curves back anteriorly to meet the
200 shaft, there is no process medially.

201 **Summary of Ontogeny-**

- 202 • Anterior margin smoothes in texture with age.
- 203 • Anterior half “fills out” proportionally with age; widening appearing as a dramatic
204 flare in AR1 and ending as a gradual widening in AR12.
- 205 • Lateral process of mandibular condyle widens and recedes closer to the bone with
206 age; appearing more knob-like rather than a drastic projection.
- 207 • Articular surface of the mandibular notch exhibits less dramatic projections with age.

208 **Fig. 4.— Right quadrate (ETVP 3295) in dorsal (A) and ventral (B) view.** Anterior is to the
209 top. Scale bar = 5 mm. Abbreviations: ar = articulatory process of quadrate; Cch = conch; ma.co
210 = mandibular condyle.

211

212 **Ectopterygoid**— Anterior lateral and ventral processes of the ectopterygoid cup the
213 lateral facet located on the posterior side of the transverse crest, dorsal to the dentigerous region
214 of the maxilla. The anterior medial process of the ectopterygoid fits into the posteromedial facet
215 of the transverse crest of the maxilla. Posterior end of the ectopterygoid overlaps the pterygoid in
216 the middle of its lateral curvature, with the posterior ventral process of the ectopterygoid
217 contacting the lateral process of the pterygoid. The thin, angled portion of the posterior of the
218 ectopterygoid fits into the groove on the dorsal side of the pterygoid.

219 **Dorsal-** Anterior end is bifurcated, producing two processes, one medial and one lateral.
220 The lateral process is anteroposteriorly broad and is not as pronounced as the medial process.
221 Lateral process is rectangular in shape, with a point at the posterior end that curves medially
222 back toward the shaft of the bone. Medial process is narrow and protrudes anteromedially from
223 the bone. Between the two anterior processes is a notch where the maxilla articulates. The shaft
224 is predominantly straight and flat; most modification is present at the ends. Posterior end angles
225 medially to allow for articulation with the pterygoid. Directly anterior to the tip, on the medial
226 side, there is the small pterygoid process that permits articulation and kinesis with the
227 ectopterygoid (Fig 5).

228 **Ventral-** Lateral process curves into itself on the ventral side. Lateral to the notch is a
229 rounded process, this process articulates with the short ridge on the dorsal side of the pterygoid.
230 The medial process does not show s difference in ventral view. Approximately 13 mm posterior
231 from the most posterior point of the lateral process a fossa is present. The fossa exhibits a crest
232 on the inferior side that curves dorsally into a short ridge that terminates ~3 mm before the
233 posterior end. Posterior end curves out laterally to terminate at a rounded, laterally angled
234 process. Medial side of the terminating process curves in medially ~5 mm to a point. The point is

235 the posterior edge of a flat, rectangular shaped process. Rectangular process is ~2 mm long and
236 the anterior point curves laterally to meet the shaft of the ectopterygoid. A short ridge is visible
237 on the medial side, beginning at the center of the rectangular process and terminating ~4 mm
238 anterior of the process.

239 **Ontogeny-** Medial process is distinctly thin in AR1, comes to point. In AR2 the shape
240 is formed, thicker, but still thinner than in AR12. Small medial process on AR2, posterior to
241 main process, not present in others. In AR1 posterior end comes to sharp point. In AR2 the shape
242 of posterior is formed, medial side of posterior does not exhibit the flat protrusion like in AR12.
243 The flat protrusion is still not form in AR10 and AR11. Hooked shape of lateral process slowly
244 forms from small to large. In AR1 the anterior of the lateral process consists of two processes, in
245 AR12 and AR2 the lateral process appears as one rounded process. Ventral process present in
246 AR12 and AR2, AR1 has a short ridge from medial process that terminates where ventral process
247 will form. Posterior end comes to a point in AR1, concave with higher sides. The ventral process
248 of the posterior end not yet formed in AR1. Medial margin remains straight to medial process in
249 AR1. In AR2 the medial side curves to pointed process then curves to medial process. In AR12
250 the medial side gently curves to the medial process with no extra processes.

251 **Summary of Ontogeny-**

- 252 • Medial process forms distinct shape with age; beginning as a thin, pointed process
253 and forming into thick, square-shaped process.
- 254 • Posterior tip thickens with age and flat protrusion forms with age.
- 255 • Lateral process begins with an additional process on anterodorsal side and morphs
256 into one rounded process with age.
- 257 • Anterior ventral process forms between AR1 and AR2.
- 258 • Posterior end forms distinct shape with age.

259 **Fig. 5.— Right ectopterygoid (ETVP 3295) in dorsal (A) and ventral (B) view.** Anterior is to
260 the top. Scale bar = 10 mm. Abbreviations: l.pr = lateral process; m.pr = medial process; mpecp
261 = maxillary process of ectopterygoid; ppecp = pterygoid process of ectopterygoid; vpecp =
262 ventral process of ectopterygoid.

263

264 **Pterygoid**— The curved anterior tip and process of the pterygoid interlocks between the
265 dorsal and ventral processes of the palatine, the posterolateral end sits against the medial side of
266 the quadrate and borders the articular of the compound bone. Groove on the dorsal side of the
267 pterygoid cups the posterior ventral process of the ectopterygoid.

268 **Dorsal**- The pterygoid has a dentigerous region that makes up a little more than half the
269 length of the bone. Dentigerous region is long and narrow, making up the anterior half of the
270 bone. Anterior tip exhibits undulations with a prominent anterior process marginally oriented
271 laterally. About half way down the bone a process begins to form by the flange widening the
272 dentigerous region medially. The process is laterally oriented and comes to a point. Located
273 posteromedially to the lateral process, on the body of the bone is a short ridge with an associated
274 groove on its lateral side. The groove receives the posterior most of the ectopterygoid and the
275 ridge fits into a complimentary groove. Posterior section of the bone consists of a broad flange
276 that curves out medially then terminates in a rounded end angled laterally. Medial edge of the
277 anterior end has a shallow groove that runs the length of the narrow dentigerous region. Groove
278 widens at the posterior end and terminates before the widening of the dentigerous region.
279 Posterior tip is rounded, with a wide groove that runs along the lateral side ~10 mm anteriorly.
280 Inside the posterior groove, the terminating end appears to be folding in on itself. The area also
281 exhibits two fossa, and has an overall folded texture (Fig 6).

282 **Ventral-** Anterior end curves medially to terminate at a narrow, rounded process. The
283 pterygoid teeth are visible in ventral view, demonstrating their recurved teeth. Approximately 13
284 mm posterior from the anterior end the bone begins to widen laterally. The narrow dentigerous
285 region remains distinct and angles medially terminating on the flange, ~9 mm before the
286 posterior end. Widening comes to a point at ~3 mm; this pointed process is oriented laterally.
287 Posterior to the pointed process the flange begins to curve out laterally, terminating at the
288 medially angled posterior end. The end is rounded, and slightly oblong shaped. Medial edge of
289 the posterior end curves out anteromedially for ~9 mm, and then curves in anterolaterally to meet
290 the narrow dentigerous region. A wide, long groove is present, beginning at the point of
291 widening and terminating at the point of inflection at the posterior end. On the lateral side of the
292 flange a dorsally curved ridge runs ~11 mm down the bone.

293 **Ontogeny-** In dorsal view a short ridge is visible down the center of the flange,
294 beginning where the flange starts in AR1; this ridge might form the rounded dorsal process as
295 seen on AR12 and AR2, though less developed. The edges of AR1 are rough rather than smooth
296 as in AR2 and AR12. In ventral view, AR1 does not have a prominent projection where the
297 dentigerous region meets the medially oriented flange. Lateral side of flange is flat in AR12,
298 mostly flat in AR2 and has a groove in AR1. Teeth not present in AR1, but tooth attachment
299 areas are visible. In ventral view of AR2 the lateral process is present but not as prominent as in
300 AR12. Anterior dorsally oriented process extends further anteriorly with age.

301 **Summary of Ontogeny-**

- 302 • Short ridge on dorsal side of flange in AR1 may form the rounded dorsal process
303 seen in AR2 and AR12.
- 304 • Medial projection where dentigerous region meets flange becomes more
305 prominent with age.

- 306 • Lateral side of flange flattens with age.
- 307 • Anterior dorsally oriented process extends anteriorly with age.

308 **Fig. 6.— Right pterygoid (ETVP 3295) in dorsal (A) and ventral (B) view.** Anterior is to the
309 top. Scale bar = 10 mm. Abbreviations: l.pr = lateral process; drpt = dorsal ridge of pterygoid;
310 lgpt = lateral groove of pterygoid.

311 **Palatine**— Right palatine has three recurved teeth while the left has four. The posterior dorsal
312 and ventral processes interlock with the curved anterior tip and anterior process of the pterygoid.

313 **Medial-** Anterior surface curves back posteriorly. A 1 mm section, directly dorsal to the
314 first tooth, is less angled than the rest of the anterior end, appearing more flat. Medial side is
315 slightly concave, with the posterior end near the articulation being more concave than the rest.
316 Posterior end exhibits a forked dorsal and ventral process. These processes articulate with the
317 anterior end of the pterygoid. The overall shape of the palatine is crescent-shaped [18]. Multiple
318 fossa are present on the medial side (Fig 7).

319 **Lateral-** The lateral side is slightly convex with the dorsal side flaring out laterally. The
320 palatine is wider ventrally, thinning as it terminates dorsally. Attachment area of each tooth
321 extends past the base of the ventral border, forming dorsally oriented grooves between each
322 tooth.

323 **Ontogeny-** AR2 has two teeth present with three, possibly four sockets. AR1 has no
324 teeth and tooth attachment areas that may not yet be sockets, they are very narrow and very
325 shallow. Dorsal side of AR1 is straight anteriorly and posteriorly curves ventrally. AR2 exhibits
326 a thin anterior tip, curving up dorsally, forming a rounded dorsal edge and curving ventrally to
327 terminate. The transition to a flat, rounded, dorsal edge is more extreme in AR2. The small
328 posterior notch seen on AR12 appears to be forming in AR2; dorsal process is present, ventral

329 process is oriented medially, not yet ventral. Posterior tip of AR1 shows a narrow groove
330 separating two projections. One (dorsal) is rounded; the other (ventral) is thin, long, with a
331 rounded tip. In medial view the two posterior processes of AR1 are more visible. One is thin and
332 long while the other is short and thick. Posterior ventral process is present in AR2, it is thin and
333 long, extending posteriorly more than in AR12.

334 **Summary of Ontogeny-**

- 335 • Dorsal border fills out it's shape with age.
- 336 • Posterior ventral process shortens and thickens with age
- 337 • Posterior notch forms with age

338 **Fig. 7.— Right palatine (ETVP 3295) in medial (A) and lateral (B) view.** Anterior is to the
339 top. Scale bar = 1mm. Abbreviations: dppal = dorsal process of palatine; vppal = ventral process
340 of palatine.

341 **Maxilla**— The maxilla articulates posterodorsally to the prefrontal; the cupped articulation
342 surface on the ascending process articulates with the maxillary facet on the anterior of the
343 prefrontal. Posterior side of the transverse crest of the maxilla articulates with the anterior
344 process of the ectopterygoid. Medial facet of the transverse crest receives the medial
345 process of the ectopterygoid while the lateral facet of the transverse crest receives the lateral and
346 ventral processes of the ectopterygoid. The maxilla does not articulate to the palatine, but is
347 connected by cartilage.

348 **Anterior-** There is a dorsally oriented ascending process that meets the ventral surface
349 of the prefrontal. Ventrally the ascending process curves laterally, forming a rounded process,
350 then medially to meet the dentigerous base. The base is wide, mostly laterally. The ventral edge
351 is textured and curves inward dorsally, bearing the fangs. The rounded process present on the

352 anterior edge of the lateral opening was found to be taxonomically important in Brattstrom [9].
353 Guo and Zhao [18] defines two types of maxilla, type A which exhibits no projection, and type
354 B which exhibits a projection on the anterior edge of the pit cavity. The maxilla observed for
355 *Tropidolaemus wagleri* falls into type B (Fig 8).

356 **Posterior-** Dorsolateral to the fang is a transverse crest, when articulated it is located
357 anterior to the edge of the ectopterygoid joint. Maxilla exhibits a large lateral opening, concave
358 and extending anteromedially and dorsally from the transverse crest. Lateral opening holds the
359 loreal pit. Dorsally oriented ascending process exhibits a cupped articular surface for attachment
360 to the prefrontal. Posterior edge of the lateral opening is curved, forming two rounded processes.
361 Lateral to the processes a long fossa is present. The fossa is longer than wide and contains an
362 additional fossa.

363 **Ontogeny-** In anterior view the tip of the ascending process is thickest in AR12, and
364 the body of the process is thickest in AR2 (Figs 9 and 10). Medial curve of the ascending process
365 curves inward medially the most in AR12. Processes of the ascending process are thicker and
366 exhibit greater curvature in AR12. In AR1 the ascending process is very thin with a gentle lateral
367 curve. Lateral flange of the dentigerous region is present in AR1 but no major curvature has
368 developed. A thickened area dorsal to the dentigerous region exhibits a lateral outward curvature,
369 appearing to be the lateral process. In AR1 the posterior is visible in anterior view, curving
370 outward laterally. Prefrontal facet of AR1 is more medially oriented and dorsoventrally longer
371 than the others. In posterior view the prefrontal facet of AR12 exhibits a square shape. In AR2
372 the prefrontal facet is rounded while in AR1 it is laterally rounded and medially straight. Lateral
373 process of ascending process is thinner and more prominent in AR12. It is rounded, thick, and
374 short in AR2 and very short in AR1. Anterior covering of the dentigerous region is extremely

375 short in AR1 while it is developed in both AR12 and AR2, with AR12 being most robust.
376 Ascending process bears a fossa posteriorly; in AR2 it is thinner and dorsoventrally shorter than
377 in AR12. In AR1 the fossa spans the majority of the length of the ascending process with the
378 inner fossa accounting for half of the major fossa. Posterior ridge dorsal to dentigerous region is
379 barely visible in AR1 and in AR2 it is thicker than in AR12.

380 **Summary of Ontogeny-**

- 381 • Maxilla overall starts thin in AR1 and becomes more robust by AR2.
- 382 • Anterior covering of dentigerous region becomes more robust with age.
- 383 • Shape and curvature of ascending process develops with age.
- 384 • Posterior fossa minimizes, moves medially, and shallows from AR1 to AR2, then
385 deepens and elongates dorsoventrally in AR12.

386 **Fig. 8.— Right maxilla (ETVP 3295) in anterior (A) and posterior (B).** Scale bar = 5 mm.

387 Abbreviations: Pfr.f = prefrontal facet; am = anterior process of maxilla; asm = ascending
388 process of maxilla; tcm = transverse crest of maxilla.

389 **Fig. 9.— Right maxilla (ETVP 3306) in anterior (A) and posterior (B).** Scale bar = 1mm.

390 Abbreviations: Pfr.f = prefrontal facet; am = anterior process of maxilla; asm = ascending
391 process of maxilla; tcm = transverse crest of maxilla.

392 **Fig. 10.— Right maxilla (ETVP 3306) in anterior (A) and posterior (B).** Scale bar = 1mm.

393 Abbreviations: Pfr.f = prefrontal facet; am = anterior process of maxilla; asm = ascending
394 process of maxilla; tcm = transverse crest of maxilla.

395 **Parietal**—Posterodorsally articulates to the supratemporal and exoccipital. Anterodorsally
396 articulates with the frontals. Posteromedially articulates to the prootic. Anteroventrally
397 articulates with the basioccipital and basisphenoid.

398 **Dorsal-** Anterior side exhibits two transverse processes, whose lateral extensions make
399 up the widest part of the bone. Transverse processes flare posterolaterally after the anterodistal
400 terminus. Posterodistal terminus forms the ventrally oriented postorbital processes. From the
401 posterodistal terminus the transverse processes curve anteromedially back toward the body of the
402 bone. After meeting the body there is no curvature and the posterior end of the bone tapers to a
403 shallow notch. The shallow notch between two rounded, short processes forms the posterior
404 extension of the parietal. Ventral to the transverse processes lateral extensions are visible on both
405 sides (Fig 11).

406 **Ventral-** The center of the parietal is moderately concave for ~8 mm toward the
407 posterior, with ventral processes on each lateral edge. Postorbital processes form a ridge that
408 curves posteromedially forming the lateral extensions and curving back toward the body
409 anteriorly to meet the central processes. Posterior to the ventral processes the dorsal attachment
410 to the body's base exhibits a wavy, wrinkled appearance. Once meeting the body, the dorsal
411 attachment flushes evenly with the body. The shallow notch exhibits borders between processes
412 and the processes exhibit short projections at the anterior curvature.

413 **Ontogeny-** In ventral view the postorbital process is ventrally oriented in AR12, in
414 AR2 and AR1 it is posteroventrally oriented (Figs 12 and 13). The anterior margin comes to a
415 sharp point in AR2 while it is more of a smooth outward curve in AR12. Ventral processes are
416 well developed in AR12, but in AR2 the anterior of the processes is more anteriorly pointed and
417 the medial margin is less smooth. A flat, straight area is present on AR1 where the ventral
418 processes would be located. Anteriorly this area is softly rounded and curved anteriorly to meet
419 the frontal facets. Dorsoventral attachment to the body is straight in AR1, mostly straight in
420 AR2, and in AR12, there are undulations. Posterior processes extend most in AR12 while in AR1

421 the area is flat and straight. In AR1 the body is open, no structures present but fossa on either
422 side posteriorly. Transverse processes are not visible when viewing in ventral view. Lateral
423 extensions of the posterior of AR1 are shorter and the medial margin extends first anteromedially
424 then anteriorly, while in AR2 the medial margin curves anterolaterally to meet the ventral
425 processes. In AR2 and AR12 the lateral extensions extend posterolaterally while in AR1 they
426 extend posteriorly. Anterior transverse processes are much wider/thicker in AR1 than the others.
427 In dorsal view the posterior is flat in AR1, shallow with a thin notch on AR2 and shallow with a
428 wide notch in AR12. Posterior processes exhibit a rounded margin in AR12; in AR2 undulations
429 are present. AR2 has many undulations on posterior border while others exhibit a flatter border.
430 Fossa of AR1 are more visible in dorsal view, transverse processes are thinner and longer in
431 AR12 and AR2, and in AR1 they are short and thick. Lateral extensions are not easily visible in
432 dorsal view of AR1, but they are posteriorly oriented and close to the body.

433 **Summary of Ontogeny-**

- 434 • Ventral processes begin as a flat edge in AR1, appear as anteriorly oriented, sharply
435 pointed processes in AR2, and anterolaterally oriented, round-tipped processes in
436 AR12.
- 437 • Dorsoventral attachment to body from ventral processes begins straight and develops
438 undulations with age.
- 439 • Body of parietal in AR1 has not fully ossified, exhibiting two openings.
- 440 • Medial margin of lateral processes shift from curving anteromedially to meet the
441 ventral processes in AR1 to anterolaterally in AR2 to mostly straight anteriorly in
442 AR12.
- 443 • Transverse processes elongate with age and begin thick in AR1, thin in AR2, and
444 thicken in AR12.

445 • In dorsal view the posterior margin is flat in AR1, shallow with a thin notch in AR2,
446 and shallow with a wide notch in AR12.

447 • Processes of posterior margin begin flat, develop undulations, and round with age.

448 **Fig. 11.— Parietal (ETVP 3295) in dorsal (A) and ventral (B). Anterior is to the top.** Scale

449 bar = 5 mm. Abbreviations: p.vpr = parietal ventral process; lep = lateral extension of parietal;

450 pop = postorbital process of parietal; tpp = transverse process of parietal.

451 **Fig. 12.— Parietal (ETVP 3293) in dorsal (A) and ventral (B). Anterior is to the top.** Scale

452 bar = 5mm. Abbreviations: P.vpr = parietal ventral process; lep = lateral extension of parietal;

453 pop = postorbital process of parietal; tpp = transverse process of parietal.

454 **Fig. 13.— Parietal (ETVP 3306) in dorsal (A) and ventral (B). Anterior is to the top.** Scale

455 bar = 1mm. Abbreviations: p.vpr = parietal ventral process; pop = postorbital process of parietal;

456 lep = lateral extension of parietal; tpp = transverse process of parietal.

457 **Prefrontal**— Articulates anteroventrally to the maxilla; the anterior facing maxillary facet of

458 the prefrontal sits in the cupped articulation surface at the dorsal end of the ascending process of

459 the maxilla. The prefrontal articulates posterodorsally to the frontal; the frontal facet on the

460 posterodorsal surface of the prefrontal fits into, and slightly ventral to, the prefrontal facet on the

461 anterior of the frontal.

462 **Dorsal**- Medial side is elevated, extending posteriorly over the prefrontal edge. An

463 elevated knob is present slightly lateral to the center. Lateral to the knob the edge is a rounded

464 and ventrally oriented lateral process. A fossa is present near the center of the bone. Anterior

465 section is somewhat flat laterally, and angled medially, with the flat area containing the maxilla

466 facet. Posterior edge is curvy, containing the frontal facet (Fig 14).

467 **Ventral-** Lateral side is concave with a short ridge, formed by the lateral process,
468 outlining the lateral edge. Medially the surface curves dorsally causing the medial side to be
469 slightly elevated. Medial side is ventral to the lateral edge, though it is still somewhat concave in
470 the center. Anterior and posterior edges are elevated forming short, rounded processes. Posterior
471 process is slightly more elevated than the anterior. Another process is visible medial to the
472 posterior process. The flat/depressed area is the articulating surface for the maxilla. Posterior
473 edge is curvy with four projections. Medial to the cup on the lateral side is a short projection.
474 Dorsal to the posterior process are two processes the medial one being more prominent and the
475 lateral one being more flat.

476 **Ontogeny-** In dorsal view the lateral side of AR1 extends further out than others. In
477 AR2 the lateral process is close to the knob, as in AR12 (Figs 15 and 16). In AR12 the lateral
478 margin is rounded posteriorly then angles medially at anterior to meet maxillary facet. In AR2
479 the rounded posterior makes up less of the lateral margin, with a straight section anteriorly that
480 then angles medially to curve into maxillary facet. In AR1 the lateral margin is rounded but thin
481 posteriorly, then curves anteromedially, gently first, then more sharply to the maxillary facet.
482 Maxillary facet is straight in AR12, in AR2 and AR1 it curves outward anteriorly. Anterior
483 medial process is rounded, thin, and long in AR1. In AR2 it is shorter, thick and rounded. In
484 AR12 it is more square-shaped, short, thick, and oriented more medially. Posterior medial
485 process is elongate, flat tipped, and curved more anteriorly than posteriorly in AR1. In AR2 it is
486 elongate, rounded, and posterior side curves in anteriorly to itself. In AR12 it is short, the tip is
487 square shaped with rounded corners, and the sides curved gently to meet the body. Dorsal knob
488 is thinnest in AR1 and extends posteriorly more than others. Posterior of the knob is oriented
489 posteromedially with a squared margin in AR1. Anterior process of the knob is anteroposteriorly

490 long and tallest in AR1. A fossa is present anteromedially to anterior process of the knob, the
491 area surrounding the fossa is concave in AR1. In AR2 the knob is mostly rounded and extends
492 posteriorly, more than AR12 but less than AR1. Anterior process is much shorter than AR1 but
493 still taller than AR12. In AR12 the anterior process is shortest. Posterior margin of knob has a
494 rounded protrusion that curves anterolaterally to meet body. The knob extends posteriorly the
495 least in AR12. Posterior margin is straight with little variations in AR1. In AR2 undulations are
496 more exaggerated while in AR12 they are more gently curved. In ventral view the lateral ridge is
497 most sharply curved in AR12, most gently in AR1. Lateral side is elongate and thin in AR1,
498 thick in AR2, and thickest in AR12. Concave area of lateral side is smooth in AR12, rough and
499 deep in AR2 and in AR1 appears as a lowered area rather than fully concave. Anterior process of
500 medial side extends furthest in AR1, is shorter and wider in AR2, and in AR12 is a curved corner
501 with a short rounded protrusion. Posterior medial process is long in AR1, tip comes to a rounded
502 point, and a ridge is present ventrally that curves out posteriorly. In AR2 posterior medial
503 process is very rounded, extends from the body, and ridge is present ventrally but does not
504 extend posteriorly. In AR12 the posterior medial process is short, wide, and anterior side extends
505 farthest. The ventral ridge has rounded and extended posteriorly to form another process in
506 AR12. Posterior lateral process is rounded and extends from the body in AR1. In AR2 it is
507 rounded, wider, and meets the lateral ridge ventrally. In AR12 it is much thinner, meets ridge
508 ventrally, and from the posterior it is angled medially to meet the body. The thicker, rounded
509 area of the lateral ridge is present in AR1 as is the anterior knob. In AR2 the ridge is much
510 thicker than AR1 and has curved in on itself. In AR12 the ridge is thickest and extends most
511 anteroposteriorly.

512 **Summary of Ontogeny-**

- 513 • Lateral margin begins thin, extending more laterally, then thickens and shrinks
- 514 closer to the body of the bone with age.
- 515 • Maxillary facet begins anteriorly curved and becomes straight/flat by AR12.
- 516 • Posterior medial process rounds and recedes close to the body with age.
- 517 • Anterior process of dorsal knob shortens with age.
- 518 • Dorsal knob recedes closer to body anteriorly with age.
- 519 • Lateral side thickens with age.
- 520 • Lateral ridge curves gently in AR1 while curving sharply in AR12.
- 521 • Anterior process of medial side shortens and recedes into body of bone until it
- 522 becomes a rounded corner with a short, rounded, protrusion.
- 523 • Posterior medial process shortens/recedes into the body and widens with age.
- 524 • Ridge on posterior medial process begins oriented posterolaterally, in AR2
- 525 extends ventrally, and in AR12 is present as a posterior facing rounded process.
- 526 • Posterior lateral process widens and recedes closer to the body with age.
- 527 • Lateral ridge thickens and elongates anteroposteriorly with age.

528 **Fig. 14.— Right prefrontal (ETVP 3295) in dorsal (A) and ventral (B) view.** Anterior is to
529 the top. Scale bar = 1mm. Abbreviations: Mx.ft = maxillary facet; Fr.ft = frontal facet; dkprf =
530 dorsal knob of prefrontal; lrpfr = lateral ridge of prefrontal.

531 **Fig. 15.— Right prefrontal (ETVP 3293) in dorsal (A) and ventral (B) view.** Anterior is to
532 the top. Scale bar = 1mm. Abbreviations: Mx.ft = maxillary facet; Fr.ft = frontal facet; dkprf =
533 dorsal knob of prefrontal; lrprf = lateral ridge of prefrontal.

534 **Fig. 16.— Right prefrontal (ETVP 3306) in dorsal (A) and ventral (B) view.** Anterior is to
535 the top. Scale bar = 1mm. Abbreviations: Mx.ft = maxillary facet; Fr.ft = frontal facet; dkprf =
536 dorsal knob of prefrontal; lrprf = lateral ridge of prefrontal.

537 **Premaxilla**— The premaxilla articulates posterodorsally to the septomaxilla; the anterior tips
538 of the septomaxilla sit on either side of the ascending process of the premaxilla. The premaxilla
539 articulates posteroventrally to the vomers; the posteriorly facing vomerine process of the
540 premaxilla abuts the anterior tips of the vomers.

541 **Dorsal**- An ascending process is present on the dorsal side, is ~1 mm tall, and does not
542 meet the nasals. Premaxilla exhibits well developed transverse processes that extend ~3 mm
543 from the center of the anterior edge. The vomerine process makes up the posterior end, extending
544 out ~1mm and tapering posteriorly. A fossa is present on each distal side of the ascending
545 process with one extra fossa on the left side (Fig 17).

546 **Anterior**- Ascending process is dorsally oriented, rounded, and thick. Ventral side of
547 the transverse process widens medially, reaching maximum a width of ~1.5 mm from the distal
548 tip before curving inward dorsally.

549 **Ontogeny**- Vomerine notch deepens and vomerine processes extend with age. Fossa
550 present on either side of the ascending process; on AR1 fossa are close to parallel, in AR2 the
551 left one is smaller and positioned more medial, and in AR12 the right fossa is barely visible and
552 positioned anteriorly. Anterior edge of AR1 is a single, gentle curve; AR2 has formed the double
553 undulated shape that is seen in AR12. On AR1 a ventral fossa is present, with AR2 appearing
554 concave in the same area, and no evidence of either on AR12.

555 **Summary of Ontogeny-**

- 556
- Vomerine notch deepens with age.

- 557 • Vomerine processes extend with age.
- 558 • Ventral process disappears with age.
- 559 • Anterior margin starts as a single gentle curve but by AR2 exhibits the double
- 560 undulated shape also seen in AR12.

561 **Fig. 17.— Premaxilla (ETVP 3295) in anterior (A) and dorsal (B) view.** Anterior is to the top.
562 Scale bar = 1mm. Abbreviations: as = ascending process of premaxilla; tr = transverse process of
563 premaxilla; vp = vomerine process of premaxilla.

564 **Dentary**— Posteriorly the dentary articulates with the compound bone, the angular, and the
565 splenial. Anterior of the splenial fits into the medial groove of the dentary, with the dorsal
566 process of the splenial connecting to the ventral half of the medial process of the dentary.
567 Anterodorsal process of the angular connects to the dorsal half of the medial process of the
568 dentary, so that the medial process connects with the angular on it's dorsal half and the splenial
569 on it's ventral half. Ventral process of the dentary also borders the anteroventral edge of the
570 angular. The anterior of the compound bone fits between the ventral and dorsal processes of the
571 dentary, enclosing it's lateral groove.

572 **Medial-** Anterior end is curved medially while the body remains uniform. Teeth are
573 aligned to the lateral side. A narrow groove is present on the medial side, open on the posterior
574 end and present as an indented line on anterior end. Dorsal and ventral edges of the groove curve
575 in on themselves dorsoventrally. The dorsal edge projects out medially producing a curved
576 process with a back and forth curved posterior end. This dorsomedial process articulates with the
577 dorsomedial process of the compound bone. As in lateral view a dorsal and ventral process are
578 produced by the bifurcating of the posterior end of the dentary (Fig 18).

579 **Lateral-** The right dentary exhibits ~13 teeth that span the entire length, with one at the

580 very posterior. Anterior teeth are the largest, with a decrease in size posteriorly. Posteriorly the
581 dentary bifurcates into thin dorsal and ventral processes. The center of the bone bears a deep
582 groove with the posterior half being open and the anterior half having bone visible from the
583 lateral side. Anterior end of the compound bone articulates with the groove. Anterior to the
584 groove is a deep fossa.

585 **Ontogeny-** In lateral view the anterior tip is somewhat ventrally angled on AR2.
586 Anterior tip is curved less in AR1 and curved the least in AR12. Anterolateral fossa is
587 anteroposteriorly long on AR1, short and shallow on AR2, and the most shallow on AR12.
588 Ventral process on the posterior of AR1 is curved dorsally. Tooth attachment areas are visible on
589 AR1, perhaps not yet sockets. In medial view the ventral and dorsal folds on the anterior of AR1
590 do not meet. The folds begin to meet in AR2, and completely meet in AR12. Dorsomedial
591 process of AR2 exhibits two short, undeveloped processes. In AR1 the two processes are visible,
592 close together, and taller than in AR2. In AR12 they are developed, rounded, and protrude more
593 than in AR2 and are thicker than both AR1 and AR2.

594 **Summary of Ontogeny-**

- 595 • Anterior lateral fossa shortens anteroposteriorly, becomes circular in shape, and
596 shallows with age.
- 597 • Ventral posterior process is angled dorsally in AR1, extends posteriorly in others.
- 598 • Dorsal and ventral folds on medial side get closer with age, eventually
599 meeting/joining in AR12.
- 600 • Dorsomedial process of dentary begins thin and elongate, thickens and shortens in
601 AR2, then elongates and thickens in AR12.

602 **Fig. 18.— Right dentary (ETVP 3295) in medial (A) and lateral (B) view.** Anterior is to the
603 right. Scale bar = 5 mm. Abbreviations: dpd = dorsal process of dentary; dmpd = dorsomedial
604 process of dentary; mgd = medial groove of dentary; vpd = ventral process of dentary.

605 **Angular**— The anteroventral edge of the angular borders the ventral process of the dentary.
606 The anterodorsal process of the angular articulates with the dorsal half of the medial process of
607 the dentary. The narrow posterior of the angular fits into the medial groove of the compound
608 bone. Anterior of the angular connects to the posterior edge of the splenial.

609 **Medial-** Anteriorly there is a dorsally oriented process, representing the anterior-most
610 end of the bone. The process exhibits a flat edge and curves back posteroventrally, causing a
611 widening of the ventral side. Approximately 2 mm from the anterior edge the curve terminates at
612 a rounded process that is oriented ventrally. Anterior and posterior edges of the rounded process
613 extend past the base of the process, forming a “pinched” appearance at the base. Directly dorsal
614 to the rounded process is a small, triangular process. Posterior to the rounded process the bone
615 tapers dorsally, thinning the posterior section. Posterior end consists of a rounded point (Fig 19).

616 **Lateral-** Ventral edge appears thicker and elevated. The elevated ridge runs posteriorly
617 from the rounded process, terminating as the rounded posterior end. Bone dorsal to the ridge is
618 gently concave with some elevation occurring at the most dorsal section of the dorsal process.
619 The bone also appears thinner in the same areas, with the exception of the most dorsal section of
620 the dorsal process. The rounded process does not appear as protruding or rounded in lateral view.
621 Dorsally the ridge terminates with a slightly rounded tip, flaring ventrally, widening the anterior
622 of the ridge. Approximately 1 mm from the anterior-most of the rounded process the curving of
623 the anterior of the ridge end in a sharp point and curves anterodorsally toward the body of the
624 bone. Posterior of the ventral side curves lightly with no other significant features. Dorsal to the

625 rounded process and ventral to the dorsal process the triangular process is more visible in lateral
626 view. Dorsal and ventral edges of the triangular process curved in their respective directions to
627 meet the body of the bone.

628 **Ontogeny-** Dorsal process of AR1's right angular has broken off (not ontogenetic).
629 Posterior tip is sharply pointed on AR1 and AR2; on AR12 it is rounded. Dorsal margin exhibits
630 most curvature in AR12 with AR2 being less curvy and AR1 the least curvy. Dorsal process is
631 thickest in AR12; in AR2 it is much thinner and less dorsally oriented. While the dorsal process
632 of the right angular of AR1 has been broken, the left angular shows a thin dorsal process, like in
633 AR2, that is less dorsally oriented than in AR12. Tip of the dorsal process is rounded in AR1,
634 square in AR12, and intermediate in AR2. In lateral view of AR2 the ventral process is thinner
635 anteroposteriorly than AR12. Groove of the ventral process is formed in AR2 and the
636 termination point is more anterior than in AR12. Ventral process of AR1 is elongate and exhibits
637 a groove; dorsal margin of the groove is long, unlike in AR2 and AR12. Ventral margin gently
638 curves out ventrally in AR2. In AR1 ventral margin is straight. On AR1 the lateral side is more
639 concave than in AR12 and AR2, with AR12 being the least concave. Anterior rounded process is
640 "pinched off" in AR12, inward curving is present on AR2, posterior to the process, but does not
641 exhibit the "pinched" shape. In AR1 the ventral margin of the anterior rounded process is straight
642 with no "pinching". Curvature from dorsal to ventral process is square in AR1, deeply curved in
643 AR2 and gently curved in AR12.

644 **Summary of Ontogeny-**

- 645 • Dorsal margin increases in curviness with age.
- 646 • Dorsal process of angular thickens and protrudes more dorsally with age.
- 647 • Posterior margin of dorsal process becomes more square-shaped with age.
- 648 • Lateral side of angular becomes less concave/more flat with age.

649 **Fig. 19.— Right angular (ETVP 3295) in medial (A) and lateral (B) view.** Anterior is to the
650 top. Scale bar = 1 mm. Abbreviations: arpan = anterior rounded process of angular; dopan =
651 dorsally oriented process of angular; Iran = lateral ridge of angular; trpan = triangular process of
652 angular.

653 **Splénial**— The posterior edge of the splénial articulates to the anterior edge of the angular.
654 The tapering anterior of the splénial fits into the medial groove of the dentary, leaving only the
655 anterior mandibular foramen open.

656 **Medial-** Anterior end comes to a point, forming a bone that is anteriorly tapering with
657 an expanded posterior end. From the anterior point the bone gradually widens posteriorly.
658 Approximately 3 mm from anterior point the widening ends where the dorsal side comes to a
659 point before curving inward ventrally, toward the body. The curve extends ~2.5 mm posteriorly,
660 before then curving outward dorsally. An anteriorly oriented process is formed by the dorsal
661 termination of the curve. Dorsal side of the process bears a small ridge, extending posteriorly and
662 ending at the articulating end. A depression is observed on the dorsal edge of the dorsal process.
663 The posterior end exhibits a curved process to articulate with the angular. Aside from the
664 process, the rest of the posterior end has slight curvatures for articulation, but is mostly uniform.
665 Ventral border of the bone is mostly straight, with slight curvature (Fig 20).

666 **Lateral-** A spine runs from the anterior-most tip, reduces in height ~3/4 way down
667 toward posterior, and terminates at the center of the posterior notch. A fossa is present on the
668 dorsal side of the spine. The posterior end exhibits more relief than in medial view, with the
669 medial side of the posterior process extending past the posterior notch.

670 **Ontogeny-** Anterior tip is sharply pointed in AR12 and AR1 with AR2 being rounded,
671 though this could be due to breakage. Anterior dorsal margin is straight and flat in AR12; AR2

672 shows little curvature and AR1 shows the most curvature; curving outward dorsally. Dorsal
673 incisure is anteroposteriorly oriented in AR12, in AR2 there is some ventral curvature, and in
674 AR1 there is a posteroventral curvature. Both AR1 and AR3 are curved on the ventral margin
675 while AR12 is mostly straight. Posterior end of AR1 exhibits four undulations, ventral process is
676 not yet extended. A fossa is present dorsal to the ventral process, not seen on AR12 or AR2. In
677 medial view the lateral ridge is visible posteriorly in AR1 and AR2 the ridge does not fully
678 extend anteriorly. In lateral view of the posterior the ventral process is present on AR2, but not
679 fully extended posteriorly. Tip of the anterodorsal process is sharply pointed in AR1 and AR2,
680 rounded in AR12. A short ridge is present on the dorsal edge of the dorsal process of AR1. The
681 short ridge on the posterodorsal process of AR2 is slightly more ventral than in AR1. On AR12
682 the ridge is long and positioned most ventral. The lateral ridge is closest to the ventral margin in
683 AR1. In AR2 the ridge is positioned more dorsally and in AR12 the ridge terminates and the
684 anterior tip. The section of bone ventral to the lateral ridge appears to thin with age. The
685 posterior notch on AR12 is curved anteriorly and the medial side of the notch extends posteriorly
686 past the lateral side. The notch on AR2 has a “V” shaped indentation on the more dorsal side and
687 the medial side extends past the lateral side of the notch. A notch has not yet formed on AR1, the
688 lateral ridge extends past the posterior edge, and the ventral margin has many undulations.

689 Margin of the incisure in AR2 is the most undulating.

690 **Summary of Ontogeny-**

- 691 • Anterior dorsal margin straightens/flattens with age.
- 692 • Dorsal incisure shifts from posteroventral curvature, to subtle ventral curvature, to
693 anteroposteriorly oriented.
- 694 • Ventral process extends with age.

695 **Fig. 20.— Right splenial (ETVP 3295) in medial (A) and lateral (B) view.** Anterior is to the
696 top. Scale bar = 1 mm. Abbreviations: dsp = dorsal process of splenial; lssp = lateral spine of
697 splenial; pns = posterior notch of splenial.

698 **Compound Bone**— Anterior tip of the compound bone articulates to the dentary between
699 the ventral and dorsal process, enclosing the lateral groove of the dentary. Medial groove of the
700 compound bone receives the posteriorly tapering end of the angular. The articular of the
701 compound bone interlocks with the mandibular condyle of the quadrate while the posterior of the
702 pterygoid abuts the articular medially.

703 **Medial-** Anterior end comes to a point consisting of a lateral ridge and two medial
704 ridges. Medial ridges curve in laterally, causing the junction to be concave. The concave area is
705 mostly open, except a thin anterior process. Dorsal to the process is a relatively short dorsally
706 elevated ridge. Approximately 13 mm from the tip of the anterior process the posterior begins to
707 curve dorsally; widening the bone and marking the anterior of the prearticular crest. Prearticular
708 crest curves out medially but does not extend past the width of the bone. Articular surface is
709 more visible in medial view, demonstrating the texture and shape of the surface. Ventral border
710 of the articular exhibits two fossa. Ventral to the anterior crest of the articular is a dorsomedially
711 oriented process (Fig 21).

712 **Lateral-** Anterior end comes to a point, gradually widens posteriorly and maintains its
713 width for ~2 mm before the bone begins to curve outward dorsally, forming the prearticular
714 crest. Posterior to the prearticular crest the bone curves inward ventrally then outward dorsally,
715 forming the anterior process of the articular. Articular surface is ~1 mm deep between two
716 processes. Posterior to the articular is the ventromedially curved retroarticular process. The
717 center of the prearticular crest exhibits a deep mandibular fossa. Anterior to the retroarticular

718 process the ventral border curves out laterally, representing the surangular crest. Anterior to the
719 termination of the surangular crest the bone remains uniform in width until the thinning and
720 termination of the anterior end. Lateral side bears two fossa; Anteroventrally to the prearticular
721 crest is a small fossa, anterior to that fossa is another smaller fossa.

722 **Ontogeny-** In AR1 the lateral edges of the prearticular crest are very rough. Mandibular
723 fossa present in all Age Ranks. Fossa anterior to the mandibular fossa is present in all, a third
724 fossa is present in lateral view of AR2. Third fossa is absent in AR1 and while the right
725 compound bone of AR12 does not exhibit a third fossa, the left does. Anterior tip very sharply
726 pointed in AR1. In AR2 and AR12 the anterior tip is rounded and edges are smooth. Medial view
727 anterior end of AR1 very thin, bent, flimsy—well formed in AR2. Posterior fossa inferior to
728 articular is large in AR1, perhaps more “open”. In AR2 it is not as open; instead it is narrow and
729 deep. In AR12 the posterior fossa inferior to articular is the most deep and narrow. Anterior fossa
730 of the posterior end is not present in AR2 and AR12. Retroarticular not yet fully formed in AR1,
731 not curved, square-shaped, and dorsoventrally thinner than in AR12. Rounded process on
732 retroarticular appears as a pointed process on AR1. Surangular crest is not yet formed on AR1.

733 **Summary of Ontogeny-**

- 734
- 735 • Margin of the prearticular crest smooths with age.
 - 736 • Surangular crest forms with age.
 - 737 • Retroarticular shortens and thickens with age.
 - 738 • Overall bone thickens with age.
 - 739 • Posterior fossa of medial side narrows anteroposteriorly and deepens with age.

739 **Fig. 21.— Right compound bone (ETVP 3295) in medial (A) and lateral (B) view.** Anterior is
740 to the right for A and to the left for B. Scale bar = 10 mm. Abbreviations: a = articular; mf =

741 mandibular fossa; pcr = prearticular crest; rp = retroarticular process; sac = surangular crest of
742 compound bone.

743 **Discussion**

744 **Ontogeny**

745 The goal for this study is to understand ontogenetic change and begin a long-term project
746 of being able to identify isolated cranial elements in the fossil record by first providing a
747 description of cranial elements and ontogenetic change in a single taxon.

748 Through ontogeny the bones that showed the most significant change were the prefrontal,
749 maxilla, and parietal. The prefrontal shows an overall increase in robustness with age (Fig 22).
750 The youngest specimens (AR1 and AR2) exhibited long, thin processes that would shorten and
751 thicken with age (AR12). Edges with extreme undulations would become gentle undulations or
752 thick processes. The maxillary facet curved outward anteriorly in the younger specimens,
753 eventually becoming straight in AR12. This straightening could be due to the development of
754 muscles and cartilage holding the prefrontal to the maxilla, allowing additional kinesis of the
755 prefronto-maxillary joint. The maxilla exhibits a thickening of the ascending process with age, as
756 well as a lengthening of the lateral process of the ascending process (Fig 23). Prefrontal facet
757 shows significant change through ontogeny, in AR1 it is laterally rounded, medially straight,
758 medially oriented, and dorso-ventrally elongate. In AR2 the facet becomes more rounded, and in
759 AR12 it exhibits a rounded square shape. The change to a more rounded facet with age could
760 also be due to the development of muscles, allowing a more kinetic articulation between the
761 maxilla and prefrontal. Parietal exhibits a shift from a basic form to a more complex form (Fig
762 24). Postorbital processes are ventrally oriented in AR12 while in AR1 and AR2 they are

763 posteroventrally oriented. Ventral processes are absent in AR1, yet in AR2 are present and their
764 anterior is pointed and the medial margin is rough with many undulations. In AR12 the ventral
765 processes exhibit a rounded anterior, and the medial margin is smooth. Ventral processes
766 develop and “round out” with age. The lateral extensions show a slight shift in orientation, being
767 posteriorly oriented in AR1 and shifting posterolaterally in AR2 and AR12. The transverse
768 processes begin thick and short in AR1; with age they lengthen and subsequently thin out. The
769 parietal of AR1 exhibits two fossa at it’s center; they exhibit rough edges, possibly indicating the
770 continuing formation of the parietal. Aside from the mentioned characteristics, the overall trend
771 appears to demonstrate small changes in proportions while the elements increase in size.

772 **Fig. 22.— Prefrontal ontogeny.** ETVP 3295 in dorsal (A) and ventral (B); ETVP 3293 in dorsal
773 (C) and ventral (D); ETVP 3306 in dorsal (E) and ventral (F). Anterior is to the top of the page.
774 Scale bar = 1 mm.

775 **Fig. 23.— Maxilla ontogeny.** ETVP 3295 in dorsal (A) and ventral (B); ETVP 3293 in dorsal
776 (C) and ventral (D); ETVP 3306 in dorsal (E) and ventral (F). Dorsal is to the top of the page.
777 Scale bar = 1 mm.

778 **Fig. 24.— Parietal ontogeny.** ETVP 3295 in dorsal (A) and ventral (B); ETVP 3293 in dorsal
779 (C) and ventral (D); ETVP 3306 in dorsal (E) and ventral (F). Anterior is to the top of the page.
780 Scale bar = 1 mm.

781 **Descriptions**

782 The description of these disarticulated cranial elements can act as a foundation for a more
783 in-depth study on ontogenetic variation. Using the descriptions, geometric morphometrics can be
784 used to map the changes through ontogeny and potentially demonstrate a greater degree of
785 change. These descriptions can also allow for comparisons with other species of the genus to

786 document how certain structures differ between species, and possibly identify new diagnostic
787 characteristics.

788 The cranial elements of Crotalinae species have played a role in many studies, and with
789 an in-depth description of disarticulated elements, *T. wagleri* could be used in more studies to
790 better understand the relationships within Asian pitvipers. Diagnostic characteristics of certain
791 taxa have been previously identified [9, 18]; thus with the addition of full descriptions of
792 disarticulated elements, additional characteristics could be identified. While ontogeny was
793 minimally approached here, the descriptions produced can allow comparisons of different age
794 groups so that ontogeny could be better understood; since *T. wagleri* exhibits such drastic color
795 changes in ontogeny [3]. *Tropidolaemus wagleri* could also add to the understanding of pitviper
796 evolution. Many authors have commented on the basal nature of *T. wagleri* within Crotalinae.
797 With an in-depth description of skull morphology the evolution and development of certain
798 characters could be mapped to estimate the sequence of evolution for pitvipers [3, 9, 12, 22, 23,
799 25].

800 Many previous studies observing the cranial osteology of members of the Crotalinae
801 compared the cranial characteristics to other specimens to hypothesize phylogeny, evolution,
802 taxonomy, and zoogeography. Among the previous studies observing cranial elements some
803 described only the differences/similarities among studied taxa, while others offered more
804 detailed descriptions. The study here provides a detailed description of multiple elements without
805 comparison to other taxa. Brattstrom [9] did reference ontogeny within the Crotalinae, stating
806 that he did not observe major shape change after birth with the exception of *Lachesis muta*.

807 Guo and Zhao [18] identified characteristics of individual skull elements that can be used
808 to identify and differentiate between five genera and nine species of Asian pitvipers. Using the

809 characters in Guo and Zhao [18] *Tropidolaemus wagleri* appears to possess the following
810 character states: Border of maxillary cavity: projection; Parietal ridge: strong; Parietal shape; T-
811 shaped; Palatine shape: crescent and forked; Ectopterygoid anterior lateral process: broad.

812 Guo et al. [21] identified 12 osteological characteristics in order to hypothesize the
813 evolution of Asian pitvipers. No specimens of *Tropidolaemus spp* were used in the study. Using
814 the 12 characters described in Guo et al. [21] *Tropidolaemus wagleri* appears to possess the
815 following character states: Dorsal process of dentary does not reach the ventral process; the
816 shape of the anterior end of the ectopterygoid is broad; thin flap on the posterior ventrolateral
817 edge of the lower jaw is present; the shape of the palatine is forked; projection on border of
818 maxillary cavity present; shape of the parietal ridge is T-shaped; pterygoid teeth extend to
819 posterior margin of articulation with ectopterygoid; squamosal does extend beyond the posterior
820 end of the braincase; splenial and angular are separated; maxillary cavity is closed.

821 Previous studies have focused on taxonomy, soft anatomy, molecular sequencing, and
822 brief osteologic comparisons and identifying characters of *Tropidolaemus wagleri*. The study
823 here is the logical next step from previous studies and opens the door for studies on identifying
824 isolated elements and understanding full ontogenetic change within one taxon, taking the next
825 step toward paleontological studies.

826

827 **Conclusion**

- 828 • *Tropidolaemus wagleri* has been focused on, mostly in a taxonomic sense and did not
829 provide data to be utilized for paleontological finds, hence this study.

- 830 • Description of cranial elements allows for identification of disarticulated elements in
831 fossilized specimens.
- 832 • Brattstrom noticed little ontogenetic change in crotalids with the exception of *Lachesis*
833 *muta*. Brattstrom observed “There is no major change in the shape of the various bones
834 of the skulls of crotalids after birth” [9:190]. Contra Brattstrom [9], my study shows the
835 greatest change occurs early on with the most dramatic change between Age Ranks 1 and
836 2.
- 837 • The bones that exhibit the most ontogenetic change in this study are the maxilla, parietal,
838 and prefrontal.
- 839 • Most ontogenetic changes appear to be the result of the isometric growth and the “filling
840 out” of the bones’ shape.

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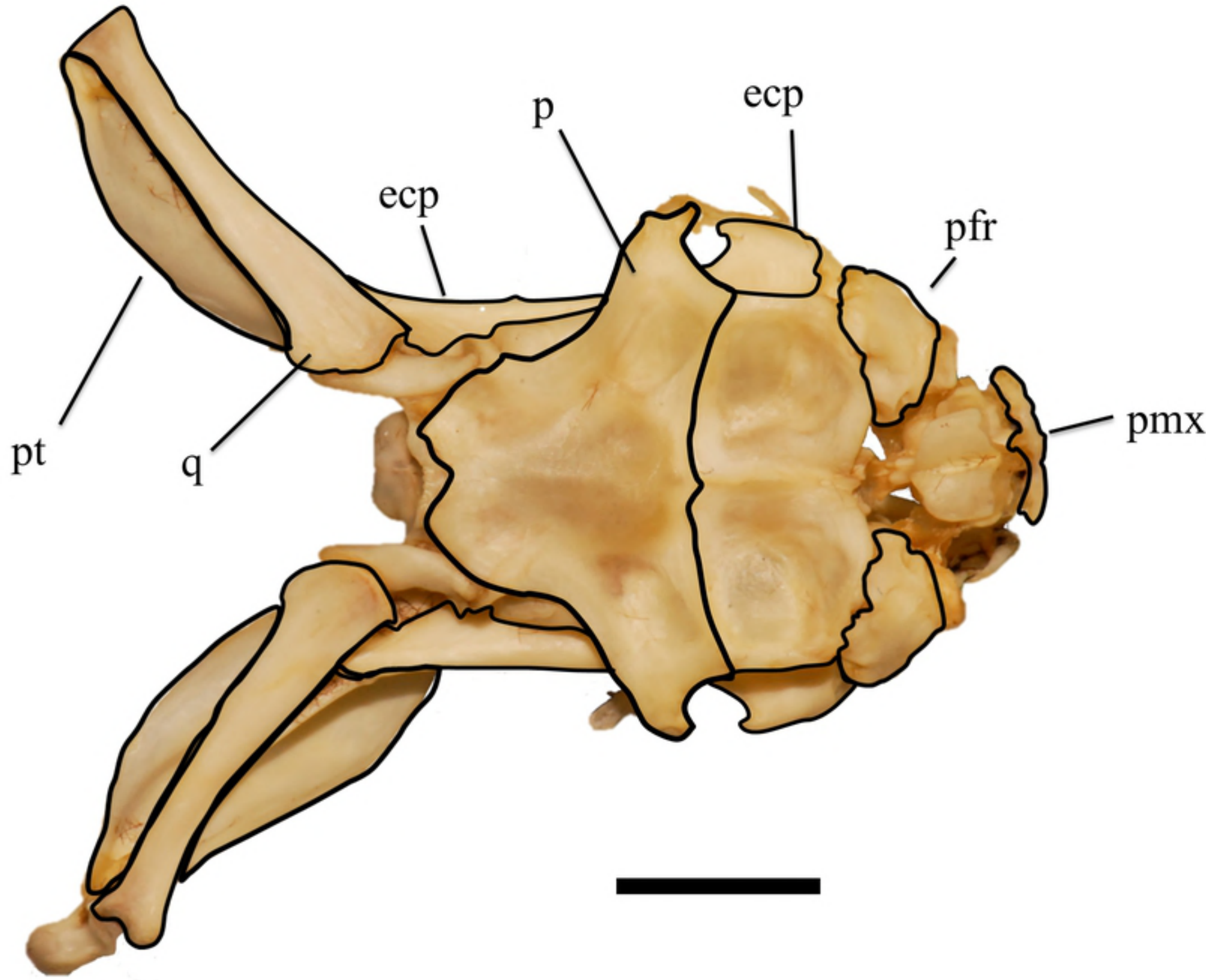
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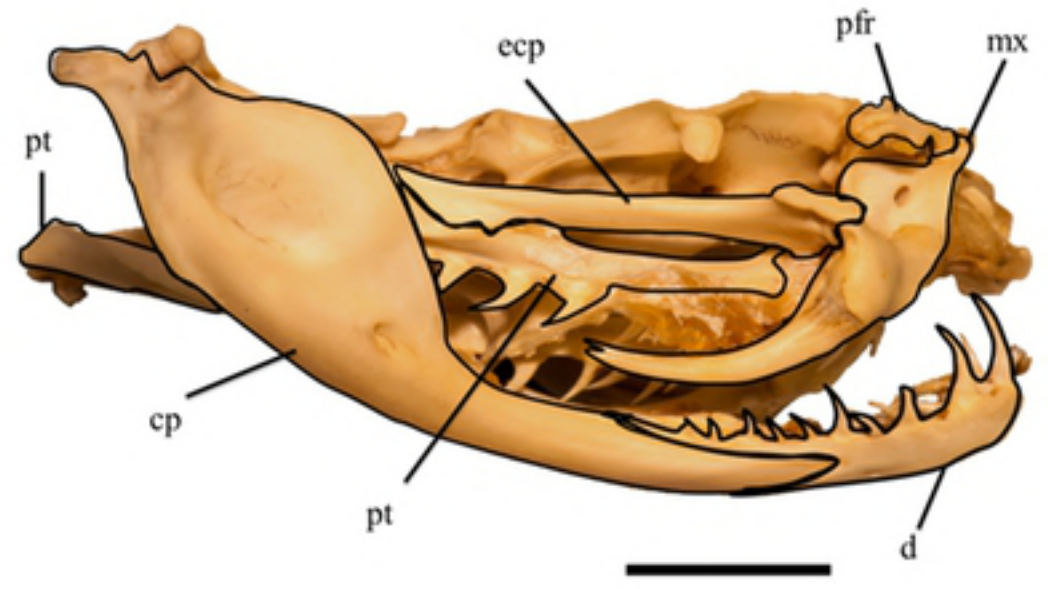
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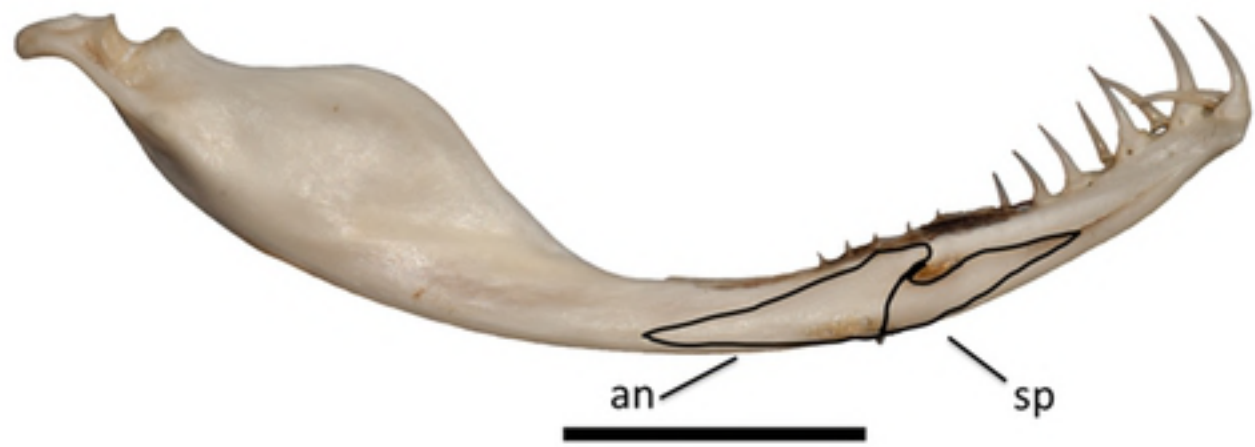
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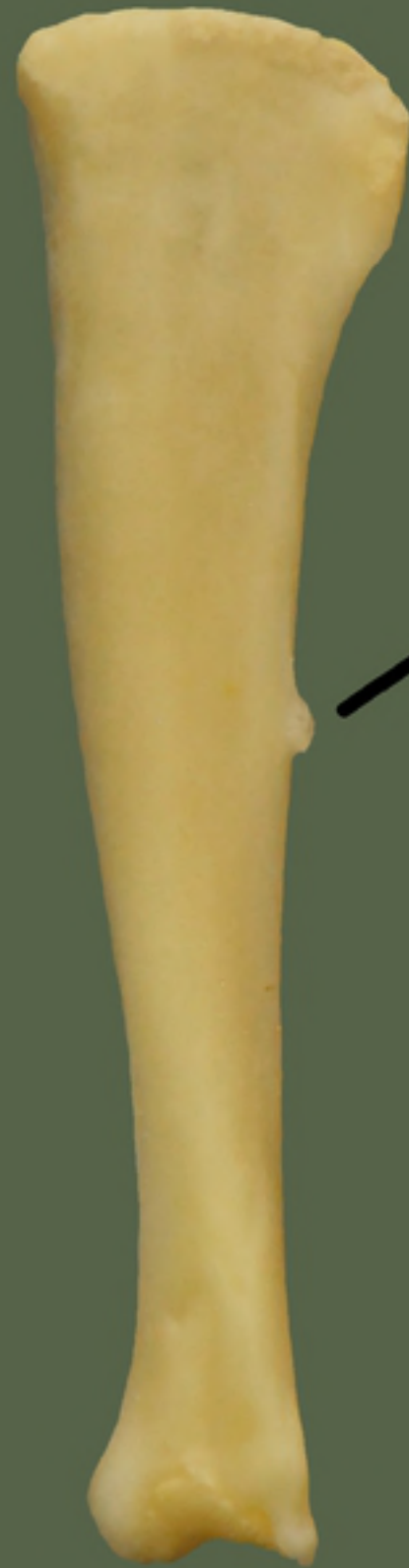






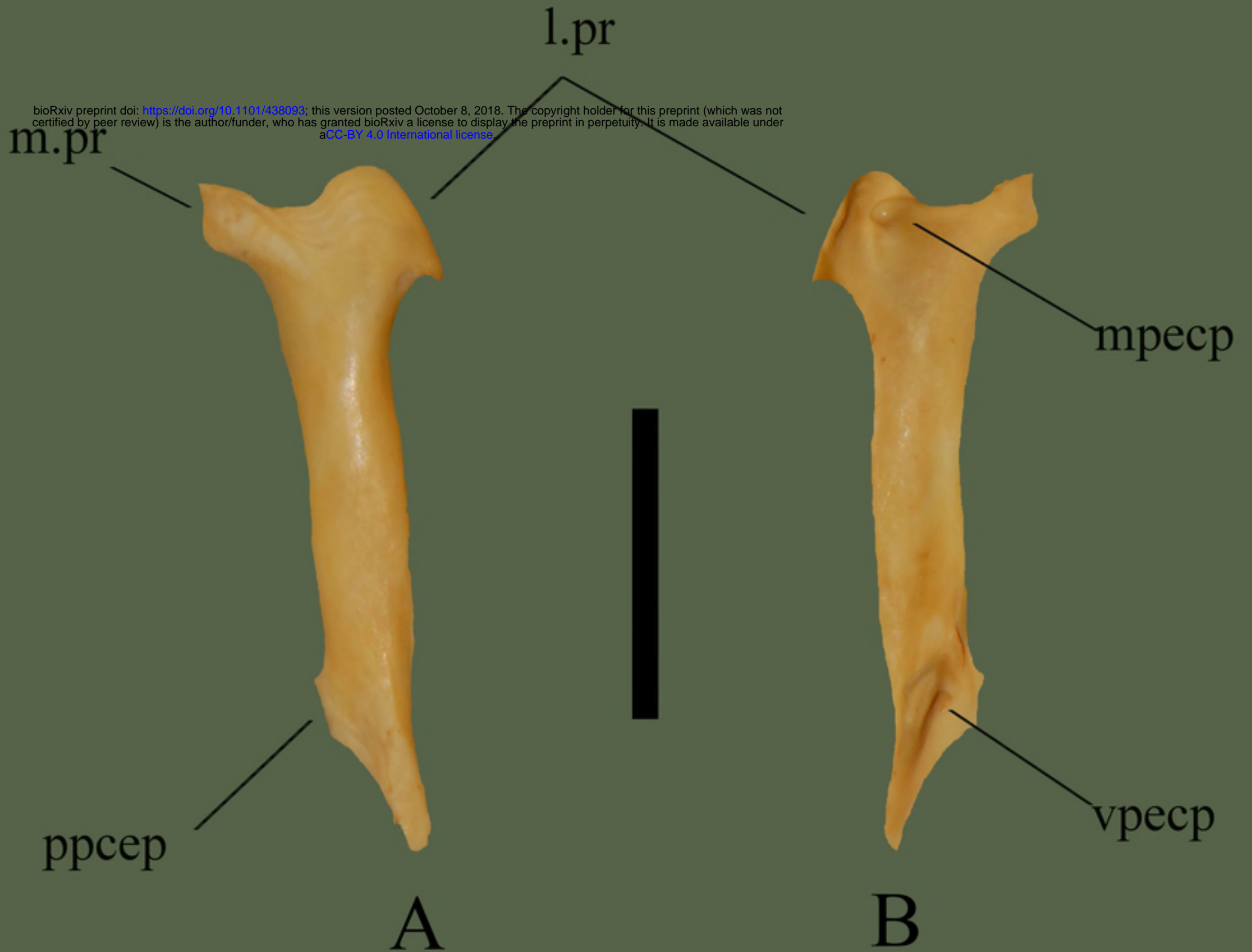
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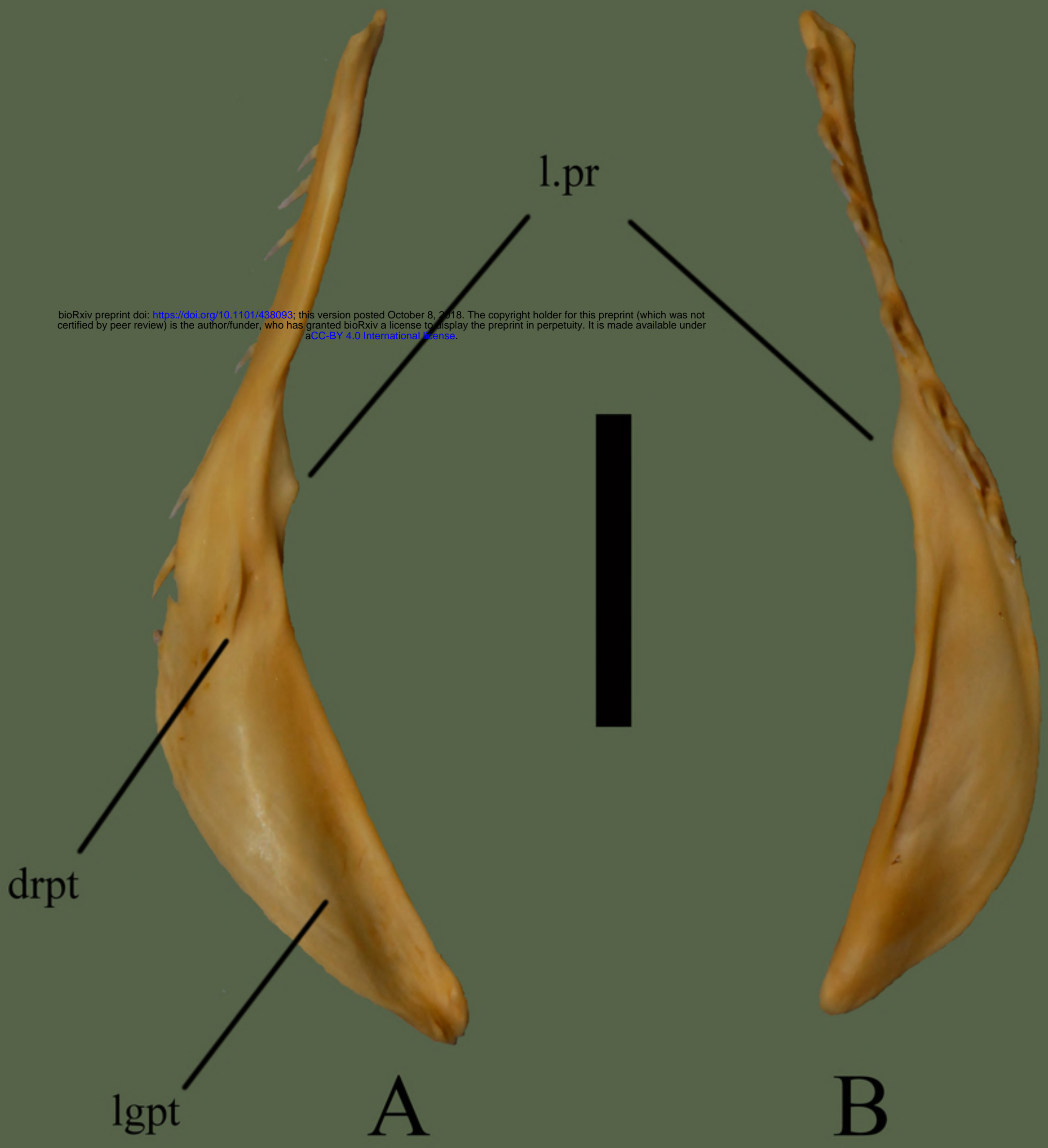


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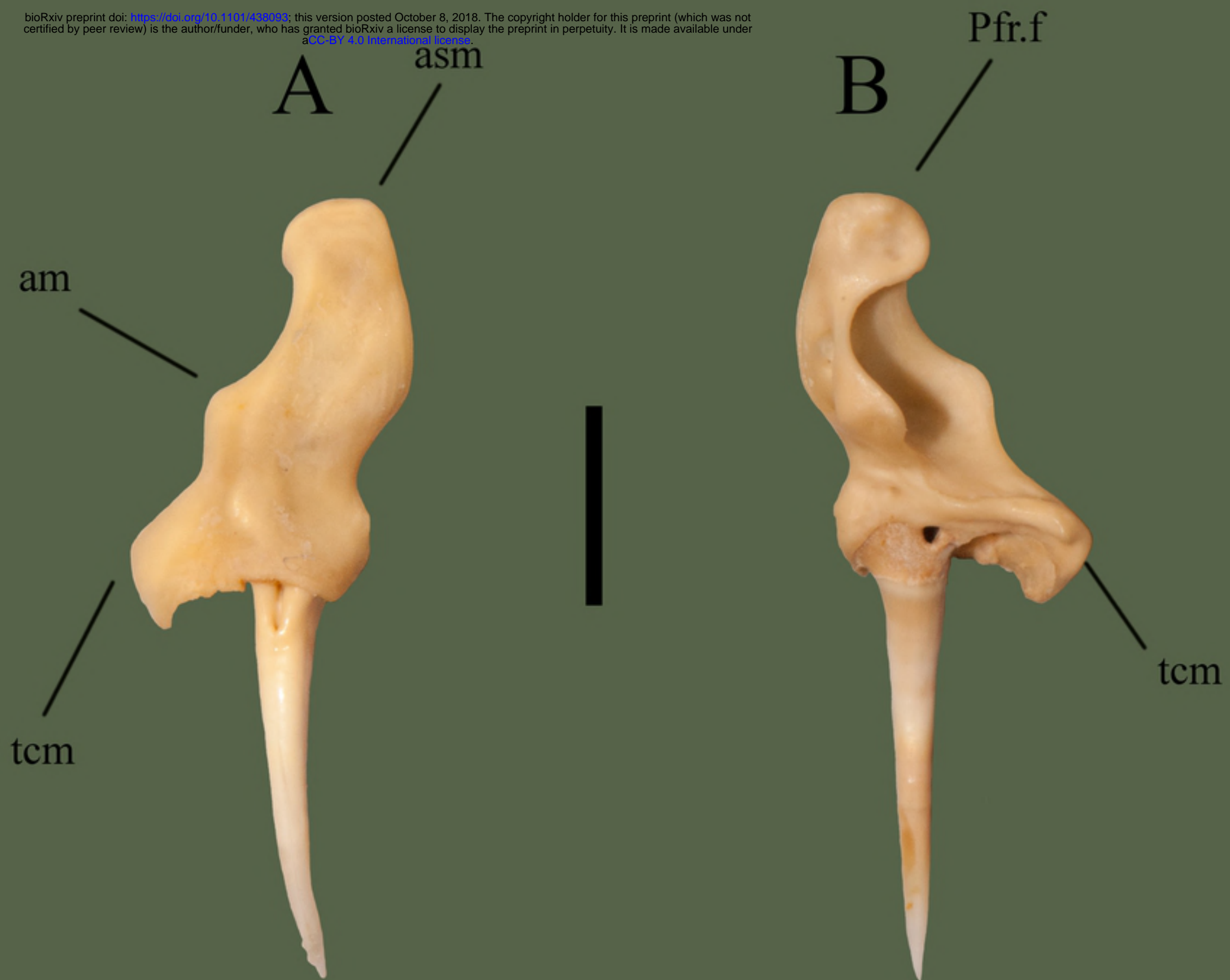
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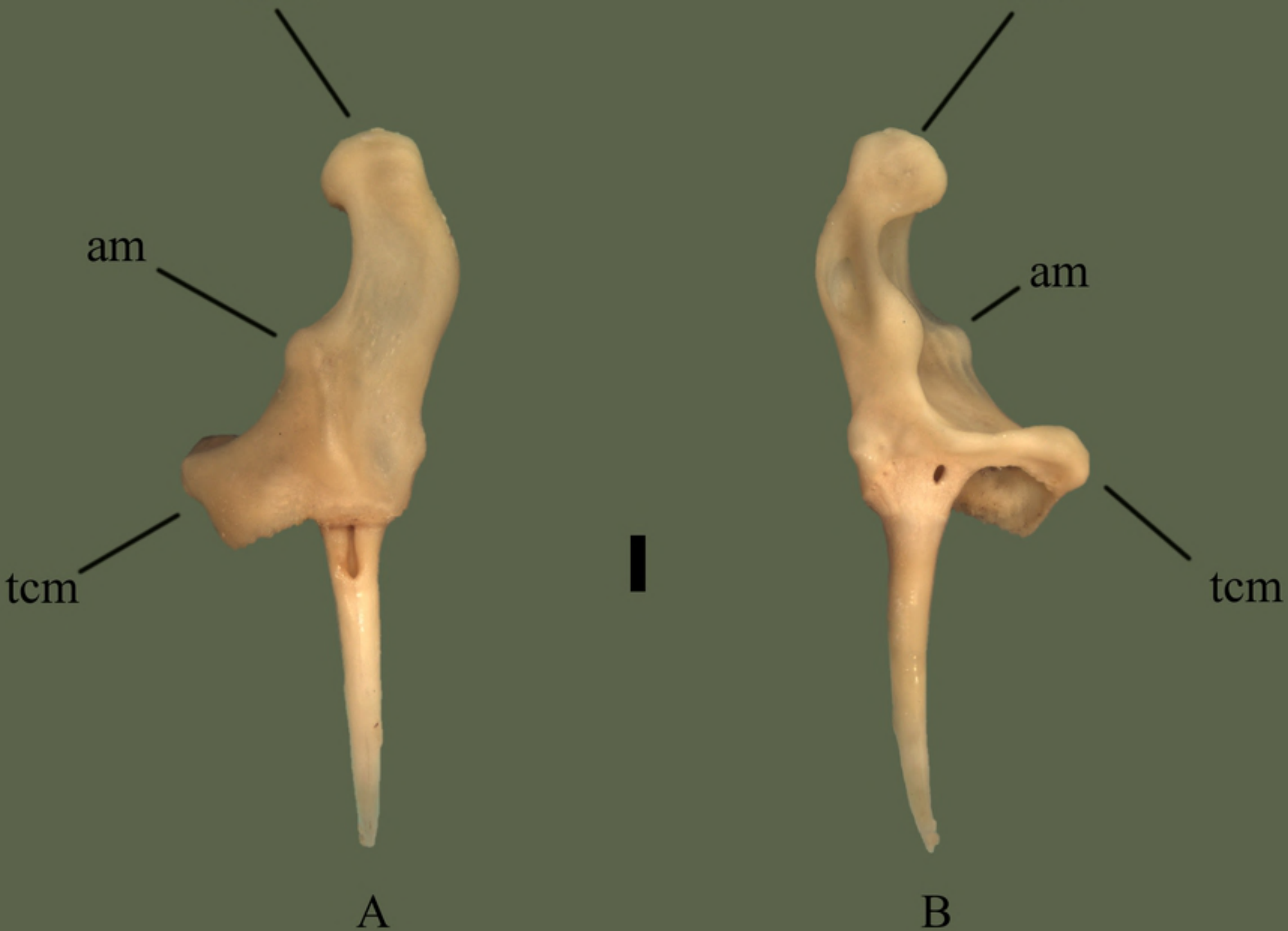
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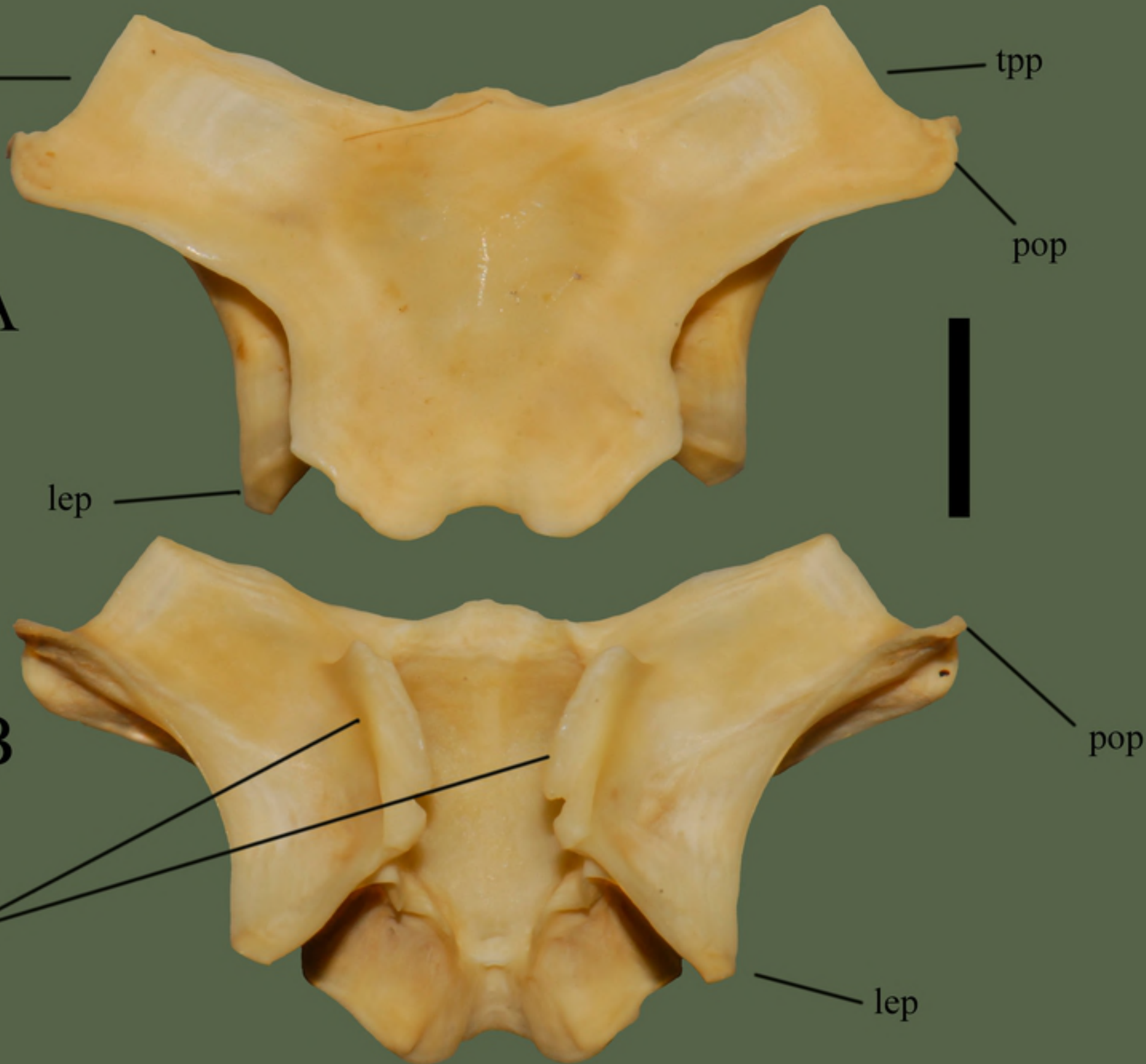


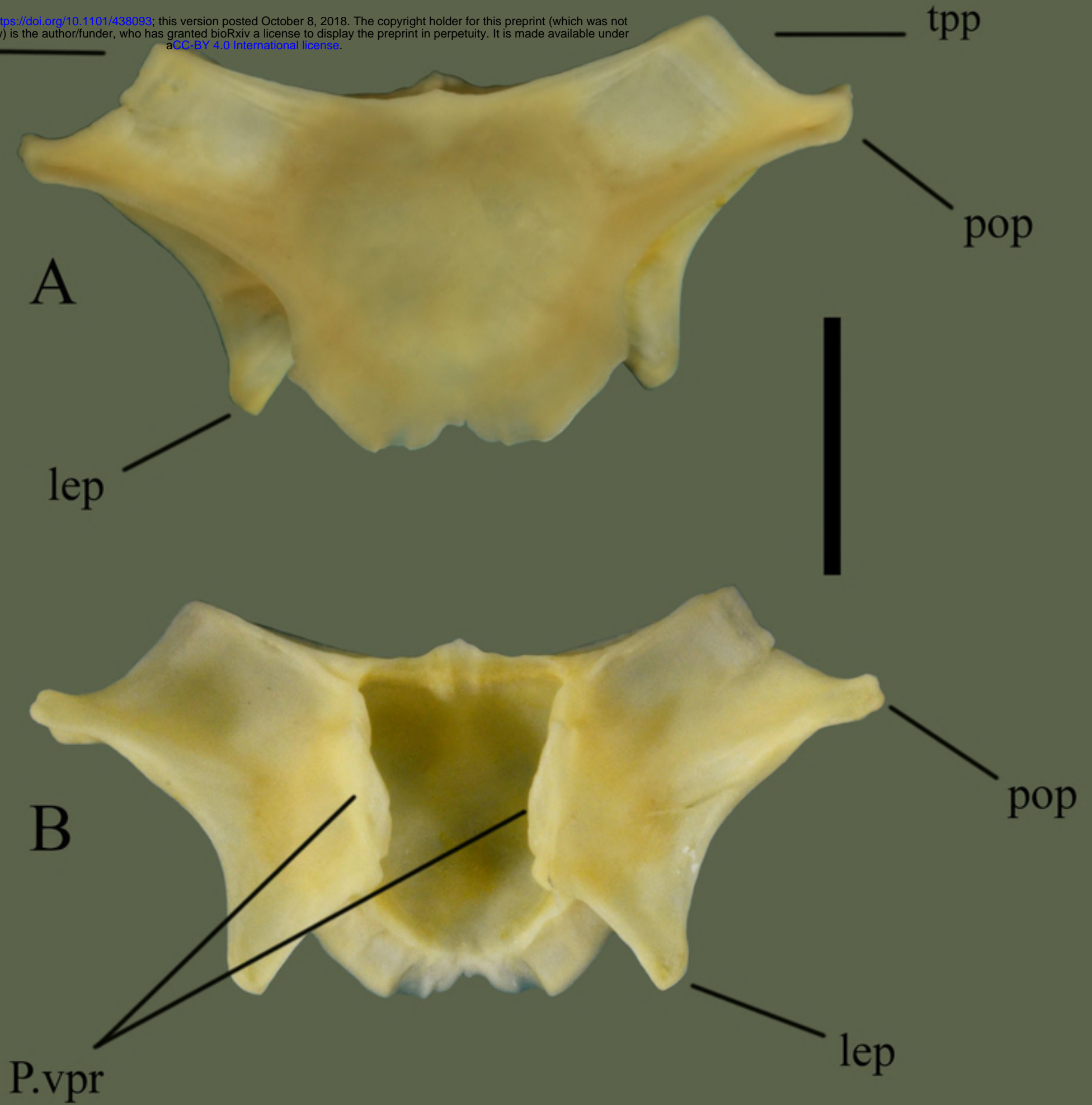
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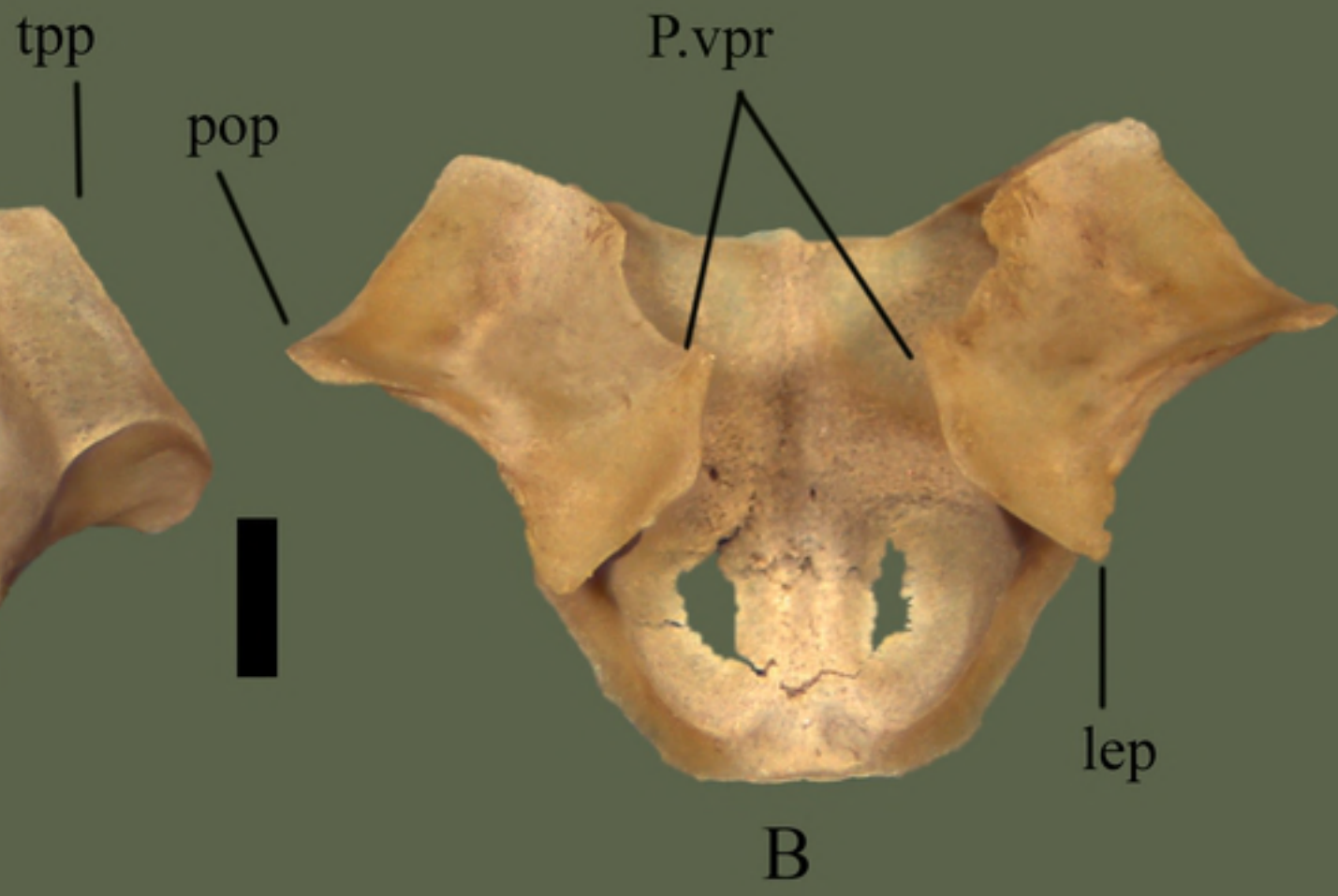
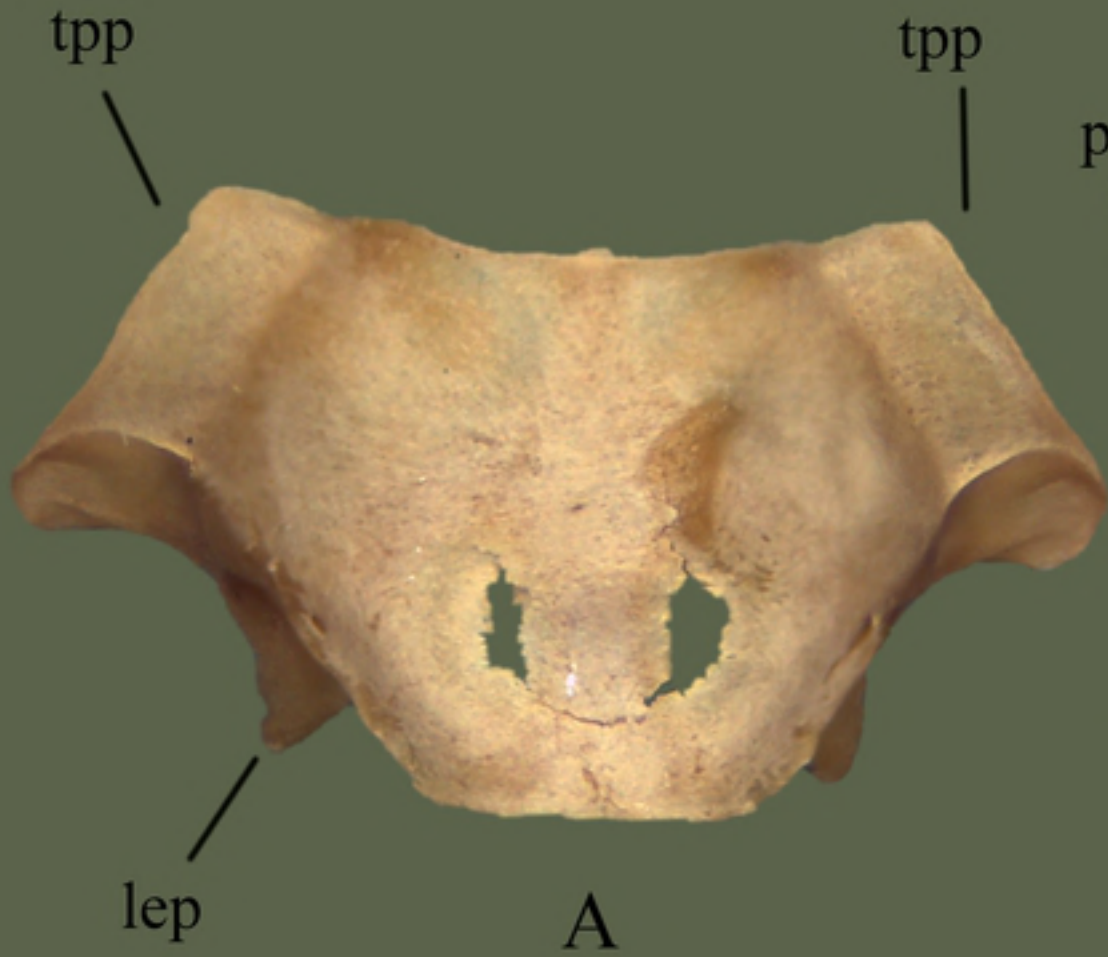
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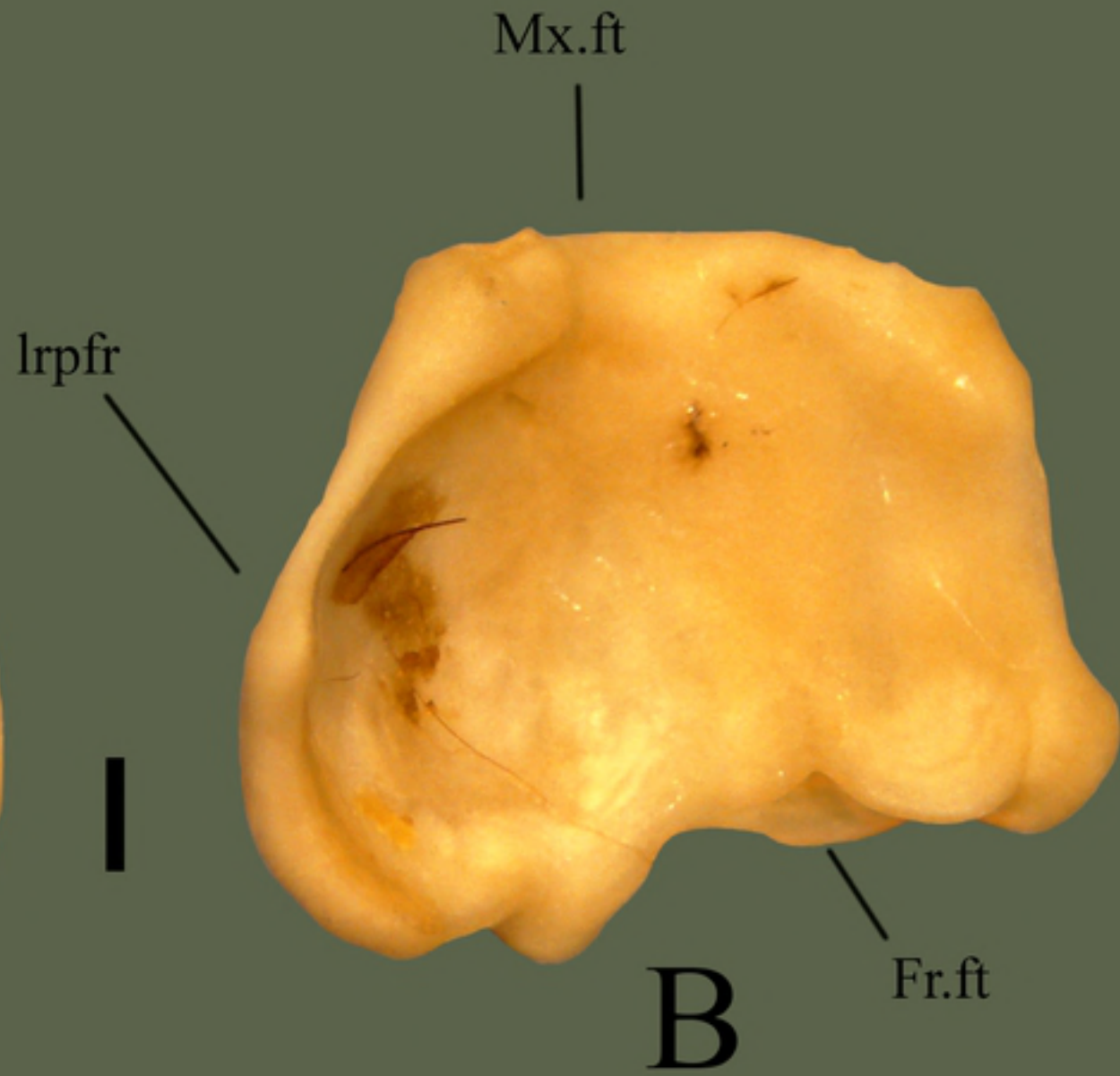
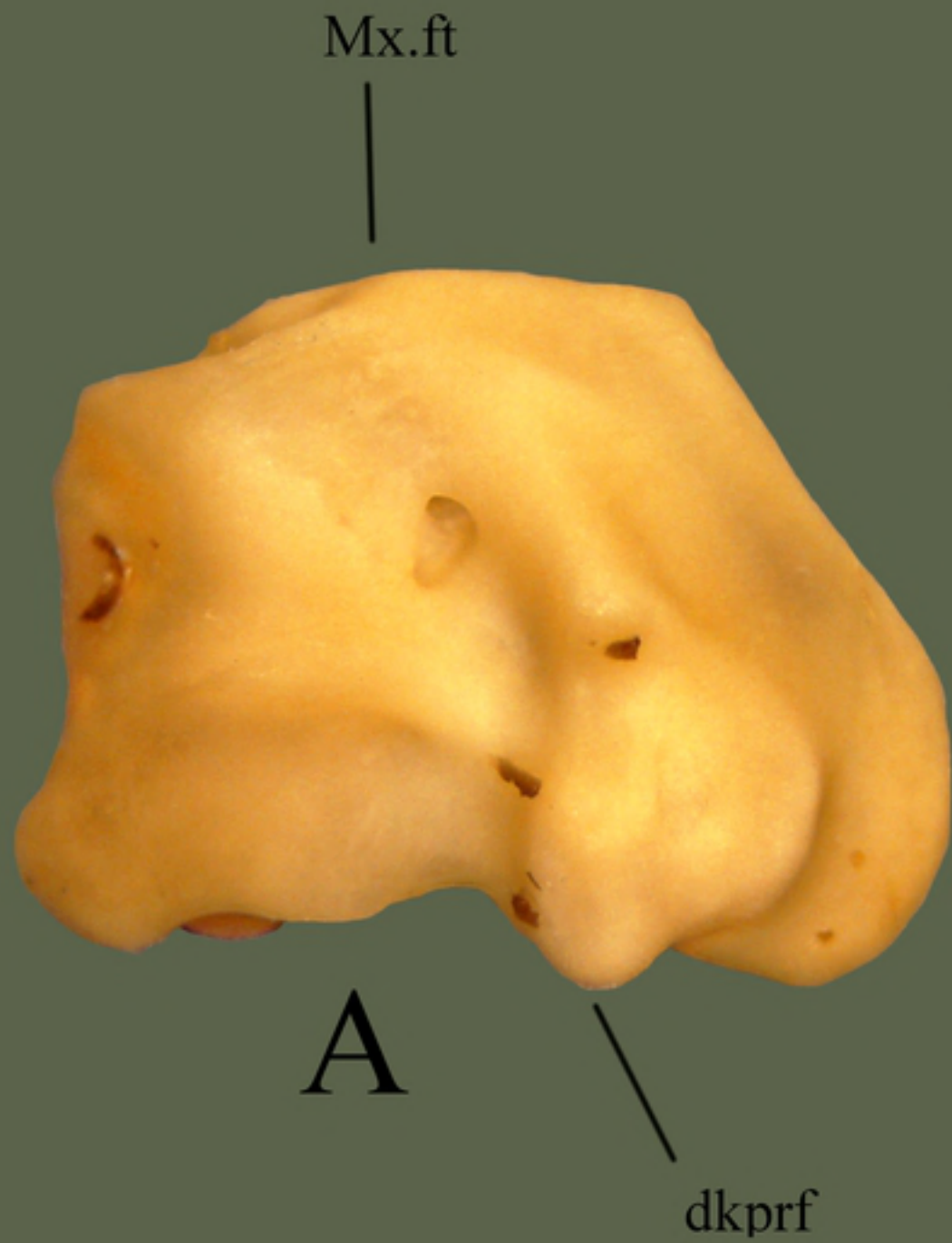
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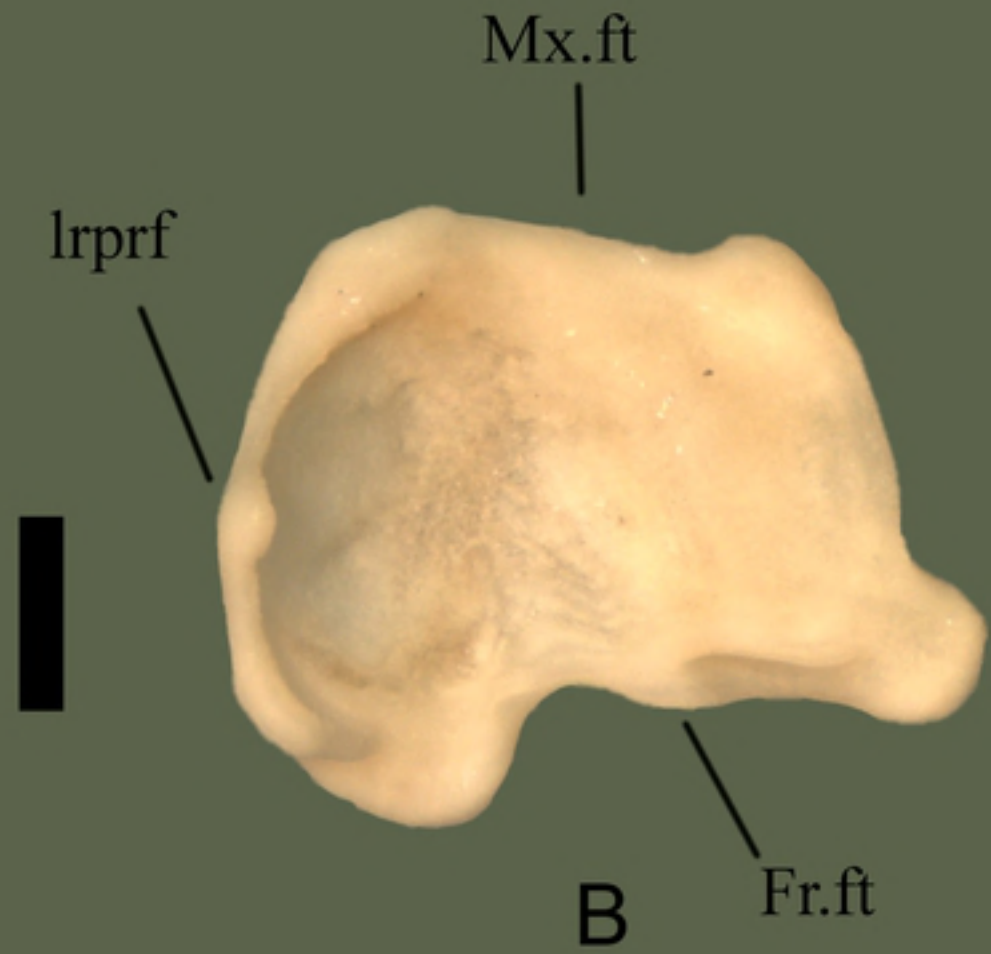
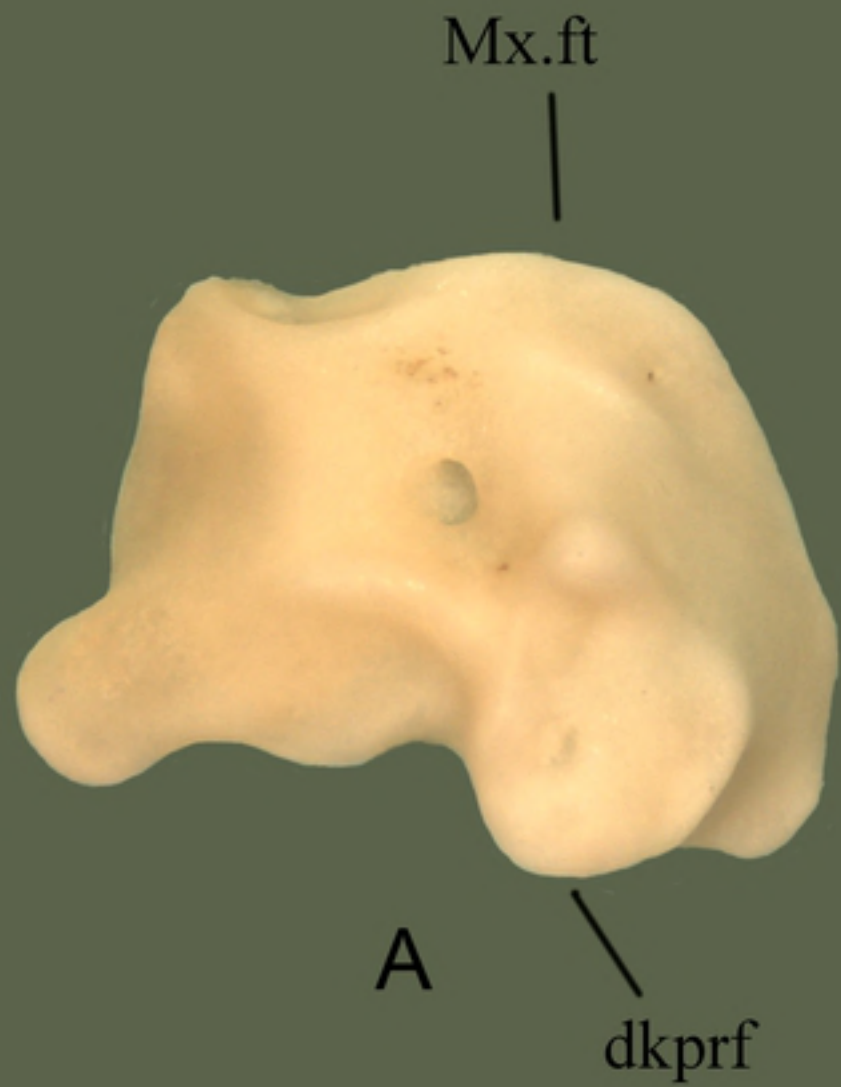
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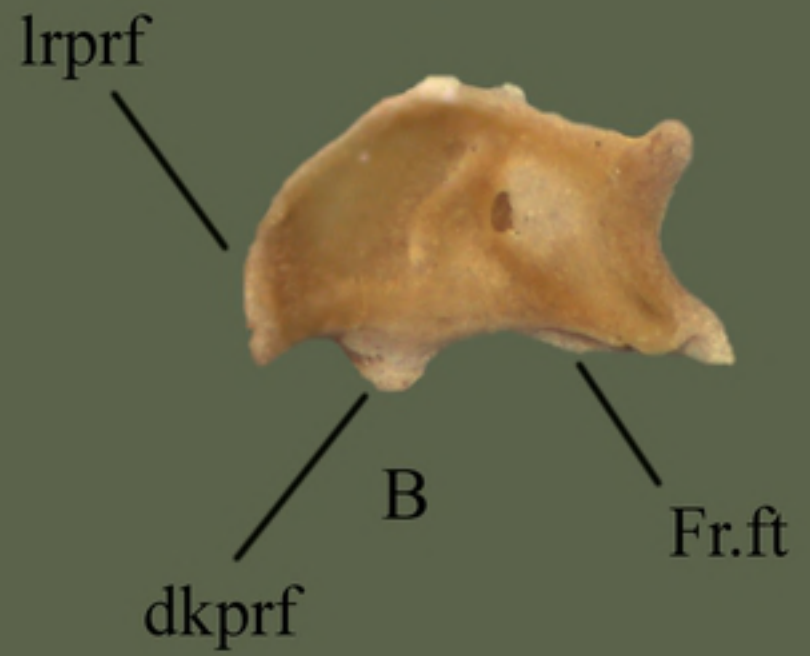


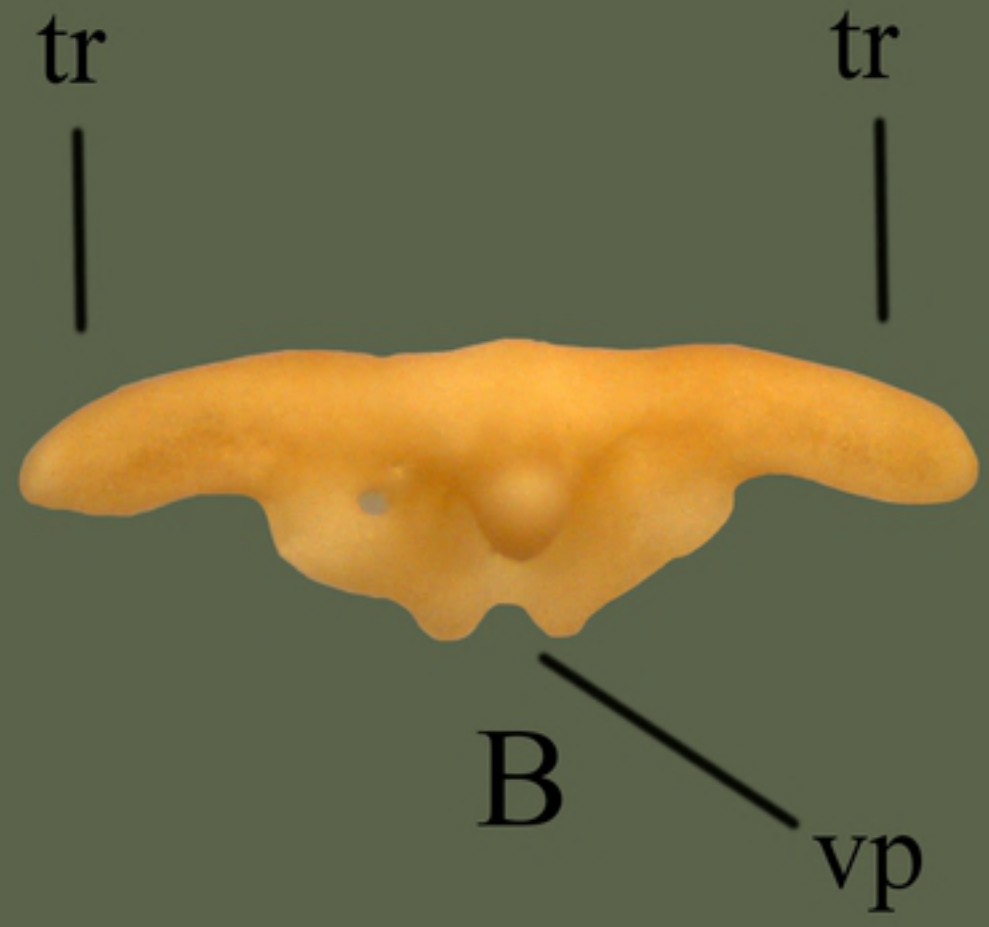
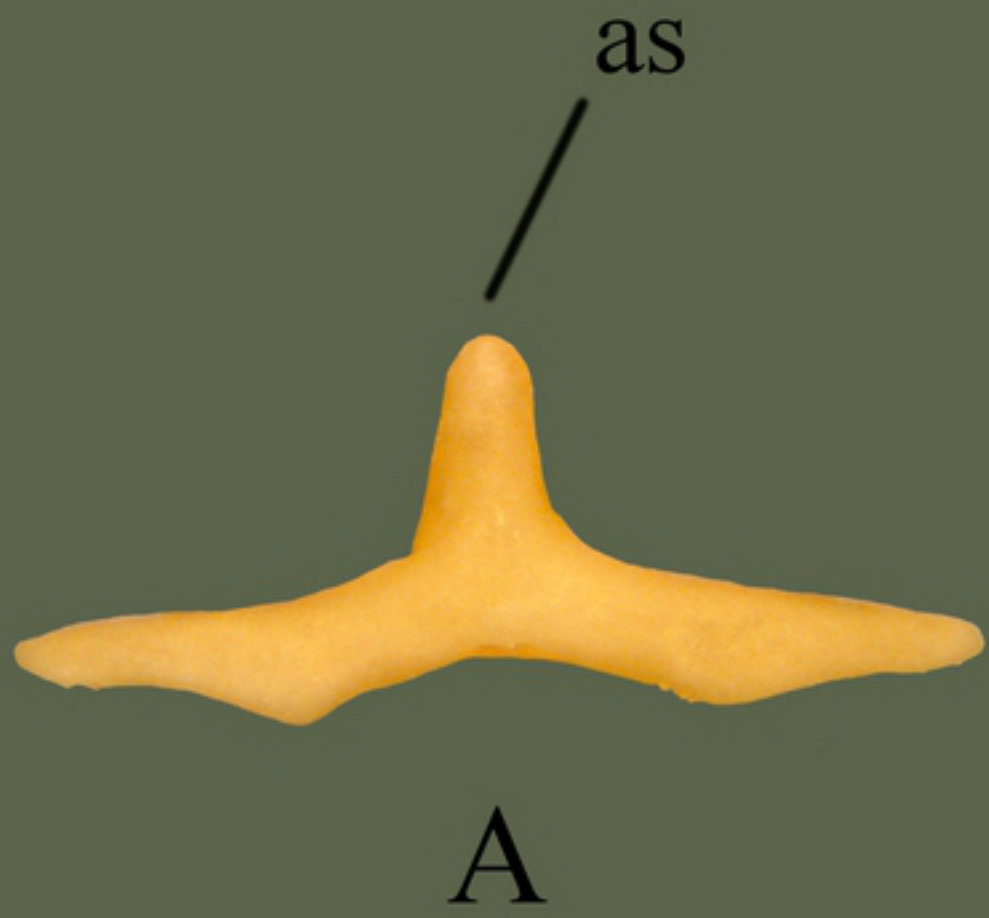












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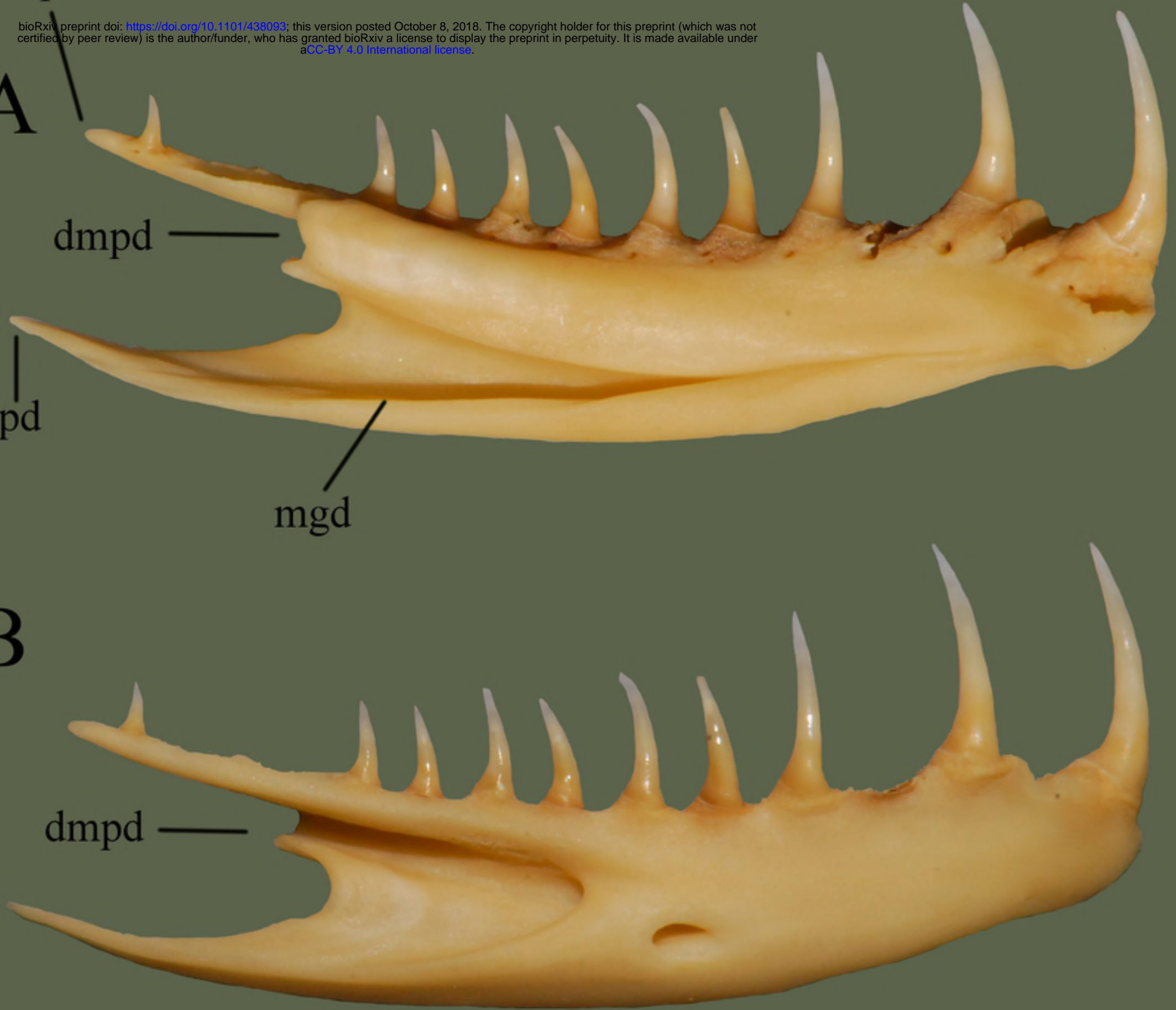
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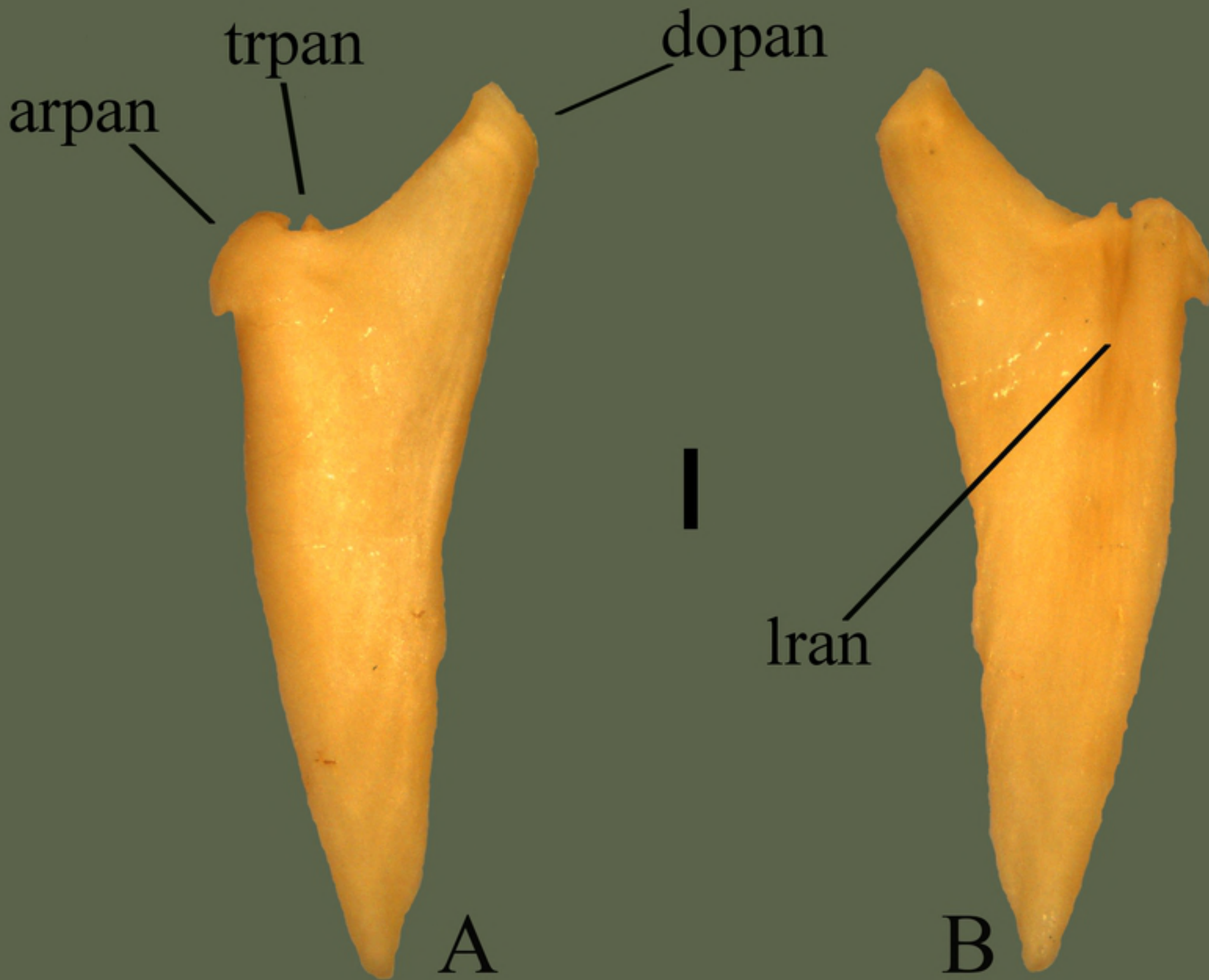
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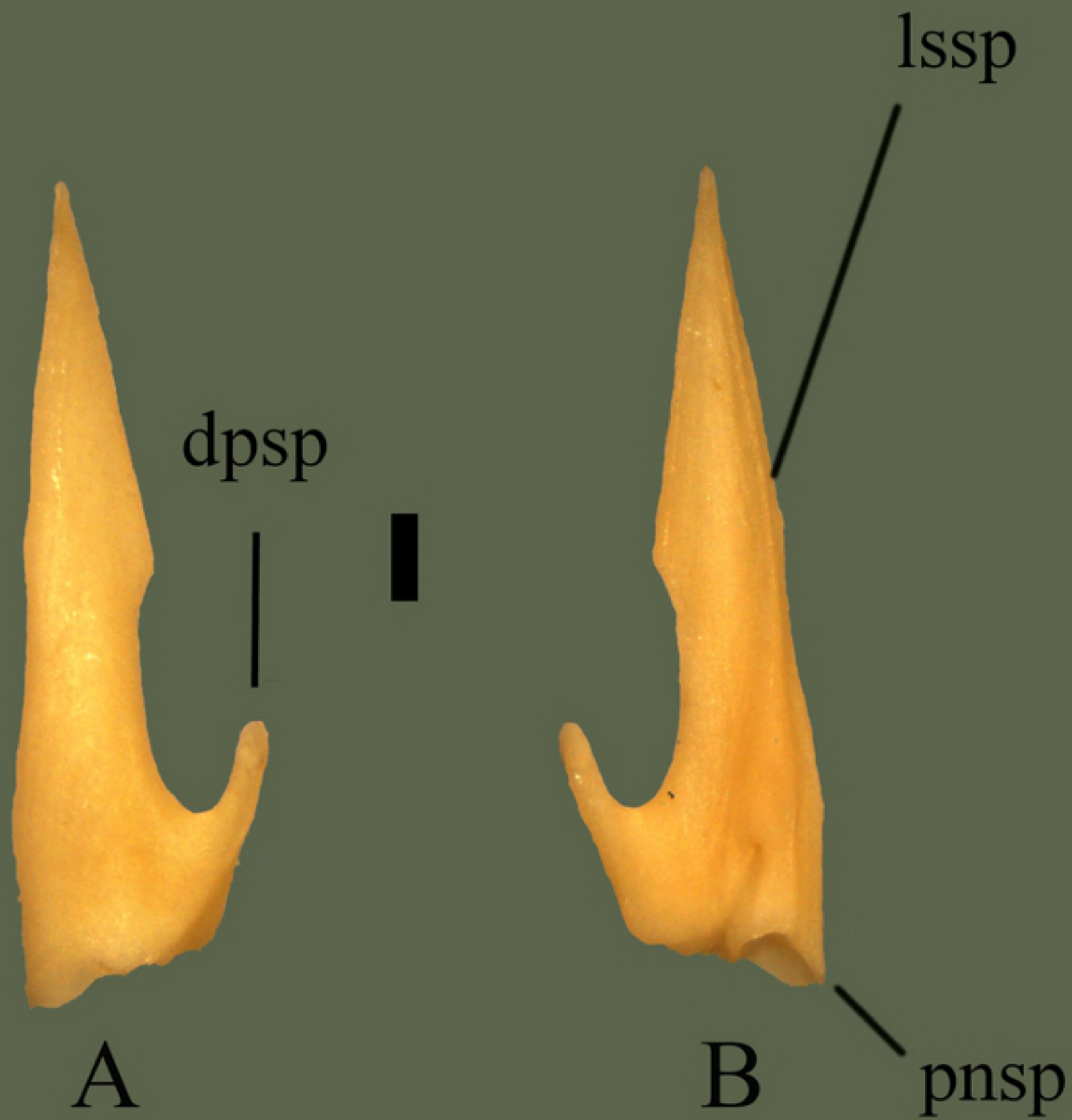
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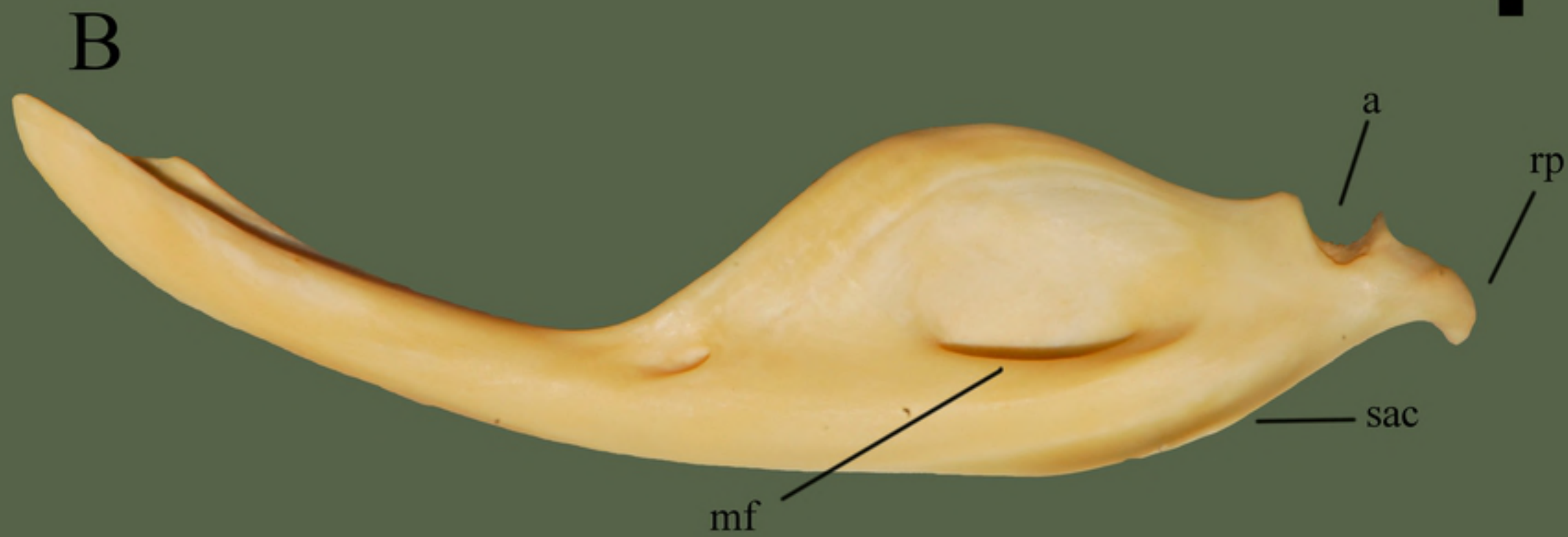
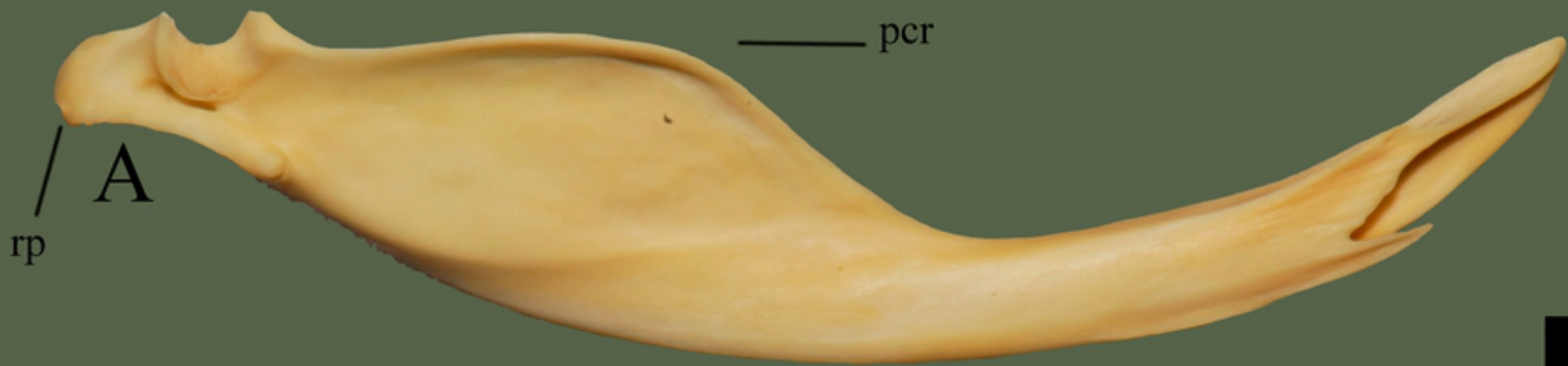
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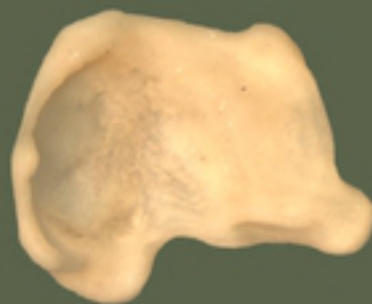


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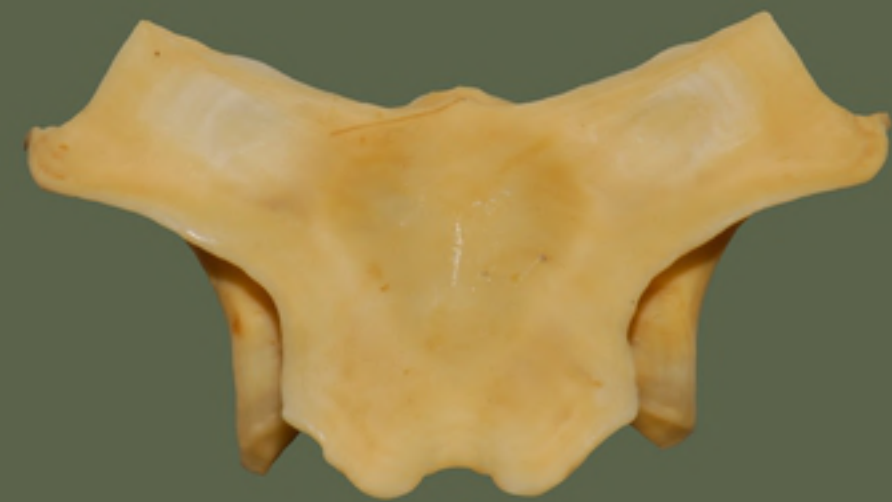


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