# The oldest record of the Steller sea lion *Eumetopias jubatus* (Schreber, 1776) from the early Pleistocene of the North Pacific

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## Abstract

The extant genera of fur seals and sea lions of the family Otariidae (Carnivora: Pinnipedia) are thought to have emerged in the Pliocene or the early Pleistocene in the North Pacific. Among them, the Steller sea lion (*Eumetopias jubatus*) is the largest and distributed both in the western and eastern North Pacific. In contrast to the limited distribution of the current population around the Japanese Islands that is now only along the coast of Hokkaido, their fossil records have been known from the middle and late Pleistocene of Honshu Island. One such important fossils specimens has been recorded from the upper lower Pleistocene Omma Formation (ca. 1.36-0.83 Ma) in Kanazawa, Ishikawa Prefecture, Japan, which now bears the institutional number GKZ-N 00001. Because GKZ-N 00001 is the earliest fossil having been identified as a species of the sea lion genus *Eumetopias*, it is of importance to elucidate the evolutionary history of that genus. The morphometric comparisons were made among 51 mandibles of fur seals and sea lions with GKZ-N 00001. As results of bivariate analyses and PCA based on 39 measurements for external morphologies with internal structures by CT scan data, there is almost no difference between GKZ-N 00001 and extant male individuals of *E. jubatus*. In this regard, GKZ-N 00001 is identified specifically as the Steller sea lion *E. jubatus*. Consequently, it is recognized as the oldest Steller sea lion in the North Pacific. About 0.8 Ma, the distribution of the Steller sea lion had been already established at least in the Japan Sea side of the western North Pacific.

## Introduction

The extant pinnipeds of the order Carnivora are divided into three families, the Otariidae, the Odobenidae, and the Phocidae (e.g., *Berta et al., 2018*). Among them, the otariids are distributed

55  mostly in the Pacific Ocean and composed of fur seals and sea lions. Sea lions are generally large
56  in body size; in particular, the Steller sea lion (*Eumetopias jubatus*) in the North Pacific is the
57  largest among them. In contrast to the relatively limited distribution of the current population of
58  the Steller sea lion in Japan, which is now only around Hokkaido (*Loughlin et al., 1984*; *1987*),
59  their distribution during the Pleistocene is thought to be relatively broad, because their
60  mandibular and tooth fossils have been known from the Pleistocene of Honshu Island. One such
61  important fossil specimens has been recorded from the upper lower Pleistocene Omma
62  Formation (ca. 1.36 – 0.83 Ma) in Kanazawa, Ishikawa Prefecture, Japan, which bears the
63  institutional number GKZ-N 00001 (*Figs. 1, 2*; *Kaseno, 1951*; *Shikama, 1953*; *Mitchell, 1968*).
64  In October 1946, a right mandibular fossil (i.e., GKZ-N 00001) was collected by the late Dr.
65  Yoshio Kaseno (then Kanazawa University) and third year students of the Biological
66  Department, Kanazawa Higher Normal School, Ishikawa Prefecture, Japan. The specimen came
67  from the upper part of the Omma Formation at a road cutting south of Gosyo village (now Gosyo
68  Town), northeastern end of Kanazawa City, Ishikawa Prefecture, central Japan. While *Kaseno*
69  *(1951)* identified GKZ-N 00001 tentatively as a species of "*Allodesmus*" which is an extinct
70  pinniped known from the Miocene of the North Pacific, *Shikama (1953)* pointed out that GKZ-N
71  00001 might belong to *E. jubatus* (*E. jubata* at that time). Later, *Mitchell (1968)* also suggested
72  that GKZ-N 00001 be studied further before being unequivocally identified as conspecific with
73  *E. jubatus*. Currently, the specific identification of GKZ-N 00001 is still ambiguous and in
74  controversy (e.g., *Kohno & Tomida, 1993*; *Barnes et al., 2006*) and has not been confirmed yet.
75  At the time when GKZ-N 00001 was found, the Omma Formation had been considered to be
76  Pliocene in age, but it turned out to be early Pleistocene (ca. 1.36－0.83 Ma) based on the
77  calcareous microfossil stratigraphy (*Takayama et al., 1988*). The extant genera in the Otariidae
78  including *Eumetopias* are considered to be branched off at the end of the Pliocene (*Repenning &*
79  *Tedford, 1977*), and the oldest fossil record of extant otariid genera is known from the late
80  Pliocene to the early Pleistocene (*Berta & Deméré, 1986*; *Kohno & Yanagisawa, 1997*). These
81  studies suggest that the early Pleistocene that may also correspond to the emergence of the genus
82  *Eumetopias* is important time to elucidate the evolutionary history of the otariids. Therefore,
83  highlighting the meaningfulness of proper identification of GKZ-N 00001 is meaningful.
84
## 85  Materials & Methods
86  In order to compare fossil specimens with modern taxa, the morphometric analyses are
87  performed using 51 mandibles of fur seals and sea lions: 12 male and 12 female individuals of
88  the Steller sea lion *E. jubatus*, three male and 10 female individuals of the Northern fur seal
89  *Callorhinus ursinus*, 10 male and one female individuals of the Japanese sea lion *Zalophus*
90  *japonicus*, two male individuals of the Odysseus sea lion *Proterozetes ulysses*, and GKZ-N
91  00001 (Table 1, Data S1). A total of 21 landmarks are defined with reference to the previous
92  morphometric research (*Berta & Deméré, 1986*; *Isono, 1998*; *Adam & Berta, 2002*; *Brunner,*
93  *2004*; *Boessenecker, 2011*; *Kienle & Berta, 2015*), and a total of 39 measurements are taken
94  using a digital caliper to the nearest 0.01 mm (Fig. 3, Tables 2, 3, S1).

95   Based on these measurements, bivariate analyses and principal component analysis (PCA) are
96   performed. PCA is implemented in R 3.5.1 (*R Core Team, 2018*). In addition, the mandibles are
97   observed with the micro-computed tomographic scanner using Microfocus CT, TXS320-ACTIS
98   at the National Museum of Nature and Science, Tokyo, Japan.
99
## Systematic Paleontology
101   MAMMALIA *Linnaeus, 1758*
102   CARNIVORA *Bowditch, 1821*
103   PINNIPEDIA *Illiger, 1811*
104   OTARIIDAE *Gill, 1866*
105   **Included Genera:** [extant genera] *Arctocephalus Cuvier, 1826*; *Arctophoca Peters, 1866*;
106   *Callorhinus Gray, 1859*; *Eumetopias Gill, 1866*; *Neophoca Gray, 1866*; *Otaria Peron, 1816*;
107   *Phocarctos Peters, 1866*; *Zalophus Gill, 1866*. [extinct genera] *Eotaria Boessenecker &*
108   *Churchill, 2015*; *Pithanotaria Kellogg, 1925*; *Thalassoleon Repenning & Tedford, 1977*;
109   *Hydrarctos* (*de Muizon, 1978*) *Berta & Deméré, 1986*; *Proterozetes Barnes et al., 2006* (after
110   *Berta & Churchill, 2011*; *Velez-Juarbe, 2017*).
111   **Emended Diagnosis of Family:** [Crown Otariidae (*C. ursinus*, northern sea lion clade, and
112   southern otariid clade)] single rooted P3, P4, p2, and p4. Pronator teres insertion positioned on
113   the proximal 40% of the radius. Secondary shelf of the sustentaculum of the calcaneum
114   developed as a wider shelf (modified from *Churchill et al., 2014*).
115
116   *EUMETOPIAS Gill, 1866*
117   **Included Species:** Only the extant species *Eumetopias jubatus* (*Schreber, 1766*).
118   **Remarks:** *Horikawa (1981)* described a partial skeleton including some isolated cheek teeth as
119   the holotype of a new species in the genus, i.e., *Eumetopias ojiyaensis*, based on comparisons
120   mainly of the upper incisor and canine with a female of *E. jubatus*.  However, the characters he
121   mentioned (e.g., overall similarity of teeth, condition of accessory cusps on the molar etc.) are
122   plesiomorphic or nondiagnostic for the sea lions and unavoidable the potential identification of
123   the holotype to a species of other sea lion genera within the Otariidae because of its
124   incompleteness. We consider *E. ojiyaensis* a *nomen dubium* and suggest a temporary pending on
125   both generic and specific identification for its holotype until much better specimens at least
126   including the mandible will be obtained from the type locality or the same formation.
127   **Diagnosis of Genus:** As for the species.
128
129   *Eumetopias jubatus* (*Schreber, 1776*)
130   **Emended Diagnosis:** *Eumetopias jubatus* is the largest species in body size (about 3.3 m in
131   males) among the family Otariidae. The upper and lower canines are large in males, particularly
132   at the apical ends of roots that are almost evergrowing (less so in females). The mandible is long
133   and the angle between the horizontal and ascending rami is large (about 130-140 degree) in
134   contrast to the smaller angle of less than 130 degree in other genera and species. The masseteric

135     fossa is deep and long, especially in older individuals. Postcanines are unicuspid with well-
136     developed labial and lingual cusples at the base (modified from *Brunner, 2004*).
137     **Dental formula:** 3/2, 1/1, 4/4, 1/1.
138     **Referred specimen:** GKZ-N 00001, incomplete right dentary with right lower canine, left p2,
139     left and right p4, left P4 and right M1; collected by the late Yoshio Kaseno (then Kanazawa
140     University) and third year students of the Biological Department, Kanazawa Higher Normal
141     School, in October 1946. Now this specimen is stored at the Graduate School of Natural Science
142     and Technology, Kanazawa University (GKZ).
143     **Locality of referred specimen:** GKZ-N 00001 was found at a road cutting south of Gosyo
144     Town, north-eastern end of Kanazawa City, Ishikawa Prefecture, Japan. The geographical
145     coordinate is 36° 34 '51 " North Latitude, 136° 40' 59" East Longitude. Currently, no
146     outcrop remains there.
147     **Formation and Age:** GKZ-N 00001 was yielded from the upper part of the Omma Formation. It
148     is consisted of homogeneous silty fine-grained sandstone in bluish color, from which many
149     fragmentary remains of molluscs such as *Acila*, *Pecten*, *Venericardia*, *Myodora*, *Cardium*, and
150     *Diplodonta* have been collected (*Kaseno,1951*). The geologic age of the Omma Formation
151     corresponds to the late early Pleistocene (ca. 1.36－0.83 Ma) based on the calcareous microfossil
152     stratigraphy (*Takayama et al., 1988*). The depositional environment of the Omma Formation is
153     thought to be cold temperate water within 0－30 m in depth, on a shoreface or inner shelf, the
154     upper part of the upper shallow-sea zone, on the basis of the habitat preferences of molluscan
155     fossils collected from a bed slightly higher than the horizon of GKZ-N 00001 (*Tsuzuku,*
156     *2018MS*).
157     **Associated Mammalian Fossils:** *Matsuura (1996)* reported some metacarpals and phalanges of
158     possibly otariid pinnipeds. In addition, many cetacean and some sirenian fossils have also been
159     found from the same formation (*Matsuura & Nagasawa, 2000*), although these have not yet been
160     described in detail.
161
162     **Description**
163     **Mandible** (Fig. 1)**:** GKZ-N 00001 is a right mandible consisting of almost complete horizontal
164     ramus and broken coronoid process. The c1 and p2 are in place on the horizontal ramus. Both
165     left and right p4 are also preserved as isolated teeth. In addition, isolated left P4 and right M1 are
166     also preserved, suggesting that the skull as well as the left mandible might also be preserved at
167     the time of its discovery. Based on the robustness of the mandible and the size of the canine
168     relative to the length of the cheek toothrow that reaches 42 %, GKZ-N 00001 is definitely a
169     male. The horizontal ramus is long and thick, and has unparallel dorsal and ventral margins. The
170     anterior border of the horizontal ramus (the portion anterior to the incisors and the canine) is
171     expanded anterolaterally. The bone surface of the ramus is rough, but not vascularized. The
172     mandibular symphysis is unfused, elliptical in shape, and upturned anteriorly. The posterior
173     border of the symphysis extends below the anterior margin of p2. The genial tuberosity is very
174     small and located below p3. There are eight distinct mental foramina on the lateral surface of the

175   horizontal ramus. They are nearly rounded or ellipsoidal in form, with the diameter varying from
176   about 3 to 15 mm. The anterior mental foramen is located beneath i3 on the anterior margin of
177   the horizontal ramus and is slit-like. Its length is about 15 mm and width is 4 mm. The middle
178   mental foramina are located between p1 and p3 on the mid portion of the horizontal ramus, and
179   the most anterior elliptical and large hole is located beneath p1 with the diameter of 11 mm in
180   major axis and 6 mm in minor axis. The second middle mental foramen is located beneath p1 and
181   p2 and rounded in outline, with a diameter of 11 mm. The third middle mental foramen is located
182   beneath p2 on the mid portion of the horizontal ramus and is very large ellipsoidal in form. Its
183   major axis is about 11 mm and minor is 6 mm. The fourth middle mental foramen is located
184   between p2 and p3, and is rounded in outline and 6 mm in diameter. The fifth middle mental
185   foramen is located between p3 and p4 and is rounded in outline and 7 mm in diameter. The sixth
186   middle mental foramen is located beneath p4 and is the smallest rounded hole and 6 mm in
187   diameter. The posterior mental foramen is located beneath the posterior margin of m1 and is the
188   rounded in outline and 9 mm in diameter. Almost all of them are directed anterodorsally, but the
189   fifth and sixth forward mental foramina are directed posterodorsally. Most of the coronoid
190   process is broken away. The ventral margin of the masseteric fossa is preserved on the lateral
191   surface and is relatively deep and large in area. It is anteroposteriorly broad at the base of the
192   coronoid process. The pterygoid process is broken at the ventral margin on the medial surface of
193   the ascending ramus. The mandibular foramen is large, with a diameter of 7 mm. The digastric
194   prominence is very weak. The mandibular condyle is broken away, but the breakage suggests
195   that it was elevated slightly high above the level of the cheek toothrow. The dentary has two
196   incisors, one canine, four premolars and one molar. The dentition converges medially from p1
197   until p3 and diverges laterally from p4 until m1. Each tooth is moderately spaced, and the
198   diastema between the c1 and p1 is slightly wider than others.
199

200   **Teeth** (Figs. 1, 2)**:** The i2 and i3 are missing, but their alveoli are preserved anterior to the c1.
201   Both are single rooted. The c1 is robust and conical. Its apex is abraded. The pulp cavity of c1 is
202   widely opened. The p1 is missing, but its alveolus is preserved on the dentary. It is single rooted.
203   The p2 is preserved in place and lanceolate in form with sharp cutting edge. It has a highly
204   developed lingual cingulum, and a well developed accessory cusp is located mesially at the base
205   of the crown. The p3 is fallen away, but its alveolus is preserved, which is single rooted and
206   bilobed in outline. The left and right p4 are preserved as detached isolated teeth. The crown is
207   lanceolate with blunt cutting edge. It has poorly developed lingual cingulum with well developed
208   accessory cusp. Their roots are bilobate and vertical to the long axis of the crown. The m1 is
209   missing, but its alveolus indicates that the m1 is distinctly double rooted.
210   The detached isolated P4 is preserved. The crown is tall and conical, and bluntly pointed at the
211   tip with single cusp. There is no sharp cutting edge with a cingulum at the base of the crown.
212   There is no well developed accessory cusp. It is bilobate single rooted, and its root is oblique to
213   the long axis of the crown. The M1 is also preserved as a detached tooth. It has conical crown,
214   blunt cutting edge, undeveloped cingulum, and slightly developed accessory cusp at the base of

215 crown. It is double rooted and oblique to the long axis of the crown. These roots are curved
216 inward and forward strongly.
217

## Results of Morphometric analyses

### Bivariate analyses

220 GKZ-N 00001 is almost as large as the mandible of male Steller sea lion and larger than that of
221 other known sea lions including the recently extinct Japanese sea lion and the middle Pleistocene
222 Odysseus sea lion (Tables 2, 3, S1). In addition to the differences of their absolute sizes, the p1
223 of the Odysseus sea lion is extremely smaller than other cheek teeth on the mandible (*Poust &*
224 *Boessenecker, 2017*), and the consequent gradient of cheek tooth sizes against the cheek
225 toothrow length are quite different to that of GKZ-N 00001 and of the Steller sea lion. All these
226 results rule out that GKZ-N 00001 belongs to the Odysseus and/or Japanese sea lions in size of
227 the mandible and to the Odysseus sea lion in proportion of the cheek teeth. Given these
228 differences, a taxonomic definition for GKZ-N 00001 as a species of *Eumetopias* is at least
229 warranted. However, given the high amount of morphological variation within species of sea
230 lions necessitates additional morphological approach to classify GKZ-N 00001 more clearly. For
231 these reasons, we made morphometric analyses for GKZ-N 00001 with *E. jubatus* and at least all
232 the North Pacific sea lions including extinct taxa mentioned above.
233 We performed 39 measurements among 21 landmarks on each mandible of 51 individuals from
234 GKZ-N 00001 and extant taxa including 13 Northern fur seals and 24 Steller sea lions and
235 extinct taxa including 11 Japanese sea lions and two Odysseus sea lions in total (Fig. 3, Tables 2,
236 3, S1). These variables were correlated heuristically to each other. Then, highly correlated
237 bivariates were considered to evaluate taxonomic significance for the mandibular fossil. As the
238 results of the analyses, three bivariates by total of six parameters were distinctive among species;
239 the depth of the horizontal ramus at c1 versus the mesiodistal diameter of c1, the depth of the
240 horizontal ramus at p1 versus that of the same portion at m1, and the major axis of the
241 mandibular symphysis versus the minor axis of the same portion (Fig.4). They were also
242 distinctively differentiated between males and females. In all bivariates, GKZ-N 00001 was
243 plotted slightly larger than the 95% confidence interval of the Ordinary Least Square regression
244 lines of the sampled male individuals of *E. jubatus*.
245 These results suggest that the difference between GKZ-N 00001 and the male *E. jubatus* is only
246 a little and that the former could be included in the variation of the latter. In fact, the *E. jubatus*
247 samples used in this study are individuals collected from around Hokkaido for a purpose to
248 prevent damage to the fisheries, so the individuals tend to be slightly smaller in the average of
249 their body size than that of the original population. For this reason, GKZ-N 00001 that is plotted
250 slightly larger than the 95% confidence interval as *E. jubatus* could be interpreted as a large male
251 individual of *E. jubatus*.
252

### Proportion of the canine root

254  Regarding GKZ-N 00001, the greatest mesiodistal and buccolingual diameters of the lower
255  canine root measured from CT image is 50.3 mm and 27.6 mm respectively (Fig. 5, Table 4).
256  Accordingly, the ratio of the buccolingual to mesiodistal diameter expressed as a percentage is
257  54.9. *Kohno & Tomida (1993)* suggested that the same ratio of the lower canines expressed as a
258  percentage for the males of *E. jubatus* ranged from 51.6 to 61.8 (the mean is 56.6; Table 4).
259  Therefore, GKZ-N 00001 is included within the range of male *E. jubatus* in regard to the canine
260  proportion.
261
262  **Principal Component Analysis**
263  The measurement data from mandibles of GKZ-N 00001 with male and female individuals of *C.*
264  *ursinus*, *Z. japonicus*, and *E. jubatus* were analyzed using PCA (Fig. 6). As a result of the
265  analysis, the first principal component (PC1) explains the majority of the variation (~88.8 %),
266  which represents variation of overall size. The larger individuals such as GKZ-N 00001 and male
267  *E. jubatus* have negative scores, while smaller individuals such as female *C. ursinus* have
268  positive scores. Sexual dimorphism can be observed in each taxon. There is only a little
269  difference between GKZ-N 00001 and the sampled male individuals of *E. jubatus*. The second
270  principal component (PC2) represents the proportion of the dorsoventral height and
271  anteroposterior length of the mandible, meaning that the lower the PC2 value, the longer the
272  mandible anteroposteriorly. It also means that the higher the PC2 value, the deeper the mandible
273  dorsoventrally.
274

## Discussion

276  GKZ-N 00001 has lanceolate, simplified cheek teeth, and lacks m2. This condition is recognized
277  to be a synapomorphy of the crown Otariidae (*King, 1983*; *Boessenecker & Churchill, 2015*;
278  *Velez-Juarbe, 2017*). In addition, the overall size of this mandible is included within the range of
279  those in the largest sea lion; i.e., the Steller sea lion *E. jubatus*. Also a result of morphometric
280  analyses for the size and proportion of the mandible for GKZ-N 00001 with extant species of a
281  fur seal and sea lions such as the Northern fur seal, the Japanese sea lion and the Steller sea lion
282  distributed in the western North Pacific suggest that GKZ-N 00001 is included in a range of *E.*
283  *jubatus* and that it is inferred to be a male individual. Therefore, GKZ-N 00001 is distinctively
284  identifiable to the extant species of the Steller sea lion *E. jubatus*. Although GKZ-N 00001 is
285  slightly larger than male individuals sampled from the Recent population, it is at the moment
286  uncertain whether this is simply the size variation among individuals of the same species or a
287  potential implication of larger average size in the early Pleistocene population of the same
288  species. At present, we consider that GKZ-N 00001 was just a large individual of *E. jubatus* until
289  the multiple specimens of mandibles are obtained from the same and/or younger geochronologic
290  formations.
291  Apart from the size difference, all the cheek teeth of the extant specimens of *E. jubatus* are single
292  or bilobate single rooted. However, the alveolus for p4 of GKZ-N 00001 is bilobate single rooted
293  in condition, and m1 is strongly bilobate and apically double rooted (Figs.7, S1). Although this

294   condition is not seen in the variation of extant specimens of *E. jubatus*,  m1 root is always
295   bilobate and its degree is strongly variable and successive among them (Fig. S1). Because the
296   otariids (and stem taxa of odobenids in the Otarioidea) have a process that the cheek tooth
297   condition is gradually changed from double rooted to single rooted to be homodont dentition
298   during their evolution (*Berta & Deméré, 1986; Boessenecker, 2011; Velez-Juarbe, 2018*), the
299   bilobate condition of p4 and the apically double rooted condition of m1 on GKZ-N 00001 are
300   considered to be plesiomorphic conditions in a series of transition to the homodonty within a
301   same species as a parallel phenomenon during their evolution. Accordingly, the condition of the
302   cheek tooth roots on GKZ-N 00001 would also simply be a primitive feature for the lineage of
303   the Steller sea lion.
304   Finally, the recognition of GKZ-N 00001 as the oldest record of *Eumetopias jubatus* could also
305   be important also for the molecular phylogenetics (see also *Parham et al., 2012*). Because only
306   the subfamilial divergence estimates among the pinnipeds had calibrated based on fossil records
307   of crown pinnipeds (e.g., *Yonezawa et al., 2007*), and because the oldest fossil record of
308   *Eumetopias* had not been traced back only until the late Pleistocene, it could be considered the
309   geologic age of GKZ-N 00001 as a good calibration point to improve divergence estimates
310   between *Eumetopias* and its closest genus *Zalophus* and also of the crown Otariidae.
311

## Conclusions

313   The mandibular fossil (GKZ-N 00001) from the lower Pleistocene Omma Formation (0.8 Ma) is
314   specifically identified as *E. jubatus* based on the morphometric analyses. Previously, the oldest
315   record of *E. jubatus* was from the upper Pleistocene of North America (*Kohl, 1974*; *Whitmore &*
316   *Gard, 1977*; *Barnes et al., 2006*), so GKZ-N 00001 from the upper lower Pleistocene (ca. 0.8
317   Ma) is now recognized as the oldest record of *E. jubatus*. This implies that the distribution of the
318   Steller sea lion was already established at about  by 0.8 Ma in the western North Pacific and at
319   least southerly in the Sea of Japan.
320

## Institutional Abbreviations

322   DCIFC:       Daté City Institute of Funkawan Culture, Daté City, Hokkaido, Japan
323   GKZ-N:       Geological collection, Kanazawa University, Kanazawa. New series. Japan
324   HM:          Hokkaido Museum, Sapporo, Hokkaido, Japan
325   NMNS-KK:   The late Kinjiro  Kubota collection, Department of Geology and Paleontology,
326              National Museum of Nature and Science, Tsukuba, Japan
327   NMNS-M:    Mammalogical collections, Department of Zoology, National Museum of Nature
328              and Science, Tsukuba, Japan
329

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342

343 **References**

344 **Adam PJ, Berta A, 2002.** Evolution of prey capture strategies and diet in the Pinnipedimorpha
345   (Mammalia, Carnivora). *Oryctos* **4**: 83－107.
346 **Barnes LG, Ray CE, Koretsky IA, 2006.** A new Pliocene Sea Lion, *Proterozetes ulysses*
347   (Mammalia: Otariidae) from Oregon, U. S. A. *Mesozoic and Cenozoic Vertebrates and*
348   *Paleoenvironments; Tributes to the career of Prof. Dan Grigorescu*, 55－57.
349 **Berta A, Churchill M, 2011.** Pinniped taxonomy: review of currently recognized species and
350   subspecies, and evidence used for their description. *Mammal Review* **42**: 207－234.
351 **Berta A, Churchill M, Boessenecker RW, 2018.** The Origin and Evolutionary Biology of
352   Pinnipeds: Seals, Sea Lions, and Walruses. *Annual Review of Earth and Planetary Sciences* **46**:
353   203－228.
354 **Berta A, Deméré TA, 1986.** *Callorhinus gilmorei* n. sp., (Carnivora: Otariidae) from the San
355   Diego Formation (Blancan) and its implications for otariid phylogeny. *Transactions of the San*
356   *Diego Society of Natural History* **21**: 111－126.
357 **Boessenecker RW, 2011.** New records of the fur seal *Callorhinus* (Carnivora: Otariidae) from
358   the Plio-Pleistocene Rio Dell Formation of Northern California and comments on otariid dental
359   evolution. *Journal of Vertebrate Paleontology* **31**: 454－467.
360 **Boessenecker RW, Churchill M, 2015.** The oldest known fur seal. *Biology Letters* **11**:
361   20140835.
362 **Bowditch TE, 1821.** An Analysis of the Natural Classification of Mammalia for the Use of
363   Students and Travellers. Paris, J. Smith.
364 **Brunner S, 2004.** Fur seals and sea lions (Otariidae): Identification of species and taxonomic
365   review. *Systematics and Biodiversity* **1**: 339－439.
366 **Churchill M, Boessenecker RW, Clementz MT, 2014.** Colonization of the Southern
367   Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined evidence
368   phylogenetic and Bayesian biogeographical analysis. *Zoological Journal of the Linnean*
369   *Society*, **172**, 200－225.
370 **Cuvier F, 1826.** Phoque. *Dicliotmaire des Sciences Naturelles* **39**: 540－559.
371 **Gill T, 1866.** Prodrome of a monograph of the pinnipedes. *Proceedings Essex Institute*
372   *Communications* **5**: 3－13.

373 **Gray JE, 1859.** On the sea bear of Foster, the *Ursus marinus* of Steller, *Aerctocephalus ursinus*
374   of authors. *Proceedings of the Zoological Society of London* **27**: 102－103.
375 **Gray JE, 1866.** Notes on the skulls of sea-bears and sea-lions (Otariadae) in the British
376   Museum. *Annals and Magazine of Natural History Series 3* **18**: 228－237.
377 **Horikawa H, 1981.** On a new fossil sea-lion from the Uonuma Group (Plio-Pleistocene), Ojiya,
378   Niigata Prefecture, Central Japan. *Earth Science* **35:** 159－178.
379 **Illiger JKW, 1811.** Prodromus Systematis Mammalium et Avium Additis Terminis
380   Zoographicis Utriusque Classis, Eorumque Versioe Germanica. Berolini. C. Salfield.
381 **Isono T, 1998.** Development of the external morphology, skull and canines of Steller sea lions.
382   *Biosphere Conservation* **1**: 149－160.
383 **Kaseno Y, 1951.** Pliocene pinniped remains from Kanazawa, Ishikawa Prefecture, Japan.
384   *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* (2): 57－
385   64.
386 **Kellogg R, 1925.** New pinnipeds from the Miocene diatomaceous earth near Lompoc,
387   California. *Contributions to Palaeontology from the Carnegie Institution of Washington* **348**: 71
388   －95.
389 **Kienle SS, Berta A, 2015.** The better to eat you with: The comparative feeding morphology of
390   phocid seals (Pinnipedia, Phocidae). *Journal of Anatomy* **228**: 396－413.
391 **King JE, 1983.** *Seals of the World 2nd Edition*. Ihaca, NY: Cornell University Press.
392 **Kohl RF, 1974.** A new Late Pleistocene fauna from Humbert County, California. *Veliger* **17**:
393   211－219.
394 **Kohno N, Tomida Y, 1993.** Marine mammal teeth (Otariidae and Delphinidae) from the Early
395   Pleistocene Setana Formation, Hokkaido, Japan. *Bulletin of the National Museum of Nature and*
396   *Science Series C (Geology and Paleontology)* **19**: 139－146.
397 **Kohno N, Yanagisawa Y, 1997.** The first record of the Pliocene Gilmore fur seal in the western
398   North Pacific Ocean. *Bulletin of the National Museum of Nature and Science Series C (Geology*
399   *and Paleontology)* **23**: 119－130.
400 **Kubota, K, Nagasaki F, Matsumoto K, Tsuboi M, 1961.** Histological studies on the growth
401   layers in the maxillary canines of fur seals as an indicator of age. Part1. the teeth at the age of
402   one to nine years. *The Bulletin of Tokyo Medical and Dental University* **8:** 261－285.
403 **Linnaeus C, 1758.** Systema nature per regna tria synonymis, locis. Tomus 1. (10th edition).
404   824pp. Stockholm: Laurentius Salvius.
405 **Loughlin TR, Rugh DJ, Fiscus CH, 1984.** Northern sea lion distribution and abundance: 1956-
406   80. *Journal of Wildlife Management* **48**: 729－740.
407 **Loughlin TR, Perez MA, Merrick RL, 1987.** *Eumetopias jubatus*. *Mammalian Species* (283):
408   1－7.
409 **Matsuura N, 1996.** Vertebrate fossils from the Omma Formation of Kanazawa area, Ishikawa
410   Prefecture, Japan. *HGI Report*: (5), 55－87.

411 **Matsuura N, Nagasawa K, 2000.** Fossil cetaceans from the distribution area of the Omma

412 Formation in Kanazawa, Ishikawa Prefecture, Japan. *Nihonkai Cetology*: (10), 37－47.

413 **Mitchell ED Jr, 1968.** The Mio-Pliocene pinniped *Imagotaria*. *Journal of the Fisheries*

414 *Research Board of Canada* **25**: 1843－1900.

415 **Muizon C de, 1978.** *Arctocephalus* (*Hydractos*) *lomasiensis*, subgen, nov. et nov. sp., un nouvel

416 Otariidae du Mio-Pliocene de Sacaco (Perou). *Bulletin de l'Institut Francais d'Etudes Andines*

417 7: 168-188.

418 **Parham JF, Donoghue PCJ, Bell CJ, Calway TD, Head JJ, Holroyd PA, Inoue JG, Irmis**

419 **RB, Joyce WG, Ksepka DT, Patane JSL, Smith ND, Tarver JE, Tuinen M van, Yang Z,**

420 **Angielczyk KD, Greenwood JM, Hipsley CA, Jacobs L, Makovicky PJ, Muller J, Smith**

421 **KT, Theodor JM, Warnock RCM, 2012.** Best practices for justifying fossil calibrations.

422 *Systematic Biology* **61**: 346-359.

423 **Peron F, 1816.** Voyage de decouvertes aux terres Australes, execute par ordre de Sa Majeste

424 l'Empereur et Loi, sur les corvettes le Geographe, le Naturaliste, et la goelette le Casuarina,

425 pendant les annees. 1800, 1801, 1802, 1803, et 1804. *Imprimerie Imperiale*. Paris, 2, 1－471.

426 **Peters W, 1866.** Über neue oder ungengend bekannte Flederthiere (*Vampyrops*, *Uroderma*,

427 *Chiroderma*, *Ametrida*, *Tylostoma*, *Vespertilio*, *Vesperugo*) und Nager (*Tylomys*, *Lasiomys*).

428 *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* **1867**: 392

429 －411, 2 pls.

430 **Poust AW, Boessenecker RW, 2017.** Mandibles of the sea lion Proterozetes ulysses from the

431 middle Pleistocene Port Orford Formation of Oregon. *Journal of Vertebrate Paleontology* :

432 e1317637 (8 pages).

433 **R Core Team, 2018.** *R: A language and environment for statistical computing*. R Foundation for

434 Statistical Computing, Vienna, Austria. https://www.R-project.org/.

435 **Repenning CA, Tedford RH, 1977.** Otarioid seals of the Neogene. *Geological Survey*

436 *Professional Paper* **992**: 1－93.

437 **Schreber JCD, 1776.** Die Saugethiere in Abbildungen nach der Natur, mit Beschreibungen.

438 Leipzig: (7), 1774－1846.

439 **Shikama T, 1953.** On a fossil remain of sea-lion, *Eumetopias* (?) *kishidai* n. sp. from Japan.

440 *Science Reports of the Yokohama National University, Series 2* (2): 10－16.

441 **Takayama T, Kato M, Kudo T, Sato T, Kameo K, 1988.** Calcareous microfossil

442 biostratigraphy of the uppermost Cenozoic formations distributed in the coast of the Japan Sea

443 －Part2: Hokuriku sedimentary basin－. *Journal of the Japanese Association for Petroleum*

444 *Technology* **53**: 10－27.

445 **Tsuzuku N, 2018MS.** Stratigraphy and Paleontology of the Pleistocene Omma Formation

446 Distributed in Kanazawa, Ishikawa Prefecture, Japan. University of Tsukuba.

447 **Velez-Juarbe J, 2017.** *Eotaria citrica*, sp. nov., a new stem otariid from the "Topanga"

448 Formation of Southern California. *PeerJ* 5: e3022. https://doi.org/10.7717/peerj.3022.

449 **Velez-Juarbe J, 2018.** New data on the early odobenid *Neotherium mirum* Kellogg, 1931, and
450  other pinniped remains from the Sharktooth Hill Bonebed, California. *Journal of Vertebrate*
451  *Paleontology* 38: e1481080 (14 pages).
452 **Whitmore FC Jr, Gard LM Jr, 1977.** Steller's Sea Cow (*Hydrodamalis gigas*) of Late
453  Pleistocene age from Amchitka, Aleutian Islands, Alaska. Geological Survey Professional
454  Paper **1306**: IV+19+[19].
455 **Yonezawa T, Kohno N, Hasegawa M, 2009.** The monophyletic origin of sea lions and fur seals
456  (Carnivora; Otariidae) in the Southern Hemisphere. *Gene* 441: 89-99.

# Figure 1

Right mandibular fossil of *Eumetopias jubatus* (GKZ-N 00001)

(A) lateral aspect (B) medial aspect (C) dorsal aspect

Photo credit: Nahoko Tsuzuku

(A)

mandibular condyle

masseteric fossa

c1

p2

pterygoid process

mental foramina

genial tuberosity

(B)

c1

p2

coronoid process

mandibular foramen

mandibular symphysis

digastric prominence

(C)

c1

p1 alveolus

p2

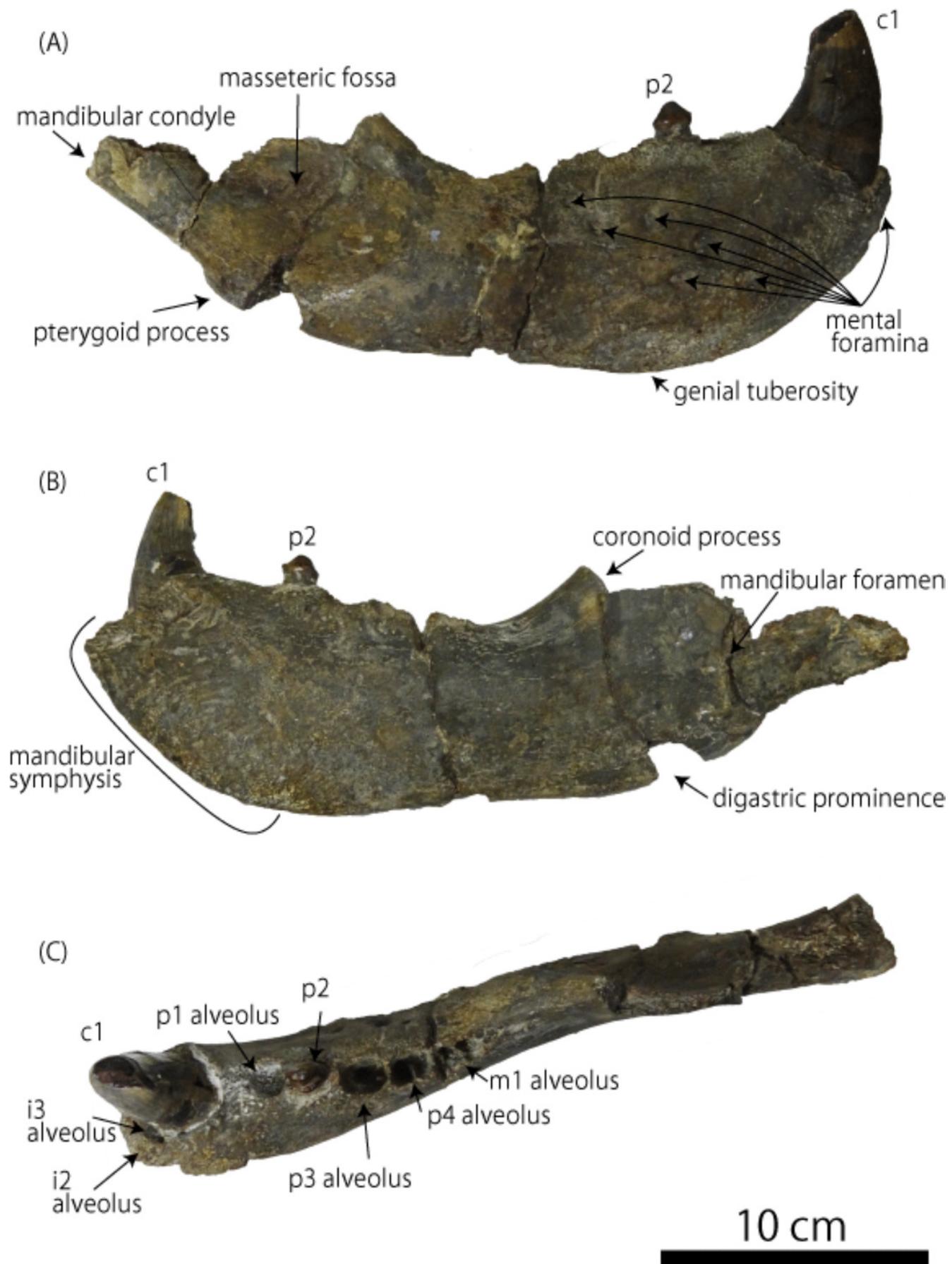
m1 alveolus

i3 alveolus

p4 alveolus

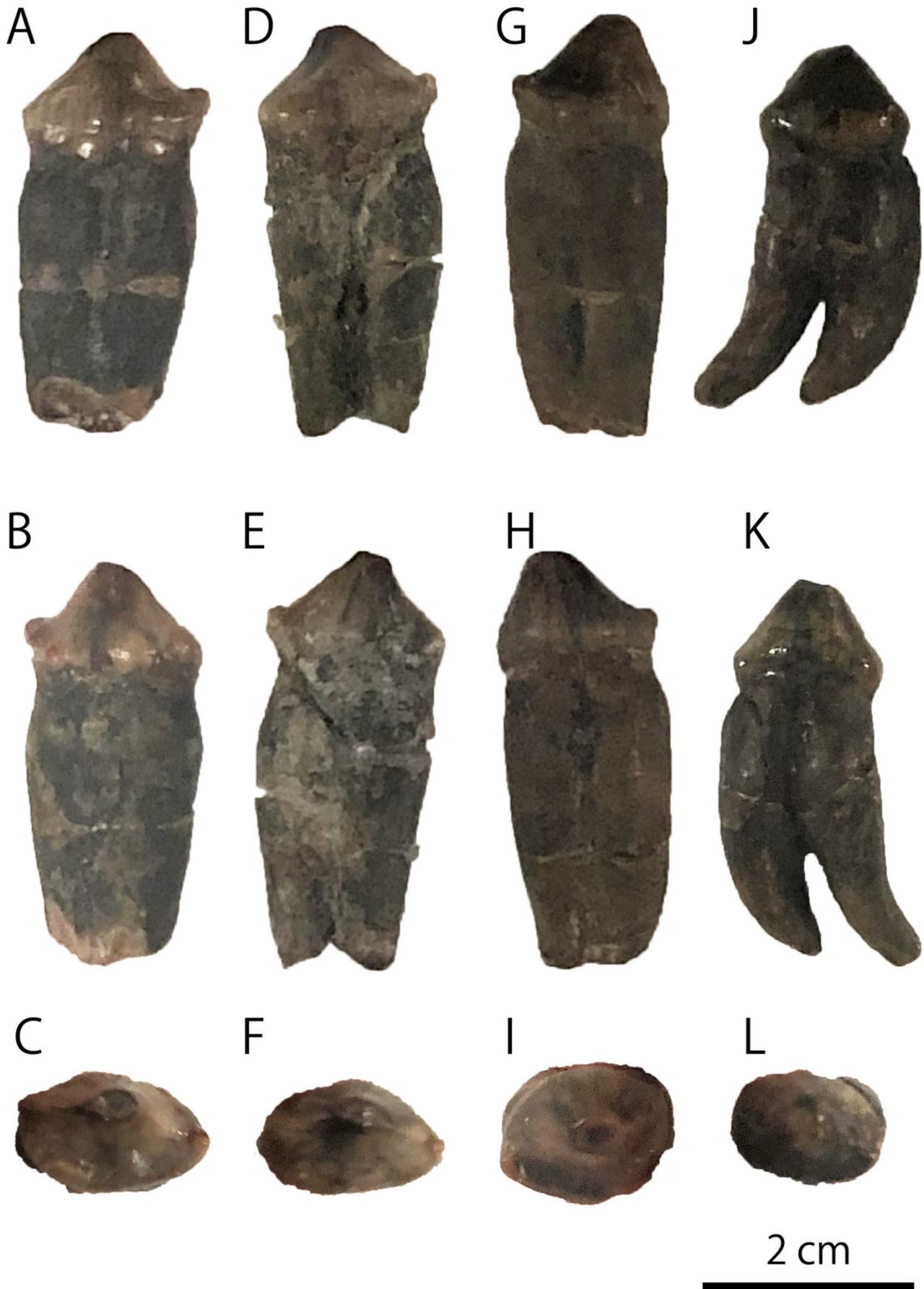
i2 alveolus

p3 alveolus

10 cm

# Figure 2

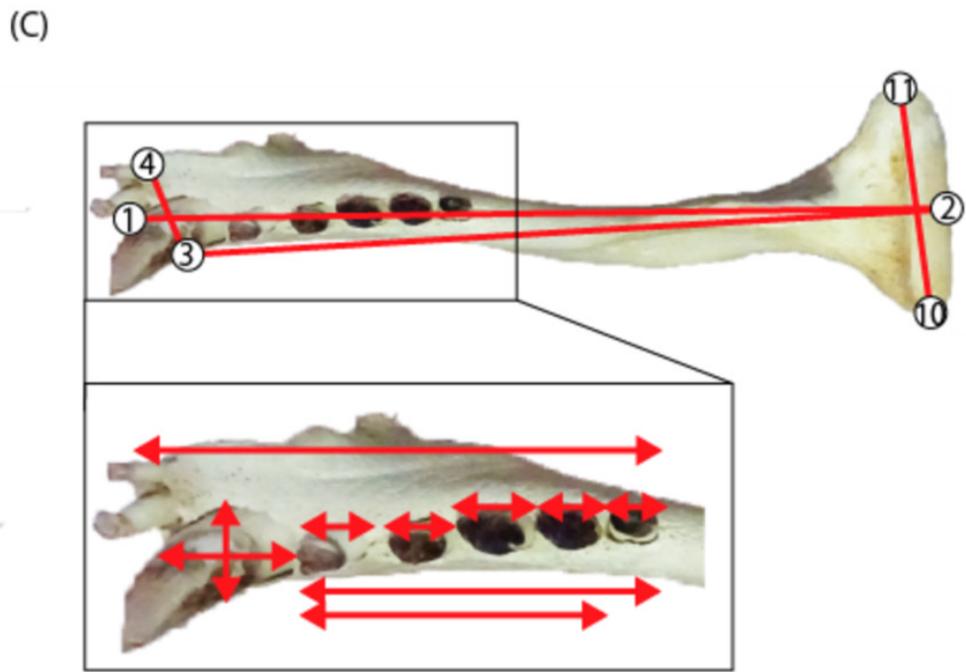
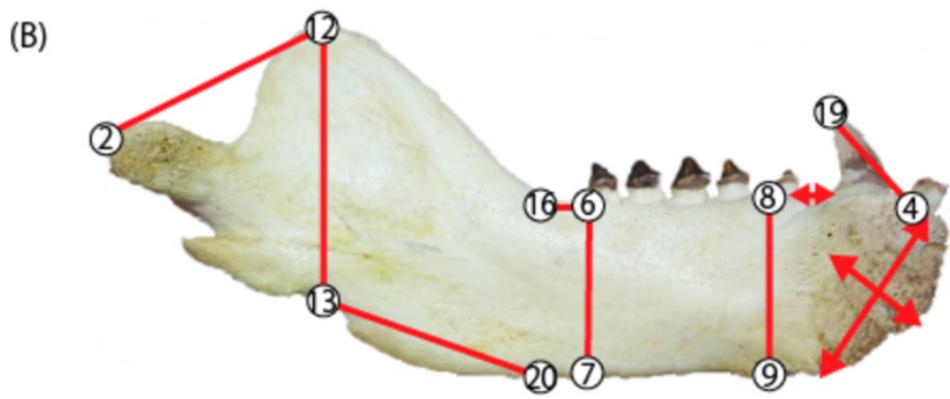
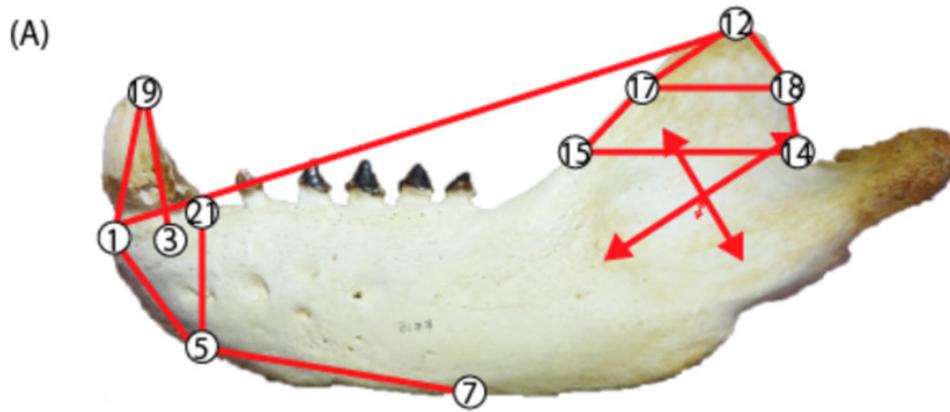
Detached molariform teeth of GKZ-N 00001

(A) lingual view of left p4 (B) buccal view of left p4 (C) occlusal view of left p4 (D) lingual view of right p4 (E) buccal view of right p4 (F) occlusal view of right p4 (G) lingual view of left P4 (H) buccal view of left P4 (I) occlusal view of left P4 (J) lingual view of right M1 (K) buccal view of right M1 (L) occlusal view of right M1

Photo credit: Nahoko Tsuzuku

# Figure 3

Mandibular landmarks and measurements used in this study

(A) lateral aspect (B) medial aspect (C) dorsal aspect

Photo credit: Nahoko Tsuzuku

# Figure 4

Result of bivariate analyses

(A) depth of horizontal ramus at c1 (I) versus the mesiodistal diameter of c1 (AF); (B) depth of horizontal ramus at p1 (J) versus that of same portion at m1 (K); (C) major axis of mandibular symphysis (X) versus minor axis of same portion (Y). Pink polygons show 95% confidence intervals of the regression lines. Characters in parentheses correspond to measurement points (Table S1).

(A)

mesiodistal diameter of c1 (AF)

depth of ramus at c1 (I)

(B)

depth of ramus at m1 (K)

depth of ramus at p1 (J)

(C)

minor axis of mandibular symphysis (Y)

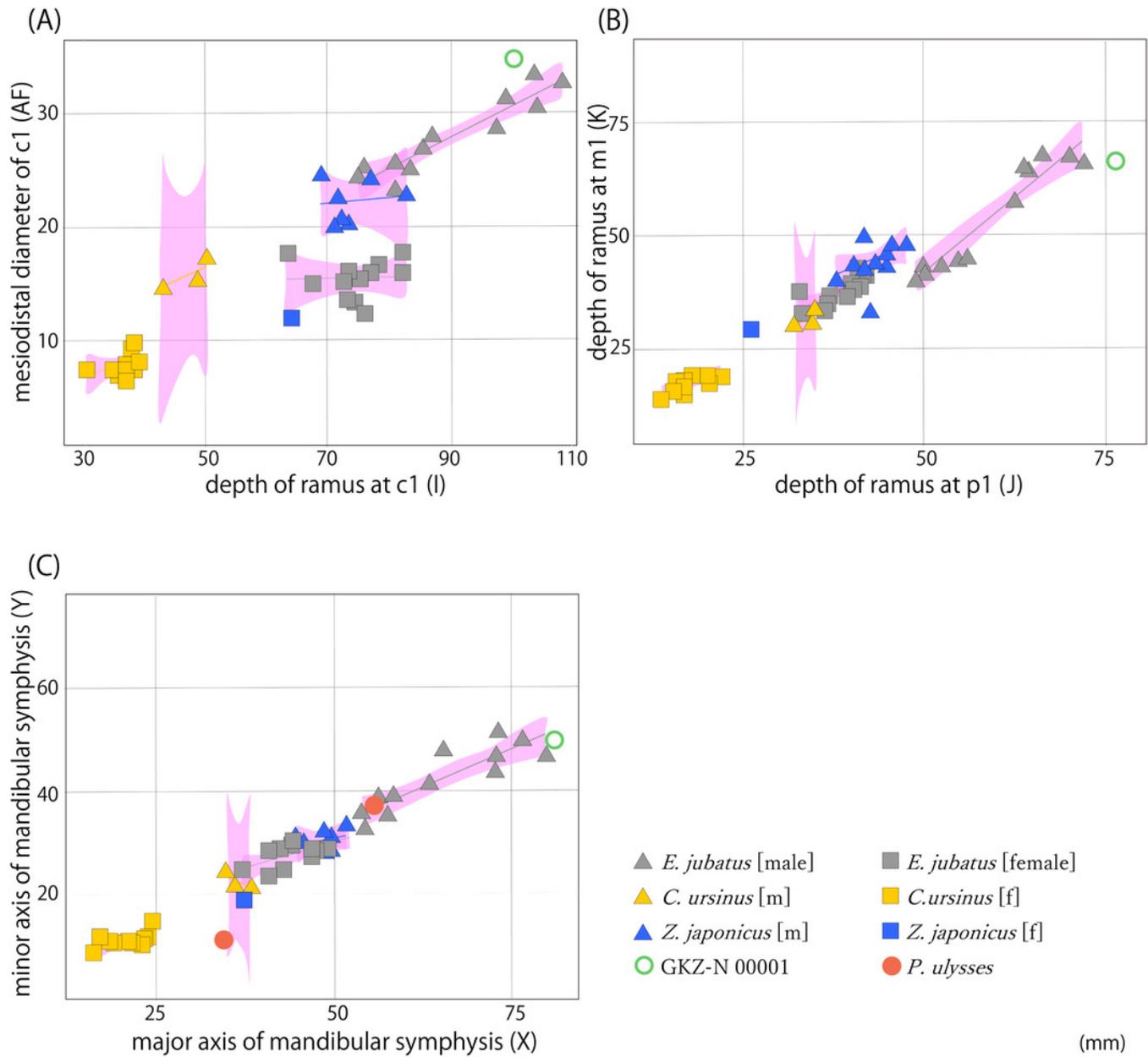
major axis of mandibular symphysis (X)

▲ *E. jubatus* [male]          ■ *E. jubatus* [female]

▲ *C. ursinus* [m]             ■ *C. ursinus* [f]

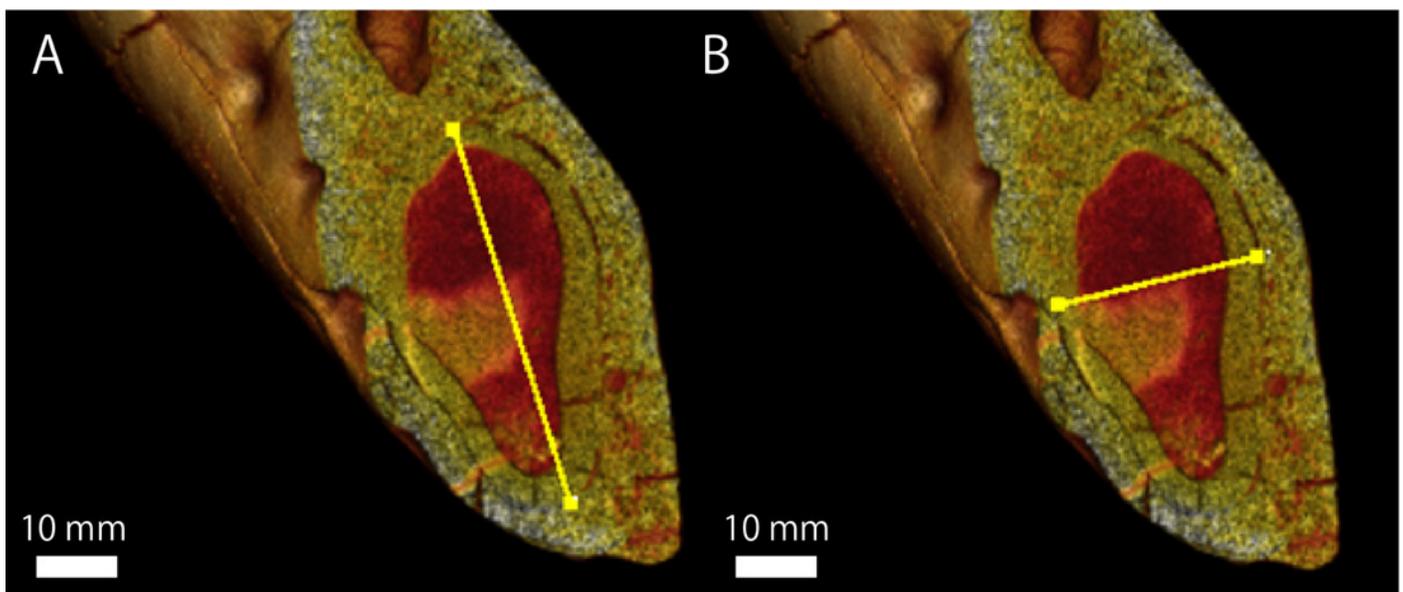
▲ *Z. japonicus* [m]           ■ *Z. japonicus* [f]

○ GKZ-N 00001                  ● *P. ulysses*

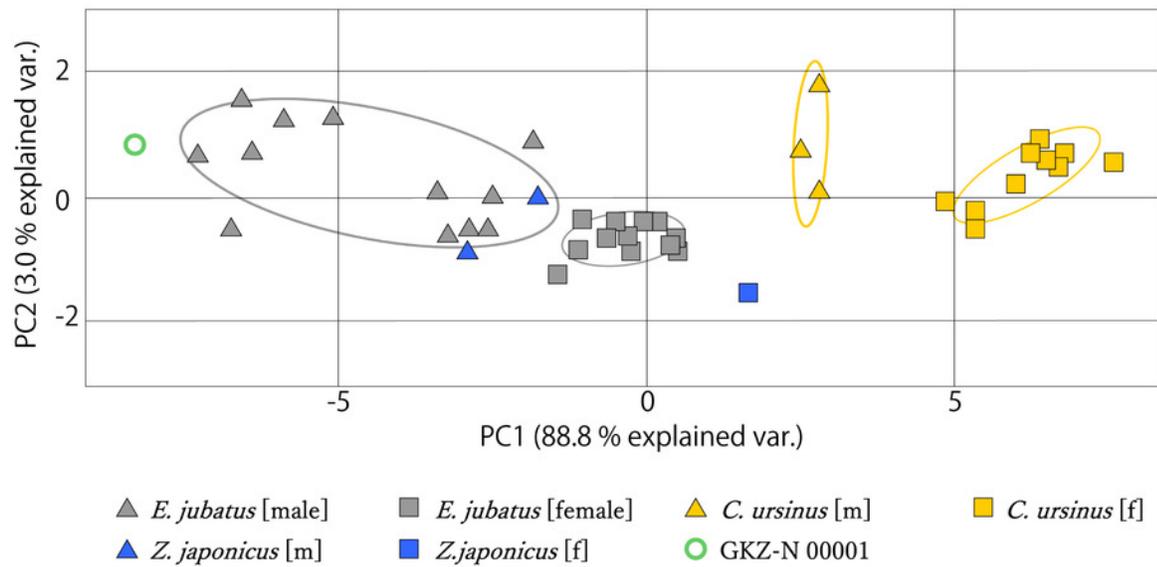
(mm)

# Figure 5

A micro CT image, showing the maximum length and width of lower canine root of GKZN 00001.

Yellow lines indicate: (A) mesiodistal diameter (B) buccolingual diameter

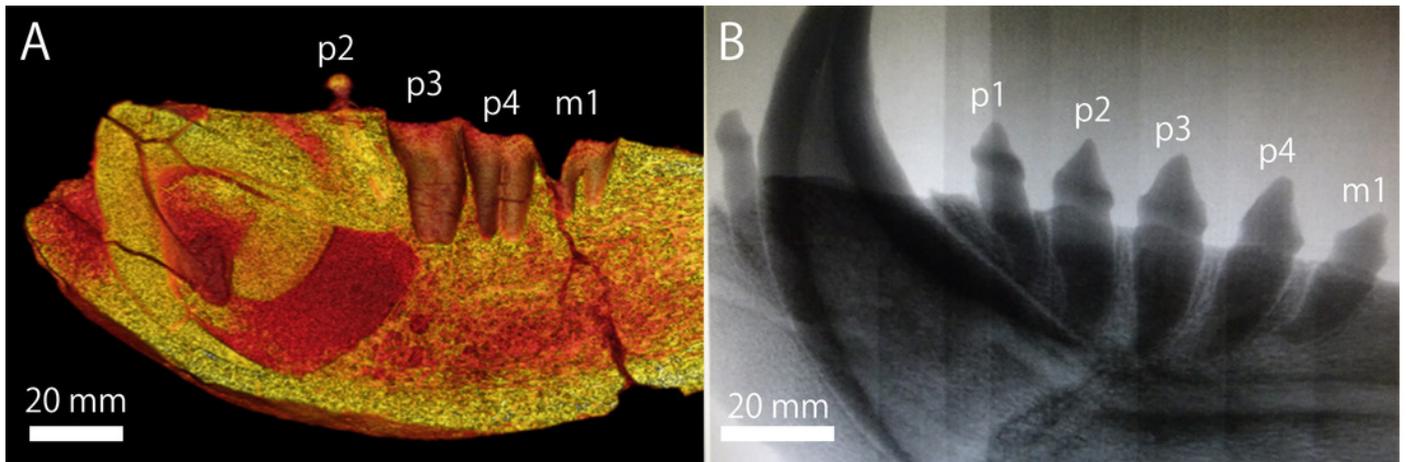
Photo credit: Naoki Kohno

# Figure 6

Mandibular PCA results comparing PC1 and PC2

Ovals represent 95% confidence intervals for each group (species and sex).

# Figure 7

Postcanine roots by CT image

(A) GKZ-N 00001 (B) *E. jubatus* (NMNS-KK 14)

Photo credits: (A) Naoki Kohno (B) Chisako Sakata

Sample list

| Scientific name | Sex | N | Registration number |
|---|---|---|---|
| *Eumetopias jubatus* | male | 12 | NMNS-KK14,15,23,51,63,69,73,167,169,192,NSMT-M5627,28387 |
| | female | 12 | NMNS-KK11,53,54,55,56,139,146,154,158,165,166,NSMT-M17123 |
| *Callorhinus ursinus* | male | 3 | NSMT-M2454,46874,17140 |
| | female | 10 | NMNS-KK05,08,10,22,24,141,151,NSMT-M42128,35148,1995 |
| *Zalophus japonicus* | male | 10 | HM-55953-18-1~8 / DCIFC-ER11H,-HM2L |
| | female | 1 | DCIFC-HM2・97R.No.30262 |
| *Proterozetes ulysses* | male | 2 | USNM 187109 (*Barnes et al., 2006*),<br>UCMP 219377 (*Poust & Boessenecker, 2017*) |

Mandibular landmarks used in this study

| 1 | rostral tip of mandible (gnathion) |
|---|---|
| 2 | caudal-most point of mandibular condyle |
| 3 | lateral edge of canine midpoint |
| 4 | medial edge of mandibular symphysis caudal to the first incisor |
| 5 | ventral edge of mandible underneath the canine |
| 6 | lateral and caudal edge of last postcanine |
| 7 | ventral edge of mandible underneath the last postcanine |
| 8 | lateral and caudal edge of p1 |
| 9 | ventral edge of mandible underneath the p1 |
| 10 | lateral-most point of mandibular condyle |
| 11 | medial-most point of mandibular condyle |
| 12 | dorsal-most point of coronoid process (koronion) |
| 13 | ventral edge of mandible underneath the tip of the coronoid process |
| 14 | caudal-most point of coronoid process |
| 15 | rostral point horizontal to caudal-most point of coronoid process |
| 16 | rostral start point of the coronoid process |
| 17 | rostral-most point on curving edge of coronoid process |
| 18 | caudal-most point on curving edge of coronoid process |
| 19 | dorsal tip of canine |
| 20 | ventral edge of mandible underneath the start of the coronoid process |
| 21 | lateral and caudal edge of canine |

Measurements (in mm) of GKZ-N 00001 for morphometric analyses

The numbers in parentheses correspond to each landmark.

| | |
|---|---|
| rostral tip of mandible－ventral edge of mandible underneath the canine (1-5) | 50.35 |
| width of mandible (3-4) | 42.76 |
| depth of ramus at c1(5-21) | 75.15 |
| depth of ramus at p1(8-9) | 76.46 |
| depth of ramus at m1 (6-7) | 66.34 |
| ventral edge of mandible underneath the canine－ventral edge of mandible underneath the last postcanine (5-7) | 100.13 |
| lateral and caudal edge of last postcanine–rostral start point of the coronoid process (6-16) | 27.60 |
| major axis of mandibular symphysis | 81.31 |
| minor axis of mandibular symphysis | 50.29 |
| major axis of masseteric fossa | 68.43 |
| minor axis of masseteric fossa | 45.73 |
| depth of masseteric fossa | 13.18 |
| tooth length | 123.89 |
| cheek tooth length□ | 84.03 |
| transverse width of c1 | 27.32 |
| mesiodistal diameter of c1 | 35.00 |
| anteroposterior length of p1 | 13.33 |
| anteroposterior length of p2 | 12.79 |
| anteroposterior length of p3 | 16.07 |
| anteroposterior length of p4 | 14.51 |
| anteroposterior length of m1 | 18.42 |
| diastema length between c1 and p1 | 10.04 |

Comparisons of measurements of the lower canines between the *E. jubatus* and GKZ-N 00001

MR: greatest mesiodistal diameter of the root BR: greatest buccolingual diameter of the root (9+)=over 9 years old (age determination is based on *Kubota et al., 1961*)

|  | N | Min-Max | Mn |
|---|---|---|---|
| *E. jubatus* :Male (*Kohno & Tomida, 1993*) |  |  |  |
| MR(9+) (mm) | 4 | 38.6-42.4 | 39.1 |
| BR(9+) (mm) | 4 | 21.4-22.6 | 21.8 |
| BR/MR×100(%) | 4 | 51.6-61.8 | 56.6 |
| GKZ-N 00001 (this study) |  |  |  |
| MR (mm) | 1 | 50.3 |  |
| BR (mm) | 1 | 27.6 |  |
| BR/MR×100(%) | 1 | 54.9 |  |