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Authors: Kimura, Toshiyuki, Hasegawa, Yoshikazu, and Kohno, Naoki

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A new species of the genus *Eschrichtius* (Cetacea: Mysticeti) from the Early Pleistocene of Japan

TOSHIYUKI KIMURA¹, YOSHIKAZU HASEGAWA¹ AND NAOKI KOHNO^{2,3}

¹Gunma Museum of Natural History, 1674-1 Kamikuroiwa, Tomioka, Gunma 370-2345, Japan (e-mail: kimura@gmnh.pref.gunma.jp)

²Department of Geology and Palaeontology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan

³Graduate School of Life and Environmental Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki 305-8752, Japan

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Abstract. The family Eschrichtiidae is presently only represented by *Eschrichtius robustus*, a relict species from the North Pacific. Because of the scarcity of fossil records of the Eschrichtiidae, their evolutionary history is not well understood. A finely preserved mysticete skeleton was recovered from the Lower Pleistocene (1.77–1.95 Ma) of Tokyo, Japan, in 1961. The fossil consists of a cranium, mandibles, cervical, thoracic, lumbar and caudal vertebrae, chevrons, ribs, and forelimb bones, including scapula, humerus, radius, ulna and digit bones. Here, we describe and diagnose this fossil as a new species of the Eschrichtiidae, *Eschrichtius akishimaensis* sp. nov. This is the first fossil species of the genus *Eschrichtius* and suggests that at least two lineages represented by the modern species of *Eschrichtius* and the new species described here survived as late as the Early Pleistocene. This expands our knowledge of the paleodiversity of the eschrichtiids.

Key words: Early Pleistocene, Eschrichtiidae, *Eschrichtius akishimaensis*, western North Pacific

Introduction

The family Eschrichtiidae is a somewhat enigmatic cetacean group that has only survived as a single genus and species. Although recent studies have elucidated their paleodiversity (Bisconti and Varola, 2006; Bisconti, 2008; Whitmore and Kaltenbach, 2008), the fossil record of the Eschrichtiidae is relatively sparse, and their evolutionary history remains unclear. The modern gray whale, *Eschrichtius robustus*, is presently found only in the North Pacific, though vagrant individuals have been sighted outside its established ranges (Scheinin *et al.*, 2011; Elwen and Gridley, 2013). Three modern gray whale populations have been recognized: a large eastern North Pacific stock, a very small, remnant western North Pacific stock, and an extinct Atlantic stock (Rice, 1998; Jefferson *et al.*, 2008). The history of the modern genus *Eschrichtius* can be dated back to the late Pliocene (Ichishima *et al.*, 2006). However, the fossil record is limited and fails to document the evolutionary details leading to the modern species.

In the summer of 1961, a nearly complete mysticete skeleton was discovered by Masato Tajima and his son, Yoshio Tajima, in the river bed of the Tama River, Akishima City, Tokyo, Japan. This fossil was recovered

and prepared by local people under the mentorship of Hiroshi Ozaki of the National Science Museum, Tokyo (now National Museum of Nature and Science). Ozaki and Akishima Chigaku Kenkyukai [the latter refers to a research group] (1962) reported the discovery of this fossil, and Akishima Chigaku Kenkyukai (1966) published a preliminary research report. The tale of the discovery and preparation of this fossil was also documented by Tajima (1994). The specimen has long been known as the “Akishima Kujira [kujira meaning whale]” and it has appeared in many publications (Ohmori, 1977; Tajima, 1994; Oishi and Hasegawa, 1994; Research Group for Fossil Footprints from the Riverbed of Tama-gawa, 2002; Taru and Hasegawa, 2002; Ichishima, 2005; Ichishima *et al.*, 2006; Ueki and Sakai, 2007 and references therein), but the specimen itself has never been fully described. The purpose of the present paper is to describe and diagnose this specimen.

Institutional abbreviations.—GMNH, Gunma Museum of Natural History, Gunma, Japan; HMT-F, Fossil collection of the Historical Museum of Teshio River, Hokkaido, Japan; KPM, Kanagawa Prefectural Museum of Natural History, Kanagawa, Japan; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; NSMT, Zoology collection of the National Museum

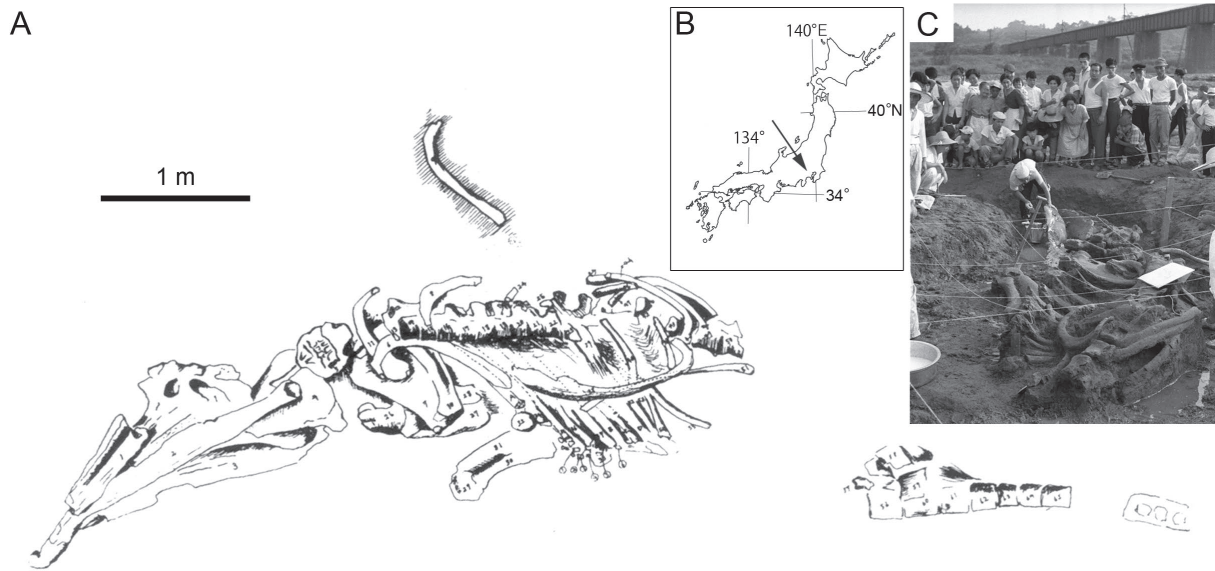


Figure 1. A, map showing the position of skeletal elements of the holotype of *Eschrichtius akishimaensis* sp. nov., GMNH-PV-3210, after Akishima Chigaku Kenkyukai (1966); B, map showing the fossil locality of GMNH-PV-3210; C, photograph of the excavation.

of Nature and Science, Tsukuba, Japan; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Systematic description

Mammalia Linnaeus, 1758
 Cetartiodactyla Montgelard *et al.*, 1997
 Cetacea Brisson, 1762
 Mysticeti Gray, 1864a
 Family Eschrichtiidae Ellerman and Morrison-Scott, 1951
 Genus *Eschrichtius* Gray, 1864b

Type species.—*Eschrichtius robustus* (Lilljeborg, 1861).

Emended diagnosis of the genus.—A genus of Eschrichtiidae having narrow and moderately arched rostrum, less telescoped cranium with frontals widely exposed on vertex, thick lateral process of maxilla, unusually large external bony nares, proportionally large nasal bones, highly reduced coronoid process of mandible; differing from *Archaeoschrichtius* by lacking well developed coronoid and satellite processes of mandible; differing from *Eschrichtioides* by having proportionally larger nasal bones, wider ascending process of premaxilla extending nearly to level of posterior termination of nasal, frontals widely exposed on vertex, zygomatic process of squamosal anteriorly directed, mandible almost straight in dorsal view, more reduced coronoid process of mandible; differing from *Gricetoides* by having postglenoid process of squamosal which is directed ventroposteriorly in lat-



Figure 2. Rostrum fragment of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210. A, dorsal view; B, dorso-lateral view. Lines indicate the suture between maxilla and premaxilla.

eral view and extends posteriorly underneath the external acoustic meatus.

Eschrichtius akishimaensis sp. nov.

Figures 1–12, 15A, E, Table 1

Diagnosis of species.—A species of the genus *Eschrichtius* differing from *E. robustus* by having dorsal surface of ascending process of premaxilla flattened, dorsolaterally facing ascending process of maxilla that is not much nar-

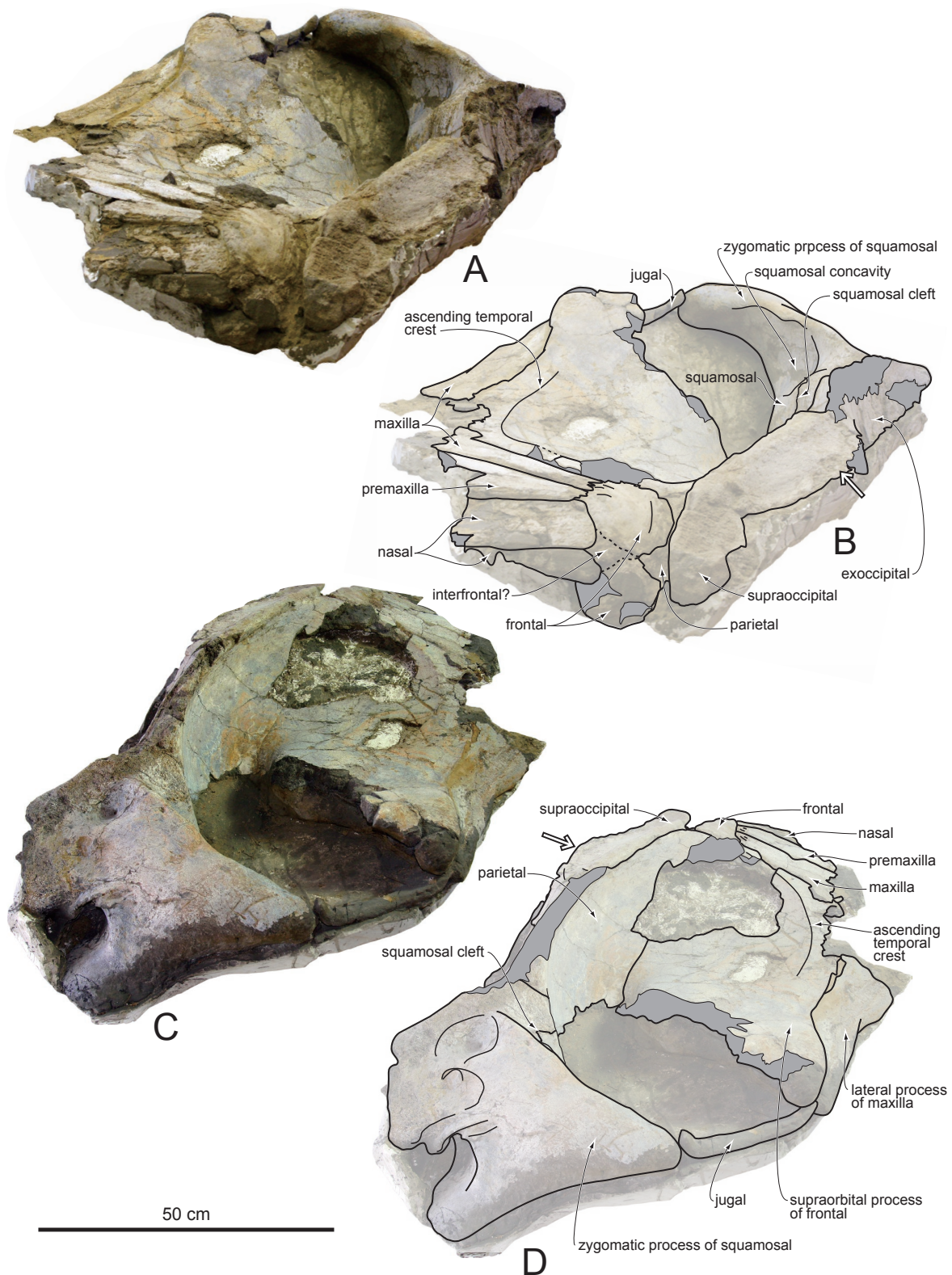


Figure 3. Cranium of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210. **A, B**, dorsal view; **C, D**, right lateral view. Gray areas correspond to major break surfaces. White arrows indicate the base of the occipital tuberosity.

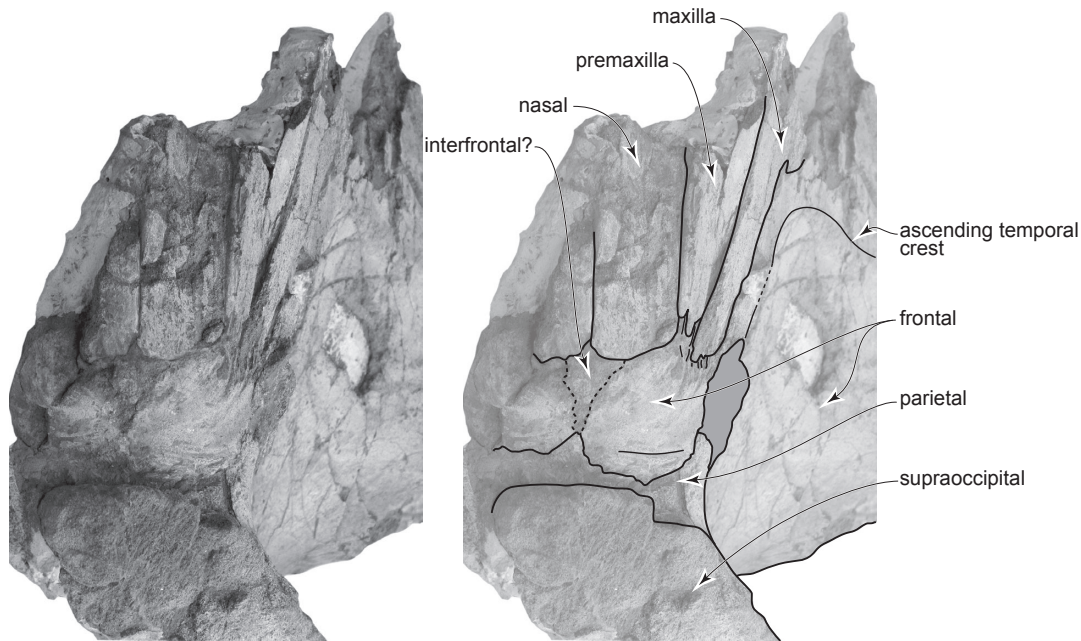


Figure 4. Cranial vertex of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210, in dorsal view. Gray areas correspond to major break surfaces.

rower in comparison with that of premaxilla, posterior border of nasal squared off, deep and large squamosal concavity.

Holotype.—GMNH-PV-3210, cranium, mandibles, cervical, thoracic, lumbar and caudal vertebrae, chevrons, ribs, scapulas, humeri, radii, ulnae, carpals, metacarpals and phalangeal bones. The holotype was discovered by Masato Tajima and Yoshio Tajima on August 20, 1961.

Type locality.—An outcrop along the Tama River, Akishima City, Tokyo, Japan (35°41'41"N, 139°21'48"E). GMNH-PV-3210 was collected from *ca.* 30 meters downstream from the pier (No. 11) of the JR Hachiko Line railway bridge crossing the Tama River.

Formation and Age.—Komiya Formation, early Pleistocene (1.77–1.95 Ma). GMNH-PV-3210 was recovered from the middle member of the Komiya Formation (Ueki and Sakai, 2007). The horizon in which the holotype was found is correlated with the Olduvai Subchron (C2n) by magnetostratigraphy (1.77–1.95 Ma: Ueki and Sakai, 2007).

Etymology.—Named for Akishima City, Tokyo, Japan, where the holotype was found.

Remarks.—An informal name “*Japonocetus akishimensis*” for this specimen has previously appeared in several literatures. However, to our knowledge, no publications have appeared in which the name was formally proposed conforming to the requirements of the Interna-

tional Code of Zoological Nomenclature (1999) for the establishment of a new scientific name.

Description

Anatomical terminology generally follows Mead and Fordyce (2009). The skeleton of GMNH-PV-3210 was well articulated and was discovered left side up (Figure 1) with most of the skeletal elements in their life positions. All the epiphyses on the preserved vertebrae are firmly fused to their centra, and both the proximal and distal epiphyses of the humerus, radius, and ulna are fused to their diaphysis. These suggest that GMNH-PV-3210 is an adult individual (Ogden *et al.*, 1981; Galatius *et al.*, 2006; Moran *et al.*, 2015).

Cranium.—The right half of the braincase and a part of the rostrum is preserved, including the premaxilla, maxilla, vomer, nasal, frontal, jugal, parietal, alisphenoid, squamosal, supraoccipital and exoccipital. The dorsal side of the cranium is well preserved, but the ventral side is badly weathered and is protected with plaster.

The point-to-point distance from the posteromedial angle of the right nasal to the preorbital process of the frontal is 686 mm, and the transverse width of the cranium at the preorbital process of the frontal is estimated as 830 mm by doubling the half-width. The preserved rostral fragment is transversely narrow. It is only slightly arched dorsally and slightly tapers anteriorly (Figure 2).

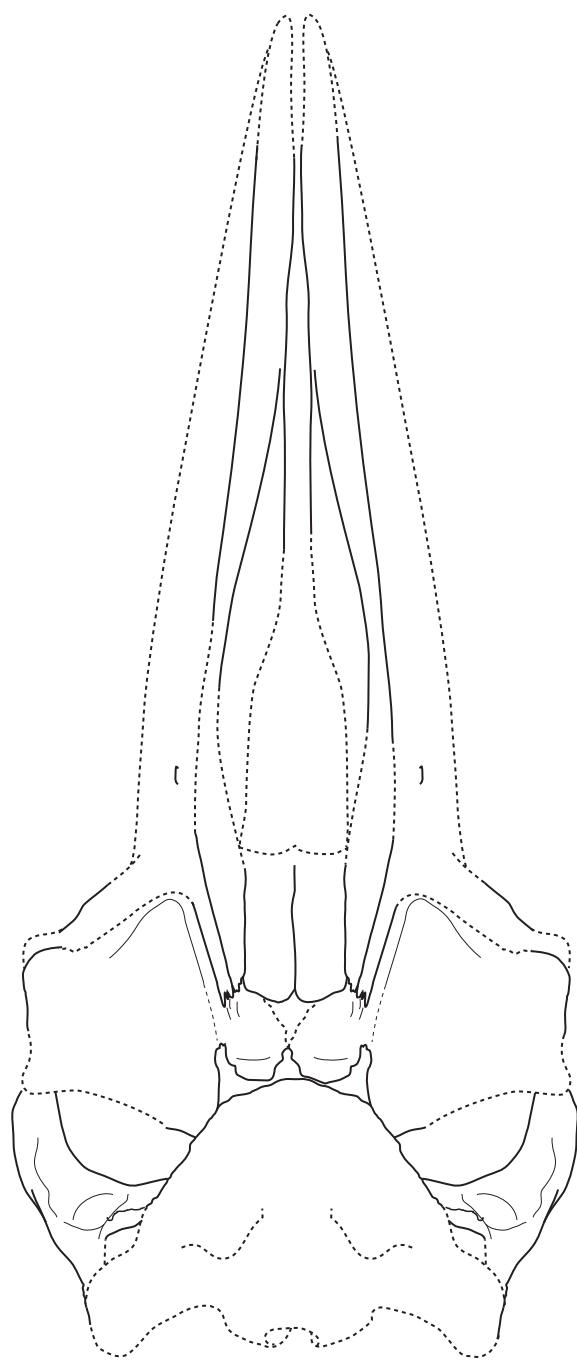


Figure 5. Reconstruction of a cranium of *Eschrichtius akishimaensis* sp. nov., with missing parts indicated by dashed lines and preserved portions symmetrically flipped.

The external bony nares are quite large.

The premaxilla is medially concave anterior to the nasal bones. Anterior to the level of the external bony nares, the left and right premaxillae nearly contact at the

midline. The ascending process of the premaxilla slightly narrows posteriorly alongside the nasal (Figures 3, 4). Its transverse widths at the anterior and posterior ends of the preserved nasal are 50 mm and 25 mm, respectively. The posterior termination of the premaxilla occurs at the level of that of the nasal. The dorsal surface of the ascending process of the premaxilla is flat and faces dorsolaterally. No premaxillary foramen is found.

The rostral part of the maxilla is narrow, and its lateral margin is straight-sided. Its dorsal surface steeply descends from the level of the maxilla-premaxilla suture to its outer edge. The maxilla abruptly widens to form an open antorbital notch at the base of the rostrum. It extends posteroventrolaterally along the anterior face of the supra-orbital process of the frontal and forms a thick lateral process of the maxilla. A large dorsal infraorbital foramen is preserved in the left maxilla lateral to the external bony nares. The ascending process of the maxilla extends to the level of the posterior ends of the nasal and premaxilla. It faces dorsolaterally and is visible in dorsal view.

The right nasal is well preserved, though its anterior portion is slightly missing; the left nasal is barely preserved. The nasal is quite large. The right nasal is 160+ mm long, and the transverse width at its posterior end is 50 mm. In dorsal view, the medial and lateral sides of the right nasal are nearly parallel, and it is rectangular in outline. The lengths of the medial and lateral sides of the nasal are almost the same, and its posterior border is squared off (Figure 4). The dorsal surface of the anterior part of the preserved nasal is raised medially and forms a longitudinal crest in the midline.

The frontals are widely exposed, and the left and right frontals widely contact each other in the interorbital region. A small bone is present between the frontals and is slightly wedged between the nasals, and this might be an interfrontal. The supraorbital process of the frontal is dorsally flat and broad anteroposteriorly. It is steeply depressed from the interorbital region and then slopes downward to its orbital rim. There is a salient orbito-temporal crest on the dorsal surface of the supraorbital process (ascending temporal crest of Bisconti, 2008). The medial portion of this crest projects anterolaterally, and the lateral portion abruptly curves laterally towards the postorbital corner of the orbit (Figures 3, 4). This ridge becomes indistinct laterally and does not reach the post-orbital process.

The right jugal is almost completely preserved. It is slender and is wedged between the maxilla and the supra-orbital process of the frontal. It posteriorly contacts to the apex of the zygomatic process of the squamosal.

The parietal contributes to most of the medial wall of the temporal fossa. Dorsally, the parietal contacts the supraoccipital and constitutes the nuchal crest. In dor-

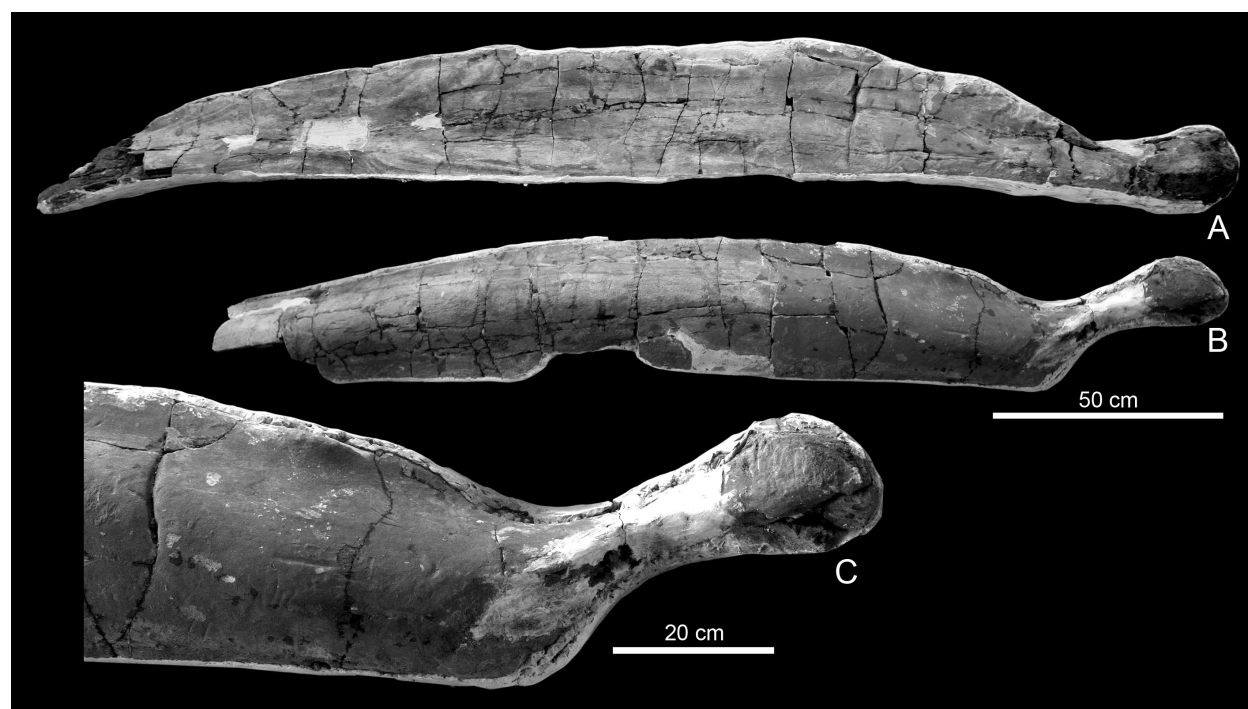


Figure 6. Mandibles of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210. **A**, right mandible in medial view; **B**, left mandible in lateral view; **C**, posterior part of left mandible in lateral view.

sal view, the parietal is not visible on the temporal surface because the nuchal crest is raised dorsolaterally and slightly overhangs the temporal fossa. The opposite parietals meet on the midline of the cranium and are narrowly exposed between the supraoccipital and the frontals.

The alisphenoid is exposed on the temporal surface. It contacts to the parietal anteriorly and to the squamosal dorsally and posteriorly.

The zygomatic process of the squamosal is short, robust and directed anteriorly. The dorsal surface of the zygomatic process is smoothly rounded, and the supramastoid crest is not well developed. In lateral view, the curvature of the dorsal profile is almost straight and descends anteriorly, while the ventral profile is slightly concave from its anterior end to the extremity of the postglenoid process. The temporal surface of the squamosal does not bulge into the temporal fossa. A large and deep excavation, the squamosal concavity [new term], is present just medial to the base of the zygomatic process (Figure 3A, B). Squamosal concavity is not homologous with secondary squamosal fossa of Sanders and Barnes (2002). Secondary squamosal fossa is located at the posterior end of the squamosal and is tied with the squamosal prominence. A squamosal cleft extends from the parieto-alisphenoid suture and ends in the squamosal concavity. Two relatively deep fossae, possibly for the attachment of muscles such as the

sternomastoideus (Schulte, 1916), are present on the lateral surface of the squamosal. The postglenoid process is directed posteroventrally in lateral view and extends posteriorly underneath the external acoustic meatus. The right external acoustic meatus is preserved. It is narrow, deeply concave and has a smooth bone surface. Parallel to the acoustic meatus, a possible fused posterior process of the periotic and tympanic is firmly wedged between the squamosal and the exoccipital.

In dorsal view, the supraoccipital shield is roughly triangular in outline. The apex of the supraoccipital is wide and rounded in dorsal view. It reaches slightly beyond the level of the apex of the zygomatic process of the squamosal. A right occipital tuberosity is barely preserved, and a small portion of its base is confirmed (white arrows in Figure 3). Anterior to the level of the occipital tuberosity, the nuchal crest slightly overhangs the temporal fossa in dorsal view. The right exoccipital is partly preserved, and is slightly concave ventral to the occipital tuberosity.

Mandible.—Both mandibles are relatively well preserved (Figure 6). The left mandible is covered medially, and the right mandible is covered laterally by a plaster jacket for protection. The straight lengths of the left and right mandibles are 2196+ mm and 2505+ mm (as preserved), respectively. The mandible is slightly arched dorsally in lateral view and is almost straight in dorsal

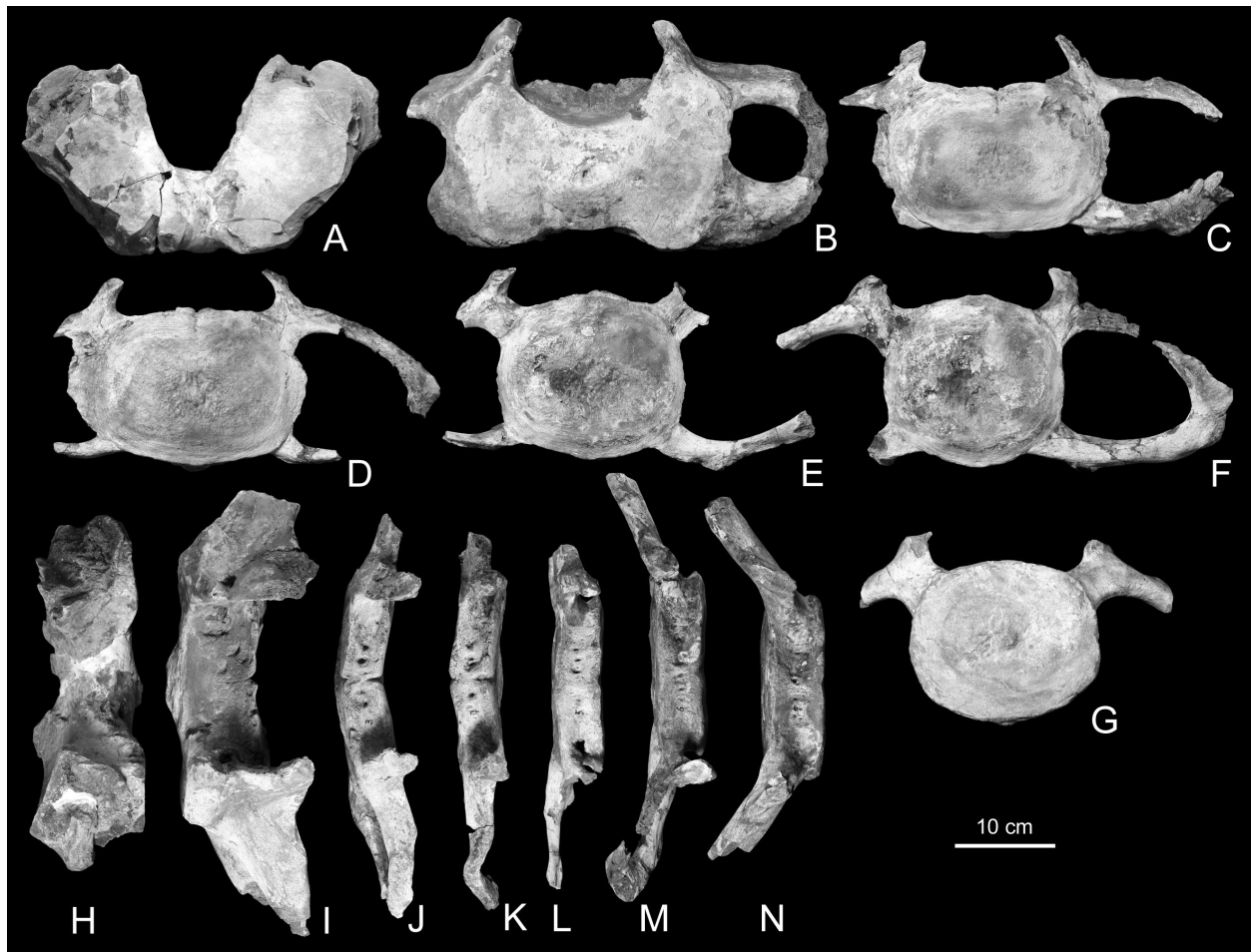


Figure 7. Cervical vertebrae of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210. A–G, anterior view; H–N, dorsal view. A and H, atlas; B and I, axis; C and J, C3; D and K, C4; E and L, C5; F and M, C6; G and N, C7.

view. The dorsoventral diameter of the mandible is largest at the middle of the body and tapers both anteriorly and also posteriorly.

The lateral surface meets the medial surface ventrally to form a well defined angular edge. The body is abruptly rotated around its axis at its anterior part and its medial surface faces dorsomedially. Except for the anterior part of the mandible, the medial surface of the mandible is noticeably flattened. The lateral surface of the mandible is uniformly convex. Anterior to the coronoid process, the greatest transverse diameter is at the midline. At the coronoid process, the greatest diameter shifts ventrally and is on the level of the ventral one-third of its height. Three mental foramina are preserved along the dorsolateral surface of the left mandible. These foramina occur at 380, 880, and 1110 mm behind the preserved anterior end of the mandible and lie at 55, 53, and 60 mm below the dorsal margin of the body, respectively. Each mental foramen

opens anterodorsally.

The coronoid process is preserved on the left mandible. It is quite low and projects dorsolaterally on the dorso-lateral edge of the mandible. This is in clear contrast to the balaenids, which have a similar quite low coronoid process but which is directed dorsally. Posterior to the coronoid process, the height of the neck of the mandible abruptly decreases. The condyle and the angle are damaged and most of the bone surfaces are eroded. The condyle is partly preserved on the left mandible and is suggested to be directed dorsoposteriorly. The right mandible preserves part of the angle, which projects posteriorly.

Vertebrae.—Forty vertebrae were associated with the skeleton and identified as seven cervical, 13 thoracic, eight lumbar, and 12 caudal vertebrae (Figures 7–9). When GMNH-PV-3210 was discovered, the vertebrae from the atlas to the sixth lumbar and the third to the ninth

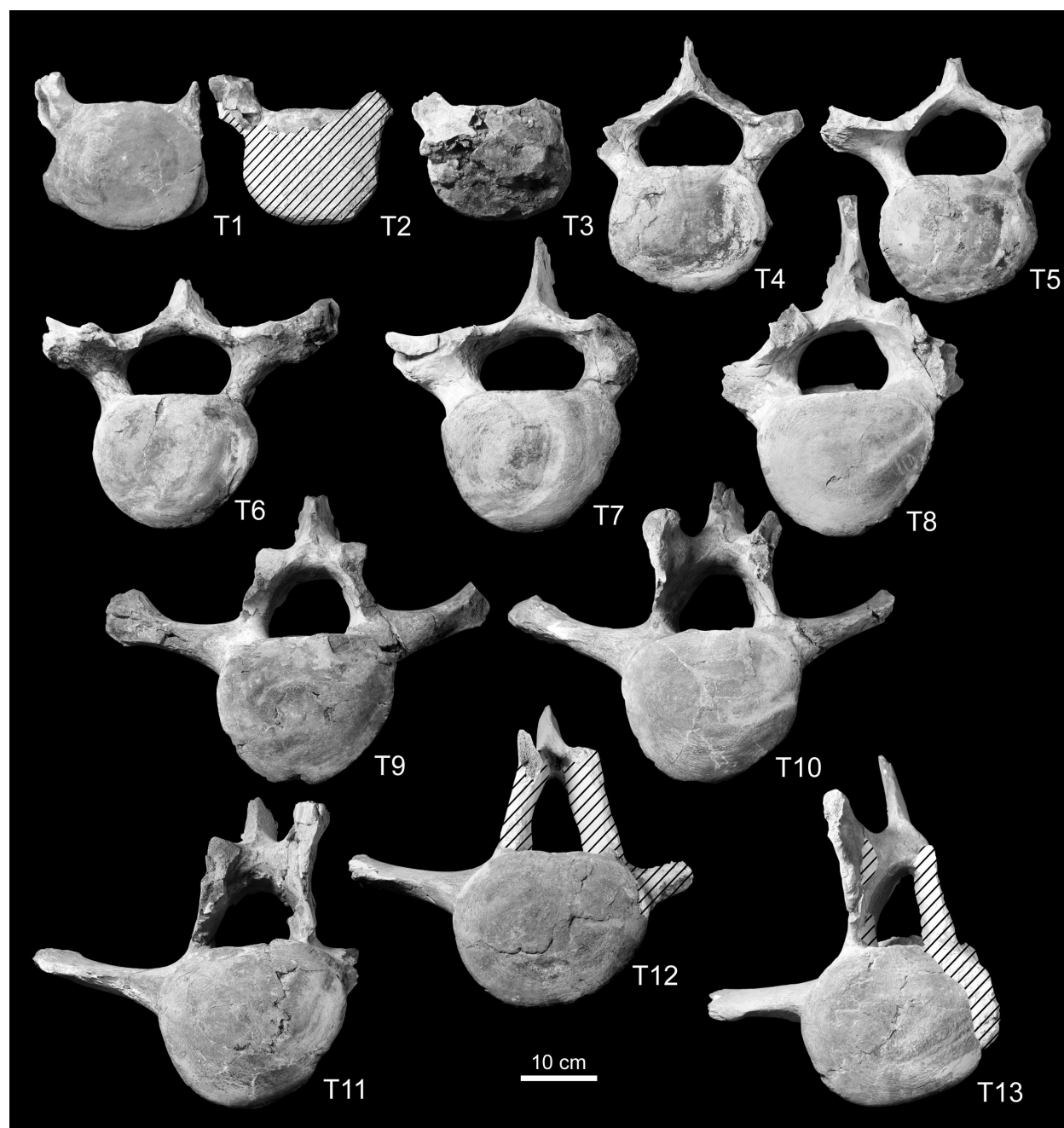


Figure 8. Thoracic vertebrae of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210, in anterior view. T denotes thoracic vertebra; see description for vertebral number assignment. Hachures indicate areas where bone is damaged and reconstructed by plaster.

caudal vertebrae were articulated and aligned along a linear axis (Figure 1). Presumably, several posterior lumbar and middle to posterior caudal vertebrae existed that were not preserved. All of the preserved vertebrae have epiphyses firmly ankylosed to the centrum. Measurements of the vertebrae are shown in Table 1.

Cervical vertebrae.—All the cervical vertebrae are

free. The atlas is incomplete and lacks the dorsal portion. The base of the transverse process is barely preserved and is directed posterolaterally. The anterior facets for articulation with the occipital condyle are concave and reniform in outline. The posterior facets for articulation with the axis are almost flat. They are transversely narrower than the anterior facets. The hyapophysial process is low

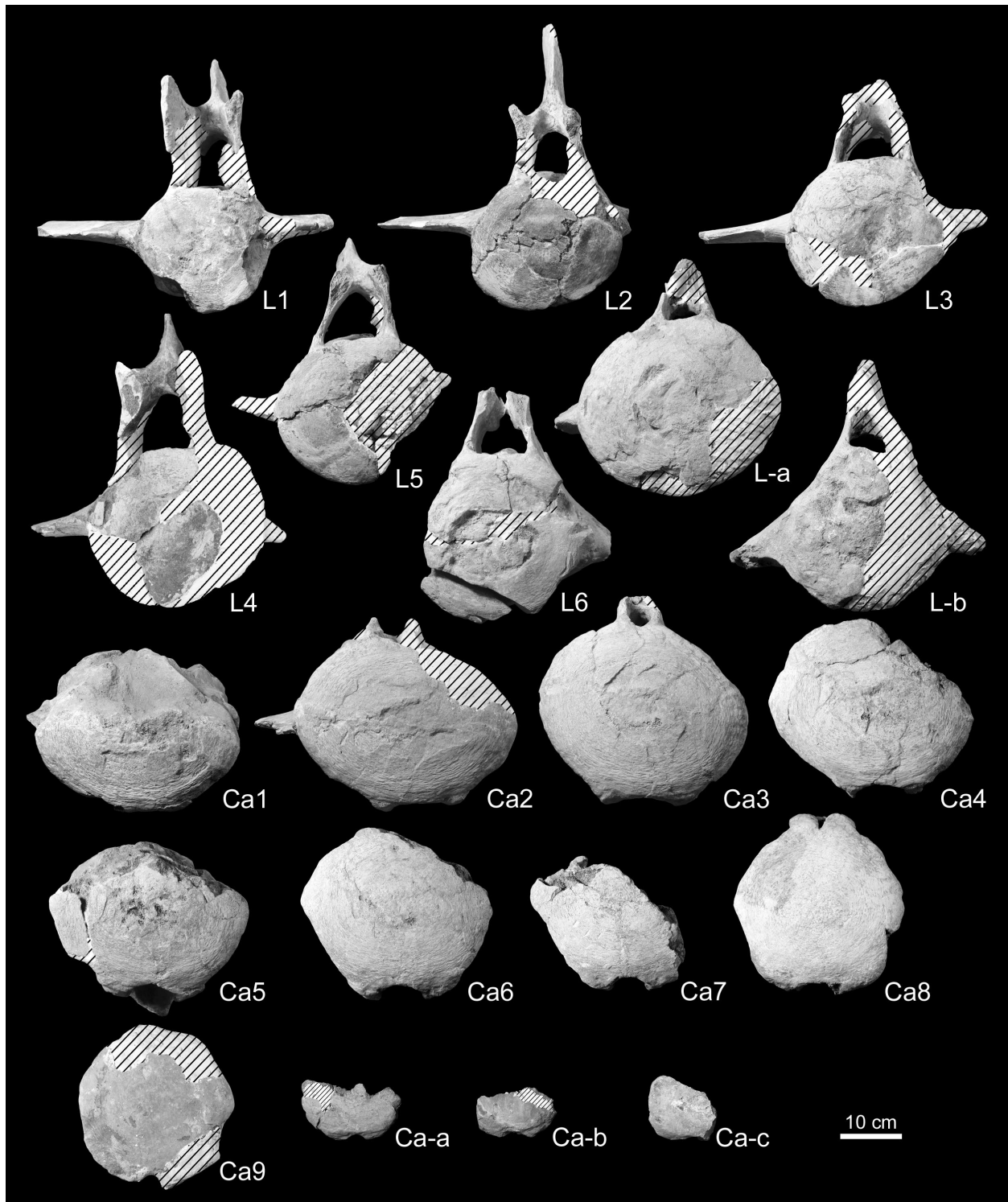


Figure 9. Lumbar and caudal vertebrae of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210, in anterior view. L denotes lumbar vertebrae, and Ca denotes caudal vertebrae; see description for vertebral number assignment. Hachures indicate areas where bone is damaged and reconstructed by plaster.

Table 1. Measurements of vertebrae (in mm) of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210. Abbreviations: +, less than true value; *AH*, anterior height of centrum; *AW*, anterior width of centrum; *PH*, posterior height of centrum; *PW*, posterior width of centrum; *L*, length of centrum; C, cervical vertebra; T, thoracic vertebra; L, lumbar vertebra; Ca, caudal vertebra.

	<i>AH</i>	<i>AW</i>	<i>PH</i>	<i>PW</i>	<i>L</i>
C1	165+	262+	163	288	107
C2	164	255+	148	225	66
C3	147	217	147	207	45
C4	146	231	162	185	44
C5	155	183	164	178	45
C6	165	173	164	179	46
C7	162	174	157	186	54
T1	159	186	157	192	70
T2	—	—	—	—	80
T3	—	—	144+	186	102+
T4	147	185	147+	191	117
T5	146	181	152	195+	121
T6	155	189	155+	190+	130
T7	157	203+	163	199+	145
T8	165	201	165	190+	155
T9	164	195	165+	203	158
T10	168	198	167+	190+	162
T11	167	195	163	209	169
T12	168	201	164	143+	171
T13	165	181+	166	185+	173
L1	157	151+	171	202	181
L2	170+	192	177	203+	182
L3	183+	200+	116+	121+	190
L4	198+	170+	185+	188+	191
L5	187	164+	197+	202+	191
L6	205+	209+	232+	188+	218
L-a	201+	232+	178+	171+	224
L-b	198+	121+	196+	130+	223+
Ca1	125+	252+	183+	276	227
Ca2	203+	269	200+	244+	221
Ca3	211	266	166+	255+	210
Ca4	203+	252	160+	238+	199
Ca5	159+	248	173+	232+	181
Ca6	205+	243	183+	220	175
Ca7	143+	199+	118+	184+	167
Ca8	226	224	190+	164+	137
Ca9	191+	209	181+	178	123
Ca-a	77+	153+	52+	133+	85+
Ca-b	65+	119+	41+	119+	76+
Ca-c	94+	106+	—	—	87+

and bluntly pointed.

The axis is well preserved although missing the right transverse processes, a part of the neural arch and the neural spine. The neural arch projects posterodorsally. The neural canal is transversely wide, measuring 138 mm at the base of the neural arch. The articular facet for the atlas is almost flat and roughly reniform in outline. The odontoid process is wide and reduced anteroposteriorly. The posterior articular facet is oval in outline and distinctly concave medially. The transverse process is posterolaterally directed and is perforated by a rather large oval foramen transversarium. This foramen measures 75 mm high and 109 mm wide.

From C3 to C7, the outline of the anterior end of the centrum changes from rectangular to circular in shape. The transverse diameter of the neural canal is wide. The diapophysis is slender and projects posterolaterally in C3, laterally in C4–C5, and anterolaterally in C6–C7. On C3–C6, the diapophyses are united distally with the parapophyses to enclose the large foramen transversarium. The parapophysis is absent in C7.

Thoracic vertebrae.—GMNH-PV-3210 has 13 thoracic vertebrae. The anteroposterior length of the centrum progressively increases from T1 to T13, and all are broader than high. The width also exceeds the length of the centrum in all the thoracic vertebrae. The outline of the anterior end of the centrum of T1 to T5 is rectangular; it is subcordate in T6–T11 and circular in T12–T13. The neural canal progressively decreases in width and increases in height from T1 to T13. The transverse process is broken off in T1–T3. It arises from the neural arch in T4–T8 and partly from the neural arch and partly from the centrum in T9–T10. It is derived from the centrum in T11–T13. The transverse process is directed anterolaterally in T4–T8 and posterolaterally in T9–T13.

Lumbar vertebrae.—Eight lumbar vertebrae were found with the skeleton. The anterior six lumbar vertebrae were found articulated with the thoracic vertebrae and were identified as L1–L6. The length of the centrum progressively increases from the anterior to the posterior lumbar vertebrae. Two other lumbar vertebrae were also recovered, but the position of these vertebrae is unclear; they are tentatively referred to as L-a and L-b from anterior to posterior on the basis of the centrum length. The transverse process originates from the dorsolateral part of the centrum in the anterior lumbar vertebrae, and the position where the process originates is progressively lowered in the posterior vertebrae. On the preserved posteriormost lumbar vertebra (L-b), it originates from the middle of the centrum. In the anterior view, the transverse process projects laterally in L1–L4 and is missing in L5; it extends ventrolaterally in L6, L-a and L-b. The height and width of the neural canal progressively decreases from the ante-

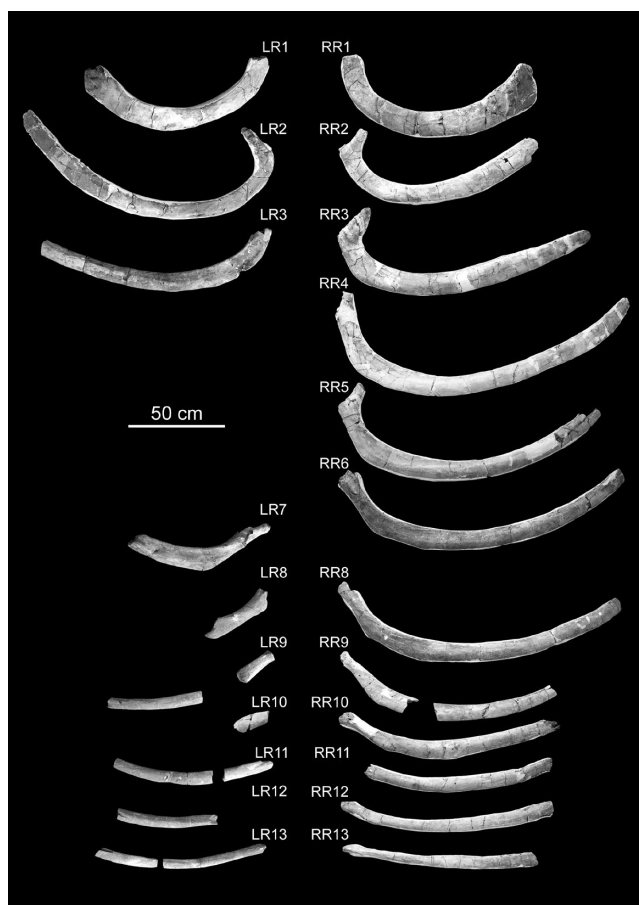


Figure 10. Right (RR) and left (LR) ribs of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210, in anterior view.

rior to the posterior vertebrae.

Caudal vertebrae.—Twelve caudal vertebrae were found with the skeleton, and seven of the preserved caudals were found in articulation (Figure 1). Ca1 is identified by having only posterior haemal tubercles, while the following consecutive caudal vertebrae (identified as Ca2 to Ca9) have anterior and posterior haemal tubercles. An additional three caudals were also recovered and identified tentatively as Ca-a, Ca-b, and Ca-c from anterior to posterior. Several caudal vertebrae are presumably missing between Ca9 and Ca-a and posterior to Ca-c. The anteroposterior length of the centrum progressively decreases from Ca1 to Ca9. The centrum is wider than its height, and its anterior face is circular in shape, at least in the anterior five caudal vertebrae, while the centrum is apparently narrower than its height in Ca9.

Ribs.—Ten left and twelve right ribs were found associated with the skeleton (Figure 10). It is suggested that GMNH-PV-3210 originally had 13 pairs of ribs given the

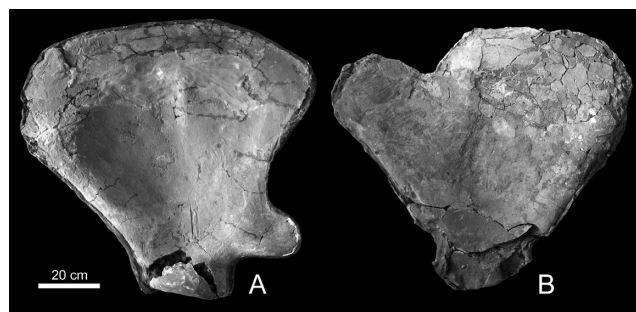


Figure 11. Scapulae of *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210, in lateral view. **A**, right scapula; **B**, left scapula.

number of thoracic vertebrae. The right rib (RR) sequence is completely preserved except for RR7. The preserved left ribs (LR) are tentatively identified as LR1–LR3 and LR7–LR13. The following description is based on the right ribs.

R1 is of uniform width in its proximal two-thirds but rapidly expands in the distal portion where it becomes the widest of the series. The anterior surface of the body is slightly convexly curved. R2–R6 possess noticeable necks with distinctly developed heads and tubercles. A similar morphology is also found in *E. robustus*, unlike other living mysticetes (Andrews, 1914; Nishiwaki and Kasuya, 1970; Nakamura and Kato, 2014). The neck extends medially, and the angle it forms with the body becomes wider from R2 to R6. In anterior view, the curvature of the proximal portion of the rib is most acute in R3 and is nearly rectilinearly angled with the body. The anterior surface of the body is convexly curved, and the body increases in thickness distally, after which the anterior surface becomes flattened. A crest develops on the dorsal edge of the rib in R2 to at least R10 just distal to the tubercle and extends distally and medially on the anterior surface of the rib. R3 possesses a shallow concavity at the region just distal to the tubercle on the anterior surface of the body.

Forelimb.—The forelimb bones are represented by scapulae, humeri, radii, ulnae, carpals and digit bones (Figures 11, 12). Both scapulae are relatively well preserved. The medial sides of both scapulae are covered by a plaster jacket and cannot be observed. The scapula is relatively high (right, 807 mm; left, 755 + mm) relative to its width (right, 859 mm; left, 881 mm). The lateral surface is slightly concave. The vertebral border is slightly convexly curved in lateral view. The posterior border is directed posterodorsally, with the anterior border more dorsally oriented. The anterior and posterior margins of the scapula are slightly concavely curved. The scapula is thickened along its anterior and posterior margins. The

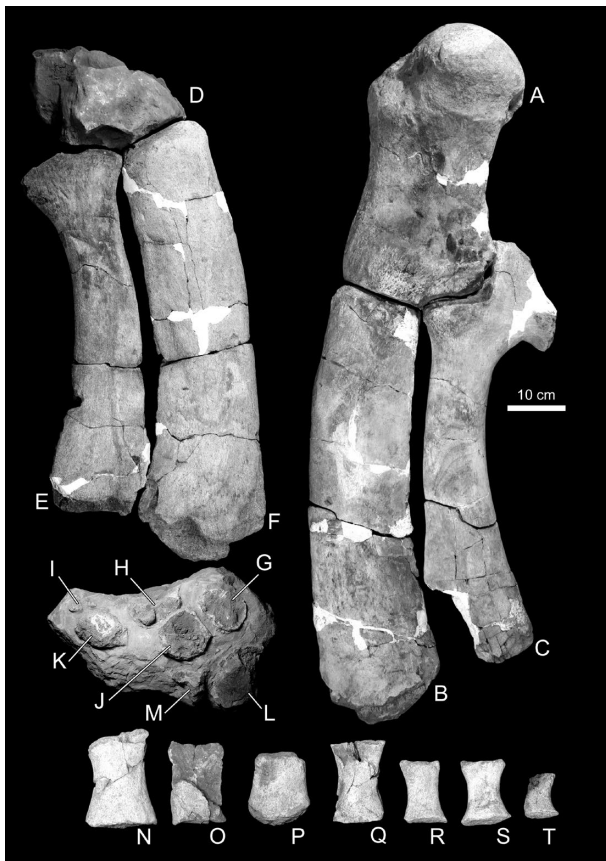


Figure 12. *Eschrichtius akishimaensis* sp. nov., holotype, GMNH-PV-3210. A–C, left forelimb in lateral views; A, humerus; B, radius; C, ulna; D–M, right forelimb in lateral views; D, humerus; E, ulna; F, radius; G, radial carpal bone (scaphoid); H, intermediate carpal bone (lunate); I, ulnar carpal bone (cuneiform); J, third carpal bone (trapezoid); K, fourth and fifth carpal bone (unciform); L, first metacarpal bone; M, second metacarpal bone; N–P, metacarpal bones; and Q–T, phalangeal bones.

angle between the anterior and posterior margins is *ca.* 70°. The right scapula preserves the acromion, which is wide and short and projects anteriorly. The supraspinous fossa is anteroposteriorly short. The glenoid fossa is preserved in the right scapula. It is shallowly concave and measures *ca.* 198 mm anteroposteriorly. The coracoid process is not preserved.

Both humeri were recovered; the left one is almost complete. The following descriptions are based on the left humerus. It retains both proximal and distal epiphyses firmly ankylosed to the body. The humerus is short and robust as in most mysticetes. The greatest length of the humerus measures 472 mm. The greatest anteroposterior diameters of the proximal and distal ends are 257 and 259 mm, respectively. Distally, the body of the humerus expands moderately. The humerus has a large and mark-

edly convex head, which faces posterolaterally; its maximum diameter is 188 mm. Anteromedial to the head is a large greater tubercle. It is broad and projects dorsomedially, but it is lower than the head. The medial face of the greater tubercle is markedly rugose. The greater tubercle is separated from the head by a shallow groove. The body of the humerus is thick. The radial surface of the body is rugose, while the ulnar surface is smooth. The radial and ulnar surfaces are both concave in lateral view. A dorsoventrally directed, crease-like structure is present on the medial surface of the body just proximal to the ulnar facet. The radial facet is flat and elliptical in shape and elongates anteroposteriorly. It is slightly wider than the ulnar facet. The ulnar facet is slightly concavely curved and extends upward on the ulnar surface of the body for the olecranon of the ulna. Both facets are separated by a crest.

Both radii are well preserved and both proximal and distal epiphyses are ankylosed to the body. The greatest length of the radius measures 738 mm (left) and 735 mm (right). The maximum anteroposterior diameters of the proximal and distal ends are 153 mm and 215 mm (left) and 155 mm and 211 mm (right), respectively. The radius is long and mediolaterally flattened. The proximal facet that articulates with the humerus is almost flat and oval-shaped. The facet on the posterior surface of the proximal end for articulation with the ulna is relatively small. The body of the radius is slightly bent posteriorly in lateral view. The medial and lateral surfaces of the body are slightly convex. The posterior edge of the body is sharper than the anterior. The distal epiphysis possesses a rugose and pitted surface of the bone, suggesting an attachment of cartilage.

Both ulnae were associated with the skeleton. The left ulna is nearly complete except for its distal extremity; the right one is missing most of the olecranon process. Both proximal and distal epiphyses are ankylosed to the body. The greatest length of the ulna measures 721 mm (left) and 615+ mm (right). The proximal facet that articulates with the humerus is deeply concave. It expands ventrally as a small facet for the radius. The olecranon process is nearly triangular in outline. In its distal portion, the dorsal and posterior surface is rugose and irregularly pitted, suggesting the presence of cartilage. The body of the ulna is slightly bent posteriorly and widens distally; just below the proximal facet, it is thick mediolaterally and becomes thin distally. The anterior edge of the body is sharper than the posterior edge. The cross section of the middle of the body is teardrop-shaped.

The five carpal and two (first and second) metacarpal bones were discovered in articulation with the right ulna and radius in life position (Akishima Chigaku Kenkyukai, 1966, p. 10), but the ulnar and intermediate carpal

Table 2. The fossil and extant eschrichtiids directly examined in this study.

Taxon	Catalog number	Geological age	Strata or stock	Remarks
<i>Eschrichtius akishimaensis</i> sp. nov.	GMNH-PV-3210	early Pleistocene	Komiya Formation	
<i>Eschrichtius robustus</i>	USNM199527	Recent	western North Pacific	
<i>Eschrichtius robustus</i>	NSMT-M34025	Recent	western North Pacific	immature
<i>Eschrichtius robustus</i>	NSMT-M52672	Recent	western North Pacific	
<i>Eschrichtius robustus</i>	KPM-NF1001988	Recent	western North Pacific	immature
<i>Eschrichtius robustus</i>	USNM187449	Holocene	Atlantic	immature
<i>Eschrichtius robustus</i>	USNM244308	Holocene	Atlantic	immature
<i>Eschrichtius robustus</i>	USNM256749		Atlantic	
<i>Eschrichtius robustus</i>	LACM54536	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM54537	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM54540	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM54541	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM54547	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM54549	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM72551	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM84011	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM84012	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM84190	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM84195	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM84202	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM84260	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM85979	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM85980	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM86047	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	LACM92044	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	LACM95661	Recent	eastern North Pacific	immature
<i>Eschrichtius robustus</i>	NSMT-M15940	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	USNM13803	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	USNM364970	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	USNM364973	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	USNM364974	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	USNM364977	Recent	eastern North Pacific	
<i>Eschrichtius robustus</i>	USNM364980	Recent	eastern North Pacific	
<i>Eschrichtius</i> cf. <i>robustus</i>	LACM122322	late Pleistocene	San Pedro Sand Formation	
<i>Gricetoides aurorae</i>	USNM182921	early Pliocene	Yorktown Formation	

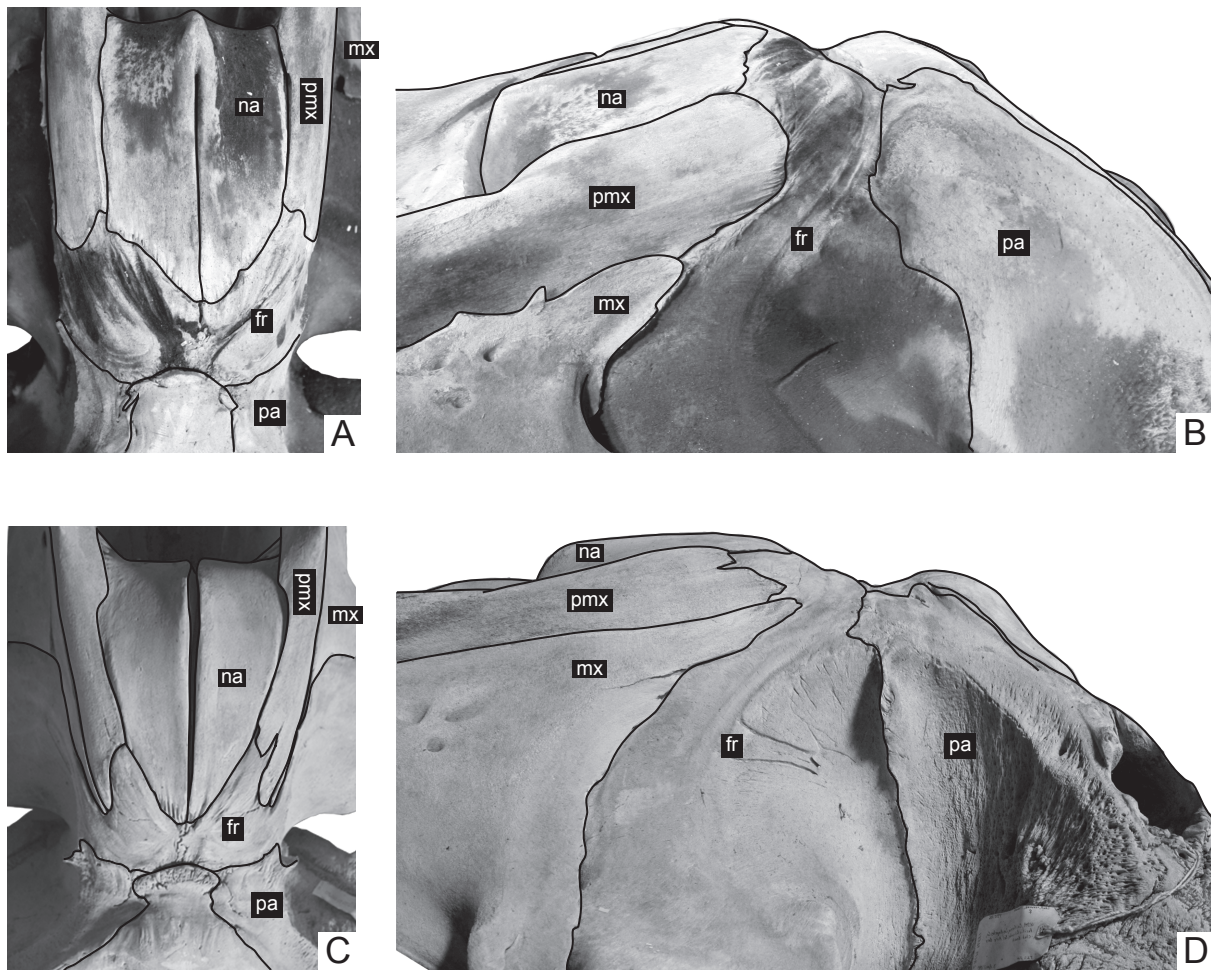


Figure 13. Relative position of maxilla, premaxilla and nasal in *Eschrichtius robustus*. **A, B**, LACM85980; **A**, dorsal view; **B**, dorso-lateral view; **C, D**, LACM72551; **C**, dorsal view; **D**, dorsolateral view (image reversed). Abbreviations: fr, frontal; mx, maxilla; na, nasal; pa, parietal; pmx, premaxilla. Not to scale.

bones and the second metacarpal bone are badly broken (Figure 12). Seven other digit bones were recovered with the skeleton and were tentatively identified as three metacarpals and four phalanges (Figure 12).

Discussion

Intraspecific variation among *Eschrichtius robustus*

All of the characters for diagnosing the genus *Eschrichtius* (see emended diagnosis of the genus) are also found in the present specimen, GMNH-PV-3210, which clearly indicates that GMNH-PV-3210 belongs to the genus *Eschrichtius*. Prior to this study, the genus *Eschrichtius* was monotypic and only included a modern species, *E. robustus*. To diagnose the present specimen, GMNH-PV-3210, it is important to assess the degree of intraspecific variation in the modern gray whale, *E. robustus*. We

directly examined 32 skeletal specimens of *E. robustus*, including all three recognized populations (Table 2). We discuss some of the intraspecific variations of the cranial morphology in *E. robustus*.

As stated before (see diagnosis of species), *Eschrichtius akishimaensis* differs from *E. robustus* in a number of morphological characters. All these morphological characters are stable and do not show apparent intraspecific variation in *E. robustus*. We will comment on several other morphological characters that have often been used in the previous phylogenetic analysis.

Posterior edge of maxilla, premaxilla, and nasal.—In GMNH-PV-3210, the posterior edges of the maxilla and the premaxilla both extend almost to the level of that of the nasal (Figure 4). The posterior extension of the medial rostral elements (maxilla, premaxilla, and nasal) is known as cranial telescoping (Miller, 1923) and has frequently

been discussed in a phylogenetic context. The relative position of the posterior edge of each bone has also been used in previous phylogenetic analyses (e.g. Bouetel and Muizon, 2006; Kimura and Hasegawa, 2010; Marx, 2011; Bisconti *et al.*, 2013).

However, the relative position shows an intraspecific variation at least in *Eschrichtius robustus*. While the posterior edges of the maxilla and the premaxilla remain anterior to that of the nasal in most individuals, it extends to the level of the posterior edge of the nasal in a few individuals (both in adult [USNM364980, USNM72551] and juvenile [LACM92044] specimens) (Figure 13). Moreover, an intraspecific variation is also found in the relative positions of the posterior edges of the maxilla and the premaxilla. The posterior edge of the maxilla extends to the level of that of the premaxilla in several adult and juvenile specimens (e.g. USNM364970, LACM72551, LACM54547, LACM92044); it remains anterior to that of the premaxilla in others (e.g. USNM364974, LACM85980, NSMT-M34025) (Figure 13B, D). Thus, it is inappropriate to diagnose on the basis of these morphologies at least for the species of *Eschrichtius*, or the character should at least be recognized as multi-states for the species of *Eschrichtius*.

Temporal crest of the parietal.—The parietal constitutes most of the temporal wall. In GMNH-PV-3210, the temporal surface of the parietal is smooth and featureless (Figure 3). In contrast, there is a salient crest, here termed as the temporal crest of the parietal, that is along and below the nuchal crest on the temporal surface of the parietal in *Eschrichtius robustus* (Figure 14A, B). It continues anteriorly to the orbitotemporal crest of the frontal and represents the attachment site for the temporal muscle (El Adli and Deméré, 2015). The degree of the development of the temporal crest of the parietal shows an ontogenetic variation in *E. robustus*. It is well marked, and between this crest and the nuchal crest, it forms a dorsolaterally facing, flattened bone surface in adult individuals (Figure 14A), though it is indistinctly developed in juveniles (Figure 14B).

However, although GMNH-PV-3210 is physically a fully matured individual, it lacks a temporal crest of the parietal. This is in contrast to *Eschrichtius robustus*. However, two specimens of *E. robustus* among those examined do not have a temporal crest of the parietal, despite not being juveniles (LACM85979, NSMT-M52672) (Figure 14C). Therefore, although it is quite rare, an intraspecific present/absent variation in the temporal crest of the parietal does exist in *E. robustus*. Thus, it may be inappropriate to diagnose at least for the species of *Eschrichtius* based on this morphology.

Squamosal and squamosal concavity.—In GMNH-PV-3210, the temporal surface of the squamosal is smooth

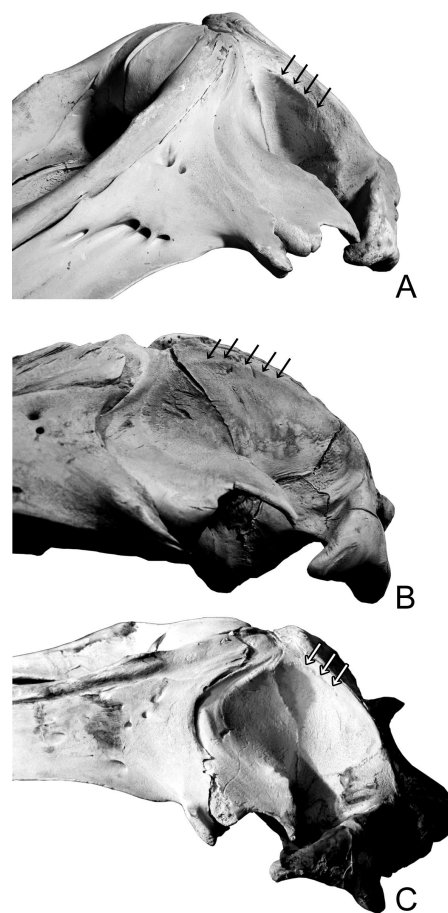


Figure 14. Temporal surface of *Eschrichtius robustus*. **A**, LACM86047; **B**, LACM54547 (immature); **C**, LACM85979. Black arrows indicate the temporal crest of the parietal. White arrows indicate a ligament remaining on the bone surface. Not to scale.

and does not well bulge into the temporal fossa (Figure 15A). In contrast, in *Eschrichtius robustus*, it well bulges into the temporal fossa, and a dorsoventrally directed, trough-like squamosal fossa is present (Bisconti, 2008) (Figure 15B). However, although it is only rarely found in *E. robustus* (one individual: USNM13803), we also found an individual with a relatively smooth temporal surface of the squamosal among the examined 25 specimens of the eastern North Pacific population (Figure 15C). This is also the case for the specimens of the western North Pacific and Atlantic populations, although the number of examined specimens is limited. A bulging squamosal is mostly present in the western North Pacific and North Atlantic population, but some individuals from these populations lack this feature. This indicates the existence of an intraspecific present/absent variation of a well marked bulge of the squamosal.

GMNH-PV-3210 has a large and deep squamosal con-

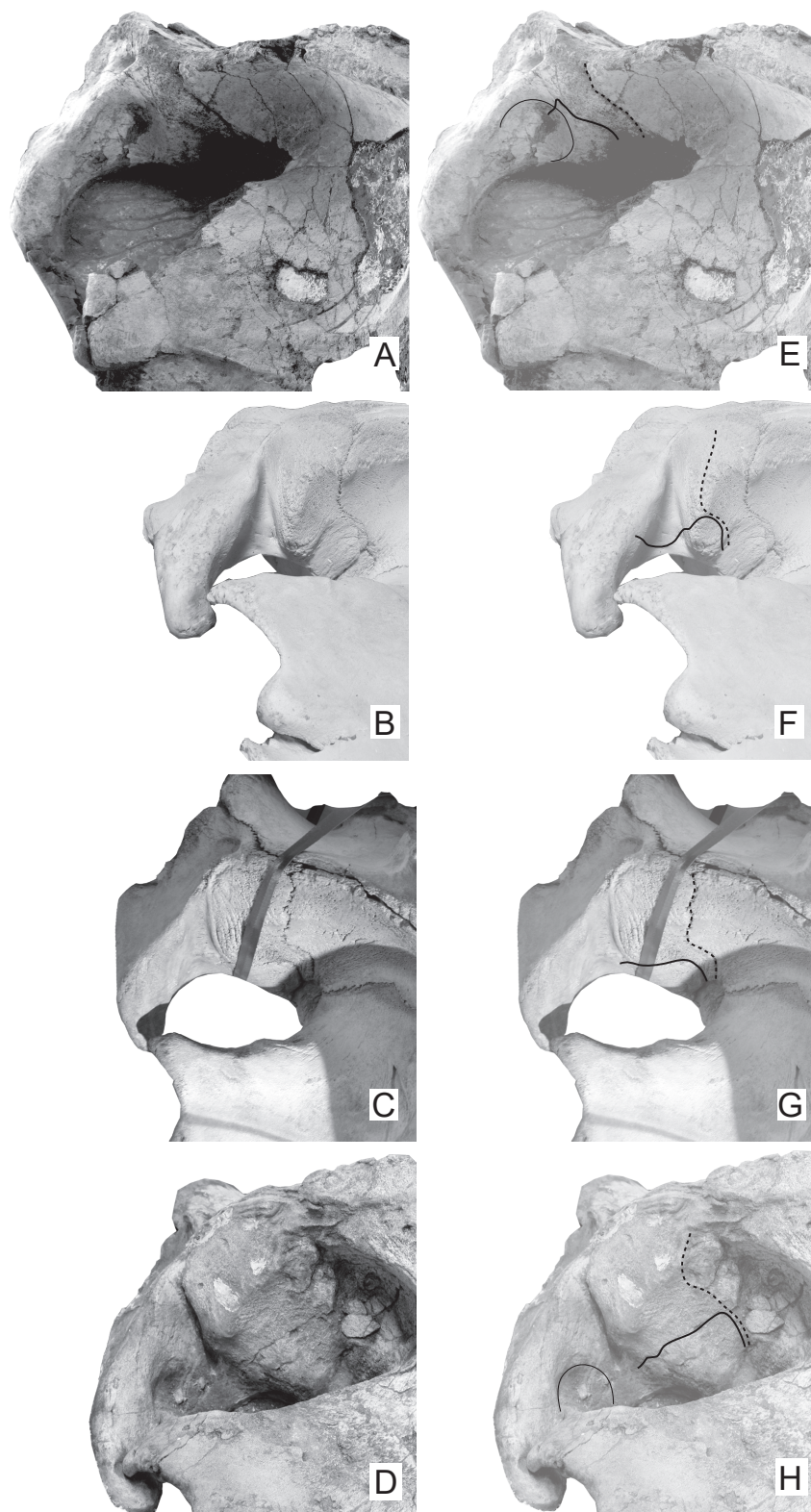


Figure 15. Squamosal portion of the cranium in anterodorsal view. **A, E**, *Eschrichtius akishimaensis* sp. nov. (GMNH-PV-3210); **B, F**, *E. robustus* (LACM86047); **C, G**, *E. robustus* (USNM13803); **D, H**, *Eschrichtius* cf. *robustus* (LACM122322). Dashed and solid lines indicate a squamo-parietal suture and a squamosal cleft, respectively. Narrow solid line represents a squamosal concavity or excavation. Not to scale.

cavity, which is just medial to the base of the zygomatic process of the squamosal. A squamosal cleft extends from the parieto-alisphenoid suture and terminates in this squamosal concavity (Figure 15A, E). No such squamosal concavity was found in any of the examined specimens of *Eschrichtius robustus*. Some individuals of *E. robustus* have a quite small and shallow concavity within the dorsoventrally directed, trough-like squamosal fossa in which the squamosal cleft terminates (e.g. LACM84260). This concavity could possibly be interpreted as a squamosal concavity, but it is quite small and shallow compared with the squamosal concavity of GMNH-PV-3210. Thus, a large and deep squamosal concavity is considered an autapomorphic character of *E. akishimaensis*.

A similar large and deep excavation is found in the fossil gray whale, *Eschrichtius* cf. *robustus* (LACM122322), from the upper Pleistocene San Pedro Formation, California (Barnes and McLeod, 1984) (Figure 15D). However, the excavation of LACM122322 is located on the medial surface of the base of the zygomatic process of the squamosal; therefore, it is more laterally positioned compared with the squamosal concavity of GMNH-PV-3210. Moreover, the distal termination of the squamosal cleft is not in the excavation but is medial to it (Figure 15H). This suggests that the excavation found in LACM122322 is not homologous to the squamosal concavity of GMNH-PV-3210. A similar, but much shallower, fossa is found in some individuals of *E. robustus* (e.g. LACM95979) and this may be homologous to the excavation found in LACM122322.

Fossil record of the genus *Eschrichtius*

Several fossil/subfossil specimens of genus *Eschrichtius* have been reported from both the Pacific and the Atlantic realms (e.g. Repenning, 1983; Barnes and McLeod, 1984; Mead and Mitchell, 1984; Post, 2005; Ichishima *et al.*, 2006; Powell and Ponti, 2007; Garrison *et al.*, 2012; Noakes *et al.*, 2013; Tsai *et al.*, 2014; Tsai and Boessenecker, 2015).

The oldest fossil *Eschrichtius* was found from the upper Pliocene Yuchi Formation (3.8–2.6 Ma), Hokkaido, Japan (Ichishima *et al.*, 2006). The specimen (HMT-F-1) consists of an incomplete cranium and some postcranial elements. Because of the incompleteness of the specimen, the authors did not discuss the details of its phylogeny and conservatively identified it as *Eschrichtius* sp. Although we do not find any morphological characters clearly suggesting that HMT-F-1 differs from the modern species of *Eschrichtius*, and though its specific identification is beyond the scope of this paper, *E. akishimaensis* is at least differentiated from HMT-F-1 by having a large and deep squamosal concavity.

A partial skeleton (LACM122322) was recovered from

the upper Pleistocene San Pedro Formation (200–300 Ka; Deméré *et al.*, 2005), California, and was described by Barnes and McLeod (1984) as *Eschrichtius* cf. *robustus*. The authors found that there was “no osteological basis for separating the fossil skull (LACM122322) from modern *Eschrichtius robustus*” (Barnes and McLeod, 1984, p. 9). Moreover, as stated before, *E. akishimaensis* has a large and deep squamosal concavity; therefore, *E. akishimaensis* is differentiated from LACM122322.

Other reported fossils of the genus *Eschrichtius* are fragmentary and/or undescribed and/or cannot be distinguished from the living species. *Eschrichtius akishimaensis*, which was recovered from the lower Pleistocene, is the first, and therefore geologically the oldest, described fossil species of the genus *Eschrichtius*. This may improve our understanding of the evolutionary history of the genus *Eschrichtius*. Since *E. akishimaensis* is differentiated from the upper Pliocene *Eschrichtius* sp. from Hokkaido and also from the modern gray whale, *E. robustus*, this clearly suggests that at least two different lineages of *Eschrichtius* survived as late as the early Pleistocene. Future discoveries of post-early Pleistocene *Eschrichtius* fossils will elucidate the evolutionary history of the genus *Eschrichtius*, especially for the western North Pacific population that is in danger of disappearing.

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