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Source: Paleontological Research, 8(1) : 1-10

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/prpsj.8.1

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Paleontological Research, vol. 8, no. 1, pp. 1–10, April 30, 2004
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Reinterpretation of some cranial structures of *Desmostylus hesperus* (Mammalia: Desmostylia): a new specimen from the Middle Miocene Tachikaraushinai Formation, Hokkaido, Japan

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Received April 10, 2003; Revised manuscript accepted September 5, 2003

Abstract. A new skull of *Desmostylus hesperus* Marsh, 1888 is described from the late Middle Miocene Tachikaraushinai Formation, Utanobori, Hokkaido, northern Japan. The specimen, GSJ-F7745, is a nearly complete skull and mandible, but the posterior halves of their left sides are missing. It was a juvenile individual, having part of the worn fourth deciduous molar (dp^4) in the right upper jaw. Another specimen (GSJ-F7743) was uncovered in the same formation near the same area where GSJ-F7745 was collected. Both fossils represent nearly the same ontogenetic stage and were of the same gender.

There are two different opinions regarding the position of the external acoustic meatus of *Desmostylus*. The cranial cavity of specimen GSJ-7745 is observable and reveals that the meatus should be identified as being the foramen on the lateral surface of the posterior portion of the zygomatic arch.

Key words: *Desmostylus hesperus*, external acoustic meatus, Middle Miocene, Tachikaraushinai Formation, Utanobori

Introduction

Desmostylus hesperus Marsh, 1888 was established on the basis of an incomplete tooth. Subsequently, additional species were described in the genus *Desmostylus*, based only on slight differences of tooth morphology. However, it was later demonstrated that the morphological variation of the teeth of *Desmostylus* was great, and some species were synonymized with the type species, *D. hesperus* (e.g., Ijiri, 1937; VanderHoof, 1937; Reinhart, 1959). Recently, *D. hesperus* and *Desmostylus japonicus* Tokunaga and Iwasaki, 1914 were reproposed as two distinct species based on some morphological differences of the skull (Inuzuka *et al.*, 1995; Kohno, 2000). However, there is little discussion about the individual variations within each species.

Two nearly complete skulls (GSJ-F7743, GSJ-F7745) and several fragmentary specimens considered to be *D. hesperus* have been uncovered in the late Middle Miocene, Tachikaraushinai Formation, Utanobori, Hokkaido, Japan (Akiyama and Kumano, 1973; Kimura *et al.*, 1978; Yamaguchi, 1978; Kimura, 1981; Yamaguchi *et al.*, 1981). These two skulls were collected within 50 m of each other at the same stratigraphic level of the Utanobori site. Furthermore, they are very similar to each other in morphology (Inuzuka, 1988), and they seem to have belonged to the same population. It is very important to compare these specimens to each other for an evaluation of individual variation in *D. hesperus*. However, only one of the two Utanobori specimens (GSJ-F7743) has been described (Inuzuka, 1988). The purpose of this paper is to describe the new specimen (GSJ-F7745), and make comparisons with the previously described skull.

Abbreviations

The following abbreviations are used for institutions: GSJ, Geological Survey of Japan, Tsukuba, Japan; NSM, National Science Museum, Tokyo, Japan; UHR, University of Hokkaido museum registered, Sapporo, Japan; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

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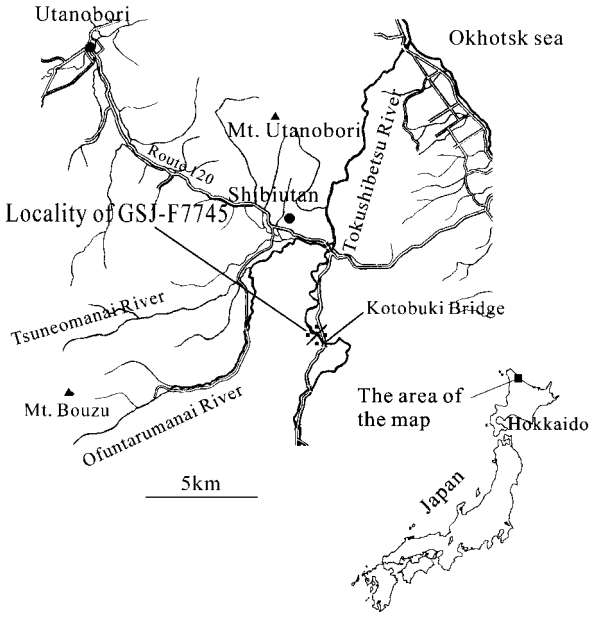


Figure 1. Locality map of GSJ-F7745. Latitude 44°43′05″N and Longitude 142°36′33″E.

Systematic paleontology

Mammalia Linnaeus, 1758
Desmostylia Reinhart, 1959
Desmostylidae Osborn, 1905
Desmostylus Marsh, 1888

Desmostylus hesperus Marsh, 1888

Diagnosis.—Canine and incisors are lost in the upper jaw. The sagittal crest is undeveloped. The posterior portion of the skull is expanded. The rostrum is high and narrow. The nasal is swollen vertically between the supraorbital processes.

New referred specimen.—GSJ-F7745, a nearly complete skull and mandible collected from the Tachikaraushinai Formation, Kamitokushibetsu, Utanobori, Hokkaido, Japan (Figure 1). Geological age based on K-Ar dating is inferred as late Middle Miocene (13.7 ± 0.7 and 13.8 ± 0.9 Ma) (Shibata *et al.*, 1981; Fujimoto *et al.*, 1998).

Description

GSJ-F7745 is a nearly complete skull and mandible, but their posterior halves are missing on the left side. They are slightly compressed and skewed. The dentition is nearly complete on each side (Figures 2–6).

Occipital.—The basioccipital and the exoccipital are preserved on the right side, and the occipital condyles and the foramen magnum are missing. The exoccipital directly connects to the squamosal, so that the mastoid is unexposed on the occiput. The supramastoid and mastoid foramina are located on the suture between the exoccipital and squamosal. The nuchal crest is undeveloped. The line of the lambdoid suture is gently convex anteriorly. The paroccipital process is stout, and its cross section is triangular. The basioccipital remains on the right side and is wide and short. A pair of tubercles for muscular attachments is present on the ventral surface of the basioccipital. The outline of each tubercle is circular, and their surfaces are slightly rough. The outline of the lacerate foramen is anteroposteriorly long and polygonal. The posterior portion of the lacerate foramen is partly continuous with the jugular foramen.

Parietal.—The parietal occupies the posterior half of the dorsal surface of the braincase. It swells posteriorly. The parietal penetrates sharply into the frontal on both sides. No sagittal crest is developed. The temporal line runs along the dorsolateral surface. The midline of the dorsal surface is slightly depressed.

Frontal.—The frontal makes up the flat anterodorsal surface of the cranium. The supraorbital process projects dorsolaterally. The orbit communicates with the temporal fossa. Several small grooves are present on the dorsal surface. The midsection between the supraorbital processes is elevated. The supraorbital foramen is present on the ventral surface of the supraorbital process. The foramen opens anteriorly, and from it a shallow groove extends anteriorly. The ethmoid foramen is invisible because of swelling of the dental sac of the M^2.

Nasal.—The nasal is retracted to the level of the orbit and is very long. The posterior half of the nasal articulates with the frontal. The nasal and surrounding portions are dorsally swollen. The nasal does not extend to the nares, and does not contribute to the outline of the nares.

Premaxilla.—The premaxilla forms the anterior portion of the rostrum. On the palate, the premaxilla extends to the middle part of the rostrum and narrows posteriorly. Dorsally, the premaxilla extends posteriorly to the nasal and covers the anterior portion of the nasal. The nares are bordered entirely by the premaxilla. The left and right premaxillae are in contact behind the nares.

Maxilla.—The maxilla forms the lateral wall of the rostrum and occupies most of the palatal surface. The zygomatic process of the maxilla extends posteriorly beyond the orbit. Ventral to the orbit, the maxilla projects posteroventrally and forms a flangelike struc-

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Figure 2. Cranium of *Desmostylus hesperus* Marsh, GSJ-F7745. **A**. ventral view. **B**. dorsal view. **C**. left lateral view. **D**. right lateral view. Scale bar equals 10 cm.

ture. The posterior end of the maxilla swells greatly because of the dental sac of the M^2. The large infraorbital foramen is located at the level of the P^4. From the infraorbital foramen, a large groove extends anteriorly. The rim of the palate is steeply elevated to form a ridge.

Jugal.—The jugal forms the ventral and posterolateral rim of the orbit and makes up a small part of the zygomatic arch. The outline of the suture between the jugal and the zygomatic process of the squamosal is gently concave. The jugal extends medially to the zygomatic process of the squamosal. A small foramen is present on the suture between the jugal and maxilla in the orbit.

Lacrimal.—No distinct bone corresponds to the lacrimal in the present specimen.

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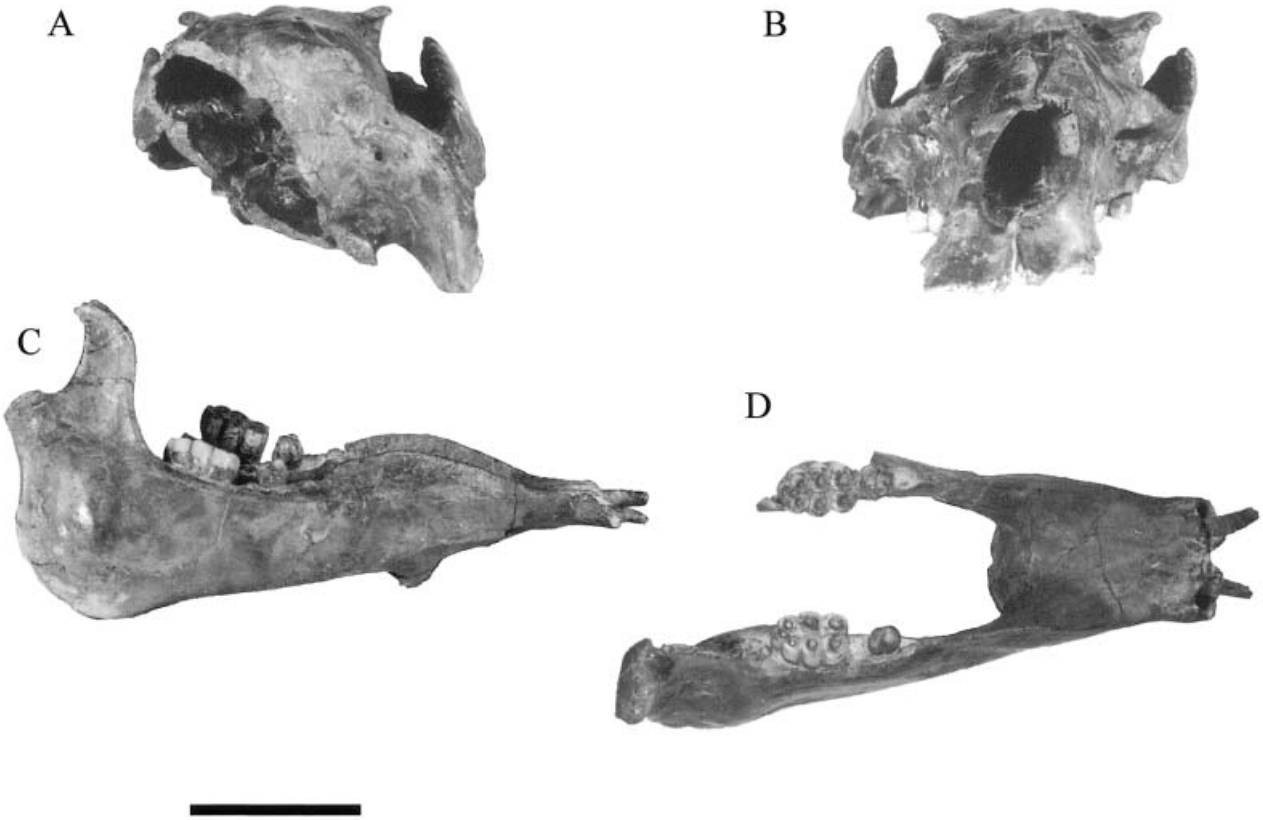


Figure 3. Cranium (**A** and **B**) and mandible (**C** and **D**) of *Desmostylus hesperus* Marsh, GSJ-F7745. **A**. posterior view. **B**. anterior view. **C**. right lateral view. **D**. dorsal view . Scale bar equals 10 cm.

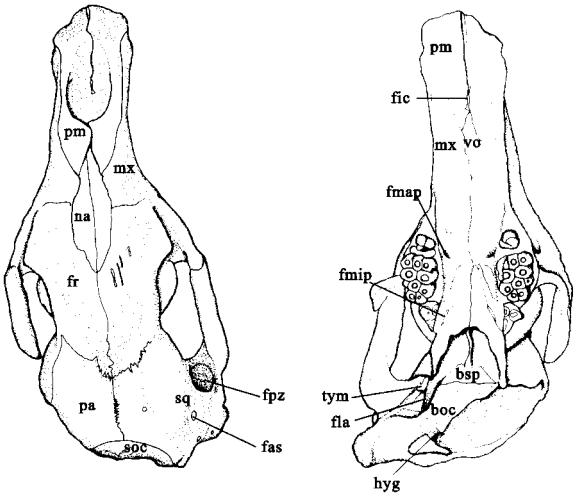


Figure 4. Sketch of *Desmostylus hesperus* Marsh, GSJ-F7745. **A**. Dorsal view. **B**. Ventral view. Scale bar equals 10 cm. Abbreviations: boc, basioccipital; bsp, basisphenoid; fas, anterior squamosal foramen; fic, incisive foramen; fla, lacerate foramen; fmap, major palatine foramen; fmip, minor palatine foramen; fr, frontal; hyg, hypoglossal foramen; mx, maxilla; na, nasal; pa, parietal; pm, premaxilla; sq, squamosal; soc, supraoccipital; tym, tympanic; vo, vomer.

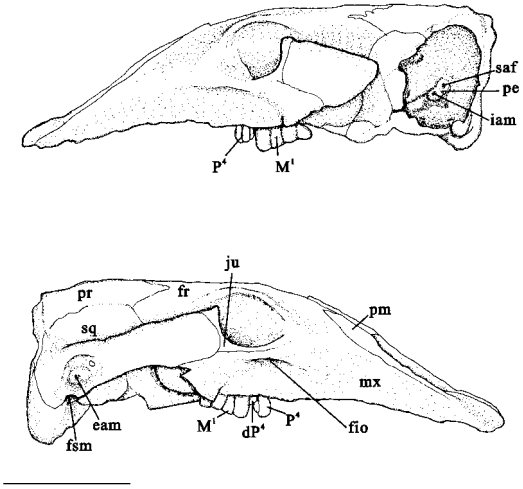


Figure 5. Sketch of *Desmostylus hesperus* Marsh, GSJ-F7745. **A**. Left lateral view. **B**. Right lateral view. Scale bar equals 10 cm. Abbreviations: dP4, fourth deciduous premolar; eam, external acoustic meatus; fio, infraorbital foramen; fr, frontal; fsm, stylomastoid foramen; iam, internal acoustic meatus; ju, jugal; M1, first molar; mx, maxilla; na, nasal; pa, parietal; pe, periotic; pm, premaxilla; P4, fourth premolar; saf, subarcuate fossa; sq, squamosal.

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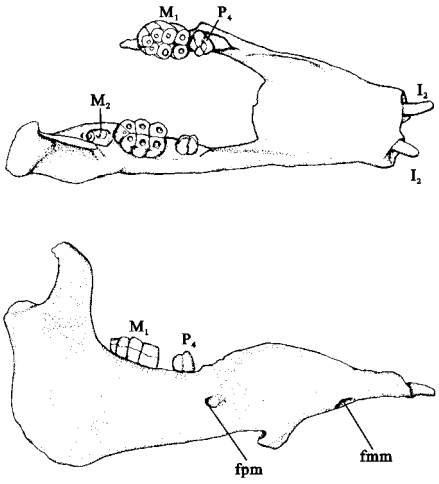


Figure 6. Sketch of mandible of *Desmostylus hesperus* Marsh, GSJ-F7745. **A**. Dorsal view. **B**. Right lateral view. Scale bar equals 10 cm. Abbreviations: fmm, middle mental foramen; fpm, posterior mental foramen; I2, second incisor; M1, first molar; P4, fourth premolar.

Palatine.—The palatine forms the posterior portion of the palate. It is narrowing anteriorly. A narrow and low ridge runs anteroposteriorly at the midline of the palate.

Sphenoids.—The wide and short body of the basisphenoid is exposed on the ventral surface of the skull. The oval foramen of the right side is preserved. It is elliptical in outline and located anterior to the lacerate foramen. On the inner side of the cranium, the hypophyseal fossa is recognized as a remarkable depression on the dorsal surface of the basisphenoid. Lateral to the hypophyseal fossa, the orbitorotundam opens anteriorly. The right foramen may be concealed by postmortem deformation.

Squamosal.—The zygomatic process of the squamosal forms most of the zygomatic arch. The zygomatic process is very deep. It extends anterodorsally. The ventral side of the posterior portion of the zygomatic process has a wide and flat surface. The glenoid fossa is elliptical in outline and slightly depressed. Its surface slopes down posteroventrally.

The external acoustic meatus opens at the posterior end of the lateral surface of the zygomatic process (this identification is discussed in the following section). The meatus is situated posterodorsal to the glenoid fossa. The structure of the meatus is like a funnel, and the medial wall is continuous with the lateral surface of the squamosal without sutures. The postzygomatic foramen is located on the dorsal surface of the posterior end of the zygomatic process of the squamosal. This foramen includes three openings; the largest and the smallest ones extend medially to the inside of the skull, and the other one passes through the zygomatic process and communicates with a small opening at the anterior portion of the external acoustic meatus. The anterior squamosal foramen opens posterior to the postzygomatic foramen.

The tympanic is anteroposteriorly compressed and shaped like a narrow ridge. It lies posteromedial to the glenoid fossa. The stylomastoid foramen faces ventrally at the base of the paroccipital process. From the stylomastoid foramen, a shallow groove extends onto the medial surface of the paroccipital process.

On the inside of the braincase, the periotic is recognized as a tubercular swelling. It bears the internal acoustic meatus and the vestibular aqueduct. The internal acoustic meatus is 5.0 mm in diameter and elliptical in outline.

Mandible.—The horizontal and ascending rami of the left side are mostly lost, but the right side is nearly complete. The dentaries are firmly fused at the symphysis. The symphysis is long and dorsoventrallly thin. The dorsal surface of the symphysis slants down posteriorly. The posterior end of the symphysis swells like a tubercle. The diastema between the incisor and the premolar is extremely long, and the rim is elevated steeply like a ridge. A middle mental foramen and a posterior one are present on the ventral side and on the lateral side, respectively, of each dentary. However, an anterior mental foramen is not clearly recognized, but only a small and slight depression is observed in the midline of the ventral side of the symphysis. The angle of the mandible is semicircular in outline. No angular process is developed. On the medial side the pterygoid fossa is barely recognizable as a small depression. The medial portion of the horizontal ramus at the M_2 is swollen because of the large dental capsule. The ascending ramus is short and thin. The mandibular condyle is situated slightly higher than the tooth row. The articular surface is transversely broad and gently convex. It slopes down posteriorly at a 45-degree angle to the long axis of the ascending ramus. The coronoid process is thin and slender. The end of the coronoid process bends posteriorly. The lateral side of the base of the coronoid process is slightly depressed. A large mandibular foramen is present on the medial side and extends ventrally along the posterior margin of the swollen dental capsule of the M_2.

A small and cancellous surface is present anterior to the P_4, but neither alveolus nor tooth is present. The alveolus of M_2 had begun to open so that part of the M_2 is visible. The opening of the gubernacular

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canal leading to the dental follicle of the M_3 is visible posterior to the M_2 alveolus.

Upper dentition.—There is neither canine nor incisor in the upper jaw. The maxilla bears the P^4, M^1 and the erupting M^2. The P^4 has three columns: two columns are transversely arranged, and the other column is situated at the buccal side behind the anterior row. These three columns correspond to the protocone, paracone and metacone, respectively. The anterior two columns are larger and taller than the other. In occlusal view, the right P^4 is rotated clockwise at 30 degrees to the long axis of the dentition, and the left one counterclockwise at 50 degrees. The occlusal facet of the right P^4 forms a flat wear surface: the left one is less worn.

The remnant of the dental root of dP^4 is only present between the P^4 and M^1 in the right maxilla (Figure 7). The crown of the dP^4 is obliterated. Diastemata are present in the other jaw quadrants between P^4s and M^1s. In the diastemata corresponding to the position of the remnant, there is no recognizable tooth or alveolus. A large interproximal facet is present on both mesial and distal margins of the remnant. The mesial facet was caused not by the P^4 but another tooth (dP^3) that had come out before the P^4 erupted, and the mesial outline does not fit that of the distal margin of the right P^4. On the other hand, the distal margin tightly contacts the mesial margin of the M^1.

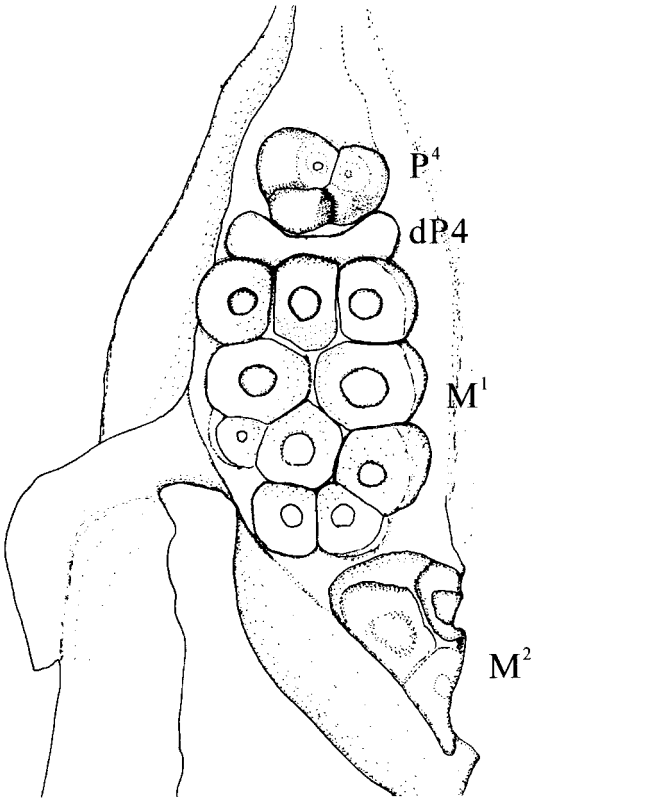


Figure 7. Right upper dentition of *Desmostylus hesperus* Marsh, GSJ-F7745. Scale bar equals 5 cm. Abbreviations: dP4, fourth deciduous premolar; M1, first molar; M2, second molar; P4, fourth premolar.

The M^1 consists of nine columns and an accessory column. They are transversely arranged in three rows. Each row has 3, 2, 2 and 2 columns, respectively, from the mesial to the distal end. The accessory column is located at the buccal side in the third row. Four columns in the second and third row correspond to protocone, paracone, metacone and hypocone. The M^1s on both sides are moderately worn. The right M^1 has a distinct interproximal facet on the mesial.

Lower dentition.—Kohno (2000) showed that *Desmostylus* has two pairs of incisors and a pair of canines in the mandible and that their eruptions are sequential from mesial to distal. He identified the incisors as I_2 and I_3, respectively. Though he did not mention the reason for the identification, it is considered to be based on a general tendency, in mammals, of reduction of the number of incisors from the mesial (Otaishi, 1984). Identification of the incisors of the present specimen, GSJ-F7745, is based upon that of Kohno (2000).

In GSJ-F7745, a pair of tusklike teeth (I_2) erupts on the anterior portion of the mandible. In a cross-sectional CT image, another pair of tusklike teeth (I_3) is recognizable dorsolateral to the pair of the erupted teeth. The I_2 is cylindrical in overall shape and protrudes anterolaterally. Part of the anterior tip of the right I_2 is missing. No distinct wear facet is visible on the I_2. A pair of large alveoli opens lateral to the I_2s. The opening of the alveolus becomes wide anteriorly and contains no septum. However, the opening is too large for just dI_3, so it is assumed to be a combination of the alveoli of dI_2 and dI_3, or dI_3 and dC.

Both P_4 have four columns and one or two accessory columns. These four columns correspond to protoconid, metaconid, hypoconid and entoconid. The P_4 does not have an interproximal facet on either the anterior or posterior margins. The right P_4 has four columns and two accessory columns. The four columns are transversely arranged in two rows, and the two accessory columns are positioned at the center of the posterior margin and at the center of the lingual margin, respectively. The buccal columns of each row are taller than the others. A slightly developed occlusal facet is recognizable on the buccal column in the anterior row.

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The left P_4 has four columns and one accessory column. The four columns are transversely arranged in two rows, and the accessory one is present at the center of the anterior margin. The left P_4 is rotated clockwise at 40 degrees to the long axis of the dentary in occlusal view.

The M_1 consists of seven columns. They are transversely arranged in four rows, and each row has 2, 2, 2 and 1, respectively, from the anterior to the posterior end. The four columns in the anteriormost and second rows correspond to protoconid, metaconid, hypoconid and entoconid. The M_1 is moderately worn. A mesial interproximal facet is visible on the margin, but there is no interproximal facet on the posterior margin.

The alveolus of the unerupted M_2 is partially open, and part of the crown is visible. The gubernacular foramen of M_3 is visible posterior to the alveolus of the M_2.

Discussion

Identification of external acoustic meatus.—Three skulls of *D. hesperus* have been previously described (USNM 8191, UHR 18466, GSJ-F7743) (Hay, 1915; Nagao, 1935; Inuzuka, 1988). In these descriptions, there have been two different identifications of the position of the external acoustic meatus.

A pit on the lateral surface of the posterior end of the zygomatic arch (A in Figure 8) was identified as the external acoustic meatus by some researchers (Hay, 1915; Abel, 1922; Ijiri and Kamei, 1961; Clark, 1991). Most of these researchers did not state the reasoning behind this conclusion, but they probably assumed an obvious foramen at the posterolateral portion of the skull to be the external acoustic meatus.

On the contrary, other researchers identified a small foramen (B in Figure 8) at the base of the paroccipital process as being the external acoustic meatus (Abel, 1925; VanderHoof, 1937; Inuzuka, 1988). Inuzuka (1988) is the only researcher to give reasons for this conclusion. In his description of a nearly complete skull of *D. hesperus*, GSJ-F7743, Inuzuka (1988) described the morphological features of the foramen (A) located almost directly above the mandibular fossa. It is a funnel-like structure, narrowing medially. The opening of the foramen connects to the surface of the squamosal without sutures. Thus, Inuzuka (1988) concluded that since these features were generally not observed in the external acoustic meatus of mammals, the external acoustic meatus should not be identified as foramen (A) but is instead foramen (B). Inuzuka (1988) instead identified foramen (A) as being the epitympanic sinus.

The posterior left half of GSJ-F7745 is not preserved, so the inner morphology of the braincase is visible. Observation of the interior of the skull shows that the position of the periotic corresponds to that of foramen (A). The features of foramen (A) are generally observed in proboscideans as Domning *et al.* (1986) and Clark (1991) pointed out. Furthermore,

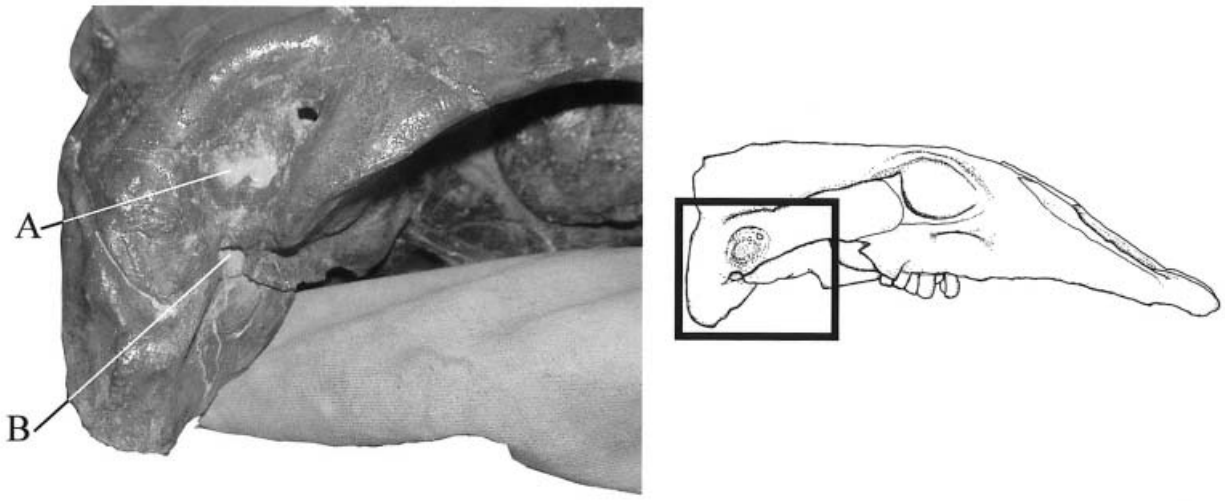


Figure 8. Position of external acoustic meatus in *Desmostylus*. **A**. External acoustic meatus (Abel, 1922; Hay, 1915; Ijiri and Kamei, 1961; Clark 1991; the present study). It was sometimes considered to be the epitympanic sinus (Abel, 1925; VanderHoof, 1937; Inuzuka, 1988). **B**. Stylomastoid foramen (Abel, 1922; Hay, 1915; Ijiri and Kamei, 1961; Clark, 1991; the present study.). It was sometimes considered to be the external acoustic meatus (Abel, 1925; VanderHoof, 1937; Inuzuka, 1988).

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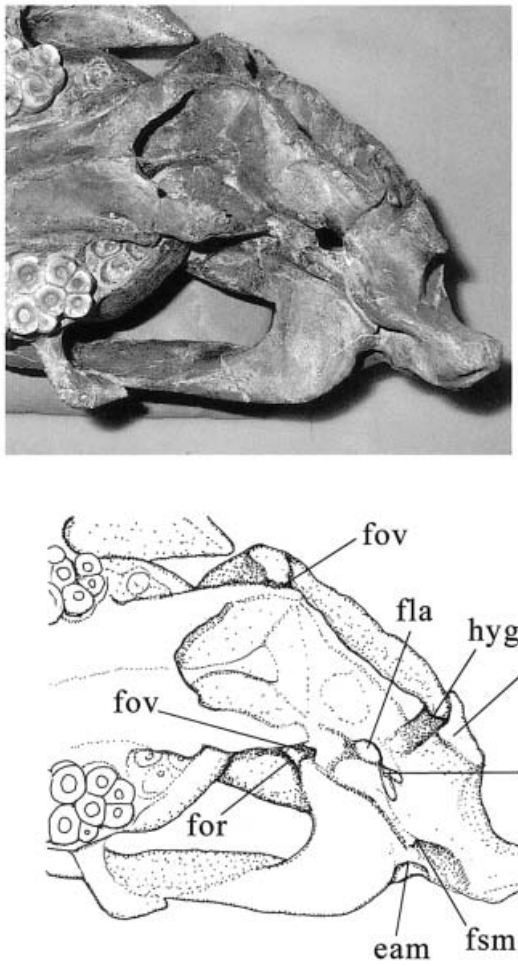


Figure 9. Basicranial foramina of *Desmostylus hesperus* Marsh, GSJ-F7745. Abbreviations: eam, external acoustic meatus; fj, jugular foramen; fla, lacerate foramen; for, orbitorotundam; fov, oval foramen; fsm, stylomastoid foramen; hyg, hypoglossal foramen; occ, occipital condyle.

foramen (B) at the base of the paroccipital process of GSJ-F7745 opens ventrally, and from the foramen (B), a shallow groove extends ventrally along the anterior surface of the paroccipital process. These features indicate that foramen (B) is one of the neurovascular foramina. Thus, foramina (A) and (B) should be identified as the external acoustic meatus and the stylomastoid foramen, respectively. The particular structures of the external acoustic meatus of *Desmostylus* are possibly an expression of particular adaptations; however, this is still open to debate.

Ontogenetic stage and gender.—Inuzuka *et al.* (1995) examined three hundred twenty isolated *Desmostylus* teeth and divided the teeth of each dental class into male and female by size difference. The M^1s of GSJ-F7745 belong to the male M1 category Inuzuka *et al.* (1995) described. It shows GSJ-F7745 may be a male individual.

Molars of *Desmostylus* erupt sequentially, and the dental class indicates the ontogenetic stage (Matsumoto, 1917; Ijiri, 1937; Inuzuka, 1989). The M^1 is worn moderately and M^2 is unerupted in GSJ-F7745. Thus, the specimen is considered to be a juvenile or young adult.

M1 sizes and states of wear of the two specimens, GSJ-F7745 and GSJ-F7743, do not greatly differ from each other, and cranial sizes also are nearly the same (Tables 1, 2). However, the P4 of GSJ-F7745 wears a little less than GSJ-F7743. In GSJ-F7745, no canine is visible in a CT image, but Sawamura and Inuzuka (2000) showed part of the developing canine in an x-ray image of GSJ-F7743. Furthermore, the remnant of the dP^4 is remained in GSJ-F7745. This suggests that the two specimens may be male and are of nearly the same ontogenetic stage. However, GSJ-F7745 is a little younger than GSJ-F7743.

Individual variation in D. hesperus.—The new specimen (GSJ-F7745) and another specimen (GSJ-F7743) were uncovered in the same formation at Utanobori, Hokkaido, Japan, and they were collected within 50 m of each other. The two specimens are considered to be from a single population. However, morphological variations are observed in the molar and premolars of the two specimens.

The P^4 of GSJ-F7743 consists of three columns, accessory columns and tubercles while that of GSJ-F7745 consists of just three columns.

In M^1 of GSJ-F7743, the most mesial columnar row is buccolingually wider than the others. A small tubercle is attached to the buccal margin between the paracone and metacone. In the M_1, the second columnar row is the widest.

On the contrary, in GSJ-F7745, widths of the first and second row are nearly equal. A distinct accessory column is attached buccal to the metacone. In the M_1, the first and second rows are nearly equal in width.

In addition, there are variations on the occlusal surface and state of premolar rotation between the two specimens. Wear of the occlusal surface of the molar of GSJ-F7743 is valleylike while the occlusal surface of GSJ-F7745 is worn flat. In premolar rotation, the P^4s of GSJ-F7743 are bucally rotated and the lower ones are lingually rotated. On the other hand, the P^4s of GSJ-F7745 are lingually rotated on both sides, and the lower one is only rotated in the left mandible.

Premolars may erupt and fall out in varied timing with molar eruption; GSJ-F7743 has erupted P^4 at the M1 ontogenetic stage, USNM 8191 has P^{3-4} at the M1

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Table 1. Measurements (mm) of GSJ-F7745. L and R indicate measurement on left and right side, respectively; e indicates transverse measurements that are half-skull measurements multiplied by two.

Measurement	Specimen	
	GSJ-F7745	GSJ-F7743
1 Condylobasal length	400	427*
2 Skull length (inion to prosthion)	409.0	424*
3 Width across postorbital processes	126.4	133.4
4 Width of braincase at glenoid fossa	128.3	237.5
5 Greatest width between zygomatic proceses	189.5e	218*
6 Width of rostrum at infraorbital foramen	101.8	96.4
7 Width of rostrum at posterior border of nares	74.4	71.4
8 Width of nares	41.8	40*
9 Length of nares	90.1	92*
10 Greatest width of zygomatic process	L –, R 17.7	L 18.9, R 21.2
11 Greatest height of zygomatic process	L –, R 40.9	L 48.7, R 53*
12 Width of glenoid fossa	L –, R 45.1	L 46, R 45.4
13 Diameter of infraorbital foramen	L –, R 15.8	L 18.6, R 16.9
14 Width of paroccipital process	L –, R 24.8	L –, R 29.7
15 Greatest width between exoccipitals	229.0e	246.0
16 Width of palatine	47.6	61.3
17 Lengh of palatine	67.6	70.6
18 Length of ridge of diastema, anterior end to P^4	L 266.0, R 294.0	252*
19 Greatest length of mandible	343.0	353*
20 Width between articular heads	156.4e	197*
21 Greatest height of horizontal mandibular ramus	333.0	344*
22 Length of mandibular symphysis	134.7	154*
23 Height of tubercle at posterior end of symphysis	18.8	21
24 Height of coronoid process	L –, R 73.9	L 72.9, R 80.7
25 Length of ridge of diastema in mandible	L –, R 174.7	L 190, R 190

* After Inuzuka (1988)

Table 2. Measurements (mm) of dentition of GSJ-F7745.

Dental class	Measurement	GSJ-F7745		GSJ-F7743	
		Left	Right	Left	Right
P^4	Length	14.8	14.7	18.1*	17.8*
	Width	19.0	18.2	18.1*	18.4*
dP^4	Length	–	6.6+	–	–
	Width	–	24.6	–	–
M^1	Length	43.7	44.8	49.0*	47.4*
	Width	32.9+	32.3	35.8*	36.0*
I_2	Diameter	11.7	10.8	11.6*	10.8*
	Protruding length	32.2	32.6	24.5*	35.0*
P_4	Length	19.8	18.1	19.7*	20.7*
	Width	16.6	14.9	19.5*	20.1*
M_1	Length	42.9	42.9	44.0*	42.4*
	Width	28.7	28.3	33.5*	33.5*

* After Inuzuka (1988)

stage, and UHR 18466 has P^4 at the M2 stage. This difference could give rise to variations of combination of upper and lower molars, and rate of progress of horizontal drift of molars. Thus, the variation of occlusal surface and premolar rotation could be visible.

Acknowledgements

We would like to express our thanks to Naoki Kohno (National Science Museum, Tokyo) for critical reading of our manuscript, for numerous suggestions and for encouragement during many phases of this work. We are grateful to Shouichi Yamaguchi (Union Consultant Company, Sapporo) for providing us the opportunity to study the specimen, GSJ-F7745. We thank James L. Goedert (Burke Museum of Natural History and Culture, University of Washington, Seat-

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tle) for correcting the English of the draft and for useful suggestions. We are grateful to Hiroshi Sawamura (Ashoro Museum of Paleontology, Hokkaido) for giving us useful advice and very important suggestions of mammal anatomy. We also thank Norihisa Inuzuka (Univ. Tokyo) for allowing us access to the specimen GSJ-F7743 in his care. We thank Akihiro Nagata (Sapporo Konan Grade school, Sapporo) and Hiroko Shimada (Sapporo City) for removing the matrix from the specimen, GSJ-F7745.

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