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A phylogeny of the North Pacific Sirenia (Dugongidae: Hydrodamalinae) based on a comparative study of endocranial casts

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Abstract. Comparisons of endocranial casts of the subfamily Hydrodamalinae (Mammalia; Sirenia) reveal some interesting evolutionary trends, especially in the changes to the shape of the cerebrum and olfactory bulbs, and the position of the optic nerve. Endocranial casts of both *Hydrodamalis spissa* Furusawa, 1988 and *H. gigas* (Zimmermann, 1780) reveal several synapomorphies (spherical olfactory bulbs, the optic nerve separate from the trigeminal nerve, and diminished fissura longitudinalis cerebri and transverse sulcus). A revised phylogeny of North Pacific Sirenia based in part on endocranial casts demonstrates that *H. spissa* and *H. gigas* are very closely related within the Hydrodamalinae. On the other hand, although they contemporaneously inhabited the North Pacific Ocean, the eastern Pacific *H. cuestae* differs clearly from the western Pacific *H. spissa*.

Key words: endocranial cast, Hydrodamalinae, morphological analysis, North Pacific, Sirenia

Introduction

As for all mammals, endocranial casts of sirenians are related to the presphenoid and ethmoid frontally, the basisphenoid ventrally, the occipital posteriorly, the temporal laterally, and the parietal dorsally. For most mammals and birds, the endocranial cast directly reflects the shape of the brain. In addition, endocranial casts reveal the size of the brain, and display other characters that can be of diagnostic value.

The first to scientifically describe the endocranial cavity of a North Pacific sirenian was G.W. Steller (1751). He studied the skull of *Hydrodamalis gigas* from the Bering Sea and stated that the brain of *H. gigas* lacked the tentorium ossium and other crests were missing also. Brandt (1846) observed some endocranial cavities of *H. gigas* and determined that the olfactory nerves were large and, therefore, the olfactory sense was fairly strong. Also, the weak optic nerves correspond very well with the narrow optic canal and small eyes. Edinger (1933, 1939) used characters of an endocranial cast as comparable features between sirenian taxa. She described six natural stone endocranial casts attributed to primitive Dugongidae, *Protosiren fraasi*, and compared them to *Eotheroides aegyptiacum* (Edinger, 1933). *Protosiren* had extremely reduced senses of sight and smell as in living sea-cows (Edinger, 1939). She later summarized studies of the evolution of the vertebrate brain (Edinger, 1949). Furthermore, she observed that there was a reduction of the olfactory apparatus with extraordinary development of the acoustic system in cetacean evolutionary history (Edinger, 1955). Pilleri (1989) described natural stone endocranial casts of Miocene *Metaxytherium* sp., the ancestor of the Hydrodamalinae, and observed that the optic nerve and trigeminal nerve were larger in size than in recent *Dugong*. Pilleri (1989) also compared *Metaxytherium* sp. with Eocene *Protosiren* and *Eotheroides* from Europe and determined that *Metaxytherium* differed in development of the frontal lobes. He also proposed that the Oligocene genus *Halitherium* occupies an intermediate position between the Eocene and Miocene and the Recent forms. Also, Pilleri (1989) stated that *H. gigas* attained the highest level of cephalization. Recently, a precise preparation method has been developed using formic acid and acetic acid to clean out the endocranial cavities of fossil sirenian skulls. A recent trend has been to utilize CT scans to study endocranial features (Gingerich *et al*., 1994; Marino, 2000). Gingerich *et al.* (1994) calculated the endocranial volume of the braincase of *P. fraasi* by digitizing a trace

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of the inside edge of the braincase derived from CT scans, and clarified the differences between *P. fraasi* and *E. aegyptiacum*. Based on CT scans, Marino *et al.* (2000) calculated the estimated encephalization quotient (EQ) of two and fully aquatic Eocene archaeocete cetacean species, *Dorudon atrox* and *Zygorhiza kochii*; both were contemporary with *P. fraasi* and *E. aegyptiacum.*

The phylogeny of North Pacific Sirenia of the subfamily Hydrodamalinae was constructed using the abundant specimens from the eastern North Pacific (Domning, 1978). He described the endocranial morphology of the North Pacific Sirenia with special attention to the bony falx and tentorium ossium. However, specimens of the Hydrodamalinae were discovered in the western North Pacific in Japan subsequent to Domning's (1978) study and it became apparent that the phylogeny and evolution of the North Pacific Sirenia was more complex than previously thought. For example, the Early Pliocene *H. spissa* displays several features that are more derived than those seen in the Late Pliocene *H. cuestae*, although, because a partial skull of *H. cuestae* (Domning and Deméré, 1984) resembles *H. spissa*, Domning (1994) indicates that *H. spissa* is a synonym of *H. cuestae*.

The purpose of this paper is to describe and compare the morphological characters of hydrodamaline endocranial casts, and to review the phylogeny and classification of the subfamily Hydrodamalinae based on these results.

Materials and methods

Abbreviations used are: LACM: Los Angeles County Museum of Natural History, Los Angeles, U.S.A.; SDSNH: San Diego Society of Natural History, San Diego, U.S.A.; SMF: Senckenberg Museum, Frankfurt, Germany; TMNH: Takikawa Museum of Art and Natural History, Takikawa, Hokkaido, Japan; UCMP: University of California Museum of Paleontology, Berkeley, California, U.S.A.; YPM; Yamagata Prefecture Museum, Yamagata, Japan.

I used endocranial casts of the following six sirenian fossils for this study representing all of the presently recognized Hydrodamalinae: *Hydrodamalis gigas* (Zimmermann, 1780) Palmer, 1895 (UCMP 23050) Recent, Bering Island, Russia; *H. cuestae* Domning, 1978 (UCMP 86433), Late Pliocene, California, U.S.A.; *H. cuestae* Domning, 1978 (LACM 25917), ?Middle Pliocene, California, U.S.A.; *H. spissa* Furusawa, 1988 (TMNH 0001), Early Pliocene, Hokkaido, Japan; *Dusisiren jordani* (Kellogg, 1925) Domning, 1978 (UCMP 77037), Late Miocene, California, U.S.A.; *Halitherium schinzii* (Kaup, 1838) Kaup, 1855 (SMF-M3921) Oligocene, Antwerp, Belgium.

Because of the small size of the orifice that the cranial nerve and connective tissues pass through, there is a portion of the temporal region that is impossible to mold. Brain volume is not debated in this paper, because most marine mammals, except for pinnipeds, have developed a thick membrane around the surface of the brain in life and as a consequence braincase capacity does not reliably reflect real brain size (Edinger, 1939; Breathnach, 1955; Kamiya *et al.*, 1979).

External morphology

The vertebrate brain is divided into six parts: the rhinencephalon (olfactory bulb); the cerebrum; diencephalon; mesencephalon; cerebellum; and medulla oblongata. Although it is possible to divide a cerebellum when it has a tentorium ossium, it is difficult, however, to distinguish these regions and form in a sirenian endocranial cast. In general, many fissures are displayed on the surface of mammalian endocranial casts. However, for example, in *Dugong dugon* (Dugongidae; Dugonginae) the endocranial cast has only two fissurae. These are the fissura longitudinalis cerebri dividing the cerebrum bilaterally, and the pseudolateral sulcus dividing the cerebrum anteroposteriorly (Kamiya *et al.*, 1979). Identification of features on the endocranial casts of fossil sirenians were based on comparisons with endocranial casts of *Dugong dugon* (Figure 1).

I interpret the frontal lobes to be the part anterior to the sulcus lateralis, the lateroposterior parts to be the temporal lobes, with the parietal lobe in the dorsal part, and the occipital lobe posteriormost. The pseudolateral sulcus is interpreted to be the sulcus lateralis. Mammalian brains in general have twelve pairs of cranial nerves ventrally; in the specimens studied it was only possible to confirm Nn.I (Nn. olfactorii), N.II (N. opticus), N.V (N. trigeminus), and N.XII (N. hypoglossus). The trigeminal nerve is represented on the endocranial casts by the material filling the sphenorbital foramen. The hypophysis cerebri, near the optic nerve chiasm, is only weakly developed.

Description

Views of endocranial casts, with a key to measurements and their values for the following specimens, are shown in Figure 2, Figure 3 and Table 1, respectively.

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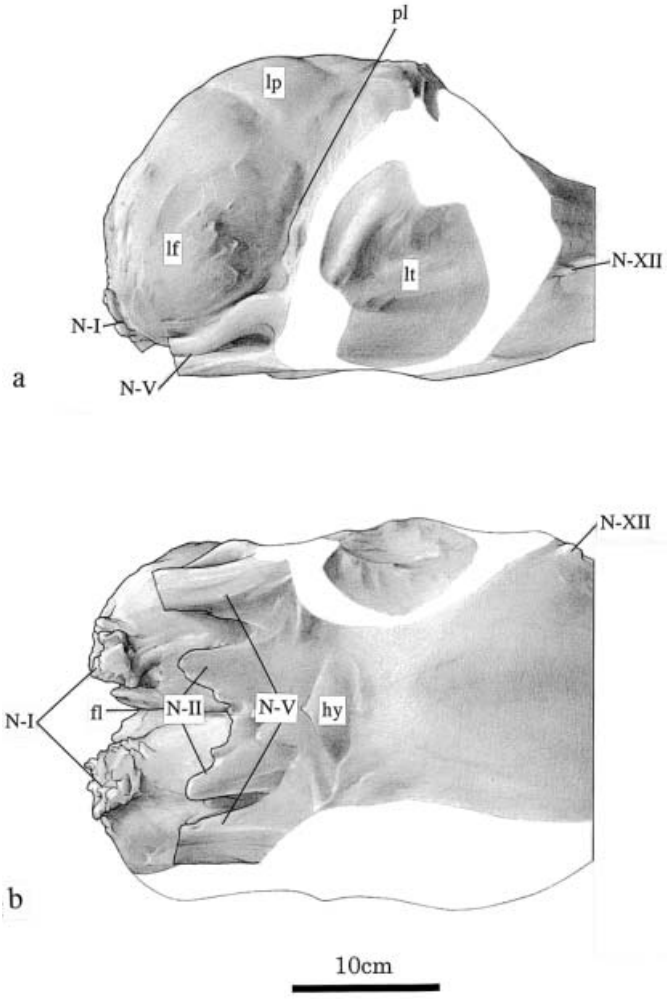


Figure 1. Endocranial cast of the holotype of *Hydrodamalis spissa* Furusawa, 1988 (TMNH 0001), Pliocene, Hokkaido, Japan. Abbreviations: cb, cerebrum; pl, pseudolateral sulcus; ch, chiasma opticum; hy, hypophysis; lf, lobus frontalis; lt: l. temporalis; lp, l. parietalis; Nn-I:Nn.; olfactorii; N-II; N. opticus; N-V, N. trigeminus; N-XII, N. hypoglossus.

Halitherium schinzii (SMF-M3921).—In lateral view, the endocranial cast is triangular in shape because the occipital lobe is larger than the frontal lobe; in dorsal view it is elliptical in shape. There is a deep sulcus between the parietal lobe and occipital lobe, and the parietal lobes are inflated. The fissura longitudinalis cerebri of the frontal lobe, reflection of bony falx, is deeper dorsally than frontally. The transverse sulcus is developed and the tentorium ossium is confined. The olfactory bulbs are long ellipses dorsoventrally. The optic nerve was small, adjacent to the medial side of the trigeminal nerve, and located dorsal to the dorsal side of the trigeminal nerve.

Dusisiren jordani.—This specimen is triangular in lateral view because the frontal lobe is low and the occipital lobe is higher, and elliptical in dorsal view. A distinct fissura longitudinalis cerebri passes through dorsally for the internal occipital protuberance. Lateral end of transverse sulcus is shallow, and surface of cerebrum is flat. The olfactory bulbs are long ellipses dorsoventrally. The optic nerve almost contacts the medial side of the trigeminal nerve, and is at the level of the dorsal side of the trigeminal nerve in frontal view. A hypophysis is posterior to the optic nerve chiasm and between the ear regions.

Hydrodamalis cuestae.—UCMP 86433 represents an immature individual, and LACM 25917 was an adult (Domning, 1978). Part of UCMP 86433 from the temporal lobe to the occipital lobe is broken away, as is the dorsal part of LACM 25917. LACM 25917 is about 17% larger than UCMP 86433, but otherwise the endocranial casts are morphologically similar, so the following descriptions are composite. They are elliptical in outline in both lateral and dorsal views. Both the fissura longitudinalis cerebri and transverse sulcus are indistinct. The olfactory bulbs are long ellipses dorsoventrally. The optic nerve was dorsal of and adjacent to the medial side of the trigeminal nerve. The hypophysis is posterior to the optic nerve chiasm and between the ear regions in ventral view.

Hydrodamalis spissa.—The endocranial cast of this specimen is rounded in shape in lateral view because of the dorsal expansion of the frontal lobe. It is elliptical in outline in dorsal view; however, the frontal lobe is also expanded laterally so that a pseudolateral sulcus is definite. The fissura longitudinalis cerebri and transverse sulcus, if present, are not recognizable. The olfactory bulbs are rounded in frontal view. The optic nerve was separate from and ventral to the trigeminal nerve. The hypophysis is posterior to the optic nerve chiasm and just anterior to the ear region.

Hydrodamalis gigas.—Every region of the endocranial cast is expanded so that it is globe-shaped. The pseudolateral sulcus is, however, remarkably conspicuous. The fissura longitudinalis cerebri and transverse sulcus are not present. The olfactory bulbs are rounded in shape in frontal view. The optic nerve was separate from, and ventral to, the trigeminal nerve. The hypophysis is immediately posterior to the optic nerve chiasm and posterior to the ear region.

Comparisons

The character states of each of these taxa, especially in the subfamilies Halitheriinae and Hydrodamalinae,

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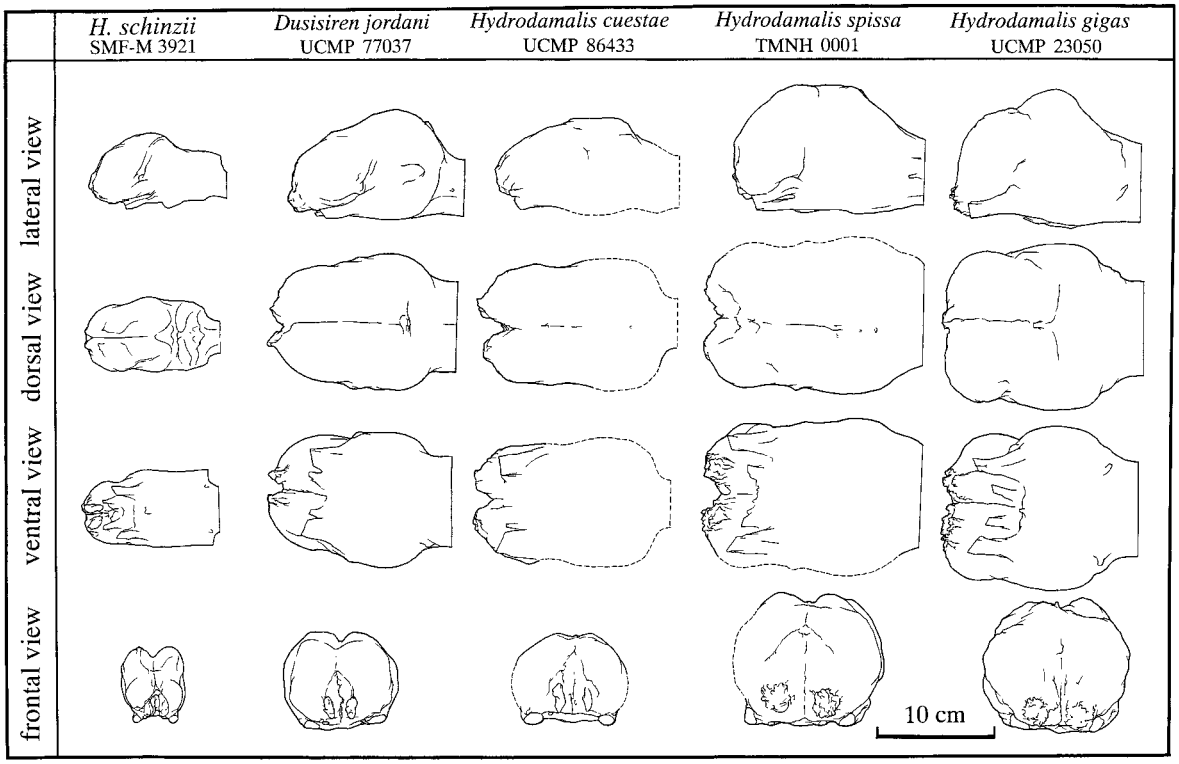


Figure 2. Comparative chart of the endocranial casts of Hydrodamalinae, Sirenia.

were compiled by detailed comparative studies of skeletons and endocranial casts (Domning, 1994). Endocranial casts of sirenians preserve important characters that can be used to compare character states of the central nervous system.

The endocranial casts of *Halitherium schinzii*, *Dusisiren jordani*, and *Hydrodamalis cuestae* have a low elliptical outline, whereas those of *H. spissa* and *H. gigas* are globose because of lateral and dorsal expansion.

Viewed anteriorly, the frontal lobe with the olfactory bulbs is elliptical in shape in *Halitherium schinzii*, *Dusisiren jordani*, and *Hydrodamalis cuestae*, whereas it is nearly spherical in *H. spissa* and *H. gigas*. The optic nerve was almost adjacent to the trigeminal nerve in *H. schinzii*, *D. jordani*, and *Hydrodamalis cuestae*. The optic and trigeminal nerves were clearly separate in both *H. spissa* and *H. gigas*.

The hypophysis extends posteriorly between the ear regions in *D. jordani* and *H. cuestae*, but is anterior to the ear region in *H. spissa* and *H. gigas*.

The fissura longitudinalis cerebri and the transverse sulcus are diminished in *H. spissa* and *H. gigas*.

Discussion

The character states of shape and position of cranial nerves clearly distinguish *Hydrodamalis spissa* and *H. gigas* from all other species of the subfamily Hydrodamalinae. This conclusion is consistent with the cladistic analysis of Furusawa (1988) wherein *H. spissa* and *H. gigas* were stated to have many shared derived characters. In this paper, the following four characters are regarded as synapomorphies of *H. spissa* and *H. gigas*, and the new cladogram (Figure 4) is a revision of Furusawa (1988):

Character 19. Swelling of anterior lobe of cerebrum.
Character 20. Fissura longitudinalis cerebri and transverse sulcus diminished.
Character 21. Olfactory bulbs spherical in shape.
Character 22. Optic nerve situated at the dorsal level of the trigeminal nerve.

In regard to *H. cuestae*, Domning (1978) stated that UCMP 86433 is modified pathologically. When more

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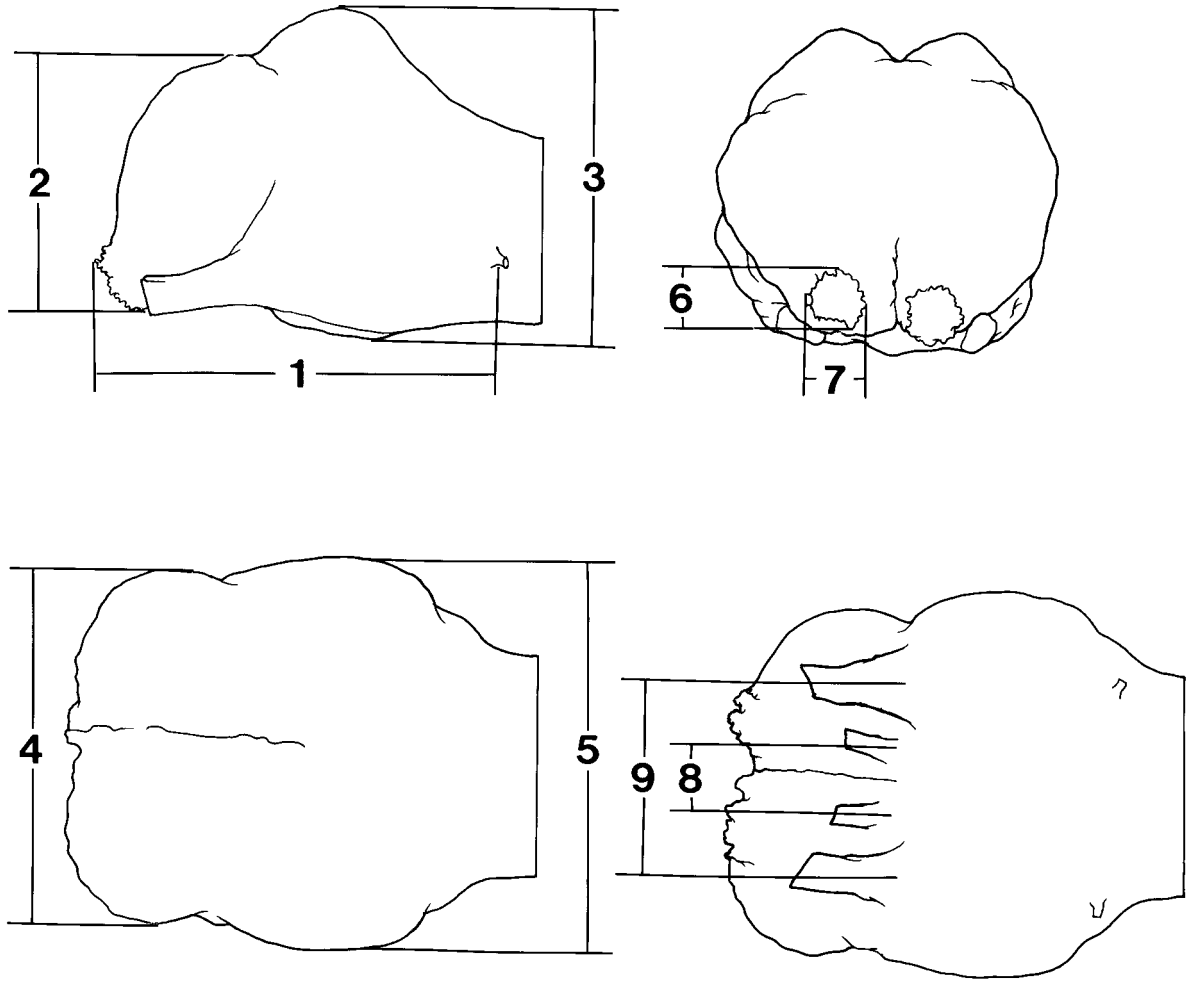


Figure 3. Key to measurements of endocranial casts, using the endocranial cast of *Hydrodamalis gigas* as a general form.

1. Total length
2. Height of frontal lobe
3. Height of occipital lobe
4. Width of frontal lobe
5. Width of occipital lobe
6. Height of olfactory nerve
7. Width of olfactory nerve
8. Width across optic nerves
9. Width across trigeminal nerves
10. Ratio of frontal lobe width (4) to total length (1)

Table 1. Measurements (1–9: in mm, 10: ratio) of endocranial casts of sirenian fossils (see Figure 3). Abbreviation: e, estimate.

		Measuring position									
Taxa	Specimen number	1	2	3	4	5	6	7	8	9	10
Hydrodamalis gigas	UCMP23050	148	95	118	127	135	30	27	25	76	0.85
Hydrodamalis spissa	TMNH0001	168	104	117	e132	e146	31	28	32	90	0.78
Hydrodamalis cuestae	UCMP86433	162	63	88	99	e120	26	14	36	71	0.61
Dosisiren jordani	UCMP77037	150	67	100	100	120	23	12	31	58	0.66
Halitherium schinzii	SMF-M3921	108	44	58	52	69	22	10	15	35	0.48

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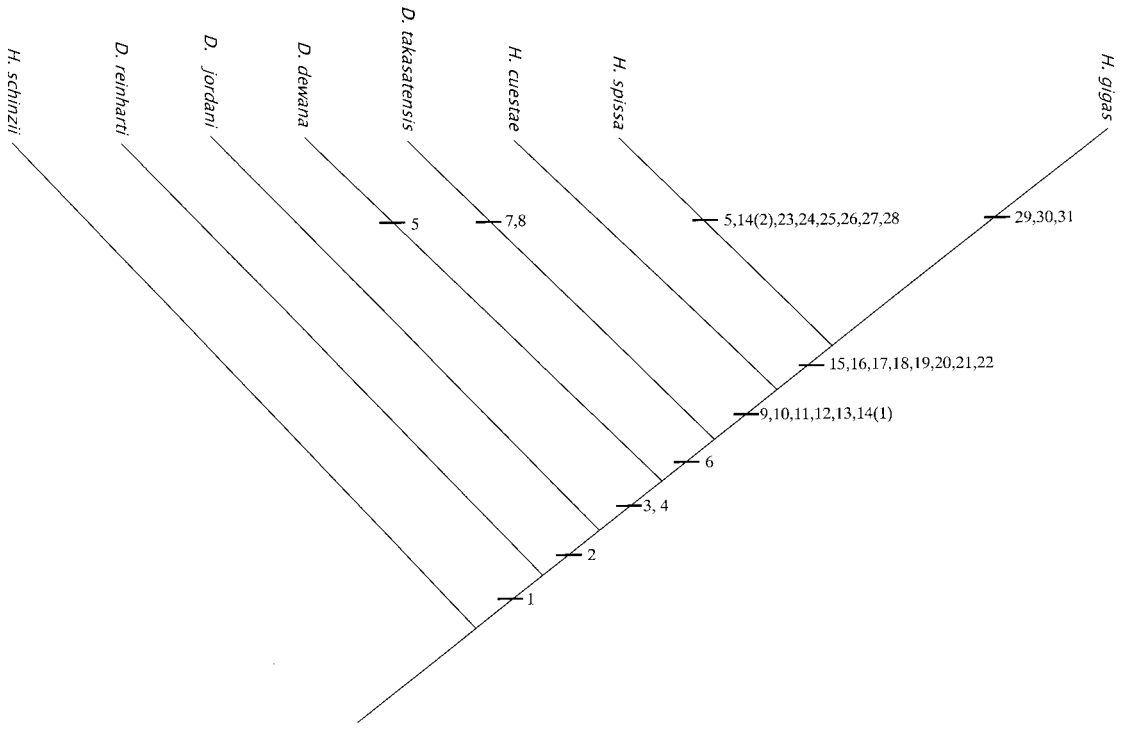


Figure 4. Cladistic analysis of North Pacific Sirenia. The taxa examined in the analysis are shown in Appendix I and II.

sirenian endocranial casts are available, UCMP 86433 should be revaluated. The endocranial and additional data from SDSNH 23736, required for comparison with *H. spissa*, could not be obtained. More casts are needed also to facilitate future comparative studies.

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Appendix I: Cladistic analysis for the species of hydrodamalines. A total of 31 osteological and endocranial characters were selected.

1. Enlargement of endocranial size: (0) = small, (1) = large.
2. Horizontal ramus of mandible: (0) = stout, (1) = slender.
3. Rib in cross section: (0) = flat ellipse, (1) = round ellipse.
4. Occlusal surface of the teeth: (0) = simple, (1) = more simple.
5. Anterior of the manubrium: (0) = no process, (1) = tongue-shaped process. – *D. jordani* and *H. spissa* have a thin and somewhat tapering process with the manubrium.
6. Lateral side of upper plate: (0) = curved laterally, (1) =straight.
7. Align of alveoli: (0) = anteroposteriorly, (1) = laterally.
8. Occipital condyle: (0) = small, (1) = large.
9. Body length: (0) = short, (1) = long. – This character is one of the most striking features which distinguish *Hydrodamalis* from *Dusisiren*. *Hydrodamalis* has almost doubled in length compared with *Dusisiren*.
10. Functional teeth: (0) = presence, (1) = absence. – This is the other most striking feature that distinguishes *Hydrodamalis* from *Dusisiren*.
11. Shaft of radius-ulna: (0) = straight, (1) curved medially. – This character is the derived state observed in *Hydrodamalis*.
12. Foramen magnum: (0) = triangle, (1) = elliptical.
13. Carpals: (0) = reduction, (1) = more reduction.
14. Pterygoid process: (0) = ordinary, (1) = weak, (2) = developed. – The pterygoid process is thick and long in *H. spissa*.
15. Humero-ulnar ligament: (0) = developed, (1) = reduction.
16. Outline of the zygomatic process: (0) = lozenge, (1) = round.
17. Notch in the posterior end of zygomatic process: (0) = curved anteriorly, (1) = straight.
18. Situation of the acromion: (0) = reached to the glenoid cavity, (1) = level of the neck.
19. Cerebrum: (0) = not swell, (1) = swell. – Anterior lobe of cerebrum swells in *H. spissa* and *H. gigas*.
20. Fissura longitudinalis cerebri and transverse sulcus: (0) = presence, (1) = absence.
21. N-I.: (0) = elliptical, (1) = spherical.
22. Situation of N-II and N-V: (0) = N-II aligned dorsal level of N-V, (1) = N-II reached ventral level of N-V.
23. Occipital: (0) = thin, (1) = thick.
24. Spines of the vertebrae: (0) = high, (1) = low. – The ratio of the height of the spine and the total height of vertebra in *H. spissa* is the smallest among other species of the hydrodamalines.
25. Thorax: (0) = narrow, (1) = wide.
26. Shaft of the humerus: (0) = straight, (1) = torsion.
27. Humerus head: (0) = round, (1) = weak curved.
28. Forelimb: (0) = developed, (1) = reduction. – This character can be especially observed in the reduction of the deltoid crest, the acromion and the spine of the scapula.
29. Posterolateral flange of the parietal: (0) = net extend, (1) = extend between the occipital and the squamosal.
30. Occipital flange: (0) = flat, (1) = developed and overhanging.
31. Mental foramen: (0) = situated at a level of the symphysis, (1) = far back caudally.

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Appendix II: Data matrix of phylogenetic analysis for subfamily Hydrodamalinae and outgroup taxa, *Halitherium schinzii*. The missing data were represented by "?".

CHARACTERS	1																														
																				2											3
TAXA	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
Halitherium schinzii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dusisiren reinharti	?	0	?	?	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
D. jordani	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D. dewana	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0
D. takasatensis	1	?	1	?	?	1	1	1	0	0	0	0	?	0	?	0	0	0	0	?	?	?	0	0	?	?	?	?	0	0	?
Hydrodamalis cuestae	1	1	1	1	0	1	–	0	1	1	1	1	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. spissa	1	1	1	1	1	1	–	0	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
H. gigas	1	1	1	1	0	1	–	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1

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