

autocorrelation coefficient for the series ($\tau = 1$ for all cases in our study). The size of effectively independent blocks was therefore $2\tau = 2$.

We also calculated the fraction of times an eruption was followed, within one year, by an El Niño-like anomaly (defined as an anomaly of 0.3°C or greater—approximately 0.75 standard deviations for the long-term NINO3 reconstruction—relative to the post-eruption 10-yr mean). An El Niño 'fraction' was defined as the number of post-eruption El Niños normalized by the number of eruptions in each list. Significance was determined by a Monte Carlo resampling procedure analogous to that described above.

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A newly discovered species of living baleen whale

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In the late 1970s eight *Balaenoptera* specimens of unknown identity were caught in the lower latitudinal Indo-Pacific waters by Japanese research whaling vessels¹. The combination of the allozyme patterns and physical maturity of the eight specimens separated them from all acknowledged *Balaenoptera* species². In September 1998 we collected a medium-sized baleen whale carcass on a coastal island in the Sea of Japan. This specimen and the previously collected eight specimens resembled *Balaenoptera physalus* (fin whale) in external appearance but were much smaller. Comparison of external morphology, osteology and mitochondrial DNA data grouped the nine specimens as a single species but separated them from all known baleen whale species. Therefore, here we describe a new species of *Balaenoptera*, which is characterized by its unique cranial morphology, its small number of baleen plates, and by its distant molecular relationships with all of its congeners. Our analyses also separated *Balaenoptera brydei* (Bryde's whale)^{3,4} and *Balaenoptera edeni* (Eden's whale)⁵ into two distinct species, raising the number of known living *Balaenoptera* species to eight.

Cetacea Brisson, 1762

Mysticeti Flower, 1864

Balaenopteridae Gray, 1864

Balaenoptera Lacépède, 1804

Balaenoptera omurai sp. nov.

Etymology. The specific name is in honour of the late H. Omura, a Japanese cetologist, for his contribution to the knowledge of Cetacea.

Holotype. Adult female, NSMT-M32505, National Science Museum, Tokyo. A complete skeleton, both complete baleen rows and frozen pieces of muscle, blubber and kidney were collected at Tsunoshima Island (34° 21' 03" N, 130° 53' 09" E) by T.K.Y., T. Kuramochi, M.O., E. Jibiki and S. Fujioka. The collection was undertaken three days after the accidental death of the animal.

Paratypes. Five females and three males, NRIFS1–8, National Research Institute of Far Seas Fisheries, Fisheries Research Agency, Shizuoka (see Table 1). The longest baleen plate, an earplug and a piece of the sixth thoracic vertebra with epiphysis were collected by trained staff from each animal. NRIFS6 includes 18 more baleen plates.

Locality. The Sea of Japan (type locality), the Solomon Sea and the eastern Indian Ocean near the Cocos Islands.

Diagnosis. *Balaenoptera omurai* differs from all of its congeners by having the following unique characters: medially expanded posterior portion of ascending process of maxilla, which conceals posterior end of premaxilla along the adjacent nasal (Fig. 1a, f); approximately 200 baleen plates on one side, which is the smallest number among all of its congeners except for *B. edeni* (the baleen plate number of which is still unknown); 21 diagnostic sites in the complete mitochondrial (mt)DNA control region sequence.

Discussion. The body length is less than 12 m (Table 1), similar to *B. edeni*^{5,6}. The skull is relatively broad and flat (Fig. 1a–c). The rostrum is tapering from its base, and its lateral margin is

conspicuously convex in dorsal view. Maximum width between the dorsomedial rims of the maxillae is at the lowest range of those for balaenopterids, occupying approximately 30% of the basal width of the rostrum. The ascending process of the maxilla broadens towards its posterior end (Fig. 1f), whereas in *B. edeni* it is slender throughout its length, giving a large space for the nasals and premaxillae (Fig. 1g, h). The frontal is only exposed as a narrow belt between the ascending processes of the maxillae and the supraoccipital, and between the nasals and a small exposure of the interparietal (Fig. 1f), whereas in *B. edeni* the frontal is exposed broadly posterior to and between the ascending processes of the maxillae, and forms a low but noticeable protuberance, which looks like a pedestal for each ascending process of the maxilla (Fig. 1g, h). The posterior end of the ascending process of the maxilla and the anterior margin of the supraoccipital are lying between levels of the antorbital and postorbital processes of the frontal. The posteromedial part of the supraorbital process of the frontal is broadly covered by the parietal, semicircularly when viewed dorsally (Fig. 1a). The hamular process of the pterygoid is broad and short, situated around the level of the posterior rim of the subtemporal fossa. The alisphenoid is separate to the squamosal (Fig. 1e), whereas in *B. edeni* it has a contact with the squamosal. The dorsal portion of the bifurcated pterygoid process of the squamosal is separate to the palatine. Two small foramina open along the suture between the parietal and squamosal in the wall of the braincase. The foramen pseudo-ovale surrounded only by the squamosal opens just posterior to the medial portion of the crest between the subtemporal and glenoid fossae, whereas in *B. edeni* and *B. brydei* the foramen pseudo-ovale surrounded by the squamosal and pterygoid opens in the glenoid fossa. Unlike *Balaenoptera musculus* (blue whale), *B. physalus* and *Balaenoptera borealis* (sei whale), the angle of the mandible conspicuously projects posteriorly, ending after the posterior edge of the condyle (Fig. 1d). The head of the first rib is not bifurcated, and its distal part is not broadened laterally like a blade. All epiphyses of the vertebrae except for NRIFSF8 are fused to each centrum. The vertebral and phalangeal formulae are given as cervical (7) + thoracic (13) + lumbar (12) + caudal (21) = 53 and I-5, II-7, IV-6, V-3, apart from four carpals and four metacarpals, respectively.

The external appearance of *B. omurai* resembles that of *B. physalus* in the following respects: the left side of the throat is widely pigmented and the remaining ventral surface is uniformly white, giving an asymmetrical appearance (Fig. 2a); the anterior edge and inner surface of both flippers are white from tip to shoulder; the ventral surface of the tail flukes is white with a black margin; the

ventral grooves extend behind the umbilicus and the total number of grooves is estimated as 80 to 90. The left gape is white in NRIFSF1 (no observation was made on the right gape). Although the surface of the head is not entirely smooth, the lateral ridges⁷ are absent, which are prominent in *B. brydei* and probably in *B. edeni*.

The baleen plates are, however, quite different compared with those of *B. physalus* in size, shape, colour and number. They are short and broad with uncurled, stiff, greyish-white fringes. The dimensions of the longest baleen plates ($n = 9$) are 26.0 ± 2.4 cm (mean \pm s.d.) in length and 21.4 ± 1.9 cm in breadth. The ratio of length to breadth, 1.22 ± 0.15 , is considerably smaller than the value of 1.48 ± 0.11 ($n = 7$) for the Antarctic *B. physalus*⁸. Baleen colour is just like that of *Balaenoptera bonaerensis* (Antarctic minke whale)^{9,10}, varying with the position in the baleen row, and displays asymmetry: in the right row of NSMT-M32505 the anterior 61 plates are all yellowish-white in colour, the posterior 40 plates are all black, and the intermediate 102 plates are bi-coloured (black externally and yellowish-white internally) (Fig. 2b); whereas in the left row of the same specimen, the anterior 178 plates are bi-coloured and the remaining 30 plates are all black; in both rows, the proportional width of the yellowish-white band becomes gradually smaller in the posterior plates. Similar transitional change of baleen colour is also seen in NRIFSF6. The proportion of the yellowish-white band to the basal width of the longest baleen plate is $30.7 \pm 6.2\%$ ($n = 5$) in the right plates and $13.7 \pm 7.3\%$ ($n = 4$) in the left plates, showing that the yellowish-white band is dominant in the right baleen row ($P < 0.001$) as in *B. physalus*^{8,11}, *B. borealis*¹², *B. bonaerensis*^{9,10} and the diminutive form of *Balaenoptera acutorostrata* (common minke whale)^{9,10}. The total number of baleen plates on one side—203 (right) and 208 (left) counted in NSMT-M32505 and 181–190 (right) estimated for NRIFSF6—is markedly smaller than that of the other *Balaenoptera* species.

The phylogenetic position of *B. omurai* relative to its congeners was examined using the complete control region sequence of the mtDNA molecule. The length of the control region in the three *B. omurai* specimens—one from the Sea of Japan (NSMT-M32505; GenBank accession number AB116095), one from the Solomon Sea (NRIFSF1; AB116096) and one from the eastern Indian Ocean (NRIFSF7; AB116097)—was 938 nucleotides, and they only differed by 4–5 nucleotides. The number of nucleotide differences between *B. omurai* and its congeners in 901 aligned sites (gaps excluded) was 62–67 for *B. brydei* (77N62 (ref. 13); AB116098), 65–70 for *B. edeni* (RMNH4003 (ref. 6); AB116099), 66–71 for *B. borealis*, 70–73 for *B. musculus*, 73–78 for *B. physalus*, 89–94 for *B. acutorostrata* and 92–97 for *B. bonaerensis*. The smallest interspecific nucleotide

Table 1 Biological information on the nine specimens of *B. omurai* sp. nov.

Museum number	Collected baleen plates	Body length (m)	Sex	Ovaries† or testes‡	Age	Physical maturity	Date of catch/stranding	Position	
								Lat.	Long.
NRIFSF1*	1 (R)	11.5	Female	1-11	29	a	24/10/1976	10° 03' S,	157° 29' E
NRIFSF2	1 (L)	9.6	Male	1.9/1.7	38	a	24/10/1976	9° 53' S,	157° 37' E
NRIFSF3	1 (L)	11.2	Female	0-6	9	A	24/10/1976	9° 57' S,	157° 41' E
NRIFSF4	1 (L)	10.0	Male	1.6/1.5	21	A	24/10/1976	9° 49' S,	157° 29' E
NRIFSF5	1 (L)	10.3	Female	1-12	23	A	24/10/1976	10° 07' S,	157° 51' E
NRIFSF6	19 (R)†	9.6	Male	2.2/2.1	34	A	24/10/1976	10° 17' S,	157° 56' E
NRIFSF7	1 (R)	10.4	Female	0-4	19	A	15/11/1978	10° 51' S,	97° 02' E
NRIFSF8	1 (R)	10.1	Female	0-3	18	n	17/11/1978	10° 53' S,	94° 29' E
NSMT-M32505	All (L&R)	11.03	Female	NC	NC	A	11/09/1998	34° 21' N,	130° 50' E

Age (column six) is indicated as the number of growth layers in an earplug. Physical maturity (column seven) was determined based on the extent of epiphyseal fusion in the sixth thoracic vertebra using the criteria: A, fused, no sign of joint; a, fused, joint visible; n, not fused, with thin cartilage. 'A' and 'a' represent physically mature whales whereas 'n' represents physically immature whale.

*Japanese inspectors took 8-mm movie footage and photographs. The description of the external appearance of the new species is based on these pictures and our direct observation on NSMT-M32505.

†The throat colour asymmetry is shown by this specimen only.

‡Nineteen baleen plates from the right (R) row were collected at every tenth position, starting from the first one and excluding the rudimentary hairs; that is, the first, the eleventh, the twenty-first, and so on. The thirteenth plate was the longest. A total number of 181–190 baleen plates is estimated for the right row.

§The left value indicates the number of corpora lutea in both ovaries, and the right value the combined number of corpora lutea and corpora albicantia. NC, not collected. Females with one or more corpora are sexually mature. None of the females were pregnant.

||Shown in kilograms.

|| Damaged or partially lost.

letters to nature

difference, 31 nucleotides, was between *B. borealis* and *B. brydei*. Thus, the difference between *B. omurai* and any of its congeners is much greater than that between these acknowledged species. Note that the difference between *B. edeni* and *B. brydei*, 35 nucleotides, is slightly greater than that between *B. borealis* and *B. brydei*, implying that they are also distinct species. The separate position of *B. omurai* in the *Balaenoptera* tree (Fig. 3) was conclusively supported irrespective of whether or not the highly variable portion (first 173 nucleotides)¹⁴ of the control region was included in the analyses.

Balaenopterid nomenclature is currently confusing¹⁵. The con-

fusion is at least partly related to the question of whether Bryde's whale is one species (*B. edeni*)⁶ or two (*B. edeni* and *B. brydei*)^{16–18}, and to the recent assertion that our eight specimens with anomalous allozymes may belong to *B. edeni*^{19,20}. However, the current molecular analyses have conclusively separated *B. omurai* from the *borealis/brydei/edeni* group, and separated *B. edeni* from the *borealis/brydei* group. Furthermore, we have confirmed that the holotype (GRM223 (ref. 5), Indian Museum, Kolkata), Sidhi Island (Indian Museum)²¹ and Pul(a)u Sugi (RMNH4003, National Museum of Natural History, Leiden) *B. edeni* skulls share the previously mentioned unique characters: the slender ascending

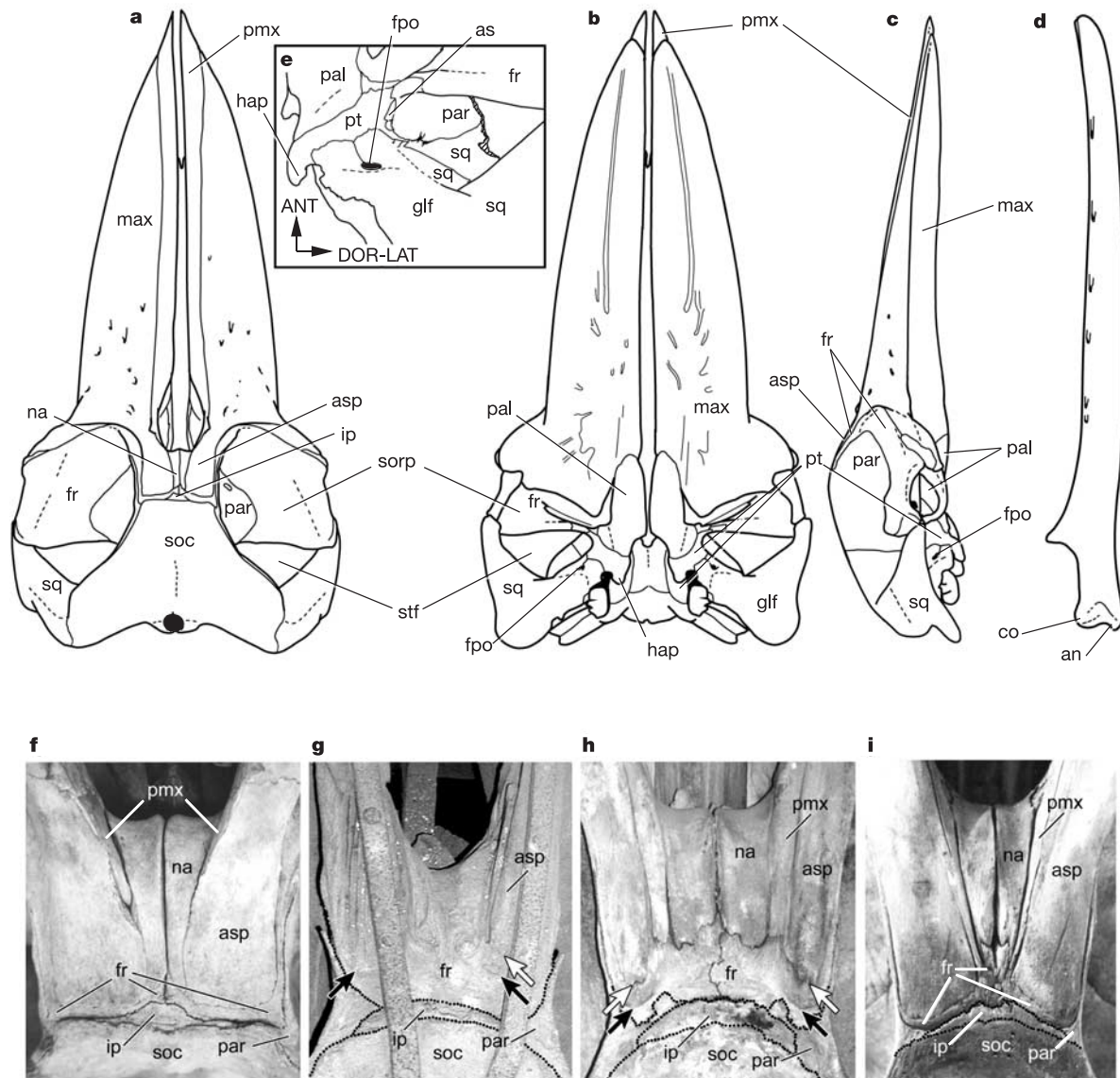


Figure 1 The holotype skull of *B. omurai* sp. nov. (NSMT-M32505). **a–d**, The skull is shown in dorsal (**a**), ventral (**b**) and lateral (**c**) views, and the mandible (NSMT-M32505) is shown in lateral and slightly oblique view (**d**) to the median plane of the skull. Length and width of the skull and length of the mandible are 2,832 mm, 1,454 mm and 2,790 mm, respectively. **e**, Ventrolateral view around the left subtemporal fossa. **f–i**, Comparison of the dorsal view of the skull at vertex among the three species. **f**, NSMT-M32505 (*B. omurai* holotype), medial margin of the left ascending process of the maxilla is broken and the posterior end of the premaxilla is exposed. **g, h**, The posterior end of the protuberance of the frontal (black arrow) is located a few centimetres posterior to the

posterior end of the ascending process (white arrow). **g**, GRM223 (*B. edeni* holotype)⁵, both of the nasals and the premaxillae as well as the left ascending process are lost. **h**, RMNH4003 (*B. edeni*)⁶. **i**, 78N33 (*B. brydei*, adult female)¹³. an, angle; ANT, anterior; as, alisphenoid; asp, ascending process; co, condyle; DOR-LAT, dorsolateral; fpo, foramen pseudo-ovale; fr, frontal; glf, glenoid fossa; hap, hamular process; ip, interparietal; max, maxilla; na, nasal; pal, palatine; par, parietal; pmx, premaxilla; pt, pterygoid; soc, supraoccipital; sorp, supraorbital process; sq, squamosal; stf, subtemporal fossa.

process of the maxilla and the broadly exposed frontal with the pedestal-like protuberance (Fig. 1g, h). These features are absent in all other *Balaenoptera* species—in *B. brydei* the ascending process of the maxilla is broad and the frontal has a small exposure without protuberance (Fig. 1i). These osteological findings, coupled with

molecular ones, corroborate our interpretation that *B. brydei*, *B. edeni* and *B. omurai* are distinct species. It is expected that, based on these diagnostic characters, more specimens of *B. omurai* and *B. edeni* will be reported from the sea as well as from museum collections. □

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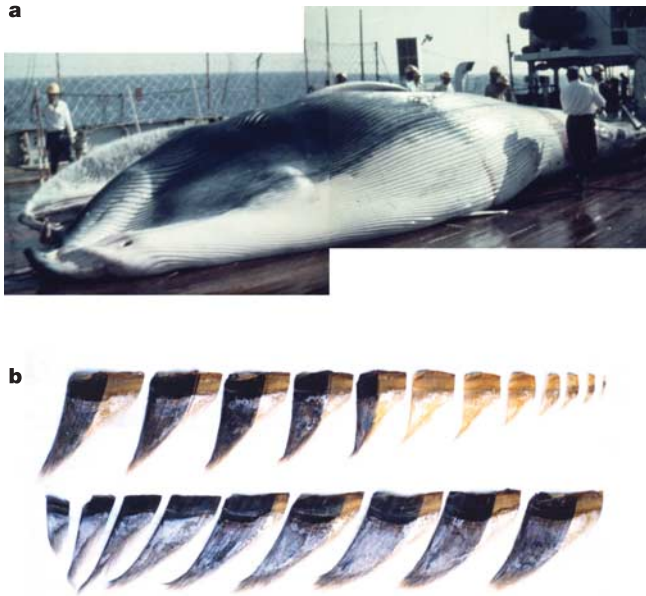


Figure 2 External morphology of *B. omurai* sp. nov. **a**, Ventral view of NRIFS1. **b**, Anterior view of 21 baleen plates (NSMT-M32505) collected from every tenth position starting from the first one of the right row.

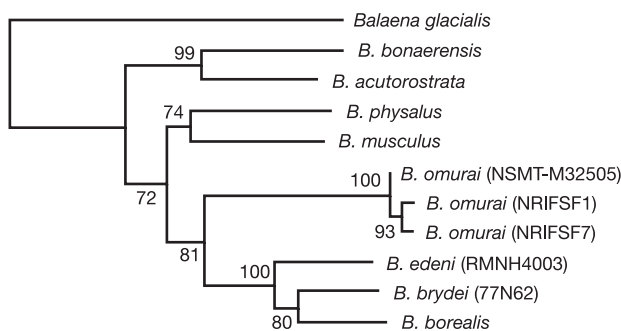


Figure 3 Neighbour-joining tree²² of the complete mtDNA control region sequences of all eight species suggested to belong to *Balaenoptera*, constructed using Kimura's two-parameter model in MEGA²³ with *Balaena glacialis* (right whale) as the outgroup. Fifty-three sites with one or more gaps were removed from the original alignment obtained by using Clustal W²⁴, resulting in a 901-nucleotide-long final alignment. Values at each node represent bootstrap values based on 1,000 replicates. The following six sequences were downloaded from GenBank: M60408 (*B. bonaerensis*)²⁵, X61145 (*B. physalus*)²⁶, X72195 (*B. borealis*)¹⁴, X72199 (*Balaena glacialis*)¹⁴, X72204 (*B. musculus*)²⁷ and X72006 (*B. acutorostrata*)¹⁴. The remaining five sequences were amplified by polymerase chain reaction using a primer set designed from X61145 and X72204—5'-ACACCTCCC TAAGACTCAAGGAAG-3' (on tRNA-(Thr/Pro)) and 5'-TAGACATTTTCAGTGTCTTGTCTT-3' (on tRNA-(Phe)). Template DNA was extracted from muscle in ethanol (NSMT-M32505), baleen plate (NRIFS1), dried soft tissue (RMNH4003) and frozen liver (NRIFS7 and 77N62 (ref. 13)). The amplified products were cloned in pGEM-T vector and sequenced for both strands.

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