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New fossil remains from the Pliocene Koetoi Formation of northern Japan provide insights into growth rates and the vertebral evolution of porpoises

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Extant porpoises (Phocoenidae) are odontocetes characterized by their small size, short and wide rostrum, late (or absent) completion of epiphyseal ankylosis in the vertebral column (= physical maturity), and short life cycles, all of which are thought to have resulted from progenetic evolution. We describe a small fossil phocoenid from the lower Pliocene Koetoi Formation of Hokkaido (northern Japan), preserving a small, narrow rostrum, as well as anteroposteriorly elongate thoracic and lumbar vertebral centra with completely fused epiphyses. Physical maturity in this specimen occurred significantly earlier than in extant phocoenids, as shown by dental data indicating that the specimen died at only four years of age. The difference between the present material and extant porpoises may be attributable to different growth rates during ontogeny. The long centra and caudally inclined neural spines of the specimen from Hokkaido are primitive characters among phocoenids. By contrast, the great height of its neural spines is highly derived, even among extant species, and suggestive of a fast swimmer. In terms of its vertebral morphology, the new specimen falls within a morphological continuum defined by the archaic *Numataphocoena yamashitai* and the highly derived vertebral morphology of *Phocoenoides dalli*. Phocoenid vertebral evolution has been complex and frequently convergent, as opposed to stepwise and unidirectional. The different vertebral morphologies of the new specimen and the contemporaneous extinct taxa *Numataphocoena* and *Piscolithax longirostris* indicate that they were adapted to different environments.

Key words: Mammalia, Phocoenidae, age estimation, growth rate, vertebral evolution, Pliocene, Japan.

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Introduction

The osteology and functional morphology of the cetacean vertebral column has been studied in some detail (e.g., Long et al. 1997; Buchholtz 1998, 2001; Buchholtz and Schur 2004; Buchholtz et al. 2005). Living cetaceans differ from most other mammals in having a relatively short neck and torso (sensu Buchholtz 2001), flattened vertebral faces, and a relatively large number of vertebrae in the torso. Taken together, these traits reduce the flexibility of the column,

and give rise to a more hydrodynamic overall body shape and enhanced swimming speed (Buchholtz 2001). In addition, some taxa, including delphinids and phocoenids, have evolved a comparatively elongate caudal tail stock. Buchholtz and Schur (2004) concluded that characters concerned with enhanced swimming speed in delphinids evolved stepwise. However, the topology of the tree they used has since been contradicted by most recent molecular phylogenies (e.g., McGowen et al. 2009), suggesting that at least some of these traits likely evolved more than once (vertebral count,

regional absence of torso metapophyses, and inclination of neural arch and spines in torsos).

Phocoenids offer an informative case study of vertebral evolution, owing to their relatively well-understood phylogeny and rich fossil record, with 16 extinct species from the period spanning the late Miocene–Pliocene. However, there are just three taxa for which the vertebral column has been described in detail: *Piscolithax longirostris* Muizon, 1983, *P. aenigmaticus* (Pilleri and Siber, 1989), and *Numataphocoena yamashitai* Ichishima and Kimura, 2000. Vertebrae of *Semirostrum ceruttii* Racicot, Deméré, Beatty, and Boessenecker, 2014 are briefly described after acceptance of this paper. Here, we describe a small fossil phocoenid (NMV-5) from the lower Pliocene Koetoi Formation of Hokkaido (northern Japan) preserving 7 cervical, 8 thoracic, and 3 lumbar vertebrae (Table 1), and discuss its implications for our understanding of the evolution of the vertebral column in porpoises.

Institutional abbreviations.—LACM, Los Angeles County Museum of Natural History, California, USA; NFL, Numata Fossil Laboratory, Numata, Japan; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London; NMV, Nakagawa Museum of Natural History, Nakagawa, Japan; NMNS, National Museum of Nature and Science, Tokyo, Japan; SMNK, Staatliche Museum für Naturkunde, Karlsruhe, Germany; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Other abbreviations.—CH, dorsoventral height of the anterior articular surface of the centrum; CL, anteroposterior length of the centrum. Our anatomical terminology follows Mead and Fordyce (2009).

Geological setting

The present material was recovered from the Koetoi Formation, which is the most fossiliferous of a series of Neogene sediments exposed in the Tempoku Basin of Hokkaido, northern Japan (Fig. 1). The latter is the northernmost of a series of north-south running basins distributed throughout central Hokkaido (Hoyanagi et al. 1986; Fukusawa et al. 1992; Sagayama and Hoyanagi 1993), and has yielded a considerable number of marine vertebrate fossils (Tomida and Kohno 1992; Uyeno 1992; Shimada et al. 1998; Kohno et al. 2002; Ichishima et al. 2006; Murakami et al. 2012a, b).

The Koetoi Formation is principally composed of diatomaceous pebbly mudstone resting on basal tuffaceous mudstone (Fukusawa 1985), and is considered to be a shelf deposit (Fukusawa et al. 1992). The Koetoi Formation conformably overlies the Wakkanai Formation, and is in turn conformably overlain by the Yuchi Formation. However, the boundaries between these formations are time-transgressive throughout of the basin. Chronologically, the Koetoi Formation has been estimated based on diatom biochronology, and ranges from

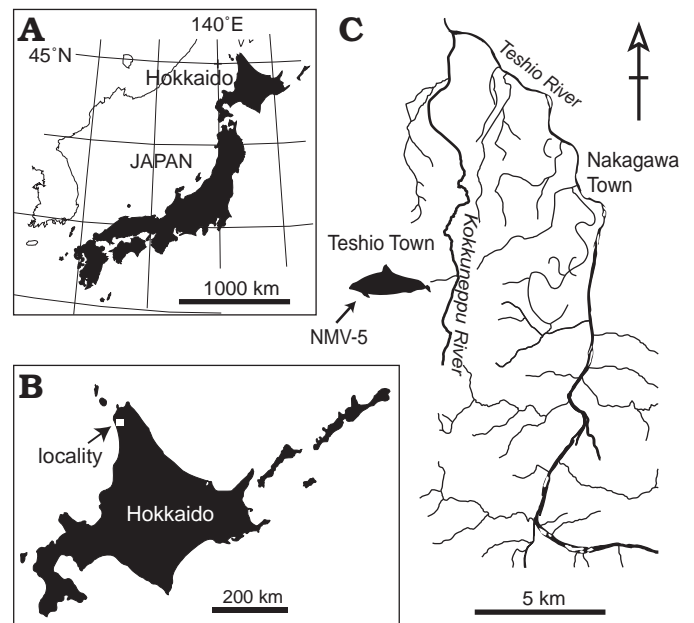


Fig. 1. The locality of a small porpoise NMV-5. **A.** The Japanese islands. **B.** The locality of NMV-5. **C.** Detailed locality of NMV-5 near the Teshionakagawa area.

the *Thalassionema hirosakiensis* s.l. Zone (Fukusawa 1985), corresponding to the *Thalassionema schraderi* Zone (8.5–7.6 Ma) of Yanagisawa and Akiba (1998), to about 2.3 Ma, as indicated by the first appearance of *Neodenticula seminae* and fission-track dating (Yasue et al. 2006).

The precise stratigraphic horizon which yielded NMV-5 is uncertain, since the latter was found in a floating calcareous concretion. However, diatoms collected from the concretion (Shimada et al. 1998) correlate with the *T. oestrupii* Subzone (5.5–3.5/3.9 Ma; Yanagisawa and Akiba 1998) and, together with the absence of *Actinocyclus oculatus* (first occurring at 4 Ma), suggest an early Pliocene (5.5–4.0 Ma) age for the material described here.

Material and methods

Age of the individual.—The individual age of extant (e.g., Perrin and Myrick 1980) and extinct odontocetes (Myrick 1979; Lambert et al. 2008) is frequently assessed by counting annually accumulated growth layer groups apparent in the dentine of the teeth (International Whaling Commission 1969; Gurevich et al. 1980). We used this method to determine the age at which NMV-5 died, based on the decalcification and staining technique (e.g., Pierce and Kajimura 1980; Kasuya 1983). For this purpose, we first coated the tooth with epoxy resin (SpeciFix-40; Struers Inc.), owing to its small size (1.25 mm in width). The tooth was then polished with abrasives until the longitudinal half section (buccal–labial section) was exposed. The latter was then glued to an acrylic slide using the instant glue Aron alpha (Toagosei Inc.). Next, we produced a thin section of the tooth using a Minitom precision cut-off machine (Struers Inc.), and polished the

section with an abrasive (#6000) under an optical microscope down to a thickness of 50 μm . Finally, we polished the thin section with a 1 μm -diamond-coated abrasive.

The thin section of the tooth was decalcified in a 5% formic acid bath for 24 hours, following which it was rinsed in running water, and stained with Mayer's hematoxylin (Merck KGaA) for 30 minutes. The thin section was then rinsed again in running water, and mounted with Entellan Neu (Merck KGaA). The growth layers of the dentine were counted under a microscope (Nikon SMZ 645 and Nikon Labophoto2-Pol) using transmitted light at a magnification of 7-90x and 40-1000x. In order to make our age determination as accurate as possible, three people independently counted the number of the dentinal growth layers three times. The mean of those nine counts was then taken as the number of annual rings of the specimen.

Vertebral evolution in Phocoenidae.—Odontocete locomotion is dependent on the vertical displacement and oscillation of the peduncle and fluke (e.g., Slijper 1961; Fish and Hui 1991), and thus the structure of the vertebral column. Vertebral modifications characterising odontocetes include an increase in the rigidity of the pre-peduncle portion of the column, as well as the flexibility of the peduncle and fluke (Long et al. 1997; Buchholtz and Schur 2004). This is achieved through (i) the reduction of the relative centrum length of the cervicals, thoracic, and anterior lumbar vertebrae; (ii) flattened central faces; (iii) increased vertebral counts; and (iv) comparatively elongated centra in the tail stock region (Slijper 1961; Buchholtz 2001; Buchholtz and Schur 2004).

In order to better understand the origins of the vertebral patterns characterising phocoenids, we traced the evolution of 16 characters related to vertebral evolution (Tables 2, 3) on a phylogenetic tree, using the parsimony algorithm implemented in Mesquite Version 2.73 (Maddison and Maddison 2010). The phylogenetic tree was based on a reanalysis of a slightly modified version of the comprehensive data matrix (72 ingroup taxa, 282 characters) of Murakami et al. (2012b), with characters 220, 221, 222, 224, and 227 excluded to avoid circular reasoning (Felsenstein 1985). The cladistic analysis was performed in PAUP 4.0 b10 (Swofford 1998), using *Georgiacetus* Hulbert, Petkewich, Bishop, Burkry, and Aleshire, 1998 and *Zygorhiza* True, 1908 as outgroups (the complete character list and data matrix are provided in the Supplementary Online Material, SOM available at http://app.pan.pl/SOM/app60-Murakami_et_al_SOM.pdf). All of the characters were treated as unweighted and unordered, and were analysed using 100 random stepwise-addition replicates and tree bisection reconnection (TBR) branch swapping, saving 30 trees per replicate. We did not include *Piscolithax aenigmaticus*, NMV-5, and *Numataphocoena yamashitai*, because specimens were either unavailable or fragmentary, generating too much polytomy to trace the characters. The cladistic analysis resulted in 121 most parsimonious trees of 1676 steps (Fig. 5), giving rise to a strict consensus tree identical to that of Murakami et al.

(2012b), except for the branches within Delphinidae. For the purpose of tracing traits related to swimming ability among phocoenids, we used *Delphinapterus leucas* Pallas, 1776 as outgroup. Vertebral counts for extant species were based on Brownell (1975, 1983), Brownell and Praderi (1984), Gas-kin et al. (1974), Heyning and Dahlheim (1988), Jefferson (1988), Jefferson and Hung (2004), Perrin (2001), Stacey et al. (1994), Stewart and Stewart (1989), West et al. (2011).

Systematic palaeontology

Order Cetacea Brisson, 1762

Odontoceti Flower, 1867

Superfamily Delphinoidea Gray, 1821

Family Phocoenidae Gray, 1825

Phocoenidae gen. et sp. indet.

Figs. 2–4.

Material.—NMV-5, a partial rostrum and mandible, all cervicals, eight thoracic and three lumbar vertebrae, and several incomplete ribs, from a small, unnamed tributary valley of the Kokuneppu River located in the Sengen district, Teshio, Hokkaido, Japan (44°49'45 N, 141°59'26 E; Fig. 1); Koetoi Formation, early Pliocene (5.5–4.0 Ma).

Description

Skull

Rostrum.—The relatively well-preserved rostrum (length: 147 mm; Fig. 2A–D), missing its distalmost 10–20 mm including the anteriormost alveolus (Fig. 2B, C), is all that remains of the skull. The greatest width of the maxillae is approximately 59+ mm (Fig. 2C), thus resembling the small extant phocoenids *Neophocaena phocaenoides* and *Phocoena phocoena* in size.

Premaxilla.—The premaxilla is slender, although it should be noted that some of the medial portion of the proximal end of the premaxilla is missing. Distally, the premaxilla slopes steeply towards the lateral border of the rostrum (Fig. 2D). As in most phocoenids, the mesorostral groove is moderately open, with the medial edges of both premaxillae being largely parallel. The suture uniting the premaxilla and maxilla is distinct along the entire rostrum.

Maxilla.—In dorsal view, the maxilla steeply slopes away laterally towards its anterior end (Fig. 2A, D). The maxillary flange is flat and narrow. As in *Piscolithax longirostris*, the anteriormost dorsal infraorbital foramen is located directly adjacent to the premaxilla. In lateral view, the maxilla is slightly curved ventrally (Fig. 2B). The ventral surface of the maxilla is transversely concave (Fig. 2D), and bears a distinct palatine sulcus and greater palatine foramen in its proximal portion (Fig. 2C). The tooth rows are clearly separated, moderately divergent posteriorly, and shortened (as in other phocoenids),

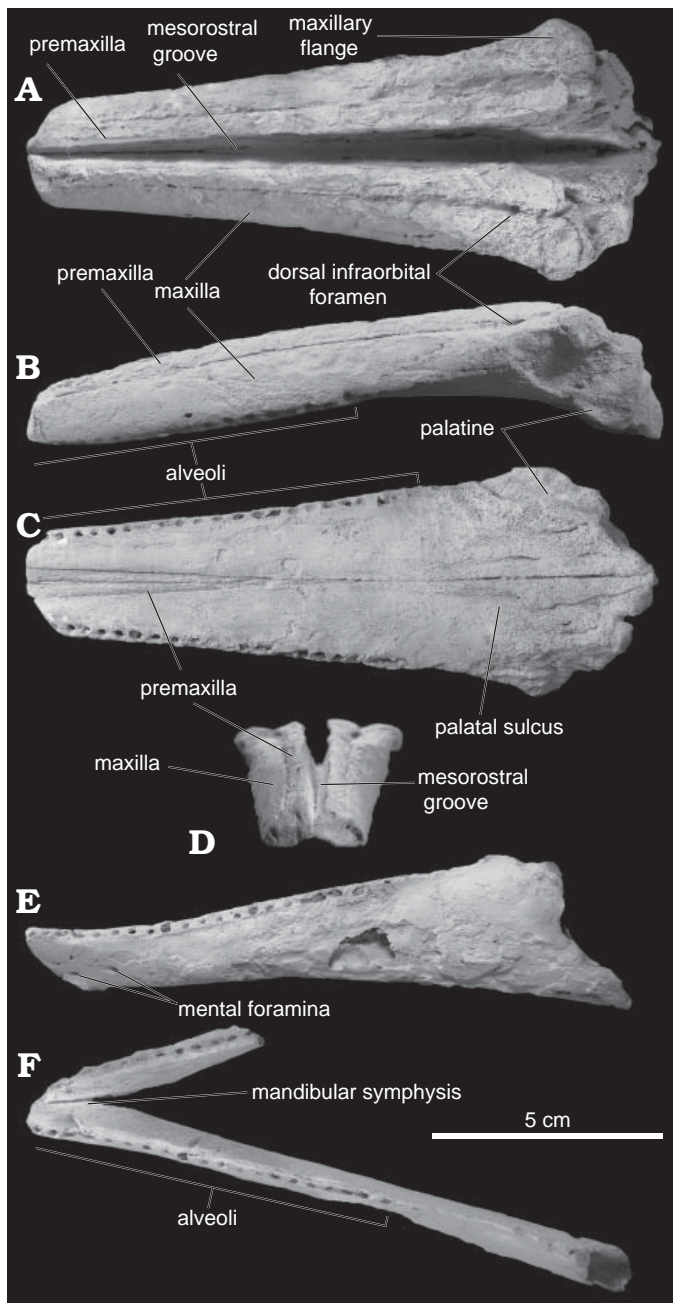


Fig. 2. The rostrum (A–D) and mandible (E, F) of the porpoise *Phocoenidae* gen. et sp. indet., NMV-5, early Pliocene of Teshio, Hokkaido, Japan; in dorsal (A, F), lateral (B, E), ventral (C), and anterior (D) views.

with the posteriormost alveolus located 32 mm anterior to the anterior edge of the palatine. 21 alveoli (length of tooth row = 88 mm) are preserved on the left side, and 20 (length of tooth row = 86 mm) on the right, with an average alveolus diameter of 2.5 mm. Six teeth lacking crowns are preserved in situ.

Vomer.—In ventral view, the vomer is narrowly exposed between the premaxillae, unlike in all other phocoenids except *Piscolithax longirostris*.

Palatine.—Only the anteriormost portions of the palatines are preserved (Fig. 2C), making accurate description impossible.

Mandible.—The left mandible is missing its anteriormost

10–20 mm and the portion posterior to the anterior border of the mandibular foramen. By contrast, only a 40 mm fragment remains of the right mandible (Fig. 2E, F). The mandibular symphysis is at least 15 mm long, and connects both mandibles at an angle of 35°. 20 alveoli are preserved in the left mandible (length of tooth row = 77 mm) and 12 in the right, with an average alveolus diameter of 1.9 mm.

Teeth.—Two small (< 3.5 mm long), isolated teeth with spatulate crowns and circular roots (1 mm in diameter) were preserved near the maxillae (Fig. 3A–D). The crowns measure 1 mm buccolingually and 1.25 mm anteroposteriorly, and are covered by smooth enamel with no accessory cusps or ornamentation.

Postcranial skeleton

Cervical vertebrae.—The seven cervical vertebrae are unfused and anteroposteriorly compressed, and resemble other extinct phocoenids in their overall morphology (Fig. 4A–D, Table 1). Weathering has resulted in the loss of most of the neural arches, as well as the erosion of the anterior face of the atlas (Fig. 4C). The ventral transverse process of the atlas is short and moderately robust, and there is no dorsal transverse process. The pedicle of the neural arch of the atlas is attached to the axis. The latter (Fig. 4D) has lost most of its neural arch and transverse processes, but preserves two deep fossae on the dorsal face of the vertebral body, which may represent attachment sites for the dorsal longitudinal ligament.

Table 1. Measurements (in mm) of the vertebrae of the porpoise NMV-5. Abbreviations: e, estimated transverse measurements (half measurement multiplied by 2); +, measured element is incomplete to some extent; CL, length of centrum; CH, height of anterior articular surface of centrum; CW, width of anterior articular surface of centrum; GH, greatest height of vertebra; GW, greatest width of vertebra; CL/CH, length of centrum/height of anterior articular surface of centrum; X, XX, XXX, precise position of vertebrae within the vertebral column unknown.

	CL	CH	CW	GH	GB	CL/CH
Atlas	22.6	36.0+	75.0e	40.0+	101.0+	?
Axis	16.7	27.8	61.0	38.6+	64.2+	0.60
3rd cervical	4.8	25.9	30.4	31.6+	37.0+	0.19
4th cervical	4.5	26.6	29.9	37.0+	34.4+	0.17
5th cervical	4.5	26.7	28.6	37.6	35.2	0.17
6th cervical	5.8	26.2	30.0	46.7	41.0	0.22
7th cervical	6.6	26.8	31.4	43.2+	55.4+	0.25
1st thoracic	11.3	26.0	27.8	41.2+	69.3	0.43
3rd thoracic	17.0	24.1	30.2	48.7+	68.8e	0.71
5th thoracic	19.8	24.7	26.0	75.8+	68.0	0.80
Thoracic X	32.7	27.8	29.2	112.0	88.9	1.18
Thoracic XX	22.3+	26.5	29.9	48.4+	105.2e	?
Thoracic XXX	33.9	28.9	29.2	118.0	139.8e	1.17
Last thoracic-1	35.4	28.8	30.5	?	158.0	1.23
Last thoracic	37.2	31.8	37.5	129.0	137.6+	1.17
1st lumbar	37.6	32.2	38.4	70.4+	159.2e	1.17
2nd lumbar	36.4	29.7	34.6	98.5	122.1+	1.23
3rd lumbar	36.1	31.4	35.9	129.9	163.0	1.15

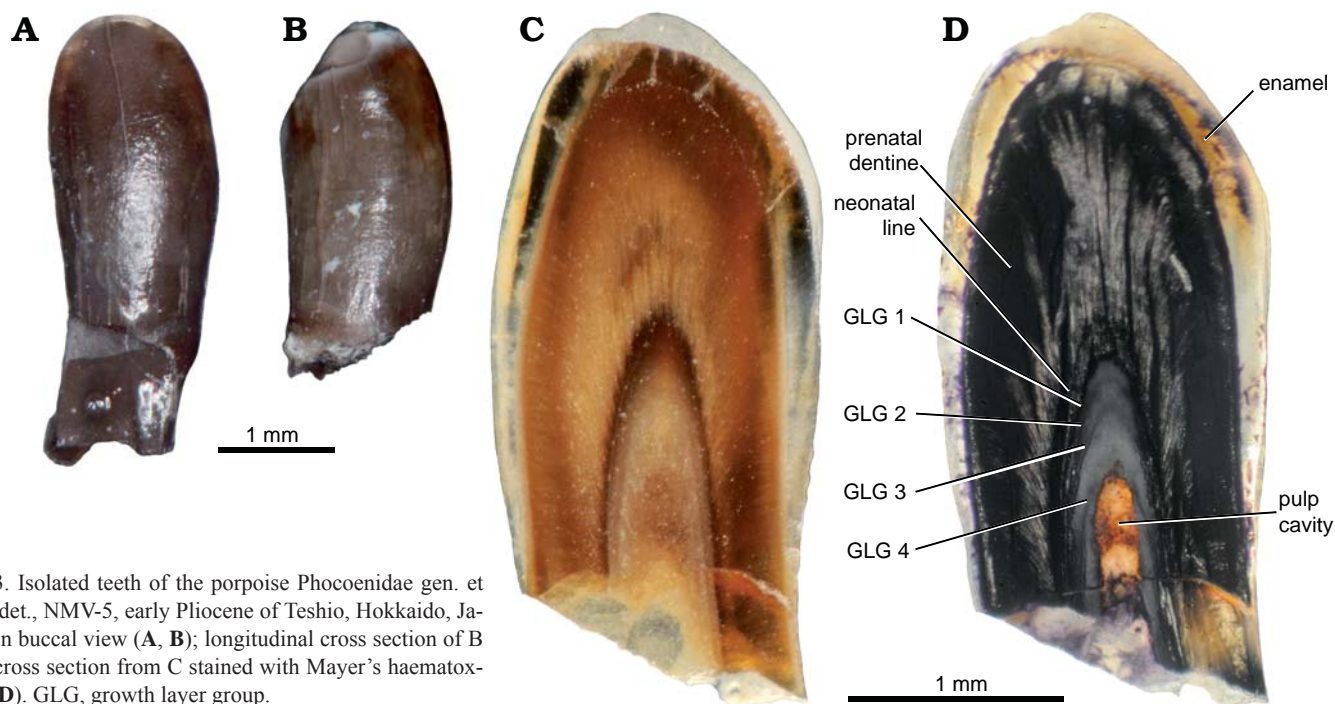


Fig. 3. Isolated teeth of the porpoise *Phocoenidae* gen. et sp. indet., NMV-5, early Pliocene of Teshio, Hokkaido, Japan; in buccal view (A, B); longitudinal cross section of B (C); cross section from C stained with Mayer's haematoxylin (D). GLG, growth layer group.

Thoracic vertebrae.—Eight thoracic vertebrae are preserved, with the posterior five having relatively long centra (Fig. 4A; Table 1). In terms of their relative and absolute centrum lengths, these vertebrae are intermediate between those of *Numataphocoena yamashitai* and extant species. All of the

preserved thoracics have flattened anterior and posterior centrum faces, as well as well-developed metapophyses. Unlike in other phocoenids, except *Phocoena sinus* Norris and McFarland, 1958 and *Phocoenoides dalli* (True, 1885), the neural spines of the posterior thoracics are tall, slender and

Table 2. Vertebral traits analysed in this study. Abbreviations: CL, length of centrum; CH, height of anterior articular surface of centrum; [], character number used in previous studies.

	Character		Source
1	Cervical vertebrae	unfused (0); only atlas and axis fused (1); C1–C3 or C1–C4 fused (2); C1–C6 or C1–C7 fused (3)	Murakami et al. 2012b [220]
2	Number of thoracic vertebrae	9–11 (0); 12–14 (1); ≥ 15 (2)	Murakami et al. 2012b [222]
3	Number of lumbar vertebrae	7 (0); 9–13 (1); 14–19 (2); 24–27 (3)	Murakami et al. 2012b [227]
4	Number of caudal vertebrae	21–26 (0); 27–33 (1); 41–49 (2)	Murakami et al. 2012b [228]
5	Lumbar count > thoracic count	absent (0); present (1)	Buchholtz and Schur 2004
6	Length of cervicals (C1–C7) as percent of height of vertebral body plus neural canal of atlas	long, >150% (0); short, <150% (1)	Murakami et al. 2012b [221]
7	Ratio of CL/CH in thoracic vertebrae	> 1.20 in more than one vertebra (0); > 0.95 in several vertebrae (1); < 0.75 in all vertebrae (2)	Buchholtz and Schur 2004 [12]
8	Ratio of CL/CH in lumbar vertebrae	> 1.20 in more than one vertebra (0); > 0.95 in more than one vertebra (1); < 0.75 in all vertebrae (2); < 0.75 in all vertebrae (3)	Buchholtz and Schur 2004 [12]
9	Length of tail stock CL of torso (lumbar + caudal vertebrae anterior to tail stock)	> CL of tail stock (0); secondary rise in tail stock CL (1)	Buchholtz and Schur 2004 [6]
10	All thoracics and lumbar amphicelous	absent (0); present (1)	Buchholtz and Schur 2004
11	Bulbous or triangular transverse process of lumbar	present (0); absent (1)	Murakami et al. 2012b [225]
12	Height of neural spines in posterior thoracics and anterior lumbar (greatest height of vertebrae/CH)	< 4.0 (0); between 4.0 and 5.0 (1); > 5.0 (2)	
13	Orientations of neural spines in posterior thoracic and lumbar vertebrae	strongly posteriorly inclined (0); posteriorly inclined or vertically standing (1); several neural spines inclined anteriorly = syncliny (2)	Buchholtz and Schur 2004 [5]
14	Regional anterior inclination of neural arches	absent (0); present (1)	Buchholtz and Schur 2004 [1]
15	Metapophyses	torso metapophyses uniformly present (0); regional absence of torso metapophyses (1)	Buchholtz and Schur 2004 [8]
16	Regionally elevated metapophyses	absent (0); present (1)	Buchholtz and Schur 2004 [1]

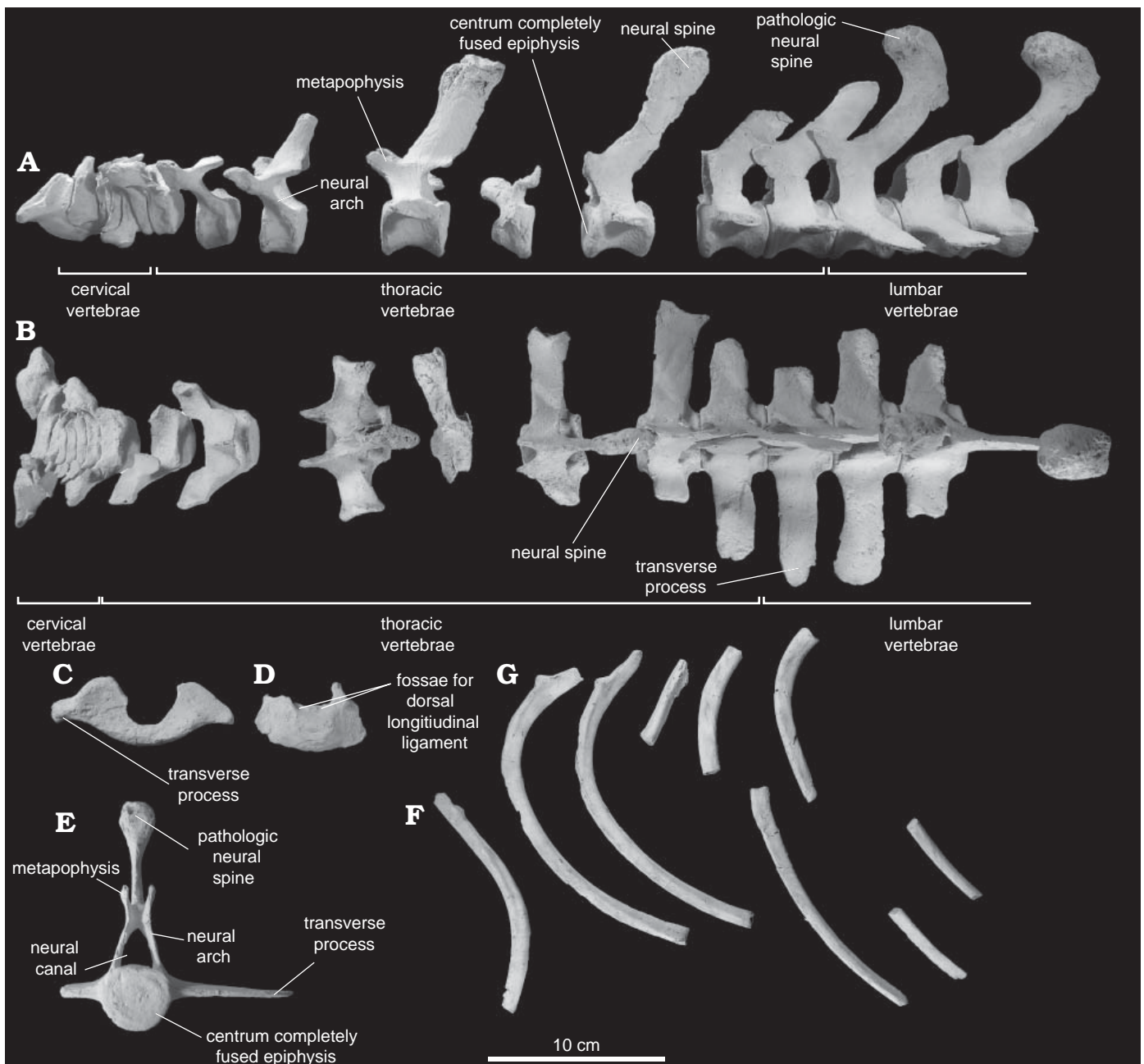


Fig. 4. Vertebrae (A–E) and ribs (F, G) of the porpoise *Phocoenidae* gen. et sp. indet., NMV-5, early Pliocene of Teshio, Hokkaido, Japan. Cervical (1–7), thoracic (1, 3, 5, 7, X, XX, XXX, last-1, last), and lumbar vertebrae (1–3) in lateral (A) and dorsal (B) views; atlas (C), axis (D), first lumbar (E), left rib fragment (F), and anterior to central right ribs (G) in anterior view.

strongly recurved anteriorly (Fig. 4A). The neural spines of *Neophocaena phocaenoides* Cuvier, 1829, are also strongly recurved anteriorly, but differ from those of NMV-5 in being distinctly shorter dorsoventrally, and longer anteroposteriorly. The neural spines of at least two of the thoracic vertebrae exhibit exostosis, with their distal tips being moderately expanded anteroposteriorly, and slightly swollen laterally.

Lumbar vertebrae.—Three lumbar vertebrae, likely representing L1–L3 are preserved, and, except for the absence of an articular surface for the rib on their transverse processes, resemble the posterior thoracics in their general morphology.

The centra of the lumbar vertebrae are distinctly elongated, both in relative (as compared to rostral width) and absolute terms. In dorsal view, the anterior and posterior edges of the transverse process of the first lumbar vertebra and an isolated posterior transverse process are parallel, whereas the transverse process of the second lumbar vertebra slightly widens anteroposteriorly (Fig. 4B). In this, NMV-5 resembles *Salumiphocaena stocktoni*, *Piscolithax longirostris* and extant species, and differs from *Numataphocaena yamashitai*, in which the transverse processes are distinctly widened distally. The neural spines on the first and third lumbar vertebrae show a remarkable degree of exostosis, making their distal tips

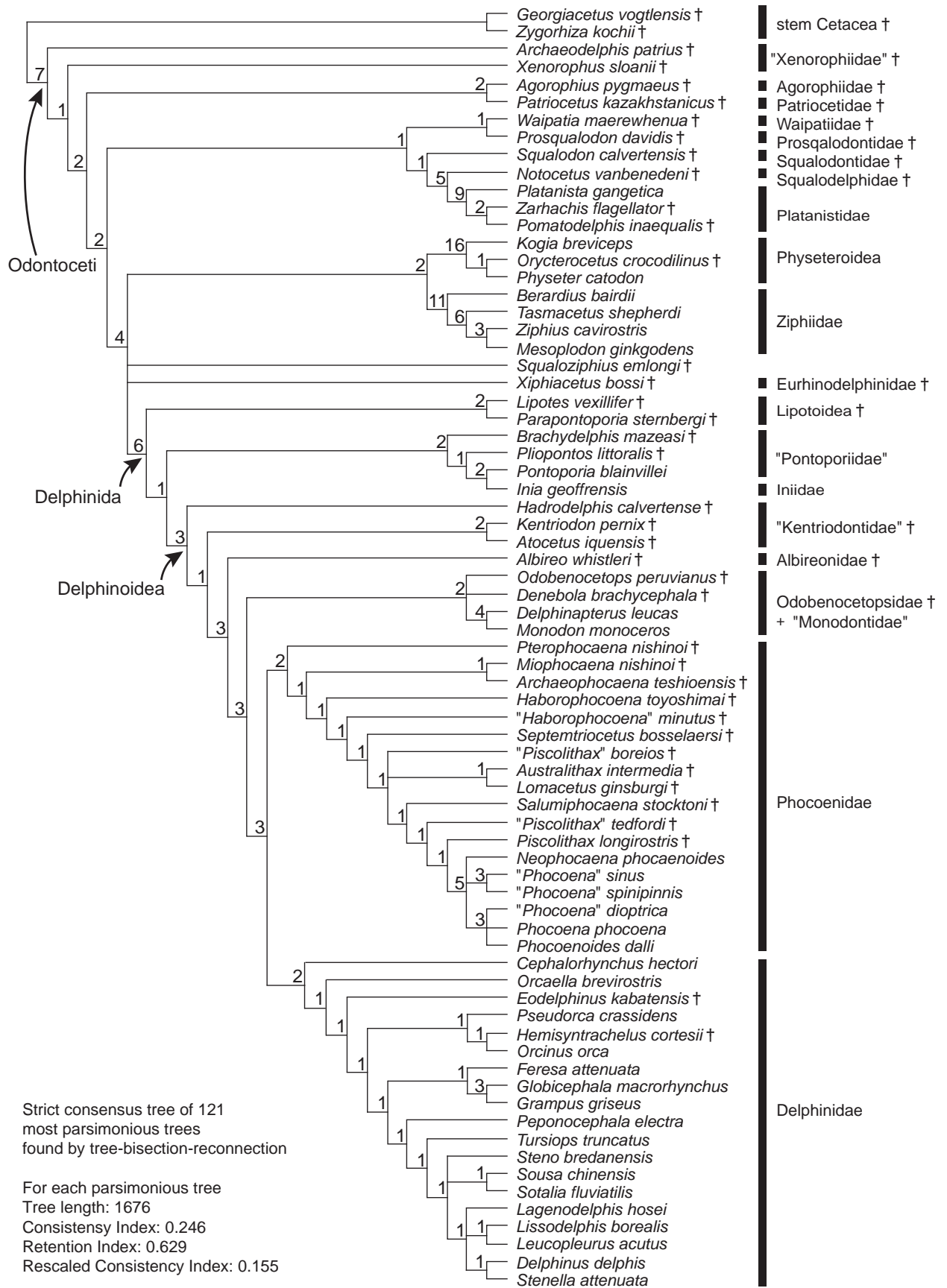


Fig. 5. The phylogeny and vertebral morphology of Phocoenidae. The phylogenetic analysis is based on the data matrix of Murakami et al. (2012b), excluding character 220, 221, 222, 224, and 227. Quotations added to taxa which are paraphyly or polyphyly in the present cladistic analysis.

Table 3. Character–taxon matrix for the vertebral traits analysed in this study.

Taxon	10	16
<i>Delphinapterus leucas</i>	0000000000	000000
<i>Cephalorhynchus hectori</i>	21[12]0110211	112101
<i>Orcinus orca</i>	3[01]10011100	101101
<i>Pseudorca crassidens</i>	3010010000	100101
<i>Steno bredanensis</i>	1121111211	112101
<i>Leucopleurus acutus</i>	1121111211	112111
<i>Stenella attenuata</i>	2[12][23][12]111211	112111
<i>Numataphocoena yamashitai</i> †	0000??00?1	0?????
NMV-5 †	0?????00?1	110???
<i>Piscolithax aenigmaticus</i> †	023???????	1?10??
<i>Pterophocaena nishinoi</i> †	0????1????	??????
<i>Archaeophocaena teshioensis</i> †	???????????	??????
<i>Miophocaena nishinoi</i> †	???????????	??????
<i>Haborophocaena toyoshimai</i> †	???????????	??????
<i>Haborophocaena minutus</i> †	???????????	??????
<i>Septentriocetus bosselaersi</i> †	???????????	??????
<i>Piscolithax boreios</i> †	0???????????	??????
<i>Australithax intermedia</i> †	???????????	??????
<i>Lomacetus ginsburgi</i> †	???????????	??????
<i>Salumiphocaena stocktoni</i> †	0?2???????	10????
<i>Piscolithax tedfordi</i> †	0?0???????1	??????
<i>Piscolithax longirostris</i> †	0?0??123?1	10????
<i>Neophocaena phocaenoides</i>	211[01]011101	100000
<i>Phocoena sinus</i>	21[12]11111?1	111011
<i>Phocoena spinipinnis</i>	2111111101	100010
<i>Phocoena dioptrica</i>	3121111101	001000
<i>Phocoena phocoena</i>	3121111101	102100
<i>Phocoenoides dalli</i>	3232112311	122110

appear globular in lateral and dorsal view (Fig. 4E). On the third lumbar, the area affected by exostosis measures 48 mm anteroposteriorly, and 24 mm laterally. The presence of exostosis indicates that this individual suffered from serious disease or injury at some point during its life.

Rib.—At least eight ribs are preserved, including five from the anterior or central portion of the right ribcage (Fig. 4F, G).

Results and discussion

Affinity of the specimen.—The spatulate teeth of NMV-5 are indicative of Phocoenidae, and resemble those of extant taxa, as well as those of the extinct species *Haborophocaena toyoshimai* Ichishima and Kimura, 2005 and *Numataphocoena yamashitai*. Among these taxa, NMV-5 is similar to the relatively basal *Haborophocaena* spp. (Fig. 5; see also Murakami et al. 2012b) in having a narrow rostrum (the rostrum of *N. yamashitai* is currently unknown). NMV-5 shares with *N. yamashitai* the presence of elongated post-cervical vertebrae, but differs from the latter in its detailed morphology (see below). Finally, NMV-5 is much smaller than *H. toyoshimai* or *N. yamashitai*, but similar in size to, *H. minutus*

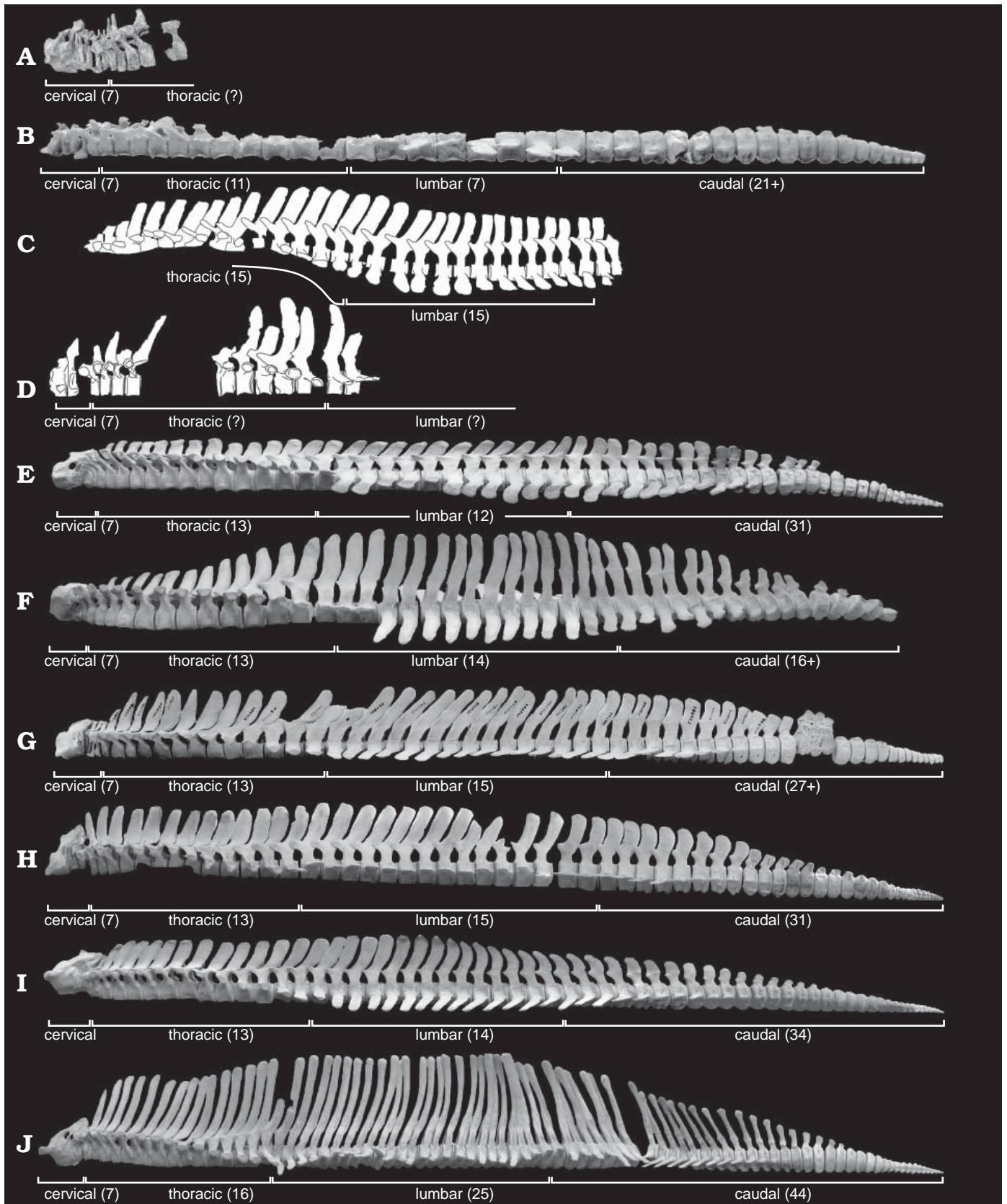
Ichishima and Kimura, 2009. However, comparisons with *H. minutus* are currently impossible owing to a lack of comparable material, except for the base of the rostrum. Overall, NMV-5 thus likely represents a basal phocoenid of uncertain generic and specific affinity.

Age estimation.—As was reported for *Phocoenoides dalli* by Kasuya (1978), but in contrast to other delphinoids, the enamel dissolved imperfectly in the formic acid. The decalcified part of the enamel stained black with hematoxylin. In addition to the enamel, the prenatal dentine, and the neonatal line, the cross section of the tooth revealed four growth layer groups (Fig. 3C, D), with each of the latter being considerably thinner than the prenatal dentine and consisting of a thin, dark-stained layer and a thick, light grey one. The presence of four growth layer groups indicates that the animal died at four years of age.

Despite its relatively young age, we consider NMV-5 to be a fully mature individual, based on the complete ankylosis of the epiphyses of all of the preserved thoracics and lumbar vertebrae (e.g., Perrin 1975; Ichishima and Kimura 2000). In achieving maturity within less than four 4 years, NMV-5 clearly differs from extant phocoenids, which reach physical maturity considerably later. Thus, *Phocoenoides dalli* reaches physical maturity at 7.16 years in males (95% confidence interval [CI] = 5.7–8.6 years) and 7.24 years in females (95% CI = 6.3–8.1 years) (Ferrero and Walker 1999). In *Phocoena phocoena*, the youngest physically mature individuals observed so far were 6-year-old male and a 7-year-old female, with estimates of the age at which 50% of individuals are physically mature ranging from 8.4 years for males (95% CI = 7.4–9.9 years) to 8.1 years for females (95% CI = 7.3–9.2 years; Galatius and Kinze 2003). Finally, *Neophocaena phocaenoides* attains physical maturity at 14–23 years (Yoshida et al. 1994). It is furthermore noteworthy that, even when the examined individuals were very old, not all of the vertebral epiphyses were completely fused to the vertebral centra in most of the specimens included in the above studies (Yoshida et al. 1994; Galatius and Kinze 2003).

The markedly early inset of sexual maturity in NMV-5 as compared to extant phocoenids might be the result of different growth rate during ontogenesis. Extant phocoenids are thought to have undergone paedomorphic evolution (Barnes 1985; Galatius and Kinze 2003; Ichishima and Kimura 2005; Galatius et al. 2011). Specifically, the presence of a relatively short and wide rostrum, a rounded cranium, incompletely fused vertebral and flipper epiphyses, and small body size have been interpreted as evidence for progenesis (Barnes 1985; Galatius and Kinze 2003; Galatius 2005; Ichishima and Kimura 2005; Galatius et al. 2006), i.e., the onset of sexual maturity at an

Fig. 6. Comparisons of the vertebral column of living and extinct phocoenids in lateral view. **A.** *Pterophocaena nishinoi* Murakami, Shimada, Hikida, and Hirano, 2012a, late Miocene of Hokkaido, Japan, NMV-7. **B.** *Numataphocoena yamashitai* Ichishima and Kimura, 2000, early Pliocene of Hokkaido, Japan, NFL 7. **C.** *Piscolithax aenigmaticus* Pilleri and Siber, 1989, late Miocene of Aguada de Lomas of Peru, SMNK-PAL 6660. **D.** *Piscolithax longirostris* Muizon, 1983, late Miocene of Sud-Sacaco, →



Peru, MNHN SAS 934. **E.** *Neophocaena phocaenoides* Cuvier, 1829, Holocene of Japan?, NMNS M 24659. **F.** *Phocoena sinus* Norris and McFarland, 1958, Holocene of Baja California, Mexico, LACM 28259. **G.** *Phocoena spinipinnis* Burmeister, 1865, Holocene of Peru, USNM 550782. **H.** *Phocoena dioptrica* Lahille, 1912, Holocene of Tierra del Fuego, Argentina, LACM 86042. **I.** *Phocoena phocoena* Linnaeus, 1758, Holocene of Hokkaido, Japan, NMNS M 27393. **J.** *Phocoenoides dalli* True, 1885, Holocene of Iwate, Japan, NMNS M 21382. Not to scale.

early ontogenetic stage, resulting in a relatively small adult retaining juvenile morphological features (McNamara 1986). Like the progenetic extant phocoenids, NMV-5 became sexually mature at an early age and retained a small body size even as an adult. However, NMV-5 seems to have been subject to considerably faster growth rates possibly pointing to acceleration (a type of peramorphosis), which is characterized by elevated growth rates during ontogeny leading to an adult form that is no larger, and indeed often smaller, than its ancestor (McNamara 1986). Acceleration may also explain the presence of a relatively long and narrow rostrum (as inferred from the long and narrow rostra of the relatively basal phocoenids *Lomacetus ginsburgi* Muizon, 1986 and *Australithax intermedia* Muizon, 1988), although the latter might also have been the result of feeding adaptations (Werth 2006).

Vertebral counts and dimensions.—All extinct phocoenids, including NMV-5 and *Numataphocoena yamashitai*, have seven unfused cervical vertebrae, as in the outgroup *Delphinapterus leucas* ([character 1-0], hereafter the character number and its state according to the present analysis are given in square brackets; see Tables 2, 3). By contrast, the first three or four cervical vertebrae are fused [1-2] in *Neophocaena phocaenoides* (Fig. 6E), *Phocoena sinus* (Fig. 6F), and *P. spinipinnis* (Burmeister, 1865) (Fig. 6G), and all, or almost all (C1–C6), of the cervicals are fused in *P. phocoena*, *P. dioptrica* Lahille, 1912 and *Phocoenoides dalli* [1-3] (Fig. 6I, H, J). Both *N. yamashitai* (Fig. 6B) and *D. leucas* have 11 thoracic vertebrae [2-0]. By contrast, *Phocoenoides dalli* and the extinct *Piscolithax aenigmaticus* have 15–18 and 15 thoracic vertebrae, respectively [2-2] (Figs. 6C, J, 7A), whereas all other phocoenids have 12–14 thoracic vertebrae [2-1]. Both *N. yamashitai* (Fig. 6B) and *D. leucas* have only seven lumbar vertebrae [3-0]. This number increases to 9–13 and 13, respectively, in *Neophocaena phocaenoides* and *P. spinipinnis* [3-1] (Fig. 6E, G), and to 13–17 in *P. sinus*, *P. dioptrica*, and *P. phocoena* [3-1 or 3-2] (Fig. 6F, H, I). *Phocoenoides dalli* has considerably more lumbar vertebrae (17–24) than other species [3-3] (Figs. 6J, 8). Finally, *N. yamashitai* and *D. leucas* have less than 26 caudal vertebrae [4-0]. This contrasts with 26–33 in *Neophocaena phocaenoides* [4-0 or 1] (Fig. 6E), 27–33 in almost all other extant phocoenids [4-1] (Fig. 6F–I), and 44–49 in *Phocoenoides dalli* [4-2] (Figs. 6J, 8).

The cervical vertebrae of even the most basal phocoenids, such as *Pterophocaena nishinoi* Murakami, Shimada, Hikida, and Hirano, 2012a (Fig. 6A) and NMV-5 (Figs. 4, 8), are considerably shorter anteroposteriorly than those of monodontids or kentriodontids. Thus, the sum of all cervical vertebral lengths as a percentage of the height of the atlas (vertebral body plus the neural canal) is less than 150% in phocoenids [6-1], but greater than 150% in *Delphinapterus leucas* [6-0]. In NMV-5, *Numataphocoena yamashitai* (Figs. 6B, 8A), and *D. leucas*, the ratio of the anteroposterior length of the centrum (CL) to the dorsoventral height of the anterior articular surface of the centrum (CH) is greater than 1.20 in more than one thoracic vertebra [7-0]. In *Neophocaena pho-*

caenoides, *Phocoena sinus*, *P. spinipinnis*, and *P. phocoena*, the same ratio equals 0.95 in several vertebrae [7-1] (Figs. 6E–H, 8B), whereas it is less than 0.75 in *Phocoenoides dalli* and *Piscolithax longirostris* [7-2] (Figs. 6I, J, 8A, B).

The CL/CH ratio is greater 1.20 in more than one lumbar vertebra [8-0] in NMV-5, *Numataphocoena yamashitai* (Figs. 6B, 8A), and *Delphinapterus leucas*, and greater than 0.95 in more than one lumbar vertebra in *Neophocaena phocaenoides*, *Phocoena sinus*, and *P. spinipinnis* [8-1] (Fig. 6E–H). By contrast, this ratio is less than 0.95 for all lumbar vertebrae in *P. phocoena* [8-2] (Fig. 6H), and less than 0.75 for all lumbar vertebrae in *Phocoenoides dalli* and *Piscolithax longirostris* [8-3] (Figs. 6D, J, 7B, 8A, B). *Numataphocoena yamashitai* (Fig. 6B) and *D. leucas* have fewer lumbar vertebrae than thoracic vertebrae [5-0]. By contrast, the number of lumbar vertebrae exceeds the number of thoracic vertebrae in extant phocoenids [5-1] (Fig. 6F–J), except *Neophocaena phocaenoides* (Fig. 6E). In *Neophocaena phocaenoides* (Fig. 6E), *P. spinipinnis* (Fig. 6G), *P. phocoena* (Fig. 6I), and *D. leucas*, the CL of the vertebrae forming the torso (lumbar + caudal vertebrae anterior to the tail stock; Buchholtz and Schur 2004) is greater than the CL of the vertebrae forming the tail stock [9-0]. Only *Phocoenoides* (Fig. 6J) displays a secondary increase in the CL of the tail stock vertebrae [9-1].

The vertebral counts in each region of the vertebral column of *Numataphocoena yamashitai* are nearly identical to those of the outgroup taxon *Delphinapterus leucas*. By contrast, other phocoenids, as exemplified in particular by *Phocoenoides dalli* (Fig. 6J), are characterised by increased numbers of thoracic, lumbar, and caudal vertebrae, implying that changes in vertebral counts across different regions of the vertebral column may be correlated. In these animals, the posterior thoracic and anterior caudal vertebrae resemble the lumbar vertebrae in terms of the height and inclination of their neural processes (“lumbarisation” sensu Buchholtz et al. 2005). Taken together, the increased vertebral counts and lumbarisation result in an expanded mid-body region, thus providing the greater rigidity to the column and skeletal support for epaxial and hypaxial muscles responsible for generating the propulsive force (Buchholtz et al. 2005). Increased vertebral counts also correlate negatively with the relative lengths of the centra, with most phocoenids having considerably shorter vertebrae than monodontids. The absolute displacement of the posterior face of a vertebra from the axis of the vertebra anterior to it decreases with decreasing centrum length, thus resulting in a more rigid vertebral column allowing high-speed swimming (Buchholtz 2001; Buchholtz and Schur 2004). Within Phocoenidae, the relative length of the centra seems to be shortest in *Phocoenoides dalli*, *Piscolithax longirostris* and possibly *Pterophocaena nishinoi*, followed by most of the extant species, NMV-5, and *Numataphocoena yamashitai* (Fig. 8).

Centrum faces.—The thoracic and lumbar vertebrae of *Delphinapterus leucas* and *Numataphocoena yamashitai* have irregular faces, ranging from amphicoelous to slightly procoelous or opisthocoelous [10-0]. By contrast, all other

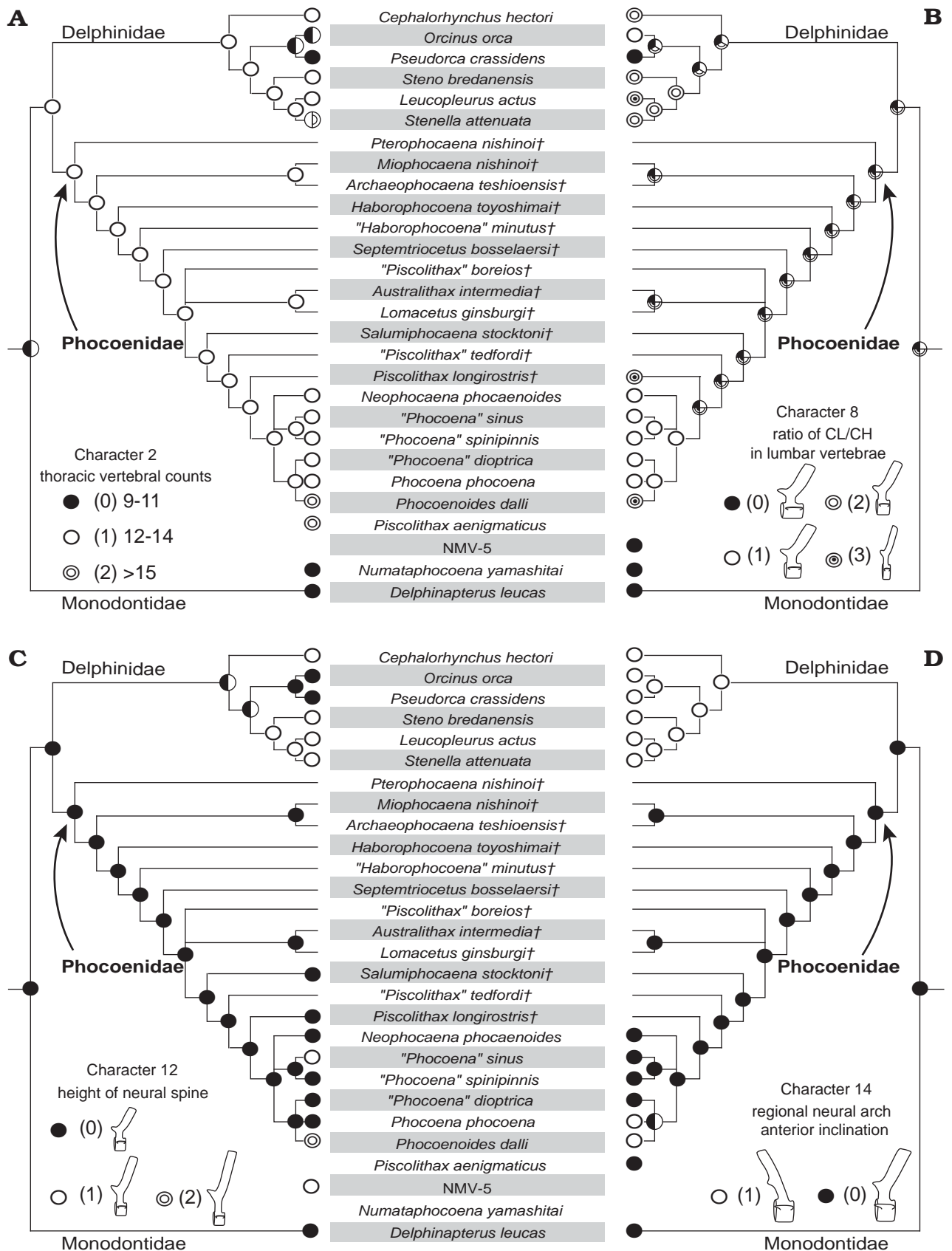


Fig. 7. Vertebral character trait evolution across phocoenids and related delphinoids. **A.** Character 2, thoracic vertebral counts. **B.** Character 8, ratio of centrum length/centrum height of lumbar vertebrae. **C.** Character 12, height of neural spine. **D.** Character 14, regional anterior inclination of neural arches. See Table 2 for detailed character descriptions.

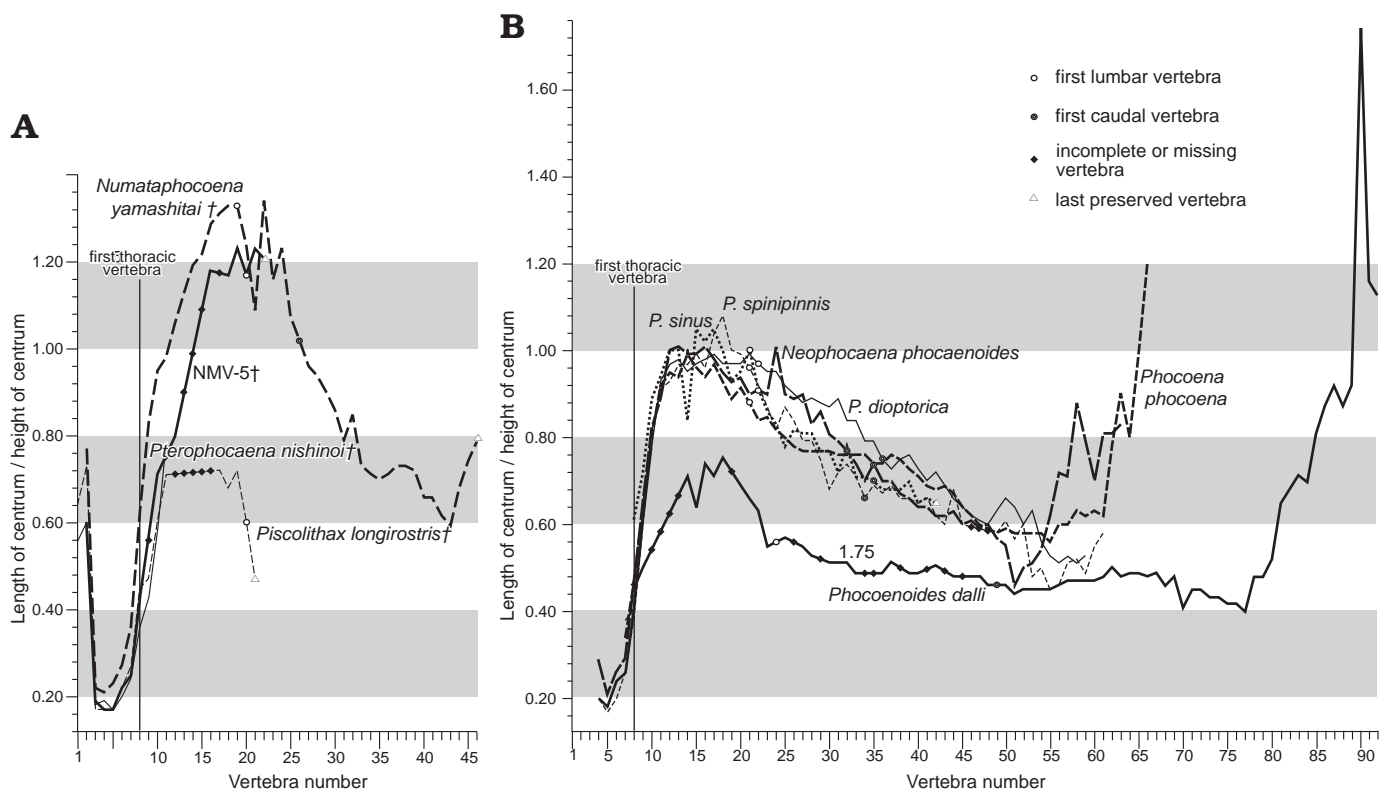


Fig. 8. Comparison of centrum length/centrum height across Phocoenidae. **A.** Extinct species: *Numataphocoena yamashitai*, NFL 7, NMV-5; *Pterophocaena nishinoi*, NMV-7; *Piscalithax longirostris*, MNHN SAS 940. **B.** Extant species: *Neophocaena phocaenoides*, NMNS M 21382; *Phocoenoides dalli*, NMNS M 21382; *Phocoena phocoena*, NMNS M 27393; *Phocoena dioptorica*, USNM 571486; *Phocoena spinipinnis*, USNM 550782; *Phocoena sinus*, NHMUK 69678 (from Noble and Fraser 1971).

extinct and extant phocoenids have amphicoelous thoracic and lumbar vertebrae [10-1]. Since flattened or amphicoelous centra increase the rigidity of the vertebral column at the expense of manoeuvrability (Buchholtz and Schur 2004), all phocoenids except *N. yamashitai* can be inferred to have a more rigid vertebral column than monodontids.

Transverse processes of the lumbar vertebrae.—The morphology of the transverse processes may affect the lateral movement of the vertebral column as it determines the anteroposterior length of the intertransverse ligaments adjacent to the vertebrae. The narrow transverse processes likely decrease the length of the ligaments, thus making the column more rigid. *Delphinapterus leucas*, *Numataphocoena yamashitai*, and *Phocoena dioptorica* retain bulbous transverse processes of the lumbar vertebrae, previously shown to be a synapomorphy of Delphinida (Muizon 1984) [11-0]. By contrast, the transverse processes of other phocoenids, including NMV-5, are anteroposteriorly narrow and have nearly parallel anterior and posterior edges [11-1] (Fig. 4).

Orientations and lengths of the neural spines and arches.—The orientation and length of the neural arches and spines correlate with the forces of the longissimus and multifidus muscles (Slijper 1936, 1961; Buchholtz 2001; Buchholtz and Schur 2004), with long neural spines providing larger attachment areas for the locomotor muscles (Buchholtz et al. 2004) and increasing the overall second moment of the cross-sectional

area of the intervertebral ligaments (Long et al. 1997). The neural spines of the posterior thoracic and anterior lumbar vertebrae are low in *Piscalithax longirostris*, *Phocoena spinipinnis*, *P. dioptorica*, *P. phocoena*, and especially *Neophocaena phocaenoides* (greatest height of vertebra/centrum height <4.0; Fig. 6D, E, G–I) [12-0]. By contrast, those of NMV-5 and of several vertebrae of *P. sinus* are relatively high (vertebra/centrum height = 4.0–5.0; Figs. 4, 6F, 7C) [12-1], with those of *Phocoenoides dalli* being yet higher (vertebra/centrum height > 5.0; Fig. 6J) [12-2].

The neural spines of the posterior thoracic and anterior lumbar vertebrae are strongly inclined posteriorly in *Delphinapterus leucas*, NMV-5, *Neophocaena phocaenoides*, and *Phocoena spinipinnis* [13-0], and somewhat less so in *Piscalithax aenigmaticus*, *Phocoena sinus*, and *P. dioptorica* [13-1] (Fig. 6D, F, H). By contrast, the neural spines in this region point anteriorly in *P. phocoena* and *Phocoenoides dalli* [13-2] (Fig. 6I, J). In *D. leucas* and most phocoenids, the neural arches of the posterior thoracic and anterior lumbar vertebrae are vertical or oriented posteriorly [14-0], whereas they are oriented anteriorly in *P. phocoena* and *Phocoenoides dalli* [14-1] (Figs. 6I, J, 7D). In the latter taxa, the anterior inclination of the neural spines likely enhances the flexion of the fluke during locomotion, as indicated by Slijper (1961).

Metapophyses.—As in *Delphinapterus leucas*, the thoracic and torso vertebrae of most phocoenids bear well-developed

[15-0], low metapophyses [16-0]. By contrast, metapophyses are reduced or absent in the vertebrae forming the torso of *P. sinus* (in which they are also elevated [16-1]), *P. spinipinnis*, and *Phocoenoides dalli* [15-1] (Fig. 6F, G, J). Elevated metapophyses increase the distance between the force application and the axis of rotation, thus enhancing mechanical advantage, but limiting angular rotation (Buchholtz and Schur 2004). Metapophyses also provide insertion sites for the main effectors of column extension (the multifidus and longissimus muscle systems); thus, their absence or reduction in *P. sinus*, *P. spinipinnis*, and *Phocoenoides dalli* likely reflects an increase in columnar rigidity (Buchholtz and Schur 2004).

Character evolution.—The evolution of vertebral traits related to swimming ability in Phocoenidae is not a simple, stepwise process (Fig. 7B, C), with several characters (3, 7, 8, 12, and 16) apparently having emerged convergently in several extant and extinct lineages (Table 3). This pattern would likely turn out to be even more complex if it were possible to determine the phylogenetic relationships of NMV-5, *Numataphocoena yamashitai*, and *Piscolithax aenigmaticus*. *Phocoenoides dalli* stands out for having evolved a suite of highly derived characters (Fig. 7, Table 3) nearly identical to that of *Leucopleurus acutus* (Fig. 7, Table 3; Buchholtz and Schur 2004; Buchholtz et al. 2005), allowing it to swim at a maximum speed of 55 km/h (Leatherwood and Reeves 1986). Among phocoenids, only *Phocoenoides dalli* and *Phocoena phocoena* show neural spine syncliny (reversed spine orientation), which was emphasised by Buchholtz and Schur (2004) as an early and critical step in the evolution of the delphinid column. Apart from *Phocoenoides dalli*, the vertebral columns of *P. phocoena*, *P. sinus*, and *Piscolithax longirostris* are also highly derived, despite these species belonging to different lineages.

Neophocaena phocaenoides has the most archaic column among extant phocoenids, with several features enhancing columnar flexibility rather than the rigidity needed for high-speed swimming. This morphology of this species may be related to its shallow coastal water or riverine habitats, where the submarine topography is undulating. The vertebral traits of *Numataphocoena yamashitai* are nearly identical to those of the monodontid *Delphinapterus leucas*, and thus likely the ancestral morphology of phocoenids as a whole. Although the swimming ability and manoeuvrability of *N. yamashitai* may have been similar to that of *Delphinapterus*, the ecology of these two species is likely not comparable owing to differences in body size, latitudinal distribution, and the morphology of the feeding apparatus. The vertebral morphology of NMV-5 is intermediate between that of *D. leucas* and *N. yamashitai* on the one hand *Neophocaena phocaenoides* on the other, although it is more similar to the former. However, the height of the neural spines of NMV-5 exceeds that of all three of these three species, as well as that of most of its extant relatives. This observation suggests that NMV-5 may have been capable of faster swimming speeds than *Neophocaena phocaenoides*, thus exemplifying the complex evolutionary

history of the vertebral column in phocoenids. In addition, the different vertebral morphologies of the contemporaneous taxa *Numataphocoena yamashitai*, *Piscolithax longirostris*, and NMV-5 (early Pliocene) may indicate their adaptation to different environments.

Conclusions

NMV-5, a new, small fossil phocoenid from the lower Pliocene Koetoi Formation, Hokkaido, northern Japan, is characterised by a unique combination of characters, including a small and narrow rostrum, long centra of the thoracic and lumbar vertebrae, and high neural spines. Dental growth layer groups indicate that NMV-5 attained physical maturity at a considerably younger age than extant phocoenids, as evidenced by ankylosis of the vertebral epiphyses. This might have resulted from a developmental pattern different from the progenesis observed in extant phocoenids, although more information is required to confirm this.

Numataphocoena yamashitai and *Phocoenoides dalli* represent the ends of an anatomical continuum in terms of phocoenid vertebral morphology, with the vertebral column of the former being the most archaic and nearly identical to that of the monodontid *Delphinapterus leucas*. Phocoenid vertebral evolution has been complex and frequently convergent, as opposed to stepwise and unidirectional (fast swimmer vs. maneuverable swimmer), as clearly demonstrated by the combination of primitive and highly derived vertebral characters in NMV-5. Its high neural spines suggest that NMV-5 had a relatively strong propulsive ability. At the same time, different vertebral morphologies observed in other, contemporaneous living and fossil taxa suggest that they were adapted to different environments.

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