

Distinctive osteology of distal flipper bones of tropical bottlenose
whales, *Indopacetus pacificus*, from Taiwan: Mother and calf,
calf with polydactyly

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Beaked whales (family Ziphiidae) are relatively large marine mammals, although they are among the least known cetaceans. The 21 described species in six genera (Dalebout *et al.* 2004) are broadly distributed around the world, but live almost exclusively in far offshore deep waters where they spend relatively little time at the surface. Observational data are further hindered by their typically undemonstrative and shy surface behavior: their blow is poorly visible, they present a low surface profile, and they spend the majority of their time deep diving, and in general, vocalizing only when deeper than 200 m (reviewed in Cox *et al.* 2006).

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Only recently, following multiple widespread live-sightings in warmer waters of the western Indian and Pacific Oceans (Pitman *et al.* 1999), and skeletal material comparisons and DNA sequence data analyses (Dalebout *et al.* 2003), has the tropical bottlenose whale, *Indopacetus pacificus* (Longman 1926) been verified as a living, distinct new ziphiid species in a separate genus. This large and robust beaked whale (estimated adult body length 7–8 m) has been previously identified from only eight strandings from the western Indian and Pacific Oceans. The first six were reviewed in Dalebout *et al.* (2003), whereas the other two are a 6.45-m adult female from Japan (Yamada *et al.* 2004) and a 5.73-m male from the Philippines (Acebes *et al.* 2005).

Description of the postcranial skeleton of the tropical bottlenose whale is extremely limited: the first five cervical vertebrae are fused, there are 10 pair of ribs, and at least 46 total vertebrae (Dalebout *et al.* 2003, Yamada *et al.* 2004). “No information is available regarding phalangeal formula [or other limb osteology]” from a review of the first six specimens (Dalebout *et al.* 2003).

We report here the distinctive osteological characterization of the manus of the ninth and tenth DNA-confirmed specimens of *Indopacetus pacificus*, a mature and juvenile pair of tropical bottlenose whales, as well as a supernumerary sixth digit in the right flipper of the juvenile specimen. Mitochondrial DNA sequences of the control region (418 bp) and cytochrome b (536 bp) from these two whales were compared with *Indopacetus* reference sequences (GenBank accession numbers AY16435–16439 for control region; AY16440–16444 for cytochrome b). Our analysis revealed that both DNA fragments of these Taiwan *Indopacetus* were identical DNA haplotypes to the adult female Maldives *Indopacetus* specimen (Dalebout *et al.* 2003, 2004). This report appears to be the first describing the distal flipper bones for this rare species and the first account of polydactyly in a ziphiid. Here we also present the first radiographic images of intact flippers from confirmed specimens of this species.

On 22 July 2005 an adult female and a juvenile male tropical bottlenose whale 5.65 m and 4.20 m in total body length (field numbers IL 2005–23-1 and IL 2005–23-2) were found alive together in the surf at Su-Ao, Ilan County, northeastern Taiwan (121°51'30.1"N, 24°37'04.6"E). These two whales were part of an unusual stranding/mortality event around Taiwan involving at least 23 odontocetes over approximately 3 wk, temporally and geographically associated with major naval exercises in the neighboring western Pacific Ocean (Yang *et al.* 2008).

Both animals stranded the next day and died soon after during transportation to a rehabilitation center. The carcasses were then transported to the Taipei City Zoo where the female was measured and necropsied on 24 July, and the juvenile male on 25 July.

In the female, significant postmortem findings included severe, diffuse vascular congestion, and marked disseminated microvascular hemorrhages associated with widespread round-to-oval cavitory lesions predominantly within the liver, kidneys, and lymph nodes (Yang *et al.* 2008) consistent with gas emboli (Fernández *et al.* 2005). The male was autolytic and not sufficiently fresh for detailed pathologic diagnosis. The female had two corpora albicantia in her left ovary and was lactating. Pale yellow viscous fluid coated the entire wall of the first stomach compartment of the juvenile. The skulls of both whales were preserved intact for subsequent specimen

Table 1. Flipper measurements (cm) of adult female and juvenile male tropical bottlenose whales. First two measurements taken at necropsy, last two taken on disarticulated flippers after storage at -15° to -20°C for 8 months.

	Adult female		Juvenile male	
	Left	Right	Left	Right
Length of flipper from cranial insertion	—	55.0	44.0	—
Axilla to tip of flipper	—	32.0	28.0	—
Maximum width of flipper	15.8	15.3	12.5	12.5
Axial flipper length from proximal end (head) of humerus to flipper tip	54.3	53.7	42.0	42.5

preparation, so the brains and ears were not examined. The left and right flippers were disarticulated at the scapulo-humeral joint, transported to the Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, and stored frozen. Standard flipper measurements were recorded (Table 1, Fig. 1).

Standard, plain-film, ventrodorsal radiographs were taken of both pairs of thawed and cleaned flippers, at the National Taiwan University Veterinary Hospital, Taipei, using a nongrid cassette, with a film-to-source distance of 100 cm, exposures of 40–50 kVp and 100–150 mA for 0.04–0.05 s, and the film was processed in an automatic processor. Each radiograph was examined by the unaided eye on a standard radiographic illuminator to determine the location and number of bones in the distal flipper.

In the adult female, separate bony epiphyses were not evident in the manus, although a fully formed epiphysis was present distally on the radius and ulna; each



Figure 1. Photograph of intact right polydactylous flipper *in situ* of a 4.20-m juvenile male tropical bottlenose whale. The ziphiid characteristic shape and relative smallness of the flipper are apparent (cranial is to the right, dorsal is to top of page). There was no external indication of the supernumerary digit, which was found by radiography and later dissected for study (scale bar = 50 cm).

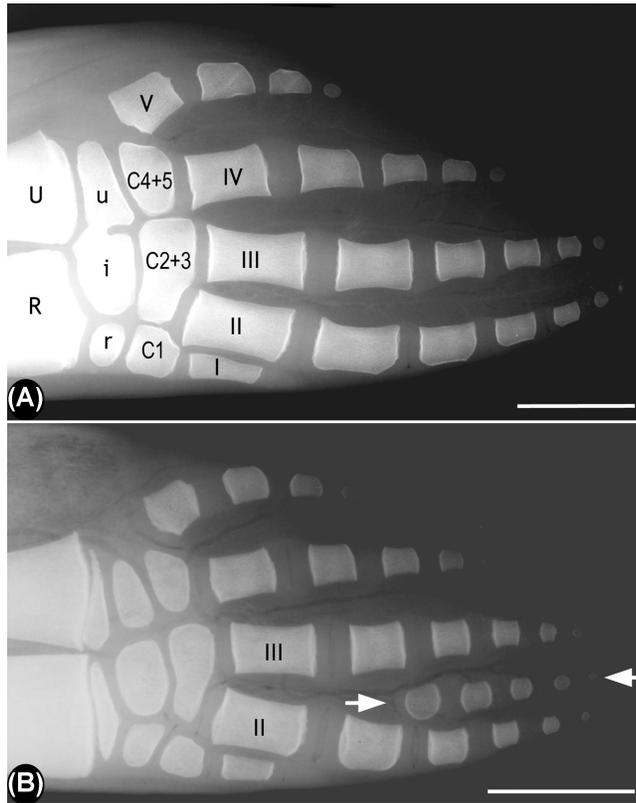


Figure 2 (A) Ventrodorsal radiograph of distal left flipper of a 5.65-m adult female tropical bottlenose whale showing the distinctive six carpal bones, five metacarpals, and phalanges in the five digits. The tiny terminal sixth phalanx of digit II is visible as a speck (image has been inverted to match view of polydactylous flipper, Fig. 2B). Note the curving of abaxial digits II, IV, and V, and the rounding of the abaxial borders of their phalanges compared with the axial digit III. R: radius; U: ulna; r: radiale; i: intermedium fused with ulnare; u: ulnare; C1: carpal 1; C2 + 3: carpal 2 plus 3; C4 + 5: carpal 4 plus 5; I–V: first through fifth metacarpal bones (scale bar = 5 cm). (B) Ventrodorsal radiograph of polydactylous right distal flipper of a 4.20-m juvenile male tropical bottlenose whale showing supernumerary digit with five phalanges (between arrows) between normal digits II and III. Overall the degree of ossification is less than in the adult (Fig. 2A), especially in the terminal phalanges but the tiny fifth supernumerary phalanx is just visible (2×3 mm; scale bar = 5 cm).

was largely fused to its respective metaphysis by multiple trabecular osseous bridges with little evidence of an intervening cartilage growth plate, being at late stage 4 of epiphyseo-metaphyseal maturation (Fig. 2A; Ogden *et al.* 1981). Both flippers had a similar pattern of six polygonal carpal bones in two rows (Fig. 2A) with intercarpal spaces of 1.5–6 mm visible radiographically: the proximal row consisted of a relatively small, squarish radiale with a rounded cranial border; a large polygonal intermedium, which articulated proximally, predominantly with the distal radius (70%), and to a lesser extent, with the distal ulna (30%), the latter by a distinctly

demarcated caudoproximal lobe; and caudally a broadly flattened trapezoidal ulnare. The transversely elongated intermedium and ulnare were conjoined by bony fusion over approximately 40% of the cranial border of the ulnare. The distal row consisted of a fully formed carpal one; a broad, mainly rectangular carpal two plus three with full articulation distally on the second and third metacarpals; and a caudal bone that we have tentatively called carpal four plus five, which had full articulation proximally with the ulnare, with the fourth metacarpal distally, and a smaller contact caudodistally with less than 50% of the fifth metacarpal bone.

In the juvenile male the same six carpal bony elements were present and in a similar pattern in both flippers (without the intermedium-ulnare bony union). The degree of ossification was less developed than in the female, there being wider intercarpal cartilaginous spaces (3–6 mm), the carpal bones were more round-edged (immature), and the distal radius and ulna had separate, almost full-width epiphyses at late stage 2 of epiphyseo-metaphyseal maturation (Fig. 2B; Ogden *et al.* 1981).

The phalangeal formula (phalanges only) for the left and right flippers in the adult was the same: I-0, II-6, III-5, IV-4, V-3 (Fig. 2A; Table 2); the terminal phalanx (6th) of digit II was 2 × 1 mm on the left and 2 × 3.5 mm on the right, the penultimate phalanx of digit II and terminal phalanges of digits III and IV were 5–7 mm in diameter, whereas the terminal phalanx of digit V was a little larger. The shape of the phalanges differed among the digits. Those of the axial third digit were rectangular with parallel cranial and caudal borders, whereas the abaxial borders of the phalanges in digits II, IV, and V had cutoff or cambered proximal and distal corners. In addition, the flipper axis extended distally from the radio-ulnar interosseous space through digit III in a relatively straight line, whereas the middle portions of the abaxial digits tended to curve concavely away from the axis.

In the juvenile male the phalangeal formula for the normal left flipper was I-0, II-6, III-6, IV-4, V-3; the terminal phalanx of digits II and III was 1 mm in diameter, and the phalangeal shape and orientation of the digits were similar to that of the adult female. The phalangeal formula for the polydactylous right flipper was I-0,

Table 2. Phalangeal formulae^a of representative ziphiids.

	Digit-I	II	III	IV	V	Total	Source
<i>Tasmacetus shepherdi</i>	0	4	3	2	1	10	Oliver (1937)
	0	4	4	2	1	11	Watson (this paper)
<i>Ziphius cavirostris</i>	1	5	5	4	2	17	Scott and Parker (1889)
<i>Hyperoodon planifrons</i>	1	6	5	4	2	18	Hale (1931)
<i>Indopacetus pacificus</i>	0	6	5–6	4	3	18–19	This paper
	0	5	5	4	3	17	Yamada ³
<i>Mesoplodon bidens</i>	0	6	5	4	2	17	Flood <i>et al.</i> (1996)
	0	5	4	3	2	14	Turner (1885)
<i>Mesoplodon densirostris</i>	1	4	4	3	1	13	Watson (this paper)
	1	3	4	3	2	13	Casinos and Filella (1981)
<i>Berardius arnuxii</i>	1	6	5	4	3	19	Hector (1878)

^aTrue bony phalangeal count, excluding metacarpals: original citations corrected and verified from radiographs and published illustrations.

II-5, [5] III-5, IV-4, V-3 (Fig. 2B), there being an additional smaller digit of five phalanges lying between digits II and III. These smaller supernumerary five phalanges extended from level with the distal end of the phalanx 1 of digit II to approximately level with the fifth (terminal) phalanx of digit II. Each additional phalanx was located serially, level with the adjacent interphalangeal space of digit II. The first phalanx of this anomalous digit was somewhat rounded, although the remaining phalanges were near normal in shape compared with the phalanges of the adjacent digits. The outline shape and size of the polydactylous left flipper was similar to the normal right flipper, and therefore externally there was no indication of the supernumerary digit (Fig. 1).

Gross dissection of the polydactylous right flipper of the juvenile male revealed the skeleton of the supernumerary digit where it lay freely in the dense fibrous connective tissue between digits II and III (Fig. 3) with a small tendon running axially on its dorsal and ventral surfaces, similar to tendons in digits II and III. The first phalanx had a small fibrous cap proximally, and lacked any apparent fibrous, cartilaginous, or bony connections with either of its adjacent digits (Fig. 3). The remaining phalanges and interphalangeal synovial joints were normal in appearance, similar to those of the neighboring digits.

The right carpus of both whales was dissected to establish the borders of the skeletal elements. The accessory carpal bone was present in both as a distinct cartilaginous element at the caudal-most aspect of the proximal row of carpal bones, where it

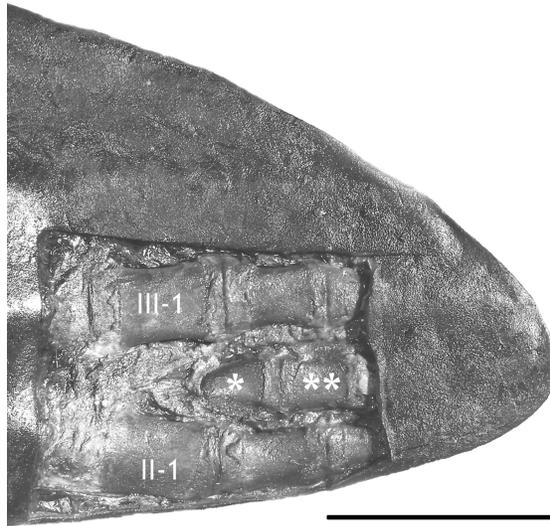


Figure 3. Ventral view of distal right polydactylous flipper of a 4.20-m juvenile male tropical bottlenose whale showing proximal two phalanges (*, **) of the supernumerary digit between digits II and III after dissection of skin and soft tissues to show ossifications (the ventral axial tendon of the anomalous and normal digits have been reflected off the bones). Notice lack of bony or cartilage connection of extra digit to either of the normal adjacent digits. II-1, III-1: first phalanx of digits II and III, respectively (scale bar = 5 cm).

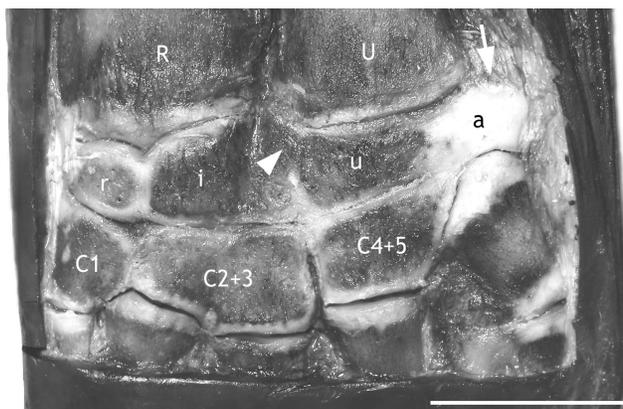


Figure 4. Ventral view of dissected right flipper of 5.65-m adult female showing the six carpal bones and associated cartilages. Union between the intermedium and ulnare is visible (arrow head), and the accessory carpal bone is present as a cartilage element (a) with muscle tendon (arrow) inserting on its proximal border. The synovial carpal joints have been opened. Labels as per Fig. 2A (scale bar = 5 cm).

extended caudal to the ulna into the free flap of tissue forming the caudal (trailing) edge of the flipper (Fig. 4). It articulated with a small area on the caudodistal limit of the ulna and distally more extensively with the fifth metacarpal bone, and it was continuous cranially with the caudal aspect of the ulnare. Its proximal-free surface received the strong tendinous insertion of flexor carpi ulnaris (Turner 1885). In the adult female the bony union between the intermedium and the ulnare was confirmed (Fig. 4). In both whales all carpo-metacarpal joints had smooth articulating cartilage surfaces and joint spaces filled with synovia. The intercarpal and antebrachio-carpal joints had varying degrees of synovial joint characteristics.

The manus of the tropical bottlenose whale is distinct morphologically from that of other ziphiids in both carpal and digital features; the ziphiids, like all odontocetes are normally pentadactylous and characteristically have hyperphalangealism (Struthers 1863, Richardson and Oelschläger 2002). In *Ziphius cavirostris*, the goosebeak whale, the carpus consists of a prominent species-specific radiale that spans both rows between the cranial half of the distal radius and metacarpal 1, caudal to which are the traditional intermedium and ulnare in the proximal row, and carpal 2 + 3, and carpal 4 + 5 in the distal row, as well as a cartilaginous accessory bone element (Scott and Parker 1889). Its true phalangeal formula I-1, II-5, III-5, IV-4, V-2, (metacarpals excluded, and numerical variations of older museum specimens reported by Paulus 1962) is unlike that of *Indopacetus*, I-0, II-6, III-5/6, IV-4, V-3 (Table 2).

Although the phalangeal formula of *Berardius arnuxii*, Arnoux's beaked whale (southern form), is similar to *Indopacetus* (the former differs in having one phalanx in the first digit; Hector 1878; Table 2), its carpus characteristically includes species-specific intra- and inter-row fusions (radiale and intermedium are united, and the ulnare is fused with carpal 4 + 5; Flower 1874, Marelli 1920), which makes the carpus of *Berardius* unique among ziphiids.

Within the beaked whales of the genus *Mesoplodon*, the carpal bones are usually six in number in two distinct rows, sometimes with the accessory bone proximocaudally (Turner 1885, 1909; Raven 1937, 1942; Mead 1989; dissection and radiographic examination of flippers by AW), and in a few species the ulnare may fuse with carpal 4 + 5 (Reyes *et al.* 1991). Characteristically, each bone is fairly blocky, almost squarish in outline, which differs from the transversely elongate (in the craniocaudal dimension) carpal bones (four of six) in *Indopacetus* (Fig. 2A). Furthermore, in the adult *Indopacetus* the intermedium and ulnare are in robust contact and coalesced over their proximal halves. The outline of the distal flipper in our adult *Indopacetus* is comparable in size and shape to that of *M. densirostris* of similar body length; however, the digits are significantly different in phalangeal number and arrangement: namely, *Indopacetus* has more phalanges in digits II–V (Table 2). Moreover, the phalanx of the first digit of *M. densirostris* is distinct and large. Small ossa centralia are infrequently observed amongst the other carpal bones in some ziphiid carpi (Turner 1909), but these elements were not seen in the two tropical bottlenose whales studied here. Observations of the manus of *Tasmacetus shepherdi*, Tasman beaked whale, have been insufficiently reported to make a comparative assessment with *Indopacetus* other than to note the former species has the six usual carpal bones in two rows (USNM 484878: radiographic image of one flipper examined by AW) and a comparatively low phalangeal count in the holotype specimen (Table 2; Oliver 1937).

Earlier sightings tentatively identified the tropical bottlenose whale as perhaps extralimnal southern bottlenose whales (Pitman *et al.* 1999); our comparative study of ziphiid carpi now reveals the peculiarity of the carpal bones in two specimens of *Indopacetus*. In the North Atlantic bottlenose whale, *Hyperoodon ampullatus*, the carpus is unique with its five separate distal carpalia (sometimes four), one at the base of each metacarpal (Turner 1909). In the southern bottlenose whale, *Hyperoodon planifrons*, there are three distal carpalia: carpal 1, a broad carpal 2 + 3, and carpal 4 + 5 (Hale 1931), which is somewhat comparable to the distal row seen in the tropical bottlenose whales of this report. The tropical bottlenose whale, however, differs from the southern bottlenose whale in at least four features of the manus. First, the widths of the distal metaphyses of the radius and ulna are equal in *Indopacetus*; in contrast, *H. planifrons* has a relatively narrower ulna (75% width of its radius, Hale 1931). Second, the intermedium and ulnare are uniquely joined in the tropical form. Third, the width of the ulnare compared to the width of the adjacent intermedium, is relatively wider in the tropical form (90%) than that in the southern form (75%). Fourth, the phalangeal formulae are distinct: in the tropical form there is one less phalanx in digit I and one more in digit V (Table 2). Study of further specimens should help clarify these observations based on the two Taiwan *Indopacetus* specimens.

Examination of the mounted bones of one flipper from another tropical bottlenose whale from Kagoshima, Japan (the seventh confirmed specimen; photographs provided by Yamada³), reveals similarities with the Taiwan specimens. This larger female

³Personal communication (e-mail) from Tadasu Yamada, Department of Zoology, National Science Museum, Tokyo, Japan, 25 April 2006. Data and flipper bones photograph of his unpublished data on the seventh confirmed specimen of *Indopacetus pacificus* from Kagoshima, Japan.

specimen (6.45 m) had all limb epiphyses closed and six well-formed carpal bones in two rows: the intermedium, ulnare, carpal 2 + 3, and carpal 4 + 5 were transversely elongate as in our adult female, but those in the Japanese specimen were more angular in outline. In the Kagoshima specimen the ulnare bone is not united with the intermedium as it is in the adult Taiwan specimen; rather, it is extended caudally beyond the border of the ulna in what appears as a conjoined ossification with the accessory carpal bone (seen as cartilage in the Taiwan specimen, Fig. 4). The pointed caudal projection of carpal 4 + 5 is also united in this accessory carpal bone part. The manifestation of the accessory carpal element is evident because the common coalescence is located caudal to the caudal border of the ulna, which is the normal topographical location for it. The phalangeal count in the adult Taiwan specimen differs from this Kagoshima specimen only in that it has one more phalanx in digit II (Table 2). The difference may be more apparent than real; this was the smallest phalanx in the manus ($2 \times 1\text{--}3.5$ mm) and the tiny phalanx was detected through our radiographic examination. All terminal phalanges seen radiographically in our two whales were confirmed on the prepared skeletons. Small and terminal phalanges are sometimes lost from decomposing cetacean carcasses or during standard museum skeletal preparations.

Polydactyly, which is the presence of additional digits (Prentiss 1903, O'Rahilly and Müller 1992), is a frequently reported congenital malformation in domestic mammal and human limbs (Tabin 1992, Palmer 1993) but is rarely observed in cetaceans. It is known in at least three odontocete species and in mysticetes of the genus *Balaenoptera*. Duplication of the fourth digit of one flipper has been described in a bottlenose dolphin (*Tursiops truncatus*; Watson *et al.* 1994), in which there was broad cartilage continuation of both digits, including their bony phalanges, from the distal end of metacarpal 4. In the vaquita (*Phocoena sinuata*), on the other hand, polydactyly is a constant bilateral trait (Ortega-Ortiz *et al.* 2000). This consistent and small supernumerary digit arises from a narrow bony projection off the caudodistal border of metacarpal 3—the cartilaginous digital ray contains 0–3 bony phalanges and lies parallel and near digit III. In the beluga (*Delphinapterus leucas*) there is variable duplication of the first digit (Kükenthal 1889–1893) or of the fourth or fifth digits (Kunze 1912, Yablokov 1974); and in each case there is chondro-osseous connection with the more proximal elements of the digital ray or metacarpal. This skeletal connection between the polydactylous digit and the normal skeleton is seen in all previous odontocete cases of polydactyly, and is consistent with findings in cats (Danforth 1947; study of four litters of alcian blue/alizarin red-stained and cleared polydactylous cat fetuses by AW) and in other domestic mammals and human beings (*e.g.*, Prentiss 1903). The lack of bony or cartilaginous connection between the polydactylous digit and a normal adjacent digit, as seen in this present case in *Indopacetus*, contrasts with the majority of mammalian individuals with polydactyly.

Polydactyly is also seen in a few balaenopterids (*Balaenoptera musculus*, Kükenthal 1890; *B. physalus*, Harmer 1927; examination of radiograph of a five-digit flipper from newborn by AW). In these cases, the rudimentary supernumerary digit lies freely between neighboring digits without bony or cartilaginous attachment, similar to that seen in the one odontocete, *Indopacetus*, here. Another similarity between the

cases in balaenopterids and *Indopacetus* is the location of the extra digit between digits II and III; although the numerical serial homology of these digits in the tetradactylous balaenopterids with those in the pentadactylous odontocetes has yet to be clarified (Cooper *et al.* 2007). At the organismal or higher taxon level, one might suggest that a polydactylous fifth digit in the normally tetradactylous balaenopterids is an atavism—expression of the “lost” ancestral condition (Gegenbaur 1882, Hall 2003). Although stem mammals and ancient cetaceans were indeed pentadactylous (Gingerich *et al.* 2001), it has been further shown that the earliest known ancestral tetrapods were not pentadactyl; they had limbs bearing six or eight digits (Clack 2002), clearly beyond the commonly expressed level of polydactyly in modern mammals. Such polydactyly, along with the resultant paddle-like limb, was suggested as an adaptation to their aquatic environment (Clack 2002). Based upon presently available information, the expression of polydactyly among living odontocetes is limited to one extra digit; there is variation, however, in which side of the manus the supernumerary digit occurs, and also in the number and size/shape of phalanges forming the additional digit. Similar variability of this malformation is noted in other mammals including human beings (*vide supra*).

In comparing these cetacean cases of polydactyly it appears that there may be either two separate developmental processes, or a persistence or resorption of proximal connecting elements in different species. Perturbations to homeobox gene expression and their complex interplay with morphogen regulators, transcription factors, and mis-regulated apical ectodermal ridge function in embryos have been suggested as possible developmental mechanisms that likely lead to dysfunction of the normal patterning of the skeletal core of the early limb bud and result in digital/phalangeal malformations in marine mammals (Watson *et al.* 1994, Ortega-Ortiz *et al.* 2000, Richardson and Oelschläger 2002; see also review of normal developmental processes in Clack 2002). Even though there may be an additional digit in the manus, it remains contained within the common sheath of skin covering the flipper and usually is undetectable externally. Functionally, it would appear to be of minimal, if any, hindrance to those affected.

In summary, our comparative study reveals the distinctive species-specific morphology of the carpal bones and digits in two genetically confirmed specimens of the tropical bottlenose whale, being a mother-calf pair. Furthermore, we have described a rare case of the congenital malformation, polydactyly, in the immature specimen. To our knowledge this provides the first such account in any ziphiid, and in this rare whale there was a supernumerary sixth digit of five phalanges between digits II and III.

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