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Morphology and Identity of the Holotype of *Megaptera indica* H.-P. Gervais, 1883

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Abstract

In 1883 a baleen whale stranded at 'baie de Bassora' (Basrah Bay), in the Chat-el-Arab river delta, Iraq, at the northwestern corner of the Persian/Arabian Gulf. Gervais obtained the complete specimen for the national museum in Paris (MNHN), and described it as a new humpback whale species *Megaptera indica* H.-P. Gervais, 1883. The authors studied the incomplete and slightly damaged holotype skull, measured and estimated craniometrics, and concluded that *M. indica* is a junior synonym of *Megaptera novaeangliae* (Borowski, 1781). No postcranial bones were found. Importantly, two cranial features suggest that *M. indica* nests between Atlantic humpback whales and other large Balaenopteridae. *Megaptera novaeangliae* has the widest skull index, i.e., breadth skull at squamosals relative to condylobasal length (57−66.9%, n=8), higher than *M. indica* which scored 54.9%, and considerably higher than other Balaenopteridae. Also the ratio of the width of skull at postorbitals (frontale) *versus* rostrum width at base in *M. indica* is smaller and barely overlaps with Atlantic humpback whales (n=4), again suggesting taxonomic significance. Gervais also reported several postcranial differences, presently unverifiably. Cranial findings support subspecific status, *Megaptera novaeangliae indica* (H.-P. Gervais, 1883), proposed also by Amaral et al. (submitted) for the Arabian Sea (*cum* Persian/Arabian Gulf) humpback whale population, based on mtDNA control region analysis. The reported pachyostosis in the Iraqi whale is suggested a possible example of phenotypic plasticity, an adaptation to the unusually high-salinity, high-density habitat of the Gulf, as to reduce buoyancy and avoid insolation.

Keywords: Arabian Sea; craniometrics; humpback whale taxonomy; Persian/Arabian Gulf; subspecies

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Introduction

In 1883, French ichthyologist Henri Frédéric Paul Gervais (1845−1915), son of renowned zoologist and palaeontologist Paul Gervais, both linked to the Muséum national d'Histoire naturelle (MNHN) in Paris, described a new species of humpback whale, *Megaptera indica* H.-P. Gervais, 1883 (see Supplementary Information). The description was based on an adult humpback whale that stranded in Iraq, at the extreme northwestern end of the Persian/Arabian Gulf (hereinafter referred to as 'the Gulf') at Basora Bay, near the present-day port city of Basrah (30°30′54″N, 47°48′36″E) (Figure 1), on an unknown date, but in or before 1883. A later, more detailed paper (H.-P. Gervais, 1888) reported that the holotype skeleton was collected at the Chat-el-Arab river delta and brought to Marseille, France, by ship in 1883. It was deposited as a trade item with a merchant in Marseille, where a certain 'Professor Marion' was able to examine it. Prof. Georges Pouchet[1] then asked Gervais to research the species to which it belonged and to assess its scientific value. Reportedly, examination of the tympanoperiotic indicated that the whale skeleton belonged to *Megaptera* (Gervais, 1888). A drawing of the diagnostic scapula by Prof. Marion confirmed this identification (Gervais, 1888). The MNHN decided to acquire the skeleton, registered in the MNHN *Journal du Laboratoire d'Anatomie comparée* (JAC) (Gervais, 1888). Only an incomplete skull remains, referred to by Robineau (1989, p. 278) as calvarium 'JAC 1883-2255', but presently bearing the collection number MNHN-ZM-AC-1883-2255. It is unknown what happened to the mandibles and postcranial bones, but they must have been transported to France as Gervais (1883a,b, 1888) had access to them.

Figure 1. Stranding location (red dot) of the holotype whale specimen of *Megaptera indica* Gervais, 1883, reported as 'baie de Basora' (Gervais, 1883a) and 'baie de Bassora' (Gervais, 1883b and 1888) in the Chat-el-Arab river delta, interpreted as present-day Basrah Bay, Iraq, situated at the extreme northwestern end of the Persian/Arabian Gulf.

Contrary to what we presently know, i.e that humpback whales have a habitual presence in the Gulf (Dakhteh et al., 2017), Gervais (1883a,b) suggested that the Iraqi whale had 'accidentally' entered the Gulf from the Indian Ocean, hence his choice of the species name. Several lines of evidence including distributional, genetic, behavioural, morphological, ecological and pathological, indicate that the humpback whale population inhabiting the Arabian Sea represents a reproductively isolated lineage, distinct from Southern Hemisphere humpback whales, long suspected to be of subspecific status (Mikhalev, 1997; Papastavrou and Van Waerebeek, 1997; Clapham and Mead, 1999; Baldwin et al., 2010; Minton et al., 2010, 2011; Pomilla et al., 2014; Jackson et al., 2014; Van Bressem et al., 2014; Willson et al., 2015, 2017). Humpback whales found inside the Gulf (Dakhteh et al., 2017), represented by the Iraqi specimen, are proposed to form part of the non-poleward migrating Arabian Sea humpback whales (ASHW), a newly recognised subspecies *Megaptera novaeangliae indica* (Amaral et al., submitted).

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[1] Georges Pouchet was a French naturalist who served as Professor of Comparative Anatomy at the National Museum of Natural History, succeeding Paul Gervais in that position. He was particularly interested in the anatomy of cetaceans.

A study visit to MNHN was conducted aiming to: (a) confirm the Iraqi whale skull as a humpback whale; (b) document its cranial morphology; (c) collect a sample for molecular genetic comparison with the ASHW population to evaluate taxonomic status and nomenclature (Amaral et al., submitted).

Material and Methods

Two of us (KVW, RB) visited MNHN on 23 May 2019 in order to examine the *M. indica* holotype and to sample bone tissue. The curator of vertebrate holotypes (CC), aided by Laurent Albenga, arranged in situ logistics, greatly facilitating our mission to the MNHN marine mammal storage facilities, which are kept in warehouses located in the Ile-de-France region.

The incomplete and moderately damaged *M. indica* skull[2] was found set in a horizontal position, dorsal side up, inside a 180 cm high wooden crate, which however obstructed lateral and ventral photographic documentation. A small wooden plate inscribed with 'Basra, Iraq' was associated with the skull and both large numericals '1883 2255' in (fading) red, and smaller ones in black, were marked on the supraoccipital bone, confirming that this specimen was indeed the *Megaptera indica* holotype (Gervais, 1883a,b, 1888; Robineau, 1989).

Three unrelated bones were found inside the same crate, including a mandible of a small sperm whale *Physeter macrocephalus*, a small-sized balaenopterid mandible[3] incompatible with the *M. indica* skull, and an unidentified whale rib, all without visible collection numbers.

A protocol with 50 standard cranial measurements was prepared (Table), based primarily on Omura (1975) and other cetacean osteology sources (Miller, 1923; Tomilin, 1967; Glass, 1973; Perrin, 1975; True, 1983). However, only about half of craniometrics could be measured due to the skull's incomplete condition. Per convention (Perrin, 1975), where feasible, left side craniometrics were selected.

The originally planned bone sampling method for genetic analysis, involving the use of a diamond core drill bit to microsample an occipital condyle, was deemed incompatible with MNHN protocols. The curator (CC) proposed an alternate methodology, proven effective before, consisting of the macrosampling of bone for later microsampling at the laboratory in sterile conditions. Indeed, the warehouse contained hundreds of marine mammal specimens, which, via aerosolized bone dust, could contaminate a locally collected microsample.

Photographs were taken, mostly in orthogonal plane to the skull, with Nikon and Canon EOS 60D cameras fitted with 18-135 mm zoom lenses. A 50 cm ruler was placed as scale. The specimen was too heavy and damaged to allow safe manipulation; thus no ventral or lateral views were obtained.

o facilitate interpretation, Gervais (1883a) was transcribed and translated from French (Supplementary Information). DeepL.com software was used to speed up translation, after which KVW thoroughly edited it for scientific accuracy.

Results

Publication History

The publication record of *Megaptera indica* is somewhat complex, as two slightly different versions were published (Gervais 1883a,b), besides a third, more comprehensive, paper (Gervais, 1888). A first account of the new species was scheduled to be orally presented by H.-P. Gervais to the Académie des Sciences in Paris at its final session ('Séance') of the year, on 31 December 1883 (Gervais, 1883a). This early published version (Gervais, 1883a, see Supplementary material), what could be considered equivalent to a preprint or a separate, was dated 31 December 1883. Apparently,

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[2] Mandibles and all postcranial bones were missing

[3] No catalogue number was visible. The size of the mandible was too small and did not match the holotype skull. However, wedged under the skull, it could not be inspected.

it was printed sometime prior to the 1883's final Académie session and was most likely available as a separate at the meeting. It shows a simple, preliminary pagination (p. 1−4), and reports the type location as 'baie de Basora' which posteriorly (Gervais, 1883b) was corrected as 'baie de Bassora'. This preprint must have been published prior to the 31 December meeting as evidenced by the fact that it was not yet known that H.-P. Gervais would not himself present his paper, but rather Mr. É. Blanchard, as reported later (p. 1566) in the volume (tome) 97 (2) (Gervais, 1883b). Therefore, we have assumed that Mr. Blanchard must have had the physical preprint (Gervais, 1883a) in his hands, to be able to present the paper, or an equivalent text, instead of Gervais.

Interestingly, Robineau (1989) cites the tome 97 (Gervais, 1883b) as the formal source of the new species description. However, this half-yearly compilation, 1578 pages long, can hardly have been printed in 1833, considering that it lists on p. 1577 '*Ouvrages recus dans la Séance du 31 décembre 1883*' (publications received on 31/12/1883) and added the detail (p. 1566) of Mr. Blanchard's reading. We conclude that tome 91(2) was completed, printed and published after the last session of 31 December 1983, i.e., in early 1884. However, the International Code of Zoological Nomenclature (ICZN) in its article 21.8. states: 'Before 2000, an author who distributed separates in advance of the specified date of publication of the work in which the material is published thereby advanced the date of publication'. In conclusion, with Gervais (1883a) being the earliest version of the work, it should be designated the formal description of *Megaptera indica.*

Condition of the Skull

The 19th century *M. indica* type specimen was described as an almost complete skeleton, including long anterior limbs and black baleen, consistent with *Megaptera* (Gervais, 1883a,b; 1888). The cause of death and the precise condition of carcass when encountered stranded were not reported, but Gervais (1888) stated it was a skeleton. Robineau (1989) found only a partial skull at MNHN, like we did. Many cranial bones were missing, including both mandibles, premaxillae, nasals, palatines (damaged), pterygoids, lacrimals, tympano-periotics and jugals. Hyoid bones and sternum were also missing. No baleen plates were present. Moreover, the maxillae were damaged apically (see below), while the vomer was bolted together because fractured in several pieces. Several pins and metal plates had also been applied to ensure the maxillae remained attached to the neurocranium and potentially for lifting/display purposes. The maxillae appeared mostly correctly placed, which is important since misaligned maxillae could bias the rostrum base width (RBW) measurement (Table 1).

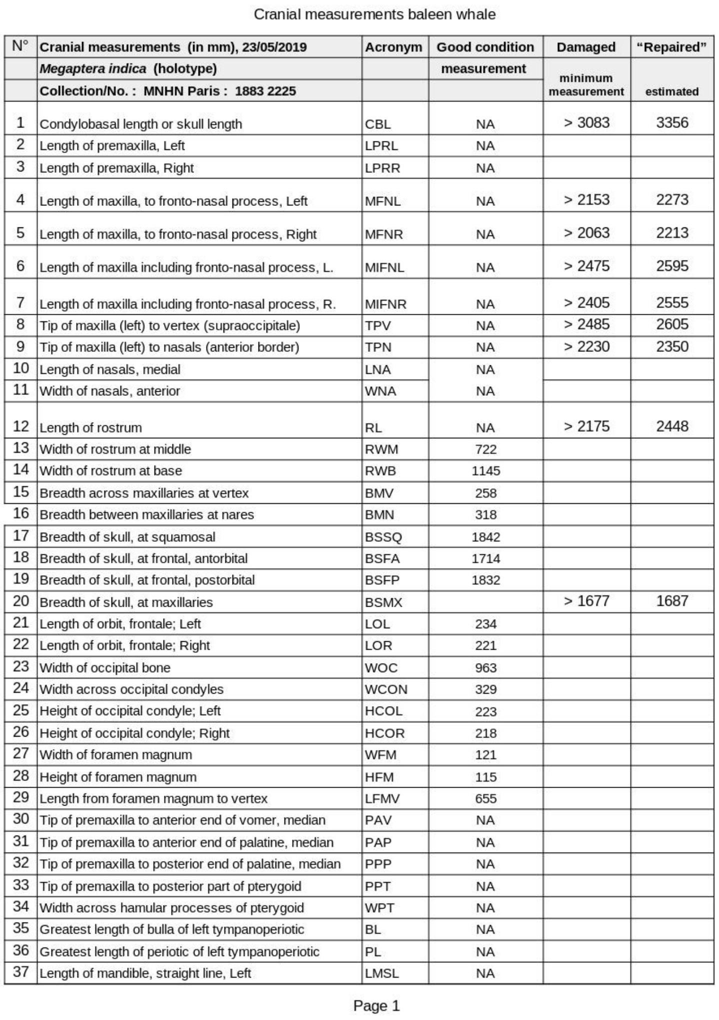
Estimation of Condylobasal Length and Body Length

The condylobasal length (CBL) and zygomatic width (ZW, typically equals maximum skull width) arguably comprise the two most important craniometrics of the balaenopterid skull, considering that the relative size of cranial bones are weighted against these. In *Megaptera,* as in other balaenopterids, the premaxillae extend beyond the maxillae anteriad and thus co-determine standard CBL. However, considering that both premaxillae of *M. indica* were missing, skull length was initially approximated as the (shorter) 'maxilla-based CBL'. Moreover, although the rostral tips of the maxillae were slightly damaged, the original outline and the length of the missing maxillary apices could be estimated from their converging left and right borders, i.e., by adding ≈120 mm (left side) and ≈150 mm (right side). The left 'maxilla-based CBL' was then estimated at 3,203 mm (3,083 mm measured + 120 mm correction).

We used good-resolution photographs of three adult *M. novaeangliae* skulls (see True, 1983; plates 29 & 32) to calculate the relative protrusion of the left premaxilla anteriad beyond the left maxilla in this species. The three skulls considered were: USNM 21492; USNM 16252; and N.N. at Milwaukee Public Museum (True, 1983). To account for the projecting premaxillae required the addition of an extra axial length of respectively, 5.13%, 5.09% and 4.13% (mean= 4.78%) of the measured 'maxilla-based CBL'. When applying this mean correction, i.e., by adding 153 mm length to compensate for the missing premaxilla, a fair estimate of the 'standard CBL' of *M. indica* is then ca. 3,356 mm.

The skull length (CBL) of an adult humpback whale is 26.5−30% of body length (True, 1983; Tomilin, 1967), while the mandible length may reach 25% (Pyenson et al., 2013)[4]. Thus, from the approximate CBL, body length of *M. indica* is estimated to have ranged between 11.87−12.91 m, indicating the whale was almost certainly sexually mature (Mikhalev, 1997). Although some variation in cranial proportions between Atlantic *Megaptera* specimens and *M. indica* is postulated (Gervais, 1883a,b; 1888), the above approximations are likely reasonably correct.

Table 1. xxx.



Cranial measurements baleen whale

N°	Cranial measurements (in mm), 23/05/2019	Acronym	Good condition	Damaged	"Repaired"
	***Megaptera indica* (holotype)**		**measurement**	**minimum measurement**	**estimated**
	Collection/No. : MNHN Paris : 1883 2225				
1	Condylobasal length or skull length	CBL	NA	> 3083	3356
2	Length of premaxilla, Left	LPRL	NA		
3	Length of premaxilla, Right	LPRR	NA		
4	Length of maxilla, to fronto-nasal process, Left	MFNL	NA	> 2153	2273
5	Length of maxilla, to fronto-nasal process, Right	MFNR	NA	> 2063	2213
6	Length of maxilla including fronto-nasal process, L.	MIFNL	NA	> 2475	2595
7	Length of maxilla including fronto-nasal process, R.	MIFNR	NA	> 2405	2555
8	Tip of maxilla (left) to vertex (supraoccipitale)	TPV	NA	> 2485	2605
9	Tip of maxilla (left) to nasals (anterior border)	TPN	NA	> 2230	2350
10	Length of nasals, medial	LNA	NA		
11	Width of nasals, anterior	WNA	NA		
12	Length of rostrum	RL	NA	> 2175	2448
13	Width of rostrum at middle	RWM	722		
14	Width of rostrum at base	RWB	1145		
15	Breadth across maxillaries at vertex	BMV	258		
16	Breadth between maxillaries at nares	BMN	318		
17	Breadth of skull, at squamosal	BSSQ	1842		
18	Breadth of skull, at frontal, antorbital	BSFA	1714		
19	Breadth of skull, at frontal, postorbital	BSFP	1832		
20	Breadth of skull, at maxillaries	BSMX		> 1677	1687
21	Length of orbit, frontale; Left	LOL	234		
22	Length of orbit, frontale; Right	LOR	221		
23	Width of occipital bone	WOC	963		
24	Width across occipital condyles	WCON	329		
25	Height of occipital condyle; Left	HCOL	223		
26	Height of occipital condyle; Right	HCOR	218		
27	Width of foramen magnum	WFM	121		
28	Height of foramen magnum	HFM	115		
29	Length from foramen magnum to vertex	LFMV	655		
30	Tip of premaxilla to anterior end of vomer, median	PAV	NA		
31	Tip of premaxilla to anterior end of palatine, median	PAP	NA		
32	Tip of premaxilla to posterior end of palatine, median	PPP	NA		
33	Tip of premaxilla to posterior part of pterygoid	PPT	NA		
34	Width across hamular processes of pterygoid	WPT	NA		
35	Greatest length of bulla of left tympanoperiotic	BL	NA		
36	Greatest length of periotic of left tympanoperiotic	PL	NA		
37	Length of mandible, straight line, Left	LMSL	NA		

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Bone Sampling and Processing

About 1 cm³ of bone tissue from the anterio-mesial edge of the left frontal bone was sampled using a Dremel rotary tool mounted with a small circular saw. Standard precautions were taken to avoid contamination (gloves, thorough cleansing of tools and sample locus with ethanol). The

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[4] In Balaenopteridae, the condylus mandibularis articulates posteriad with the zygomatic process of the squamosal at the level of the exoccipital. Hence, mandibular length is only slightly shorter than CBL, explaining the similar % of body length.

macrosampling yielded good-quality DNA (Amaral et al., submitted), despite the age (136 yrs) of the skull.

The CITES export-import permit procedure of the sample and actual delivery to the American Museum of Natural History (AMNH) in New York, was coordinated by CC, TC & RLB. The process was severely complicated by Covid-19 pandemic restrictions. Ancient DNA extraction, amplification and comparative analysis with ASHW specimens were implemented by experts in *M. novaeangliae* phylogenetics (Amaral et al., submitted).

Taxonomic Confirmation as Megaptera

The size of the skull and moderate ankylosis between cranial bones indicated that the *M. indica* type specimen was cranially mature, albeit not an old individual (Figures 1 and 3). For instance, suture lines between the temporal and frontal bones were still clearly visible. Gervais (1883a,b) reported it as an adult individual. Despite multiple missing and damaged cranial bones, the overall cranial morphology (Figures 2–4) confirms the study specimen to be a *Megaptera* sp., distinct from *Balaenoptera* spp. The below characters are of particular relevance.

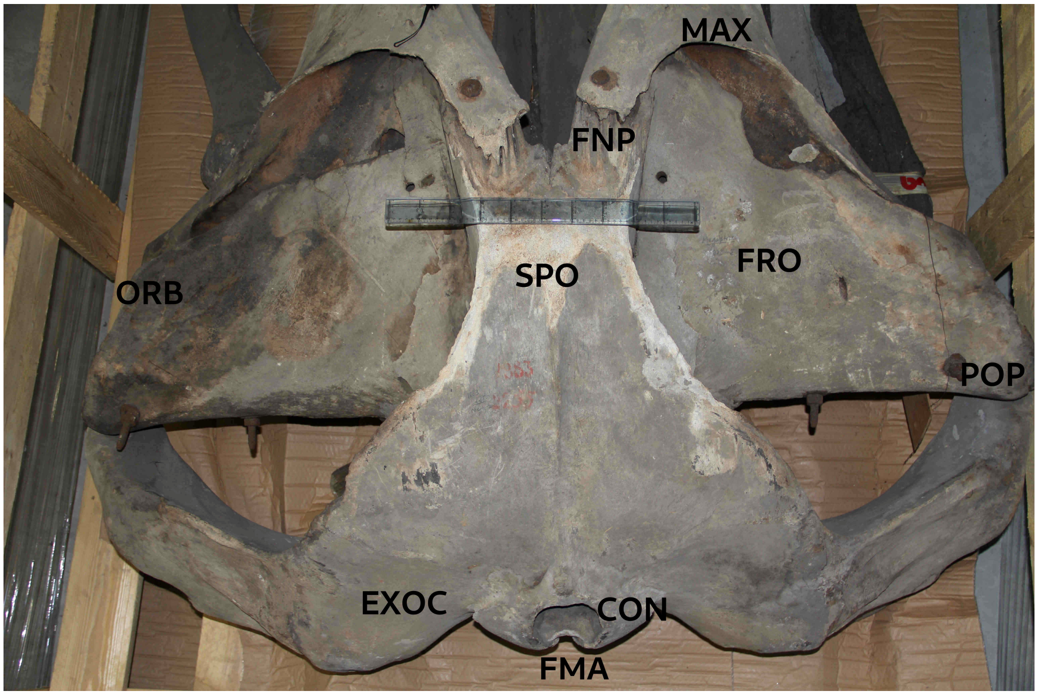

Figure 2. Dorsoposteriad view of the cranium (holotype) of *Megaptera indica*. It shows the occipital condyles (CON), foramen magnum (FMA), exoccipital (EXOC), supraoccipital (SPO), frontal bone (FRO) with orbit (ORB), postorbital process of frontal (POP) and damaged fronto-nasal processes of maxillae (FNP). Scale is 50 cm. Photo ©KVW.

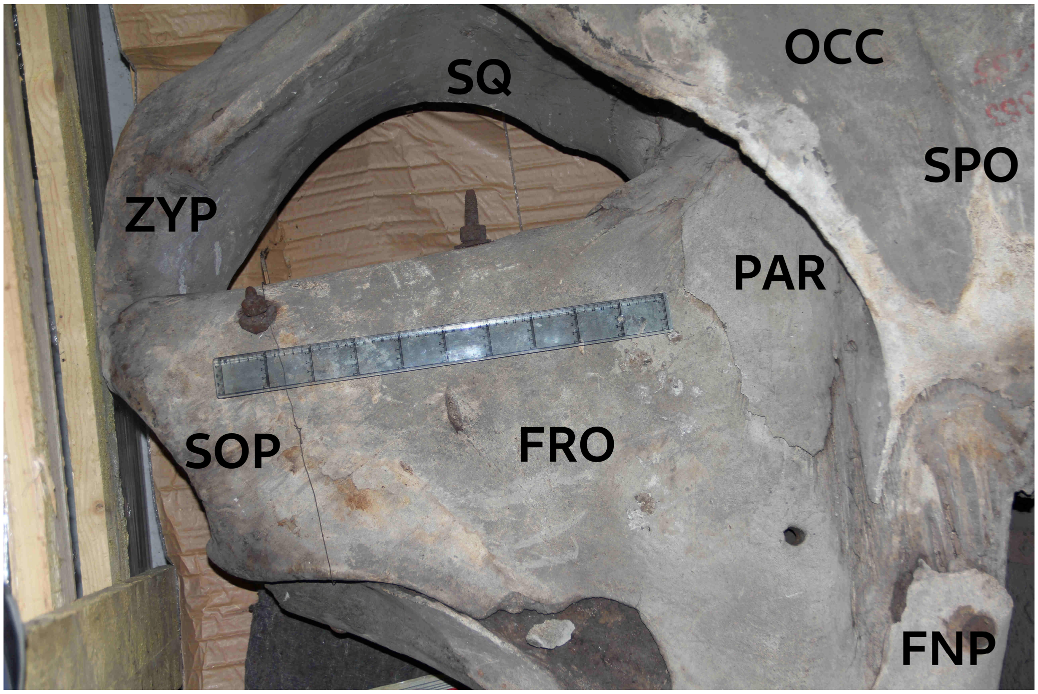

Figure 3. Dorsolateral view of the *M. indica* holotype skull showing multiple cranial bones, including the right frontal bone (FRO), the (incomplete) fronto-nasal process (FNP) of the right maxilla, the parietal (PAR), occipital bone (OCC), and supraoccipital (SPO) at the skull's crest. Note the prominent supraorbital process (SOP) of the frontal bone (FRO) narrowing markedly towards the orbit. The anterior margin of the squamosal (SQ) is smoothly rounded and U-shaped including the zygomatic process (ZYP). Both features are diagnostic for *Megaptera.* Scale shown is 50 cm (10 x 5 cm). Photo © KVW.

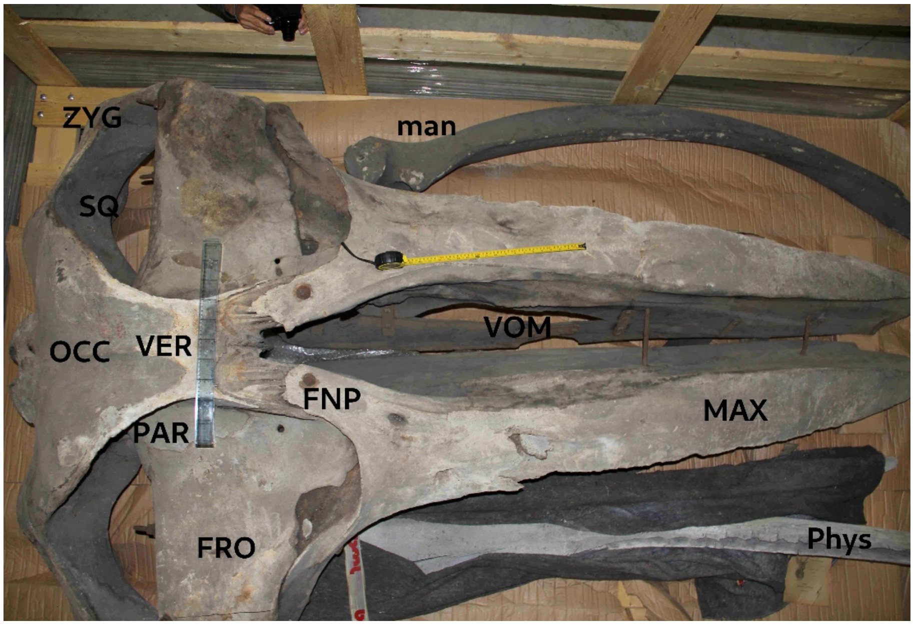

Figure 4. Dorsal view of *M. indica* skull exposing: occipital bone (OCC), vertex (VER), frontal (FRO), parietal (PAR), squamosal (SQ) with zygomatic process (ZYG), fronto-nasal process (FNP) of maxilla (MAX) and vomer (VOM), which is incomplete and fractured but assembled with metal components. Naso-frontal processes of maxillae, although damaged, do not expand in width posteriad, characteristic for *Megaptera*. Premaxillae and nasals are missing. Two unrelated bones were present in the crate: non-matching left mandible (man) of a smaller balaenopterid; mandible of a small-sized *Physeter macrocephalus* (Phys). Photo © KVW.

(i) A key anatomical cue for *Megaptera* is the strongly prominent supraorbital processes of the frontal bones (see Gray, 1866 [his Figure 14]; True, 1983 [Plates 29 and 32]; Jefferson et al., 1993 [p.60], 2008 [p.501], which is also evident in *M. indica* (Figures 2 and 3). Tomilin (1963; p.246) accurately emphasized the different shape of the supraorbital processes compared to these in *Balaenoptera* spp.: 'processes [in *Megaptera*] are considerably expanded along the axis of the cranium, but greatly narrow towards the orbit'. Jointly with (ii), it is the most striking morphological feature, readily identifying a *Megaptera* skull at ocular inspection.

(ii) As evident in *M. indica* (Figure 2 and 3), the anterior margin of the squamosal is rounded or U-shaped in *Megaptera,* while pointed or V-shaped in *Balaenoptera* spp. (see Jefferson et al., 1993, Figure 179; Jefferson et al., 2008; p.501). Also, squamosals in *M. indica* are heavily built (Figure 2 and 3), consistent with other *Megaptera* (Tomilin, 1963). Archer et al. (2018) described it as 'in *Megaptera*, unlike other balaenopterids, the anterior margin of the squamosal is marked by a smooth and continuous surface'. The result, diagnostic for *Megaptera,* is the lack of a distinct fold in the squamosal (a 'squamosal crease') as it transitions from the temporal wall to the zygomatic process at the rear of the temporal fossa (Figure 2 and 3) (Deméré et al., 2005; Archer et al., 2018).

(iii) In *Balaenoptera* spp. the breadth of the skull (BSFP) at the postorbital processes of frontals does not exceed 1.5 times the rostrum width at base (RWB) (Reyes and Molina, 1997), differentiating it from *M. novaeangliae* which are reported to have a breadth of skull ratio of about 2 (Reyes and Molina, 1997). Published photos of four North Atlantic *M. novaeangliae* skulls (True, 1983) allowed this ratio to be estimated, with a range of 1.72−1.96 (mean= 1.85). In *M. indica* the ratio ranged between 1.60 and 1.73 (mean= 1.665), calculated respectively from cranial measurements and photogrammetry. Thus, the highest *M. indica* estimate only slightly overlaps with the lowest value for Atlantic humpback whales, but amply exceeds other balaenopterids.

Jefferson et al. (2008) presented an inverted ratio, but equivalent to Reyes and Molina (1997): the RWB is only about 0.50 of cranial width (BSFP) in *M. novaeangliae* while at least 2/3 cranial width (0.666 or higher) in other balaenopterids. In *M. indica* this ratio was 0.625, again outside the *Balaenoptera* spp. range.

(iv) In *M. indica,* as in other humpback whales (see True, 1983: Plates 29 and 32), the imaginary line that unites the external borders of the orbital processes of the maxillae passes behind the nasals (Figure 3), whereas it passes over the nasals in other balaenopterids (Reyes and Molina, 1997). The nasal bones were lacking in *M. indica* but their relative location at the skull's vertex was evident.

(v) Tomilin (1967) indicates that, among large balaenopterids, *M. novaeangliae* has the maximum zygomatic process width index (i.e., breadth skull at squamosals = BSSQ) relative to CBL (57−66.9%, n=8), somewhat higher than *M. indica* which scored 54.9%, and considerably higher than fin whale *B. physalus* (44.6−52.2%, n=10), sei whale *B. borealis* (43−50.8%, n=9) and blue whale *B. musculus* (47.2−52.5) (Tomilin, 1967). Here again, *M. indica* scores in between *M. novaeangliae* and other balaenopterids, suggesting some taxonomic significance.

(vi) The naso-frontal process of the maxillae normally[5] expands posteriad in width in all *Balaenoptera* spp., but not in *Megaptera* (Tomilin, 1967; Reyes and Molina, 1997). Although proximal parts of the naso-frontal processes of the *M. indica* holotype are slightly damaged, their outline is evident and there is no indication of a distal expansion (Figures 1 and 3).

(vii) Another feature reported for the *Megaptera* skull is a downward rostral curvature, characterized by Tomilin (1967) as 'dorsal contours of the maxillary and premaxillary more intricately curved than in *Balaenoptera*'. However, such curvature is not diagnostic, considering that sei whale *B. borealis* Lesson, 1828, also shows an arched head with slightly down-turned rostrum tip (see Andrews, 1916; images p. 98 & 101; Gambell, 1985).

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[5] At least in some juvenile Antarctic minke whales *Balaenoptera bonaerensis* Burmeister, 1867 there is neither any expansion (e.g. specimen KVW-2298 deposited at CEPEC, Pucusana, Peru). Unpublished data.

(viii) The *Megaptera* scapula is unique among Balaenopteridae, for it lacks coracoid and acromial processes, while sometimes represented by rudimentary tubercles (Gray, 1866; Miller, 1923; Tomilin, 1967; True, 1983, Plates 34 and 36). Gervais (1883a,b) noted that the scapula of *M. indica* was lacking an acromion and that the coracoid process was represented by a small bony protrusion, consistent with known *Megaptera* features.

(ix) Gervais (1888), without specifying why, reported that the examination of the (presently missing) tympanoperiotic complex confirmed that the whale was a *Megaptera.* Gray (1866; e.g., his Figures 20 and 53) recognized 'great differences' in form of tympanic bones to separate whale species from one another.

Other Features of Interest

(a) Gervais (1883a,b) underscored that, in comparison with *Megaptera Boops* of the North Atlantic, *M. indica* had thick (dense) osseous tissue affecting many bones including vertebral bodies and their spinal and transverse processes, especially in the first cervicals, but also affecting pterygoids, palatine bones, sternum and metacarpals. These bones were not available for examination. This systemic condition is interesting as it may be pathologic, but might also be equivalent to the 'swollen' (pachyostosis) and dense (osteosclerotic) bones of Sirenia, a skeletal adaptation to reduce buoyancy (Domning, 2018). Unusually heavy bones could help whales to remain fully immerged and avoid insolation, despite the high-salinity, high-density waters of the Gulf (Swift and Bower, 2003; Paparella et al., 2022). Besides that unusual condition, no deformations or osteopathy were reported (Gervais, 1883a,b; 1888; Robineau, 1989). We did notice a small foramen (2-3 cm in diameter) perforating the dorsal edge of the left occipital condyle (Figure 5), osteolytic, non-traumatic in origin. Considering its small size, it is unlikely that this foramen caused any ill health effects. The occipital condyles and adjacent occipital bone presented a somewhat rough surface, apparently also from osseous lysis (Figure 5).

Figure 5. Dorsal view of the basioccipital area including the occipital **condyles.** Note the (abnormal) small foramen at the upper rim of the left. condyle (arrow), set among mild idiopathic bone lysis. Photo © KVW.

(b) Gervais (1883a,b) reported that the occipital bone of *M. indica* shows a strong central ridge, as do two of four humpback whale skulls pictured in True (1983). However, this feature is not unique to *Megaptera*, e.g., *Balaenoptera physalus* (Linnaeus, 1758) can also show such an occipital ridge (see True, 1983, Plate 1).

(c) The unique shape of the sternum in *M. indica* was emphasized by Gervais (1883a,b; 1888), however variation in shape between and within balaenopterid species is known to be naturally high. Klima (1978) confirmed great individual variability in the shape of sterna of *M. novaeangliae* that one could call triangular, heart-shaped, trilobate or U-shaped. Hence, diagnostic value is very limited, if not nihil.

Discussion and Conclusions

Contemporary cranial data presented here and historical descriptions of postcranials, e.g., on scapular morphology and long pectoral fins (Gervais, 1883a,b; 1888) confirm that *Megaptera indica* is a humpback whale. A comprehensive phylogenetic comparison between *M. indica* and Arabian Sea humpback whales from the Gulf of Oman is consistent with this finding (Amaral et al., submitted).

Some cranial indices demonstrated *M. indica* to be morphologically intermediate between *M. novaeangliae* and *Balaenoptera* spp. This supports the arguments based on mt-DNA control region (Amaral et al., submitted) to recognize *M. indica* as a distinct subspecies. Considering the historical publication record, it should be referred to as *Megaptera novaeangliae indica* (H.-P. Gervais, 1883).

Unusually thick postcranial bones (pachyostosis) were described by Gervais (1883a,b), which we suggest to be an example of phenotypic plasticity (Price et al., 2003) a likely adaptation to reduce excessive buoyancy (and damaging sun exposure), due to the high-salinity, high-density waters of the Gulf. The pachyostotic phenotype may have been acquired after long permanence in the Gulf (multiple months or years).

While detailed case studies are scarce, negative anthropogenic impacts affecting threatened humpback whales in the Persian/Arabian Gulf and the Arabian Sea are of major concern. Of seven documented records in the Gulf (Dakhteh et al., 2017), only two humpback whales were seen alive, one of which, a juvenile, was net-entangled in a drift gillnet and the other was severely injured by a propeller with unclear survivability. Among the five dead whales, at least three were juveniles. One was a confirmed fatality by ship collision, and three cases were probable collision victims as they were suspiciously found floating inside a port or in the general vicinity of a portarea (Dakhteh et al. 2017). In fact the Iraqi specimen, found near the port of Basrah, may well have died from a hit by a vessel. Globally, humpback whale, after fin whale, is the second-most commonly killed whale species by ship collisions (Van Waerebeek and Leaper, 2008) which for a remnant population as the ASHW is likely to be a significant factor. Some ship-stricken whales may have been killed considerable distances from the reporting location since they are often transported, wrapped around the ship's bulbous bow (Van Waerebeek and Leaper, 2008), therefore interpretation of the precise conflict area should be carefully evaluated. Other plausible threats in the Gulf and Arabian Sea may include bycatch and entanglement in fisheries (Dakhteh et al., 2017; Minton et al., 2022), organic (eutrophication) and chemical pollution and oil spills (e.g., Robineau and Fiquet, 1994; Preen, 2004; Shokat et al., 2010) as well as infectious diseases (e.g., Van Bressem et al., 2014; Minton et al., 2022). Systematic whale surveying linked to environmental data should shed light on the factors that make the Gulf a suitable long-term habitat, if not permanent residence, for humpback whales. This shallow sea apparently offers favourable feeding or reproductive conditions (i.e., avoiding calf predation by killer whales *Orcinus orca*), or both (Dakhteh et al., 2017).

Supplementary Materials: The following supporting information can be downloaded at: Preprints.org.

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