



# Taxonomic revision of the South Asian River dolphins (*Platanista*): Indus and Ganges River dolphins are separate species

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## Abstract

South Asian river dolphins (*Platanista gangetica*) are among the most endangered of the world's cetaceans. The two subspecies in the family Platanistidae, Indus, and Ganges river dolphins (*P. g. minor* and *P. g. gangetica*), are both threatened by dams and barrages, declining river flows, fisheries bycatch, and pollution. We examine differences in external and skull morphology between dolphins in each river system to clarify their taxonomic status. Skulls from each river system could easily be differentiated using diagnostic differences in the shape of the frontal bones behind the nasals. This feature was present in all individuals irrespective of size, age, and sex. Ganges river dolphins are sexually dimorphic with females larger than males, but there was no evidence of dimorphism in the small sample of Indus river dolphins. There were no mitochondrial DNA haplotypes shared between the two river systems, and five fixed differences suggested a long-term (approximately 0.55 million years) absence of gene flow. Diagnosable differences in morphological and genetic characteristics indicate long-term reproductive as well as geographic isolation of Indus and Ganges river dolphins. We conclude that Indus and Ganges

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river dolphins should each be recognized as distinct species, and elevate the Indus subspecies, *Platanista gangetica minor*, to species level, *Platanista minor* Owen, 1853. Formal re-descriptions are provided for both species.

#### KEYWORDS

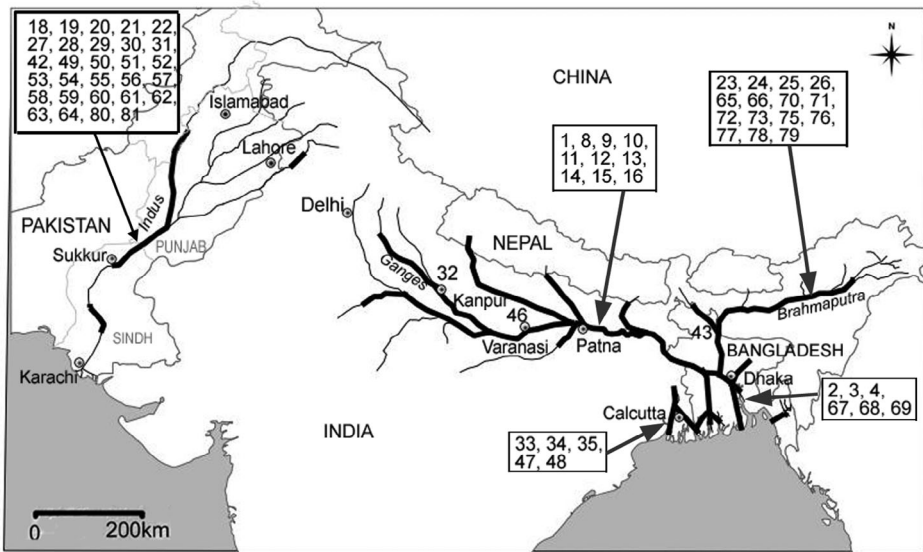
endangered species, river dolphins, speciation, taxonomy

## 1 | INTRODUCTION

The great challenge of gathering samples from species with vast, remote, and inaccessible geographic ranges, means that there are still significant knowledge gaps in cetacean taxonomy, and it is certain that numerous cetacean species and subspecies are still unrecognized to science. For example, it is estimated that at least 40 of the 90 recognized cetacean species have additional unnamed taxa (Taylor, Perrin, et al., 2017). Increased availability of molecular evidence to supplement more traditional morphological data has, in the last decade, resulted in a number of new species and subspecies being described or resurrected (e.g., Archer et al., 2019; Jefferson & Rosenbaum, 2014; Wada et al., 2003; Wang et al., 2008; Yamada et al., 2019), as well as to changes to high level cetacean systematics (Perrin et al., 2013; Vollmer et al., 2019) but there are still many taxonomic relationships that remain unresolved (Committee on Taxonomy, 2020). Among the Cetacea, one of the highest priorities for taxonomic research is the family Platanistidae, because of the high level of threat the animals face in the wild, and the possibility that there are additional species in the family which if not recognized might prevent them from receiving the conservation attention they warrant (Reeves et al., 2004; Taylor, Perrin, et al., 2017).

The dolphins inhabiting the Ganges River were named *Platanista* by Pliny the Elder in his *Historia Naturalis* published around 77 AD, meaning that this is one of the earliest cetaceans to be named. The Platanistidae (Wagler, 1830) are the only extant members of the superfamily Platanistoidea which was one of the earliest cetacean lineages to diverge (34–24 million years ago during the Oligocene), and previously included numerous species widely distributed across the world's oceans (de Muizon et al., 2018, Hamilton et al., 2001). Currently, only a single relict species in the family is recognized: the South Asian river dolphin *Platanista gangetica* (Lebeck, 1801). It is currently composed of two subspecies that occur in geographically separate, adjacent, freshwater river systems: the Indus river dolphin (*P. g. minor*), which is endemic to the Indus River system principally in Pakistan, and the Ganges river dolphin (*P. g. gangetica*), which inhabits only the Ganges-Brahmaputra-Meghna, and nearby Karnaphuli-Sangu River systems of Bangladesh, India, and Nepal (Figure 1). Indus and Ganges river dolphins each number only a few thousand individuals, have suffered extensive declines in distribution, and are both listed as Endangered on the IUCN Red List (Braulik et al., 2012; Smith et al., 2012). Perhaps because Indus and Ganges river dolphins look very different to most other dolphins, and are superficially similar to each other, they have in many previous works been treated as a single species, despite the fact that there was insufficient reliable scientific evidence on which to base any taxonomic classification (Rice, 1998). However, from the late 1970s until the late 1990s, Indus and Ganges river dolphins were classified as distinct species (*Platanista indi* and *Platanista gangetica*, respectively), but they were then downgraded to subspecies status due to a lack of rigor in the previous taxonomic studies which failed to present a strong case for species level differentiation (see Table 1 for a full history of the taxonomy of *Platanista*; Kasuya, 1972; Reeves & Brownell, 1989; Rice 1998).

Recent paleo-fluvial studies all agree that the Indus and the Ganges-Brahmaputra river systems have been entirely distinct, separate, and in approximately their current geographic locations, for around 45–55 million years, since the rise of the Himalayan mountains they drain (Burbank et al., 1993; Clift & Blusztajn, 2005). The dolphins occur only in fresh (and sometimes brackish) waters. The dispersal of animals between the respective river mouths around the Indian Peninsula would involve traversing approximately 4,600 km of marine waters and is highly



**FIGURE 1** The Indus, Ganges-Brahmaputra, and Karnaphuli-Sangu River systems in South Asia and the geographic origin of samples used in this study (numbers refer to skull ID numbers listed in Table SM1).

implausible for these obligate freshwater dolphins (Braulik, Barnett, et al., 2015). The two subspecies are thus completely geographically isolated within the separate river systems.

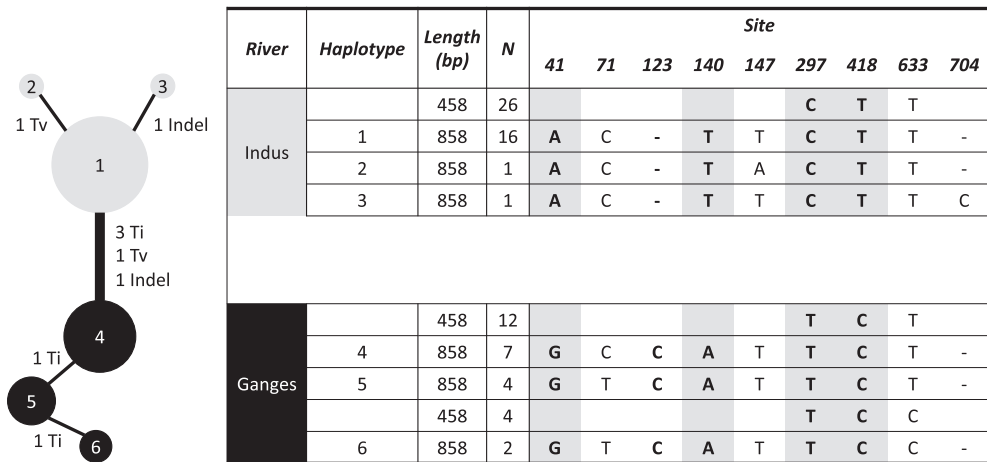
A recent genetic study found five fixed differences and no shared haplotypes between the 18 Indus and 13 Ganges complete (856 bp) mitochondrial DNA control region sequences examined (Figure 2; Braulik, Barnett, et al., 2015). An externally calibrated molecular clock estimated that Indus and Ganges river dolphins diverged around 550,000 years ago (95% posterior probability 0.13–1.05 million years ago). It was suggested that ancient *Platanista* relatives first colonized the larger Ganges basin, and subsequently dispersed into the Indus during one of the documented east to west river drainage capture events that occurred over the last million years (Braulik, Barnett, et al., 2015; Clift & Blusztajn, 2005). These results indicate an absence of gene flow and suggest that dolphins in the two river systems are reproductively isolated and on separate evolutionary trajectories (Braulik, Barnett, et al., 2015). If the long-term isolation and genetic difference suggested by the molecular study (Braulik, Barnett, et al., 2015) are such that Indus and Ganges river dolphins cannot effectively breed with one another, they likely have also developed diagnosable morphological differences indicative of species-level differentiation. Both morphological data and genetic data can be taken as proxies for reproductive isolation and irreversible divergence; a finding of congruent divergence for each distinct kind of data can be taken as strong support for species designations (Reeves et al., 2004).

Comparative studies of animals in the two river systems are complicated by the fact that they occur in neighboring countries separated by an unfriendly international border, with the result that there are very few scientists that have ever been able to observe both in the wild. Thus, sharing of samples or data between countries is extremely challenging. Dead animals are uncommon because they either float downstream, sink, or are buried quickly. Museum collections worldwide contain few specimens, most of which are damaged. For all these reasons, obtaining sufficient samples and data for taxonomic studies has been a challenge. In this study, we examined the largest compiled data set of external and cranial morphology to date, in conjunction with new analyses of published genetic data, and a survey of coloration patterns to evaluate the degree of differentiation between Indus and Ganges river dolphins with the ultimate aim to clarify the taxonomy of this ancient and highly endangered cetacean family.

**TABLE 1** Taxonomic history of the South Asian river dolphins, *Platanista* spp.

Year	River	Species	Subspecies	Notes	Reference
1801	Ganges	<i>Platanista gangetica</i>		Original description of Ganges River dolphin	Lebeck (1801); Roxburgh (1801)
1853	Indus			Mention of var. minor in the Indus River (discovered in 1976)	Owen (1853)
1859	Indus	<i>P. indi</i>		Original description of Indus River dolphin	Blyth (1859)
1879	Ganges	<i>P. gangetica</i>	<i>P. g. gangetica</i>	Based on external morphology, skull and skeletal morphology concluded that evidence did not allow identification of different species	Anderson (1879)
	Indus		<i>P. g. indi</i>		
Mid-1970s	Ganges	<i>P. gangetica</i>		Differences in nasal crests on the skull, the sixth and seventh cervical vertebrae, composition of blood proteins, the ratio of free-esterified cholesterol lipids in the blubber and in the length of the tail.	Pilleri (1971); Pilleri & Gühr (1971); Kasuya (1972); Pilleri & Gühr (1976); De Monte & Pilleri (1979); Pilleri et al. (1982)
	Indus	<i>P. indi</i>			
1976	Indus	<i>P. minor</i>		Earlier Indus description discovered	Owen (1853); van Bree (1976)
1998–present	Ganges	<i>P. gangetica</i>	<i>P. g. gangetica</i>	Small sample sizes, few adult specimens and no statistical analyses mean none of the earlier arguments were adequate to recognize two species	Reeves & Brownell (1989); Rice (1998)
	Indus		<i>P. g. minor</i>		

Note. Gray shading highlights the consensus on the correct taxonomic classification in each time period.



**FIGURE 2** Median-joining network and table of variable sites from complete mtDNA control region haplotypes for the cetacean family Platanistidae reproduced from Braulik, Barnett, et al., (2015) Figure 2 and Table 2. Values in circles correspond to the haplotype numbers for the 858 bp sequences in the table. Circle size is proportional to the number of individuals representing that haplotype ( $N$  in table). Values next to branches indicate the number of transitions (Ti), transversions (Tv), and indels between haplotypes. Rows in tables without haplotype numbers are for the three shorter 458 bp sequences (1 Indus, 2 Ganges haplotypes). Note that the total number of 858 bp sequences does not add up to the number of 458 bp sequences.

## 2 | METHODS

This study involves multiple analyses, some using subsets of the same or overlapping data sets. For clarity, Table 2 provides a summary of the number of samples according to river and sex used in each data set in the analyses described below.

### 2.1 | Body growth

Data on the total body length measured as a straight-line distance from the tip of the rostrum to the tail notch (centimeters), weight (kilograms) using a digital scale, and sex of *Platanista* were compiled from previously published reports (Herald et al., 1969; Kasuya, 1972; Pilleri, 1970; Sinha et al., 1993) and from stranded or rescued dolphins in India and Pakistan (data gathered by U.K., M.I., and R.K.S.). Those from the Indus come mostly from live animals rescued from irrigation canals, while those from the Ganges-Brahmaputra (referred to hereafter simply as “Ganges”) are mostly dead bycaught individuals. To examine possible differences in the pattern of growth of dolphins between river systems, we estimated asymptotic length (size at which growth is zero) by fitting a Bayesian von Bertalanffy growth model to the body length and weight data (Fabens, 1965; Siegfried & Sansó, 2006). The growth model was defined as:

$$\text{length} = L_{\text{asympt}} \left[ 1 - e^{-k(\text{weight} + x)} \right]$$

where  $L_{\text{asympt}}$  is asymptotic length,  $k$  is the growth rate, and  $x$  is a nuisance parameter defined as an offset used to estimate length when weight is zero. The prior for  $L_{\text{asympt}}$  was a Uniform distribution ranging from 1.1 times the minimum observed length to 1.5 times the maximum observed length. For  $k$ , an uninformative prior was given as a Uniform distribution ranging from 0 to 1, and for  $x$ , a Normal distribution with a mean of 0 and precision of 0.0001.

**TABLE 2** Sample sizes for each dataset in the study. Number of samples for males (M), females (F), and unknown sex (U) are listed separately where available.

Data set	Subset	Indus			Ganges			Total
		M	F	U	M	F	U	
Body length and weight		48	32		25	21		126
Skulls measured		8	9	12	22 (+1) <sup>a</sup>	10	13 (+5) <sup>a</sup>	80
Skulls with ages		6	8		15	7		36
Tooth counts <sup>b</sup>	GUTC	24			33			57
	GLTC	23			32			55
Multivariate (PCA and Random Forest) <sup>c</sup>	<i>AbsAll</i>	6	9	9	18	6	12	60
	<i>AbsAdult</i>	2	2	1	6	3	5	19
	<i>RatioAll</i>	7	9	9	19	6	12	62
	<i>RatioAdult</i>	2	2	1	6	3	5	19
	<i>CombAll</i>	6	9	9	18	6	12	60
	<i>CombAdult</i>	2	2	1	6	3	5	19
mtDNA <sup>b</sup>	458 bp	26			16			42
	858 bp	18			13			31
Coloration <sup>b</sup>		11			26			37

Note. GUTC = Greatest upper tooth count; GLTC = Greatest lower tooth count.

<sup>a</sup>One male and five unknown sex individuals were assigned to the Ganges based on the shape of the frontal suture.

<sup>b</sup>Values are for all sexes, not just males.

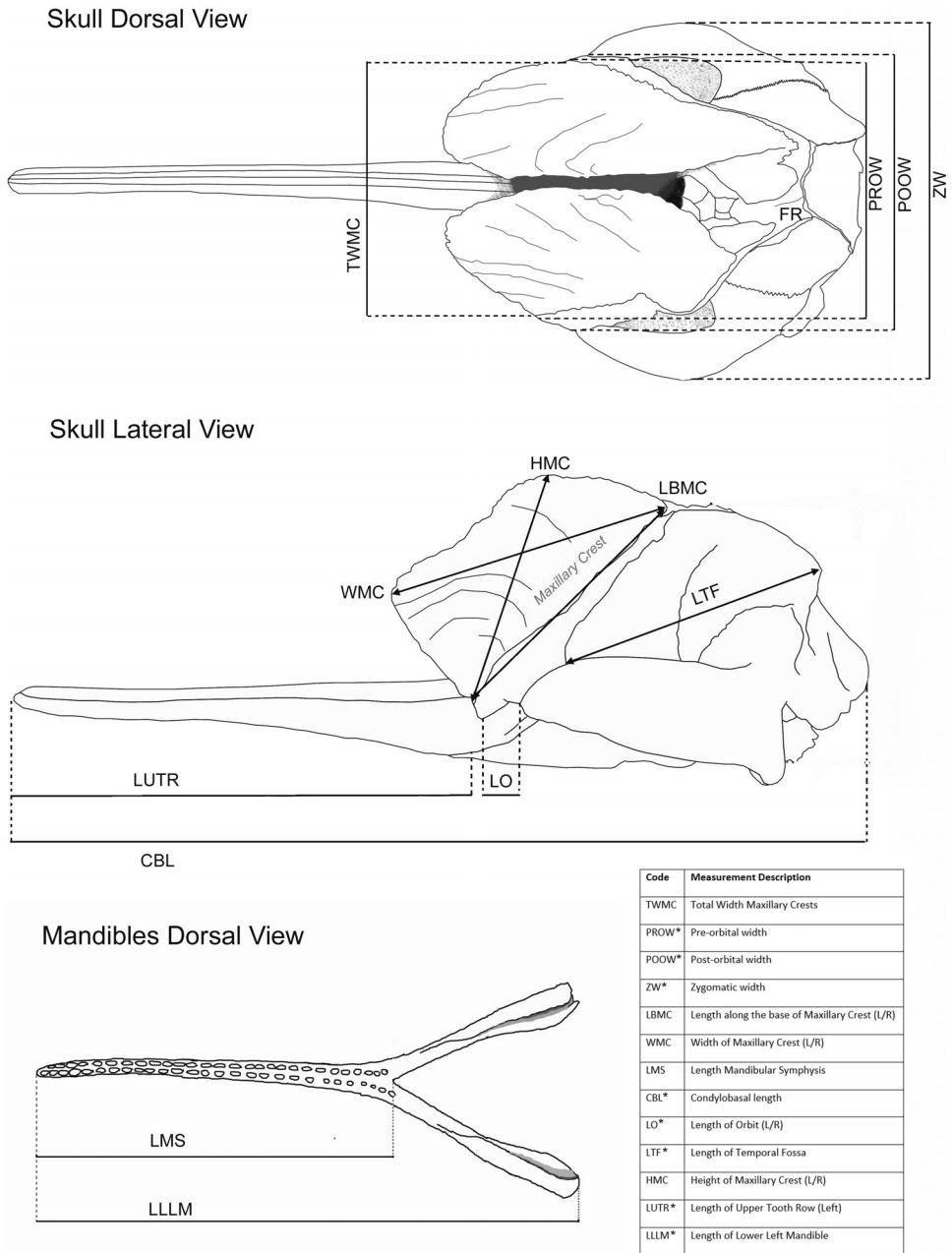
<sup>c</sup>Sample sizes from optimum IMDO data set.

Parameters were estimated for data from each river system and sex separately using the *rjags* package (Plummer, 2018) in R version 3.5.3 (R Core Team, 2019). Six independent chains were run for each model, with 10,000 adaptation iterations, 10,000 burn-in iterations, and 100,000 samples from the posterior taken, thinned every 100 samples, leaving a total of 1,000 samples for each posterior. We then created “delta” posteriors by subtracting the posterior samples of all pairs of treatments (river × sex) from each other. We highlight comparisons with notable differences between river systems or sexes, which we identify as those with delta posteriors with more than 95% of their mass greater or less than zero.

## 2.2 | Skull morphology

An extensive worldwide search was made to locate *Platanista* skeletal material. Specimens were located in international museum collections (principally in Stuttgart, Germany, Edinburgh, Scotland, and Tokyo, Japan) or were held at institutions in South Asia (Figure 1 and Table SM1). Where possible, each skull was identified as being from the Indus or Ganges river basins based on accompanying notes. If information regarding origin was lacking, or if it predated the partition of British India in 1947 and was identified only as from “India,” its river of origin was noted as unknown. Most of the specimens had no associated information on sex or total body length.

Eighteen standard measurements, which included a subset of those described by Perrin (1975) were taken for each skull with measuring calipers by G.B. (Figure 3). Measurements greater than 10 mm were taken to the nearest millimeter; those less than 10 mm to the nearest 0.5 mm. We measured the orbit on both the left and right sides of the skulls and calculated the ratio of the two (L<sub>Oratio</sub> = L<sub>LO</sub>/L<sub>RO</sub>). We also calculated the ratio of the upper tooth row to lower mandibular symphysis (L<sub>UTR.LMS</sub> = L<sub>UTR</sub>/L<sub>MS</sub>).



**FIGURE 3** Measurements taken from *Platanista* skulls.

Skulls from the family Platanistidae are notable for the presence of maxillary crests (MC) that extend forward in a cone obscuring the nasal area and making measurements of the nasals and other parts of the skull impossible. Where possible, we measured the height, width, and length at base (HMC, WMC, and LBMC in Figure 3) of maxillary crests on both the left (L) and right (R) sides of all skulls. We captured differences in the size, shape, and area of the maxillary crests, as well as differences between the left and right crests, which can be notable in these skulls, by computing the following eight values:

- $MCareaL$  &  $MCareaR$  ( $= WMC * HMC$ ): Area of the maxillary crests calculated separately for both the left and right crests.
- $WHMCratioL$  &  $WHMCratioR$  ( $= WMC/HMC$ ): Ratio of the width to the height of the maxillary crests calculated separately for both the left and right crests.
- $WMCratio$  ( $= WMCL/WMCR$ ): Ratio of the widths of the left and right maxillary crests.
- $HMCratio$  ( $= HMCL/HMCR$ ): Ratio of the heights of the left and right maxillary crests.
- $LBMCratio$  ( $= LBMCL/LBMCR$ ): Ratio of the base lengths of the left and right maxillary crests.
- $AreaRatio$  ( $= MCareaL/MCareaR$ ): Ratio of the left and right maxillary crest areas.

Preliminary analyses showed differences in patterns of growth for measurements along the length of the skull relative to those describing the width of the skull. Thus, to examine differences of measurements relative to overall skull size, we scaled 16 of the standard measurements: LUTR, LMS, and LLLM were scaled by dividing by CBL, while the other 13 were scaled by dividing by PROW, which was a width measurement with the least amount of missing data.

In this paper, we will refer to the 18 standard measurements in Figure 3 and the two computed measurements of the maxillary crest area ( $MCareaL$  and  $MCareaR$ ) as “absolute” measurements (20 in total). The 16 scaled measurements and remaining eight ratio values ( $LOratio$ , LUTR.LMS,  $WHMCratioL/R$ ,  $WMCratio$ ,  $HMCratio$ ,  $LBMCratio$ , and  $AreaRatio$ ) are referred to as “ratio” measurements (24 in total), giving a total of 44 measurements in the initial data set. Pairwise scatterplots of both absolute and ratio measurements were examined to identify outliers, which were recorded as missing values.

In addition to the 44 measurements above, following Jefferson and Van Waerebeek (2004) the number of teeth in the left and right tooth rows in each maxillary and lower mandible were counted, but only the largest of these counts were used in the analysis. Therefore, only the greatest upper (GUTC) and lower (GLTC) tooth counts were analyzed for each specimen.

Finally, it was noted that the morphology of the frontal suture behind the maxillary crests had one of two discrete states on every skull: flat or forward-protruding (Figure 4). Given that it was not possible to measure this feature using calipers because it was partially obscured by the maxillary crests and was curved in shape, we only recorded its status.

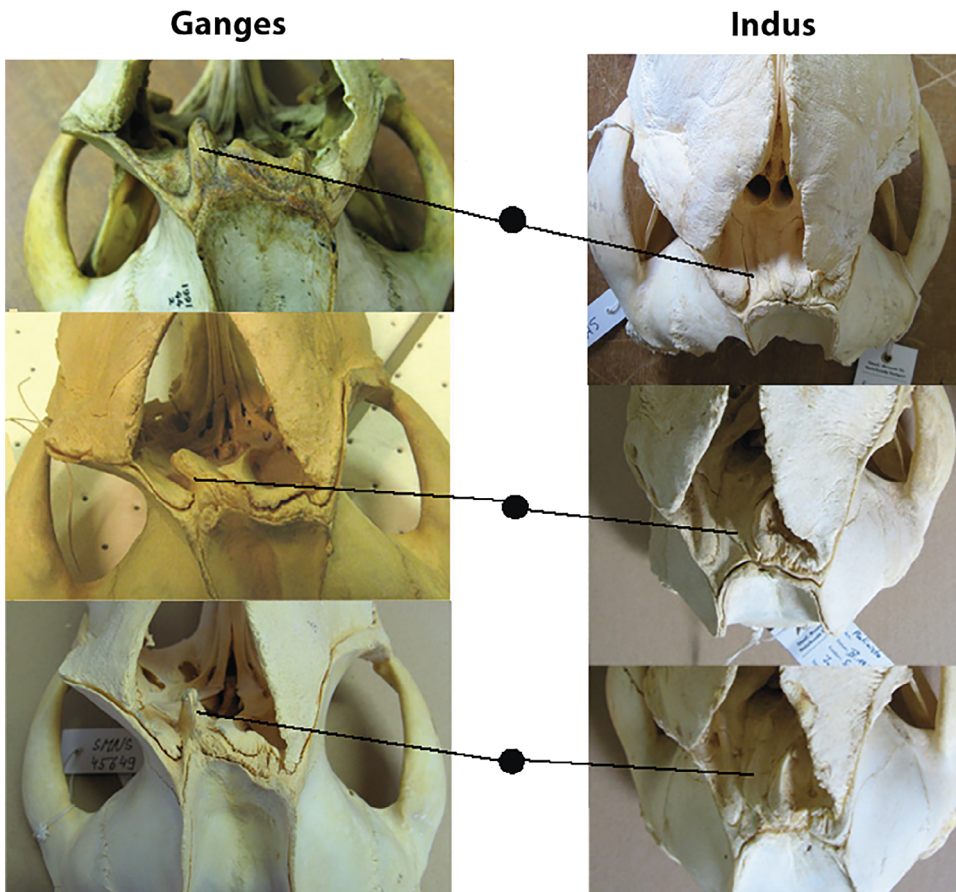
## 2.3 | Skull growth

Teeth from some of the skulls we measured had previously been aged by Jefferson, SWFSC, NOAA (unpublished), Kasuya (1972), or Lockyer and Braulik (2014). We estimated growth curves and asymptotic values for each of the 20 absolute measurements using a Bayesian von Bertalanffy growth model, constructed as for external morphology above, with age substituted for weight as the independent value, and the respective measurements substituted for length as dependent value. As above, growth parameters of each measurement were estimated for skulls from each river system and sex separately.

## 2.4 | Univariate morphometrics

As there are no known independent indicators of maturity in this family (e.g., fusion of the premaxillaries), we used the distribution of CBL and PROW relative to estimated age to identify the cutoff values above which, for the analysis, skulls would be considered as adult and below which they would be classified as immature and juvenile. First, we examined scatterplots of CBL relative to age, and PROW relative to age, and for each identified an approximate length above which most skulls appeared to be adult (Figure 5a and b). We then plotted CBL against PROW, which





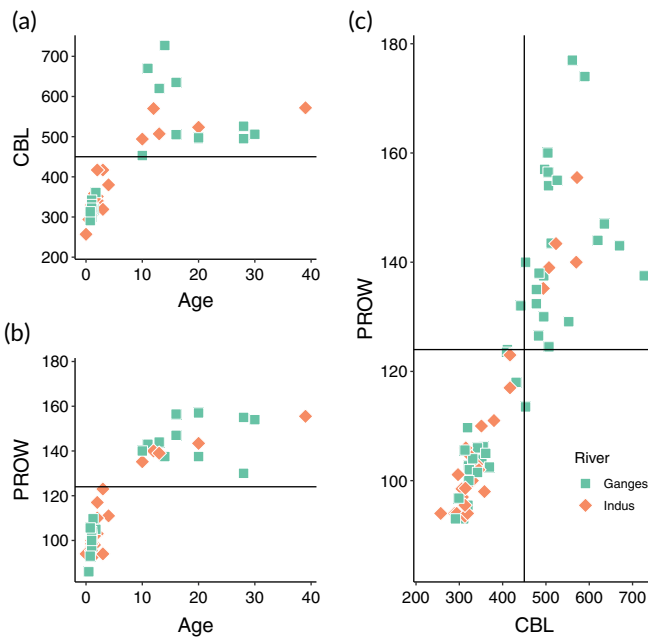
**FIGURE 4** Close up images of three skulls from the Ganges and three from the Indus illustrating the extension anteriorly and to the left of the frontal suture in Ganges River dolphins and how it differs clearly from animals in the Indus.

allowed the use of a larger data set of skulls (including those for which age was not available) to refine these values such that no skulls were classified as adult by only one of the two measurements. Because these two measurements are positively correlated, this equates to skulls falling in the upper-left or lower-right quadrants in a scatterplot (Figure 5c). This procedure maximized the number of skulls which could confidently be called adults based on both CBL and PROW.

There was a relatively small number of skulls from individuals with known sex in each river system. These were tested for univariate differences of the measurements between rivers with nonparametric Kolmogorov–Smirnov (KS) tests using the *ks.test* function in R (R Core Team, 2019), thereby avoiding distributional assumptions that are difficult to assess reliably on small samples.

## 2.5 | Tooth counts

To examine the ability to use tooth counts to assign skulls to river systems, we fit a simple Bayesian logistic model of the form:



**FIGURE 5** Distribution of (a) Condylolbasal length (CBL,  $n = 45$ ) relative to age, (b) pre-orbital width (PROW,  $n = 46$ ) relative to age, and (c) PROW vs. CBL ( $n = 71$ ) for Ganges (green squares) and Indus (orange diamonds) skulls. Note that (c) contains skulls without ages. Empirically derived cutoffs for adults are denoted by black lines:  $CBL \geq 450$  mm, and  $PROW \geq 124$  mm.

$$\Pr(\text{Indus}) = \frac{1}{1 + e^{w-T}}$$

Skulls from the Ganges and Indus rivers were coded as 0 or 1, respectively,  $w$  is the number of teeth when the probability that it was from the Indus,  $\Pr(\text{Indus}) = 0.5$ , and  $T$  is either the GUTC or GLTC tooth count. The model was also fit in *rjags* using a logit-link where  $\Pr(\text{Indus})$  was Bernoulli distributed, and a noninformative prior for  $w$  was drawn from a Uniform distribution ranging from the minimum to maximum observed number of teeth. The same number of chains, adaptation, burn-in, and sampling iterations were used as in the external morphology and skull growth models above.

## 2.6 | Multivariate morphometrics

Most multivariate analyses require complete suites of measurements (no missing data) for all cases in the analysis. In our data set, the condition of many of the skulls meant that not all measurements could be taken for most skulls. Therefore, to select an optimal data set for analysis maximizing the number of skulls representing each river system but also minimizing the number of measurements that had to be excluded from analyses, we developed the “Iterative Missing Data Optimization” (IMDO), procedure conducted as follows:

1. Create a data set of all skulls with complete data for all 44 absolute and ratio measurements and the two tooth counts. This data set is  $D_i$  where  $i$  is the current iteration. Thus, the first data set of skulls with complete data for all measurements is  $D_1$ .
2. The remainder of the skulls not in  $D_i$  which therefore had some missing values, comprise a second data set called  $D_{\text{missing}}$ .
3. Partition  $D_{\text{missing}}$  into groups of skulls, where each group has the same set of measurements missing.
4. Select the group of skulls from Step 3 (created from  $D_{\text{missing}}$ ) for inclusion in the analysis that has (in order of priority):

- a. skulls from both river systems,
  - b. skulls from the river system with the smallest sample size in  $D_i$ ,
  - c. the largest ratio of number of skulls to be included to the number of measurements to be excluded,
  - d. the largest mean maximum correlation coefficient of measurements to be excluded (measurements missing in the group) to measurements in  $D_i$ .
5. Add the group of skulls identified in Step 4 to  $D_i$  to make  $D_{i+1}$ .
  6. Remove the measurements that were missing in the group that got added in Step 5 from both  $D_{i+1}$  and  $D_{\text{missing}}$ .
  7. Repeat steps 3–6, incrementing  $i$  and stopping when no more skulls are in  $D_{\text{missing}}$  or  $D_i$  has only two measurements.

Of the  $D_i = 1 \dots n$  data sets from the  $n$  iterations of the above procedure, we identified the “optimal” data set ( $D_{\text{opt}}$ ) as the one that incorporated the largest number of skulls while retaining the largest number of measurements. This was done by plotting the number of skulls against the number of measurements for each data set, drawing a line from  $D_1$  to  $D_n$  and identifying the  $D_i$  that had the greatest perpendicular distance to this line (Figure SM1). We ran this procedure on data sets using absolute and ratio measurements separately as well as all measurements combined. Additionally, for each set of measurements, we used all skulls as well as the subset of skulls identified as adults using the CBL and PROW thresholds described above. Thus, we produced six  $D_{\text{opt}}$  data sets for the multivariate analyses described below, referred to as *AbsAll*, *AbsAdult*, *RatioAll*, *RatioAdult*, *CombAll*, and *CombAdult*.

A principal component analysis (PCA) was conducted separately on the optimal *AbsAll*, *AbsAdult*, *RatioAll*, and *RatioAdult* data sets using the *prcomp* function in R to identify sets of measurements responsible for variation in skull size and shape. Measurements were centered and scaled to have unit variance. We conducted nonparametric Kolmogorov–Smirnov tests of differentiation on all component scores to identify components that differed between river systems.

We conducted a Random Forest analysis on the optimal *CombAll* and *CombAdult* data sets to quantify the diagnosability of skulls in each river basin using all of the measurements. One feature of Random Forest models is the ability to quantify the importance of measurements to the classification performance of the model. This is achieved by computing the Mean Decrease in Accuracy (MDA) of each measurement via a permutation procedure (Liaw & Wiener, 2002). The removal of a measurement with low MDA is not expected to significantly affect the classification ability of the model, however, given the distribution of missing data in our data set, its removal may permit the addition of other skulls which would increase the stability of the model. To examine this effect, we conducted a series of stepwise Random Forest analyses, where we started with the optimal *CombAll* and *CombAdult* data sets generated in IMDO, and then sequentially removed measurements with the lowest MDA while adding skulls that would then have complete data with these measurements removed. We stopped when there were only two measurements remaining in the Random Forest analysis. We selected the optimal model to be the one that had the largest classification accuracy, breaking ties by selecting the one with the largest number of skulls, then the one with the fewest measurements.

All Random Forest models were balanced by selecting the same number of individuals for each tree (half of the smallest sample size) to avoid bias from unequal sample sizes (Archer, Martien, & Taylor, 2017). Models were run using the *randomForest* package (Liaw & Wiener, 2002) in R, with a total of 10,000 trees grown for each forest. Statistical significance of MDA importance scores for the optimal model was computed with the *rfPermute* package from 1,000 replicates (Archer, 2018).

## 2.7 | mtDNA analysis

Based on analyses of empirical cetacean data sets, Martien et al., (2017) and Taylor, Archer, et al., (2017) recommend computing Nei's net nucleotide diversity ( $d_A$ ) and diagnosability to evaluate the taxonomic status of putative

cetacean subspecies or species using mitochondrial control region sequences. We computed these values for the 459 bp ( $n = 42$ ), and 859 bp ( $n = 31$ ), *Platanista* control region sequences published in Braulik, Barnett, et al., (2015).  $d_A$  was calculated with the Tamura-Nei substitution model using the *strataG* package (Archer, Adams, & Schneiders 2017) in R. Tamura-Nei was chosen as the optimal model with jModelTest2 (Darriba et al., 2012). Diagnosability was calculated following Archer, Martien, and Taylor (2017) using the *randomForest* package (Liaw & Wiener, 2002).

## 2.8 | Coloration

Indus and Ganges river dolphins are a relatively uniform light brown/gray color and in field identification guides are typically depicted as having identical coloration. Field observations and photographs suggest that there may be some differences in the color hue between the animals from each river system, however, evaluating these subtle differences empirically is challenging since it is not possible to view carcasses side by side and photographs can have variable exposure and lighting, or can be altered digitally, and color can be misleading. Therefore, we solicited expert opinion regarding the color of dolphins in each river system by developing a very simple digital questionnaire to ask those experienced with observing them in the wild what color most accurately described them. Recipients were first asked whether they were “very familiar” observing Indus and/or Ganges river dolphins in the wild. If they were not very familiar no more questions were asked. If the answer was positive, they were then asked to choose from the following list the color that best described the dolphins from the river system where they work: (1) gray, (2) grayish brown (more gray than brown), (3) brownish gray (more brown than gray), (4) brown, or (5) other - describe. A final question asked which specific location within the range of the dolphin they had experience working (e.g., Nepal, Bangladesh, India, Brahmaputra River, Ganges River, Sundarbans, etc.).

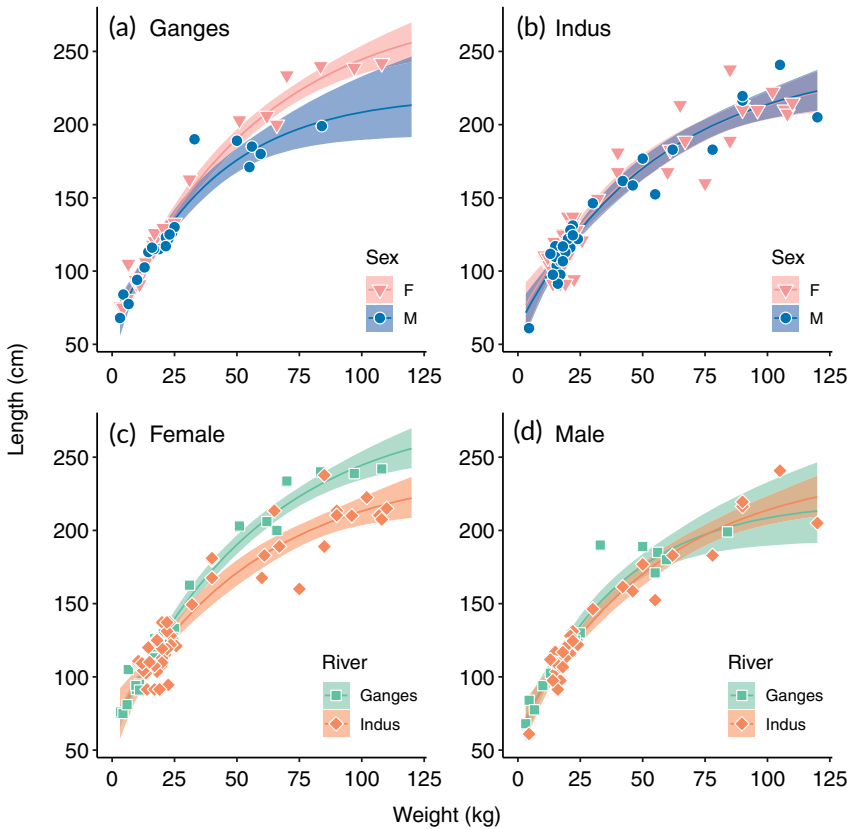
## 3 | RESULTS

### 3.1 | Body size and growth

Data on body length, weight and sex were available for a total of 126 individuals, comprising 80 from the Indus (48 females, 32 males) and 46 from the Ganges (25 females, 21 males). The longest Ganges river dolphin recorded was a 267 cm long female (no weight was recorded for this animal), while the heaviest Ganges female weighed 108 kg and was 242 cm in length. The heaviest Indus river dolphin was a 120 kg male, while the longest Indus river dolphin was a 241 cm male. The smallest Ganges river dolphin was a 68 cm long male, and the smallest Indus river dolphin was a male 61 cm in length. The results of the Bayesian growth model indicate that Ganges females have asymptotic lengths approximately 60 cm longer than Ganges males (Figure 6 and Table SM2). Ganges females were also approximately 40 cm longer than both Indus females and Indus males,  $\text{Pr}(\delta > 0) = 0.89$  and  $0.91$ , respectively, while Ganges males were approximately 22 cm shorter than Indus males and females,  $\text{Pr}(\delta > 0) = 0.23$ . We found no significant difference in the estimated asymptotic length between Indus males and females,  $\text{Pr}(\delta > 0) = 0.49$ . The growth curves also demonstrate that Indus individuals are on average heavier than Ganges animals of equivalent length, irrespective of sex.

### 3.2 | Skull morphology

A total of 80 *Platanista* skulls were measured: 29 from the Indus, 45 from the Ganges and six of unknown origin. Sex was unknown for 30, 19 were labeled as females (9 Indus, 10 Ganges) and 31 as males (8 Indus, 22 Ganges, 1 unknown origin). The six skulls of unknown origin were sampled by Braulik, Barnett, et al. (2015) for genetic



**FIGURE 6** Von Bertalanffy growth curves of external length (cm) relative to body weight (kg) for specimens of *Platanista* spp ( $n = 126$ ). Top row shows fits of curves by sex within each river system, while bottom row show fits of curves by river system for each sex. Solid lines are the median of the Bayesian posterior, while shaded polygons give the 95% credible interval.

analysis; however, they were all originally collected in the 1800s, and insufficient DNA was obtained to permit genetic identification to the river system.

The most notable feature of the *Platanista* skulls was the shape of the frontal bones above the nasals and behind the maxillary crests (Figure 4). In all 45 skulls from the Ganges, the frontal suture above the nasals extends forward and to the left in a clear protuberance up to 20 mm in length, while in the 29 skulls from the Indus, the frontal suture was flat, or almost completely flat. This difference was clearly observable by eye and was found in every skull irrespective of age and sex.

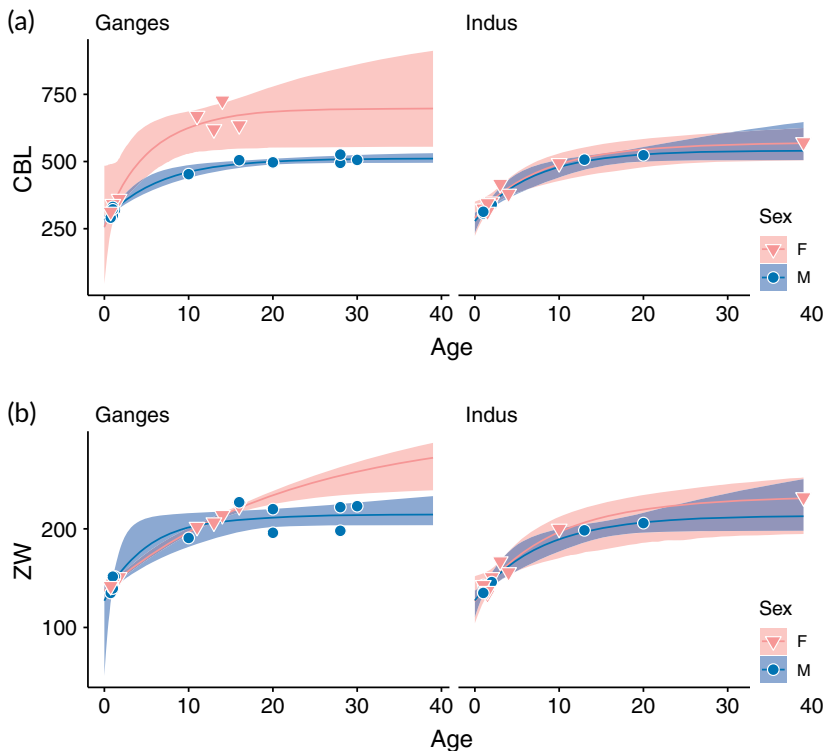
All six skulls of unknown origin (1 male, 5 sex unknown) had a protruding frontal suture. Because the morphology of this feature was diagnostic for all skulls for which the river system of origin was known, we used this to assign the unknown skulls to the Ganges, increasing the sample size from this river system to 51. One skull of unknown sex from the Indus (P18) was identified as having unusually large measurements, particularly those related to skull width. The analysis could not verify if these measurements were erroneous, resulted from issues of preservation or preparation, or if the skull had some other unusual morphology. Thus, to be conservative, we treated this skull as an outlier and removed it from further analyses, leaving 28 skulls from this river system, and a total of 79 skulls across both river systems with usable measurements.

A second skull, a male Ganges river dolphin, (P65) had a relatively large maxillary crest, so we set the seven measurements related to this feature (WMCL/R, HMCL/R, LBMCL/R, and WMC) to missing for this skull to remove its

effects as an outlier. Additionally, three skulls from the Ganges (P02, P14, P46) and one from the Indus (P55) had an unusually long or short ratio of LUTR in comparison to LMS. Other key measurements in these skulls, such as CBL and ZW, were within the distribution of the other skulls, so LUTR and LMS were set to missing for these skulls under the suspicion that they were erroneously recorded or were not representative of the population at large.

### 3.3 | Skull growth

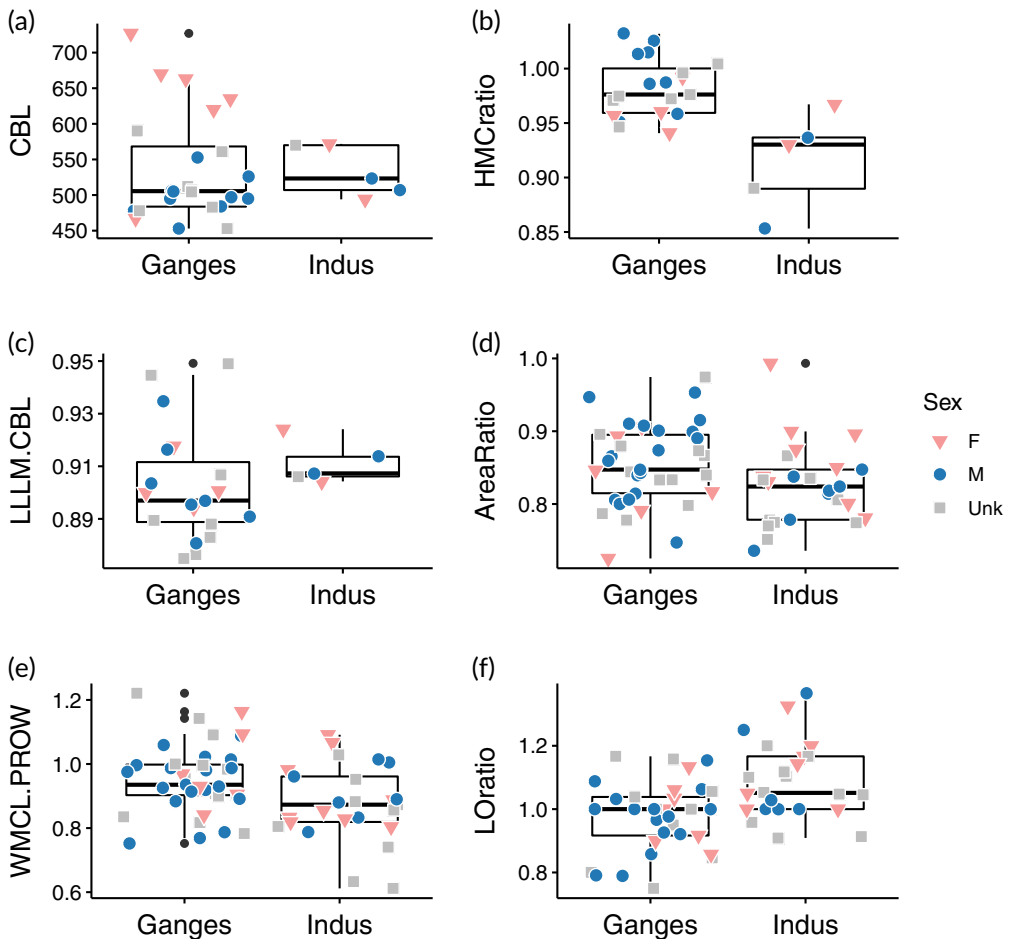
Ages were available for 14 Indus (8 females, 6 males) and 22 Ganges (7 females, 15 males) skulls. Estimated ages ranged from less than 1 to 39 growth layer groups (1 GLG is assumed to equal 1 year). Table SM3 gives the distribution of sample sizes and summarizes the asymptotic length posterior from each of the 18 growth models. Given the small number of skulls from old individuals of both sexes, there was large uncertainty around parameter estimates for many measurements. Nonetheless, as in the external morphology growth models, there was strong evidence of sexual dimorphism in Ganges skulls, with females estimated to have larger asymptotic values for CBL, LLLM, LMS, LUTR, and ZW than males (Figure 7 and Table SM3). The first four of these measurements describe features involving the length of the skull, in particular the rostrum, and were on average 185 mm longer in females. Conversely, there was no difference in the asymptotic length of any measurements between sexes for skulls from the Indus. Although Ganges females had substantially longer asymptotic skull lengths than Indus males, Ganges males had smaller asymptotic values than Indus males for all measurements except length of the orbits (LLO and LRO). For measures along the length of the skull, the average median difference between Ganges and Indus males was 55 mm.



**FIGURE 7** Von Bertalanffy growth curves of (a) condylobasal length (CBL) and (b) zygomatic width (ZW) relative to age for *Platanista* spp. skulls ( $n = 35$ ). Curves are plotted for female (pink triangles) and male (blue dots) skulls separately. Solid lines are the median of the Bayesian posterior, while shaded area gives the 95% credible interval.

### 3.4 | Univariate morphometrics

Based on the distributions of skull length and width on age, we designated skulls with  $CBL \geq 450$  mm, or  $PROW \geq 124$  mm if  $CBL$  was unavailable, as adults, which corresponded to animals approximately 10 years of age or older (Figure 5). Under these criteria, there were 25 adult Ganges skulls (6 females, 10 males, 9 unknown sex) and five adult Indus skulls (2 females, 2 males, and 1 unknown sex). A summary of measurements for adult skulls by river and sex is given in Table SM4. The sexual dimorphism seen in the skull growth models for Ganges river dolphins is evident in the adult distributions of  $CBL$ ,  $LUTR$ ,  $LMS$ , and  $LLLM$ , where the same five female Ganges river dolphins are consistently larger than males from the same river (Figure 8a). The fact that the dimorphism is also present in the ratio measures  $LUTR.CBL$  and  $LMS.CBL$ , but not in  $LLLM.CBL$  or in  $LUTR.LMS$  indicates that it is just the rostrum that grows to proportionately greater lengths in Ganges females, rather than the entire skull.



**FIGURE 8** Comparison of skull measurement distributions from the two river systems for (a) Condylbasal length ( $CBL$ ), (b) ratio of heights of the left and right maxillary crests ( $HMCratio$ ), (c) ratio of the length of the lower mandible to the condylbasal length ( $LLLM.CBL$ ), (d) ratio of the area of the left and right maxillary crests ( $AreaRatio$ ), (e) ratio of the width of the left maxillary crest to preorbital width ( $WMCL.PROW$ ), and (f) ratio of the left and right orbital length ( $LOratio$ ). Plots for  $CBL$ ,  $HMCratio$ , and  $LLLM.CBL$  show adult skulls, while those for  $AreaRatio$ ,  $WMCL.PROW$ , and  $LOratio$  show all skulls. Sample sizes for each measurement are provided in Table SM4.

We tested differentiation of both absolute and ratio measurements for adult skulls with all sexes and unknown sex animals combined (Table SM4). We did not test for differentiation between adult skulls by sex given the small number of adult Indus skulls. We found no significant difference ( $KS p < .05$ ) among the river systems for any of the 20 absolute measurements in the subset of 30 adult skulls. However, Ganges river dolphins had a significantly higher left maxillary crest relative to the right crest (HMCratio) compared to the Indus river dolphin, which might indicate less skew in the skulls from the Ganges (Figure 8b). Additionally, the ratio of the length of the lower left mandible to condylobasal length (LLM.CBL) was significantly different between rivers (Figure 8c) as was the ratio of the maximum height of the mandible to the preorbital width (HM.PROW). However, the difference between medians of both these latter values was relatively small.

We also tested differentiation of ratio measurements for all skulls (both adults and immature) with sexes and unknown sex animals combined and sexes separately (Table SM4). As reported above, ratios related to sexual dimorphism in the length of the skull (LUTR.CBL, LLLM.CBL, and LUTR.LMS) showed significant differentiation between rivers. Two of these (LUTR.CBL and LUTR.LMS) were the only ratios found to be significantly different between river systems for the subset of female skulls. Additionally, several ratios involving the size of the maxillary crests were significantly different (Table SM4). In particular, HMCratio and AreaRatio were significantly greater in Ganges skulls than Indus skulls, and were in fact also significantly different between Indus and Ganges male skulls alone (Figure 8d). This indicates that there is more asymmetry in the size of Indus maxillary crests (left smaller than right) than in the Ganges, where they tend to be more evenly sized. The ratio measurements TWMC.PROW, WMCL.PROW, and WMCR.PROW were also significantly greater in the Ganges skulls, which indicates that each maxillary crest was generally rounder in shape on the Indus river dolphin, compared to the more elongated oval crests on the Ganges river dolphin (Figure 8e). This difference in asymmetry seen in the maxillary crests was reversed in the length of the orbit ratio (LORatio), which was significantly smaller for Ganges skulls than Indus skulls (Figure 8f). Finally, the length of the temporal fossa as a proportion of preorbital width (LTF.PROW) was significantly greater in Ganges skulls than in Indus skulls.

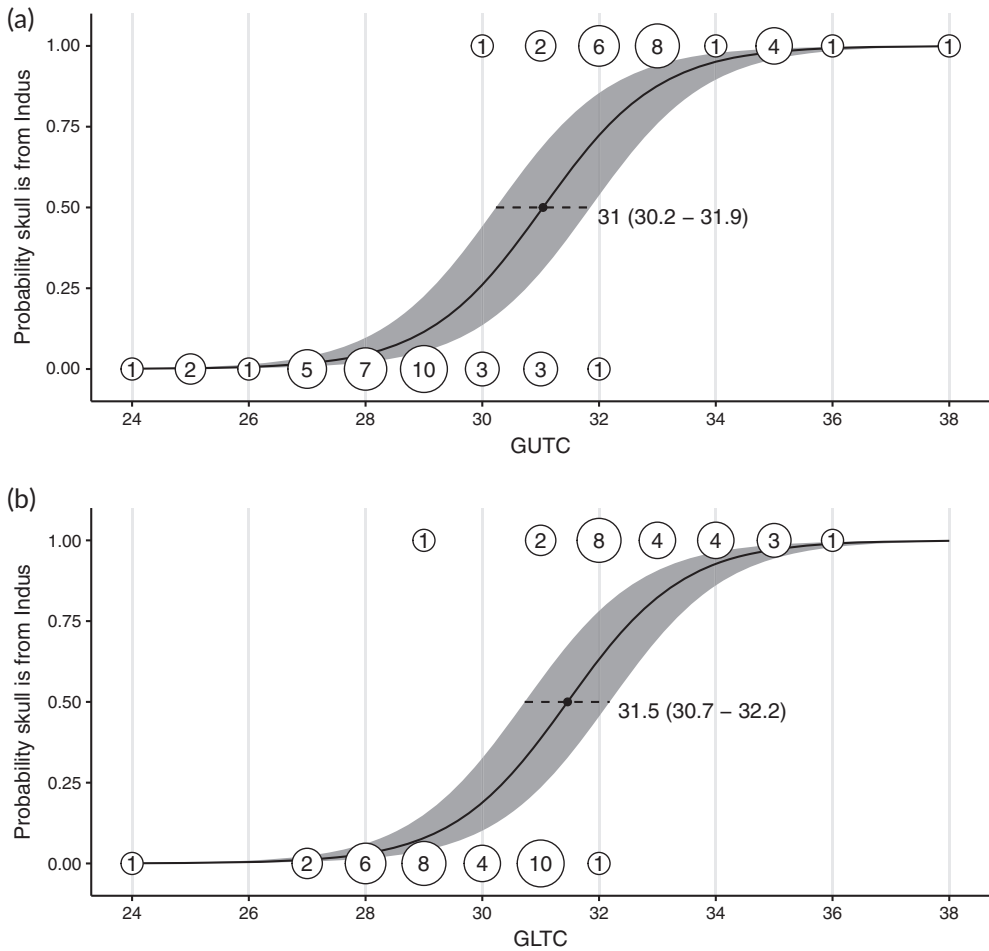
### 3.5 | Tooth counts

Indus specimens have on average five more teeth than those from the Ganges in each of the upper and lower tooth rows. Indus skulls have an average of 33.2 teeth in the upper tooth row and 32.9 in the lower tooth row, whereas those from the Ganges have on average 28.4 in the upper tooth row and 29.4 in the lower tooth row (Table 3). Additionally, while Indus river dolphins tended to have an equal number of teeth in the upper and lower tooth rows, Ganges river dolphins tended to have one more tooth in the lower tooth row. The differences between river systems in tooth counts and the difference between the upper and lower tooth rows were consistent across both sexes and all

**TABLE 3** Summary and Kolmogorof-Smirnov  $p$ -value for tests of differentiation for greater upper tooth count (GUTC), greater lower tooth count (GLTC), and tooth count difference (TCdiff). Shown is sample size (top), mean and standard deviation (middle), and median with 95% credibility interval (bottom) for each measure.

Measurement	Ganges	Indus	Median difference	KS $p$ -value
GUTC	33 28.4 (1.8) 29 (24.8–31.2)	24 33.2 (1.79) 33 (30.6–36.9)	–4	<.01
GLTC	32 29.4 (1.68) 29 (26.3–31.2)	23 32.9 (1.6) 33 (30.1–35.5)	–4	<.01
TCdiff	28 – 1 (1.43) – 1 (–3.3–1.3)	23 0.4 (1.31) 0 (–1.4–3)	–1	.1





**FIGURE 9** Logistic curves showing the ability of greatest upper tooth count (GUTC) (upper plot) and greatest lower tooth count (GLTC) (lower plot) to predict which river system the skull originated from. Where  $\text{Pr}(\text{Indus}) = 0$  the skull is from the Ganges and where  $\text{Pr}(\text{Indus}) = 1$  it is from the Indus. Numbers in circles indicate the number of skulls with each tooth count, and circles are scaled to sample size. Solid lines are the median of the Bayesian posterior, while shaded polygons give the 95% credible interval. Black dot indicates median tooth count at  $\text{Pr}(\text{Indus}) = 0.5$  from the Bayesian posterior, with dashed line indicating central 95% of posterior at  $\text{Pr}(\text{Indus}) = 0.5$ .

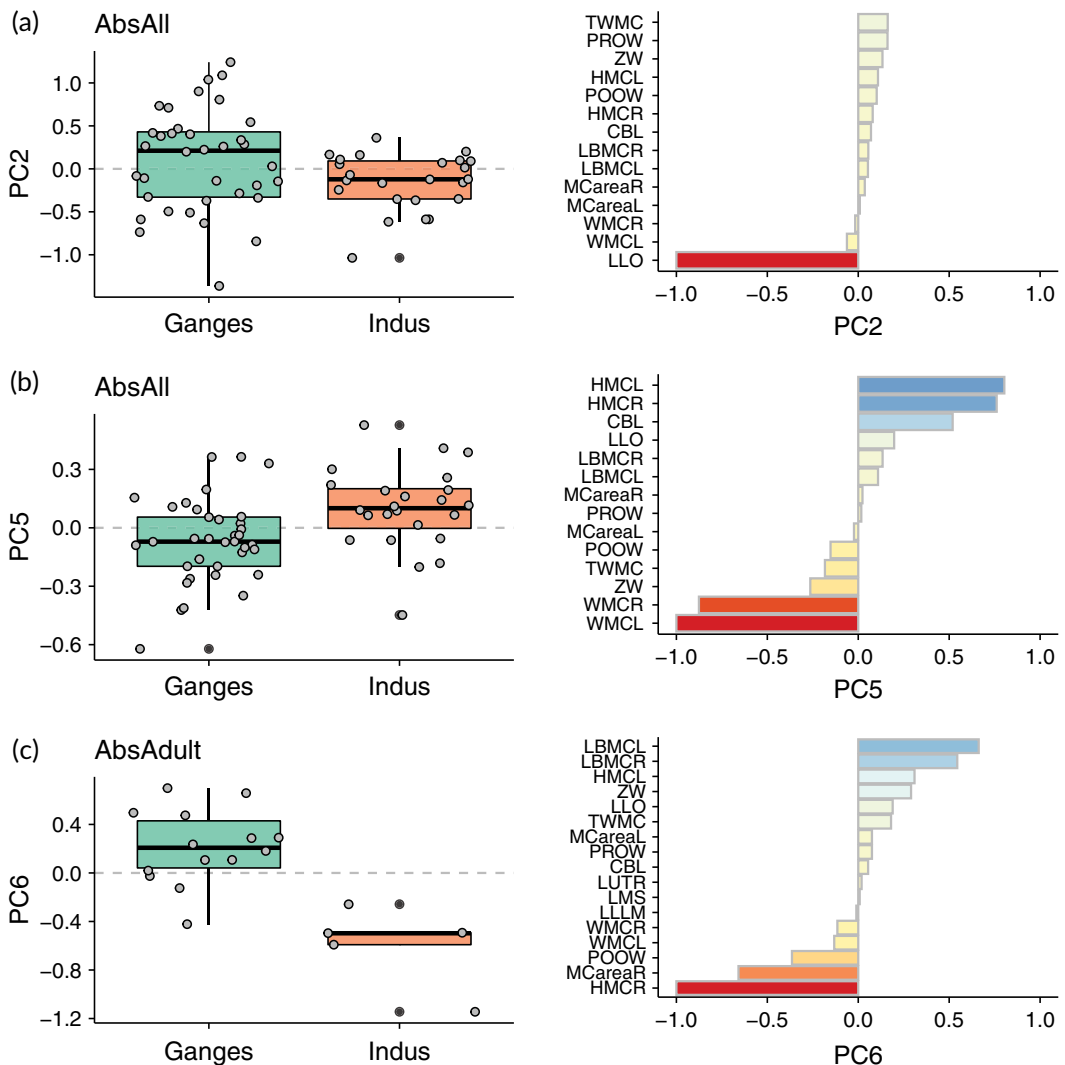
ages and skull sizes. There was a zone of overlap in upper tooth counts from 30 to 32 teeth, which included nine Indus river dolphin skulls, and seven Ganges river dolphin skulls and corresponded to approximately 28% of the total sample (Figure 9). The Bayesian logistic model estimated a threshold value between the river systems of approximately 31 teeth for both upper and lower tooth counts (Figure 9). When this threshold was used to classify skulls, only one out of 33 (3%) Ganges skulls and three out of 24 (12%) Indus skulls were misclassified for both GUTC and GLTC making for a total of about 92% correctly classified.

### 3.6 | Multivariate morphometrics

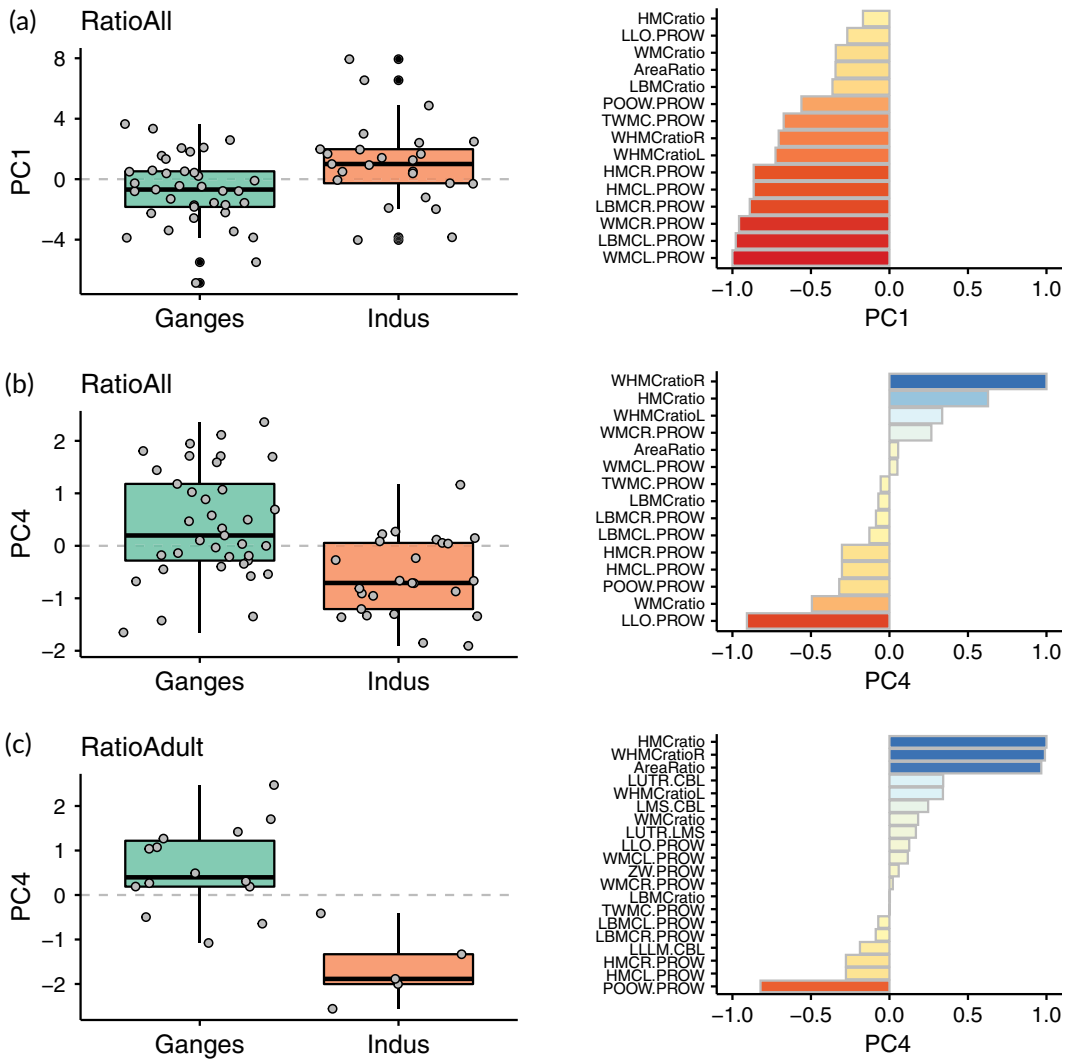
Of the 18 initial measurements collected (Figure 3), an average of 2.4 (range = 0–16) were missing for each skull. We used the iterative missing data optimization (IMDO) procedure described above to compile six optimal complete data

sets ( $D_{opt}$ ) for the multivariate PCA and Random Forest models, representing all skulls as well as the subset identified as adults for absolute, ratio, and a combination of all measurements (Figure SM1 and Table SM5). The three optimal data sets for all skulls (*AbsAll*, *RatioAll*, *CombAll*) were composed of 60–62 individuals, while those for adult skulls (*AbsAdult*, *RatioAdult*, *CombAdult*) contained 19 individuals.

In the PCA of *AbsAll*, the first two components accounted for approximately 96% of the variation in the measurements (Figure SM2a and Table SM6). As normal in a PCA on absolute measurements, the first component described variation in overall skull size, but there was no significant differentiation of the river basins on this component. The second component was primarily defined by large negative loadings of the left orbit (LLO). The Kolmogorov–Smirnov (KS) test indicated significant differentiation ( $p = .003$ ) between the rivers for this component, with skulls from the Indus having slightly more negative scores on average (larger orbital measurements) than those from the Ganges (Figure 10a). There was also significant differentiation between river systems on the fifth



**FIGURE 10** PCA axes with significant ( $p < .05$ ) differences in Kolmogorov–Smirnov tests between river systems for absolute measurements. Left panel for each component shows scores of skulls for each river system. Right panel shows loading of measurements on the component ordered from greatest at top to least on the bottom.



**FIGURE 11** PCA axes with significant ( $p < .05$ ) differences in Kolmogorov–Smirnov tests between river systems for ratio measurements. Left panel for each component shows scores of skulls for each river system. Right panel shows loading of measurements on the component ordered from greatest at top to least on the bottom.

component (KS  $p = .001$ , accounting for 0.4% of the variance, Figure 10b), which was a contrast between the height and width of the maxillary crests (HMCL and HMCR vs. WMCL and WMCR), with skulls from the Indus tending to have higher crests relative to their width than those from the Ganges.

When only adult skulls were examined in the PCA of *AbsAdult*, the first two components accounted for approximately 86% of the variation in the measurements (Figure SM2b and Table SM7). Again, the first component described variation in overall skull size, while the second component primarily described variation in the length of the skull (LMS, LUTR, CBL, and LLLM) influenced principally by the three Ganges females with extremely long skulls. However, skulls from the two river systems did not show significant differentiation on either of these components in the KS tests. For this data set, only the sixth component, which explained 1.3% of the variance, showed significant differentiation ( $p = .001$ ) between river systems (Figure 10c). This component was defined as a contrast between measurements of the right and left maxillary crests (HMCR and MCareaR vs. LBMCL and HMCL). Indus skulls were significantly larger for the right crest measurements, while Ganges skulls were larger for the left measurements.

Data set	Original river	Classified river		% Correct (95% CI)
		Ganges	Indus	
All	Ganges	31	5	86.1 (70.5–95.3)
	Indus	5	19	79.2 (57.8–92.9)
	Overall			83.3 (71.5–91.7)
Adults	Ganges	12	3	80 (51.9–95.7)
	Indus	1	4	80 (28.4–99.5)
	Overall			80 (56.3–94.3)

**TABLE 4** Confusion matrices from Random Forest classification models. Values in final column show actual percent correctly classified with 95% confidence intervals from binomial distribution in parentheses.

**TABLE 5** Summary of mitochondrial control region sequences.

Sequence length	# Individuals	# Haplotypes	$d_A$	Variable sites	Fixed differences	Percent diagnosable
458	42	3	0.00452	3	2	100
858	31	6	0.005016	7	5	100

Of the 24 ratio measurements, 15 were selected in the optimal *RatioAll* data set (Table SM5). Of these, 13 were related to the maxillary crests, while the other two were the length of the left orbit and postorbital width scaled to the preorbital width (LLO.PROW and POOW.PROW). In the PCA of this data set, the first two components accounted for 65% of the variance (Figure SM2c and Table SM8). There was significant differentiation of scores between river systems on the first component ( $KS\ p = .024$ ), which had high negative loadings of the six scaled measurements of the maxillary crest (Figure 11a). The lower scores of Ganges skulls on this component relative to those from the Indus indicated that they tended to have larger maxillary crests relative to skull width. The only other component that showed significant differentiation ( $KS\ p = .0007$ ) was the fourth (Figure 11b), which accounted for 7% of the variance and was primarily a contrast between the scaled length of the left orbit (LLO.PROW) and the ratio of the width to the height of the right maxillary crest (WHMCratioR). On this component, Ganges skulls tended to have larger values of WHMCratioR relative to LLO.PROW, while the reverse was true for Indus skulls. The PCA of ratio measurements for adult skulls (*RatioAdult*) showed roughly similar patterns across components as in *RatioAll* (Figure SM2d and Table SM9). In this analysis, the fourth component, accounting for 9% of the variance was also significantly different between river systems (Figure 11c). On this component, Ganges skulls had larger values of HMCratio, WHMCratioR, and AreaRatio relative to POOW.PROW.

The optimal Random Forest classification model could correctly classify 83% of all skulls and 80% of adult skulls using the *CombAll* and *CombAdult* data sets (Table 4). In the *CombAll* model, the predictors that had a significant (permutation  $p \leq .05$ ) MDA importance score were (in order of decreasing importance) LLO.PROW, WHMCratioR, TWMC.PROW, WMCL.PROW, HMCratio, and LLO. For the optimal model on *CombAdult*, only HMCratio, LLLM, CBL, and WMCL.PROW were selected and had significant MDA importance. As a test, we also added GUTC and GLTC to the data sets (removing skulls for which they were missing) and reran the stepwise Random Forest analysis. These tooth counts were consistently chosen as the most significant of all predictors, and their addition improved classification scores by approximately 10%, to about 90% overall, which was similar to the results of the logistic model on tooth counts alone.

### 3.7 | Genetics

As reported in Braulik, Barnett, et al., (2015), there were no shared mtDNA haplotypes between sequences from the Ganges and Indus, two fixed differences in the 458 bp data set ( $n = 42$ ), and five fixed differences in the 858 bp data

set ( $n = 31$ ) (Figure 2). Thus, all sequences could be correctly assigned to river system, producing a diagnosability of 100%. Nei's net divergence ( $d_A$ ) between Ganges and Indus samples for the 459 bp and 859 bp mtDNA control region data sets was 0.0045 and 0.0050, respectively (Table 5).

### 3.8 | Coloration

The questionnaire was directly emailed to 42 people known to currently work on, or to have recently (within the last 5 years) worked on South Asian river dolphins. We received 33 responses; 26 recipients asserted that they were "very familiar" observing Ganges river dolphins in the wild and 11 claimed to be "very familiar" observing Indus river dolphins in the wild; only four people were familiar with both. Eighty-eight percent of respondents (23/26) classified Ganges river dolphins as either gray, or grayish brown in color. The category selected with highest frequency was pure gray, representing 58% of all responses. Nobody classified Ganges river dolphins as purely brown. Responses for the Indus river dolphin were more mixed and included all four color categories, but the most frequent two selections, each with an equal number of responses, were "brownish gray" and "grayish brown." These options combined accounted for 73% (8/11) of responses. Several respondents from both rivers noted that there was often a pinkish hue to animals, especially on the underside (this is common in many cetacean species that live in warm waters and is due to flushing of blood to the body surface during thermoregulation) and also that color may change a little with age.

## 4 | DISCUSSION

The results of our morphometric and genetic analyses strongly support the presence of two clearly distinct forms of South Asian river dolphins. Currently, these two are recognized as subspecies (*P. gangetica minor* and *P. gangetica gangetica*; Committee on Taxonomy, 2020). However, the evidence from our results, in conjunction with other published studies (Braulik, Barnett, et al., 2015; De Monte & Pilleri, 1979; Kasuya 1972; Pilleri & Gehr, 1971; Pilleri & Gehr, 1976), suggests that they should more appropriately be considered full species.

It is well recognized that taxonomy is an imprecise science, delimiting the evolutionary continuum into discrete categories. The problem of delineating species has given rise to a large number of species concepts. As noted by de Queiroz (2007), it is useful to recognize that each of these concepts focuses on a different outcome or feature along the continuum towards speciation. As such, different lines of evidence from various data types can be appropriate for evaluation by different concepts. Below, we evaluate the available evidence of isolation, and the degree of morphological and genetic differentiation between Indus and Ganges river dolphins with respect to several criteria for species delimitation, and then discuss the implications of these for the taxonomic status of *Platanista* in the Indus and Ganges river systems.

### 4.1 | Geographical isolation

One of the most popular paradigms for evaluating taxonomic hypotheses is the Biological Species Concept (BSC). Under the BSC, species are delineated by the presence of barriers that prevent interbreeding and gene flow (Mayr, 1963, 2000). In sympatric or parapatric populations, where the potential to interbreed readily exists, these barriers can be evaluated. For allopatric populations, interbreeding cannot be evaluated because the animals do not come into contact with each other, and other lines of evidence, such as morphological or genetic differentiation are needed as proxies of reproductive isolation. However, the presence of geographic separation over long stretches of

time is also used as an important context demonstrating that the species are likely on independent evolutionary trajectories.

In the current study, samples were obtained from throughout the range of both Indus and Ganges river dolphins, including the disjunct Karnaphuli-Sangu River system in the east, the Brahmaputra in the northeast, the Meghna in the south, and the Ganges river in the west; only the northern range limit in Nepal and the Beas River in northwest India were not sampled (Figure 1). The Indus river dolphin has undergone an 80% decline in range and all samples came from the remaining concentration of animals in the Indus mainstem. The theory, cited by Rice (1998), that there was once a single “Indobrahm” river that drained the Himalayas and later split into the Indus and Ganges systems has long since been debunked, and modern studies of paleo-fluvial geomorphology agree that the Indus and Ganges River systems have been separate and in their current approximate locations for over 40 million years (Cliff et al., 2001). Therefore, the Indus and Ganges river dolphins have, for a considerable period of time, existed in geographically isolated river systems and these physical barriers (land, and marine waters) ensure that interbreeding cannot occur (Braulik, Barnett, et al., 2015).

Based on a Bayesian calibrated molecular clock, it was estimated by Braulik, Barnett, et al., (2015) that Indus and Ganges river dolphins diverged around 550,000 years ago (95% posterior probability 0.13–1.05 million years ago) and by McGowen et al., (2009) as 520,000 years ago (95% posterior probability 0.12–1.09 million years ago). An estimated divergence time of many millions of years would constitute strong evidence that lineages are separately evolving (Martien et al., 2017). This length of separation is considerably longer than for many other known species pairs. For example, a recent speciation event, the divergence of two finless porpoise species (*Neophocaena*), was estimated to have occurred, based on mitochondrial and microsatellite sequences, 18,000 years ago (Wang et al., 2008), and using whole genome sequences as about 100,000 years ago (Zhou et al., 2018); both estimates are substantially shorter (1/30 to 1/5 as long) than the time that it is estimated that Indus and Ganges river dolphins have been reproductively isolated. Although we are unlikely to ever be able to directly test for reproductive isolation between Indus and Ganges river dolphins, it is clear that they have been separated for more than enough time for speciation to have occurred.

## 4.2 | Diagnosability

In the commonly used Phylogenetic Species Concept (PSC), species are delineated by the presence of derived, diagnostic characters indicative of descent from a common ancestor (Cracraft, 1983; Eldredge & Cracraft, 1980). By placing an emphasis on diagnosability, the PSC focuses on a consequence of reproductive isolation central to the BSC—the development and establishment of unique characters by separately evolving units (Cracraft, 1983). Thus, species are often more readily evaluated under the PSC, as diagnosability can be determined from multiple sources of commonly collected data such as morphology and genetics (Archer, Martien, & Taylor, 2017).

In a previous study of 31 mtDNA control region sequences of 858 bp, Braulik, Barnett, et al., (2015) identified six haplotypes, three in each of the two river systems. With only nine variable sites, diversity was extremely low, among the lowest reported in any cetacean. Five of these variable sites, consisting of one transversion, one insertion–deletion, and three transitions were fixed for different bases in Indus and Ganges haplotypes (Braulik, Barnett, et al., 2015), making dolphins from the two river systems 100% diagnosable using the mtDNA control region.

However, even in the face of five fixed differences, Braulik, Barnett, et al., (2015) were not able to demonstrate reciprocal monophyly of Indus and Ganges sequences, which may at first seem counterintuitive. As seen in Figure 2, three of the other four nonfixed variable sites were defined by a substitution in a single haplotype. It is clear that despite the fixed differences, the distribution of these nonfixed substitutions among haplotypes generates conflicting phylogenetic information, such that it is not possible to firmly resolve the patterns of descent in each river system. Given that *Platanista* does not have any close relatives, the outgroups used by Braulik, Barnett, et al., (2015)

(*Berardius bairdii*, *Hyperoodon ampullatus*, *Kogia breviceps*, and *Physeter macrocephalus*) are all relatively distantly related (McGowen et al., 2009, 2020; Xiong et al., 2009), making polarization of these sites to infer ancestral states difficult. The low genetic variability within *Platanista* in conjunction with the high variability between *Platanista* and the nearest outgroups result in an unresolvable polytomy of the three Ganges haplotypes (figure 3 in Braulik, Barnett, et al., 2015a). Thus, although the Indus haplotypes are monophyletic, it is difficult to generate support for monophyly in the Ganges. If these four variable sites were not present, there would be only one haplotype in each river system separated by five fixed substitutions, and a tree would show the trivial result of reciprocal monophyly as the two haplotypes would be more closely related to each other than their nearest relatives. These sequences are an interesting counterexample to the subset of interpretations of the PSC that have monophyly as a central requirement for species delimitation (Gutierrez & Garbino, 2018; McKittrick & Zink, 1988; Rosen, 1978). In this case, the lack of monophyly is not evidence of gene flow among river systems, but rather a lack of the ability to resolve patterns of descent.

The diagnosability seen in the mitochondrial sequences is also mirrored in a striking feature of the shape of the frontal bones on the skull. This bone was found to be flat in all Indus skulls and protruding in all Ganges skulls, allowing skulls to be diagnosed with 100% accuracy to the correct river system. This feature was clearly visible in all skulls examined, irrespective of age, size, or sex. It was even identifiable in a skull obtained from what is presumed to have been a fetus with a tiny and unfused braincase (specimen P16, Table SM1).

In the only other study of *Platanista* skull morphology, Pilleri and Gihir (1971), using six specimens from the Indus and six from the Ganges, state,

“a characteristic peculiar to *Platanista* is a nasal crest formed by the two frontals and situated on the caudo-dorsal edge of the neurocranium. It varies in height according to species. In *Platanista gangetica* it projects above the frontals in a clearly visible ridge...while in *Platanista indi* (Indus) it is distinctly lower.”

Unfortunately, diagrams of measurements for this feature were not given, so we cannot definitively state that the “nasal crest” in this description refers to the shape of the frontals rather than the maxillary crest or some other feature, but it seems probable that this was the case and that Pilleri and Gihir (1971) were referring to the same skeletal feature identified in this study. Regardless, it is clear from our data that the shape of the frontals is diagnostic and can be used to correctly classify *Platanista* sp. skulls to river system without the need for other traditional skull measurements or classification algorithms.

While not a perfectly diagnosable character, there was also very little overlap in the distribution of tooth counts from each river system. Indus river dolphins had on average 5 more teeth than Ganges river dolphins. Although 28% of the skulls overlapped in upper tooth counts, using a threshold of 31 teeth, a Bayesian logistic model could correctly assign 92% of skulls to river system. Differences in tooth counts between each river system are also seen in the data table presented in the Pilleri and Gihir (1971) study, but the authors only present tooth count ranges for all skulls combined and do not mention differences between rivers.

We note that although we observe 100% diagnosability in the shape of the frontal suture above the nasals and the mtDNA sequences, this is only an estimate of the true distribution of these features in the entire population. That is, there is some probability that if we sampled every individual, we would observe that some feature was not truly fixed between river systems. We can estimate what this error would be by calculating the binomial probability of observing a given number of fixed differences if the true probability was less than 100%. For example, if a single feature was truly fixed in only 95% of all individuals, we would expect to see it totally fixed in a random sample of 31 individuals 20% of the time. Likewise, if it was only fixed in 90% of all individuals, we would expect a random sample of 31 individuals to show it being totally fixed only 4% of the time. The tail of this distribution quickly drops to less than 1% if the true proportion of animals for which the feature is fixed is only 86%.

These results from a binomial distribution are for a single feature, expected to be randomly distributed. In the case of mtDNA, it does not take into account differences in haplotype frequencies. Regardless, with the realization

that we have observed six independent fully diagnostic features (five sites in 31 individuals and one morphological feature in 76 individuals), we can multiply the probabilities for a given true misclassification error to estimate how likely one would be to misclassify a random individual. If we assume that each feature has a true misclassification rate of 5% rather than the observed 0%, the probability of misclassifying an individual based on all six features is  $7 \times 10^{-6}$ . Given that there are likely less than 10,000 individuals of both species combined (Braulik & Smith, 2017), this suggests for all practical purposes some combination of these features is 100% diagnostic for every individual.

### 4.3 | Sexual dimorphism

The data on growth from both body and skull measurements clearly demonstrate differences in the extent of sexual dimorphism between dolphins from the Ganges and Indus. Ganges females grow to longer lengths and heavier weights than males. Ganges females have skulls that are similar to males in all dimensions except for a substantially longer rostrum that starts to develop at around 4 years of age. In contrast, body measurements and the limited skull data set suggest that Indus males and females exhibit a similar pattern of growth, reach similar size and weight as adults and have similar rostrum lengths. Ganges females reach longer lengths than Indus males and females (which grow to approximately equal size), and Ganges males are the smallest of all. Although data are limited, the length at birth for both sexes appears to be approximately equal, at 60–70 cm, in both river systems (Brownell, 1984; Harrison, 1972; Kasuya, 1972). Kasuya (1972) noted that the growth pattern of Ganges river dolphins shows peculiarities and continues for a longer period than most other cetaceans, especially in females. It is important to note that the data on external morphology used in this study were recorded by different, noncoordinated research groups over a long period of time and should therefore be treated with some caution.

Patterns of growth differ between the sexes of many cetacean species and result in some degree of sexual dimorphism (Dines et al., 2015). Females are slightly larger than males in Baird's beaked whale (*Berardius bairdii*), franciscana (*Pontoporia blainvillei*), baiji (*Lipotes vexillifer*), harbor porpoise (*Phocoena phocoena*), dolphins in the genus *Cephalorhynchus*, and most mysticete species (Chivers, 2009; Dines et al., 2015). It has been suggested that the sexual dimorphism in rostrum length is a reflection of ecological differences between the sexes, rather than playing a role in reproduction (Mesnick & Ralls, 2018); however, it is also possible that larger females also have a higher degree of reproductive success. If, as the data suggest, there is sexual dimorphism in the Ganges river dolphin and not in the Indus river dolphin, this is a substantial difference that indicates there are intrinsic differences in growth between dolphins in each river system. This may be explained by differences in habitat, diet, food availability, reproductive behavior or some other biological factors (Sibley, 1957; Shine, 1989). As an example, differences in the extent of sexual dimorphism of body and head size between closely related species of sea snakes have been related to sex-specific differences in feeding biology and prey opportunities across the range of each species (Shine et al., 2002).

### 4.4 | Other morphological differentiation

Our data suggest that while the overall difference in color may be small, most Ganges river dolphins are predominantly gray in color, while Indus river dolphins have more of a brownish gray tone. There is a possibility that the color of the river water, which varies between locations from brown to gray to blue, affects the observer's perception of the color of the dolphin, however, the above conclusions corroborate the coloration differences seen in many published photos.

Aside from the differences in the degree of sexual dimorphism discussed above, our univariate and multivariate analyses found significant differences between the size and shape of the maxillary crests of Indus and Ganges skulls. The left and right maxillary crests of Ganges skulls tended to be oval in shape and more similar to each other, while in Indus skulls they were more round and asymmetrically sized. Apart from the diagnostic difference in the frontal bones, little of the remaining variation in skull size and shape was specific to differences between river systems,



nevertheless, 80% of the skulls could be correctly classified based on these measurements. Thus, while no skull features captured by the measurements collected were perfectly diagnostic, differences were such that error of assignment was relatively small.

We note that the degree of diagnosability using the skull measurements does not take into account the previously discussed differences in tooth counts and shape of the frontal bones. Having observed the diagnostic pattern of the frontal bones, in this study we elected to explore differentiation of the other skull measurements independently. However, it should be emphasized that taken as a whole, *Platanista* skulls are 100% diagnosable to their river system of origin. This diagnosability is by virtue of an aspect of the skull that is clearly visible by eye, even to untrained observers, and does not require the taking of measurements or any additional analyses to correctly assign individual skulls to the correct river system.

#### 4.5 | Genetic differentiation

In a comparison of metrics for delineating cetacean populations, subspecies, and species using mtDNA sequence data, Rosel, Hancock Hanser, et al. (2017) identified Nei's net nucleotide divergence,  $d_A$  as being the most informative.  $d_A$  measures the proportion of nucleotide divergence due to differences accumulated between populations over time after removing the within-population variability (Martien et al., 2017). Given this, Taylor, Archer, et al., (2017) utilized  $d_A$  in conjunction with a measure of diagnosability to develop a set of guidelines and thresholds for delimiting subspecies and species with mtDNA control region data. Under these guidelines, subspecies are distinguished from populations by having  $d_A > 0.004$  and diagnosability  $>95\%$ , while species are distinguished from subspecies by having  $d_A > 0.02$ . In addition, there must be evidence that male-mediated gene flow can be ruled out, as these thresholds were developed for maternally inherited mtDNA.

Although the control region sequences demonstrate 100% diagnosability between Indus and Ganges river dolphins,  $d_A$  is only slightly larger than 0.004. Although sufficient to delineate subspecies, this amount of divergence is not close to being sufficiently large to meet the species threshold of 0.02 set in Taylor, Archer, et al., (2017). However, Taylor, Archer, et al., (2017) also noted that taxonomic classification errors based on  $d_A$  could occur where haplotypic diversity is low, where effective population size is very large, or where divergence is very recent. As previously discussed, mtDNA haplotypic diversity is notably low in *Platanista*, which likely accounts for relatively low  $d_A$  values, despite the fixed differences, and the fact that the two forms likely diverged within the past 500,000 years. By contrast the two species of finless porpoise (*Neophocaena phocaenoides* and *N. asiaorientalis*) are estimated in one study to have diverged only 18,000 years ago and have  $d_A = 0.0033$  (Wang et al., 2008; Jefferson & Wang, 2011; Rosel, Hancock Hanser, et al., 2017).

Taylor, Archer, et al., (2017) also proposed that if  $d_A < 0.02$  (the species threshold is  $>0.02$ ), but diagnosability is  $>95\%$ , and there is also at least one additional line of evidence, independent of the mtDNA data, that meets the species definition then species status can still be warranted. The morphological differences between river systems previously discussed, primarily in the shape of the frontal bones, means that this condition is met and therefore using the Taylor, Archer, et al., (2017) guidelines Indus and Ganges river dolphins would be designated as species. In a similar sense, consistent morphological differences between *N. phocaenoides* and *N. asiaorientalis* support their species status in the face of low values of genetic divergence (Jefferson & Wang, 2011; Rosel, Hancock Hanser, et al., 2017).

#### 4.6 | Limitations of this study

As with many studies conducted on endangered species our skull data set is not large, and the presence of sexual dimorphism meant that the sexes had to be analyzed separately, further reducing sample sizes. This, combined with the fact that the skulls were often damaged, there were few adult specimens, especially from the Indus, and the fact

that the nasals, one of the more variable parts of cetacean skulls, were often obscured by the maxillary crests, meant that fully describing skeletal differences between river systems was challenging. However, the sample size was similar to that in many other taxonomic studies (see Rosel, Taylor, et al., 2017 for a review).

Given the condition of many of the skulls, we were left with a data set with a wide range of missing data. To maximize the potential to detect differentiation in our multivariate analyses in as robust a manner as possible, we developed an iterative method (IMDO) that objectively generated data sets composed of the largest possible number of skulls and measurements. While we believe that this allowed us to perform a thorough multivariate analysis of this data set, the use of more advanced techniques such as geometric morphometrics may enhance the ability to detect finer differences in size and shape of *Platanista* skulls in the future and provide more insights into the extent of sexually dimorphic differences between river systems. It should be noted that for this study we compiled measurements from virtually every *Platanista* skull that could be located in museums and collections around the world (Table SM1). Given that skulls from stranded or bycaught animals are rarely collected and archived, it is unlikely that this data set will grow appreciably in the foreseeable future.

There were also limitations in the genetic data available for this analysis. Although we have used 459 and 859 bp of the neutral, hypervariable mtDNA control region, it is important to note that it is a single, nonrecombining locus. We can only infer a single gene tree from these sequences which may or may not correspond to the species tree (Nichols, 2001; Rubinoff & Holland, 2005). Ideally, the patterns of differentiation observed in this locus would be corroborated with larger suites of nuclear loci, such as Single Nucleotide Polymorphisms (SNPs) from which one would be able to accurately estimate current levels of gene flow and historical patterns of abundance (Andrews et al., 2016; Brumfield et al., 2003; Morin et al., 2004). However, the difficulty of collecting and preserving a sufficient number of samples from these dolphins means that much previous genetic work used ancient DNA extracted from museum specimens. Because of the challenges of gathering samples from animals that cannot be biopsied and seldom strand, and then coordinating sample analyses across countries, it is unlikely that substantially more samples will be collected in the near future. It is possible that evolving next generation sequencing methods might allow for more sensitive nuclear genotypes to be generated from museum specimens (Besnard et al., 2016; Ewart et al., 2019; McGowen et al., 2020) to give more insights into the evolutionary history of *Platanista*.

The data on coloration is not as quantitative or unequivocal as the other data sets presented in this work. Given that there was a suspicion of subtle differences in coloration between the two species, finding a way to articulate those was thought to be very important, however, quantifying subtle coloration hue differences in animals that cannot be compared side by side, and where photographs would be misleading, is extremely challenging, if not impossible. The solicitation of expert opinion was thought to be an innovative way to try to characterize possible differences where no other feasible methods were available, but the results should be considered as preliminary, treated as a broad indication of the color of each species, and ideally confirmed in further studies.

## 4.7 | Concluding summary

Indus and Ganges river dolphins occur in geographically isolated freshwater river systems, and, as such, there is no possibility of contemporary gene flow. Geological evidence suggests that the two rivers have been separate for at least 40 million years, and it has been estimated, based on mtDNA data, that Indus and Ganges river dolphins diverged approximately 550,000 years ago. The skulls of Indus and Ganges river dolphins can be quickly and easily assigned to a river system based on a consistent feature, the shape of the frontals, which is present in all animals irrespective of age and sex. There were no mtDNA control region haplotypes shared between river systems and there were five fixed differences between them. The consistent conclusions from these two separate lines of evidence are that there are clear diagnosable differences in both genetics and morphology that are indicative of the geographic and reproductive isolation of Indus and Ganges river dolphins, supporting recognition as separate species.

In addition to these primary lines of evidence this study suggests differences in growth and in the pattern of sexual dimorphism between dolphins in each river system, with Ganges river dolphins clearly sexually dimorphic and no evidence of dimorphism in Indus river dolphins. Other studies have suggested that there are differences in external morphology, in particular the shorter length of the tail in the Ganges compared to the Indus (Kasuya, 1972), differences in cervical vertebrae (Pilleri & Gahr, 1976) and blood composition (De Monte & Pilleri, 1979); these have yet to be fully investigated. Our data also suggest that the maxillary crests of the skull exhibit differences in shape, that Indus river dolphins have on average five more teeth in each jaw compared to Ganges river dolphins, and that the color of dolphins in each system is slightly different. Considering the weight of the combined evidence from multiple sources, we conclude that the Indus and Ganges river dolphins are sufficiently distinct to warrant their reclassification as separate species: Indus river dolphin (*Platanista minor*) and Ganges river dolphin (*Platanista gangetica*). We therefore elevate the Indus River subspecies, *Platanista gangetica minor*, to species level, *Platanista minor*. Formal redescrptions are provided for both species.

## 5 | TAXONOMIC TREATMENT AND SPECIES REDESCRIPTIONS

### 5.1 | Review of *Platanista* taxonomy and nomenclature

The superfamily Platanistoidea (Gray, 1863) previously included all the extant obligate river dolphins (*Platanista*, *Lipotes*, *Inia* and *Pontoporia*), but it now includes only *Platanista* and 15–22 extinct fossil genera, many from as long ago as the late Oligocene (De Muizon et al., 2018; Fordyce & Barnes, 1994). The platanistoids are considered to be monophyletic based on two main characters: the loss or reduction of the coracoid process and the supraspinous fossa of the scapula (De Muizon et al., 2018).

Several different genus names have been used for this group, including *Susu* Lesson, 1828, *Platanista* Wagler, 1830, *Sousou* F. Cuvier, 1836, *Soosoo* Hamilton, 1837, and *Platanistina* Neave, 1940. The genus name *Susu* actually has date priority over *Platanista*, but Rice (1987) applied to the International Commission on Zoological Nomenclature (ICZN) to conserve *Platanista*, due to its long history of widespread use and the ICZN (1989) agreed to suppress *Susu*, and to conserve *Platanista* as the valid name of the genus.

Finally, it has recently been shown by Smeenk (2018), that two names that were previously considered by some biologists to be synonyms of *P. gangetica* (i.e., *Delphinus rostratus* Shaw, 1801 and *Delphinus shawensis* Blainville in Desmarest, 1817) are actually both junior synonyms of *Inia geoffrensis* Blainville in Desmarest, 1817.

#### ***Delphinus gangeticus* Lebeck, 1801**

This nominal river dolphin species was first described in two separate accounts, both published in 1801, and both using the name *Delphinus gangeticus*, one by Heinrich Julius Lebeck and the other by William Roxburgh. There has been controversy about which author has priority. All early works considered that Lebeck had priority over Roxburgh (Ellerman & Morrison-Scott, 1951; Eschricht, 1851; Flower, 1884; Hershkovitz, 1966; Lesson, 1828). In the 1970s, Pilleri (1971, 1978) made a case for Roxburgh being the original describer, largely based on the notion that Lebeck was the junior and less experienced naturalist, and that he had seen Roxburgh's early account and plagiarized it. After extensive research, Kinze (2000) found original elements in both accounts and rejected Pilleri's argument of plagiarism; he further deduced a publication date of 24 August 1801 for Lebeck's account and although no exact date could be ascertained for Roxburgh's account, it was shown that it must have been published after September 1801, and thus priority was returned to Lebeck.

Home (1818) claimed that *Delphinus gangeticus* was described by the late Dr. Roxburgh in the seventh volume of the Asiatic Researches, published in 1781. However, the journal "Asiatic Researches; or Transactions of the Society instituted in Bengal for enquiring into the history and antiquities, the arts, sciences and literature of Asia" only began

with Volume 1 in 1788 and we therefore assume the year stated by Home was incorrect, and was in fact 1801 as noted by all other authors.

Lebeck's type description is based on an adult male specimen collected in November 1797 from close to Calcutta, India, and it is thought that this is the same material that Roxburgh based his description on (thereby making Roxburgh's name a junior objective synonym). The type specimen was deposited in the Hunterian Museum (Home, 1818; Owen, 1853) (specimen No. 2482). This type specimen was apparently destroyed in World War II, but fortunately there is a cast of the rostrum and part of the mandible still in the Natural History Museum of the United Kingdom (NHMUK No. 1884.5.3.1). *Delphinus gangeticus* Lebeck, 1801 is considered the senior synonym and valid name of the Ganges river dolphin. It was Gray (1835) who first used the present name combination *Platanista gangetica*.

### ***Delphinus gangeticus* Roxburgh, 1801**

See detailed description above under *Delphinus gangeticus* Lebeck, 1801. The Roxburgh type description is moderately detailed and includes an illustration of the external features. Roxburgh's name represents an unusual case, which is considered both a junior objective synonym and junior objective homonym of *D. gangeticus* Lebeck, 1801.

### ***Susu platanista* Lesson, 1828**

This name was cited in Hershkovitz (1966) as a synonym for the Ganges river dolphin, but in Lesson's monograph, he uses "sousedou plataniste" only as a common name, and the Latin name he uses in the description on p. 215 is *Delphinus gangeticus* Lebeck. "*Susu platanista*" only appears in the index on p. 440. Therefore, *Susu platanista* Lesson is not a true scientific name, and should thus be considered a *nomen nudum*.

### ***Platanista minor* Owen, 1853**

Owen (1853) noted in his catalogue, a specimen of a river dolphin from "the Indus" based on a skull presented by Dr David Wallich MD (specimen No. 2481 in the Royal College of Surgeons, London) which he described as a smaller variety of the Ganges river dolphin, *P. gangetica*, var. *minor*, and not a species or subspecies. The Owen type specimen was in the Hunterian Museum, part of the Royal College of Surgeons collection, and it was destroyed when the museum sustained a direct hit during a World War II bombing raid; tens of thousands of osteological specimens (60% of the total, including most mammals) were lost (Fforde, 1992; Pilleri & Gihir, 1977). There has been a lack of clarity over the years as to whether this is a valid name, but the ICZN has determined that such names are available in zoological nomenclature and this is the senior synonym of the Indus river dolphin (see van Bree, 1976).

### ***Platanista indi* Blyth, 1859**

Edward Blyth (1810–1873) was the curator of zoology at the museum of the Asiatic Society of India in Calcutta. He described *P. indi* as a new species (Blyth, 1859), based on a skull collected by Sir Alexander Burnes. The collection location is not known, but Alexander Burnes wrote an account of an expedition he conducted in 1831 sailing up the Indus River from the sea to Lahore, hence he had ample time to collect a specimen (Burnes, 1835). The disposition of the type is not mentioned in the original publication (Blyth, 1859), but Hershkovitz (1966) stated that the type skull was in the Asiatic Society of India Museum, Calcutta (now known as the Indian Museum). Pilleri and Gihir (1977) stated that neither Blyth's, nor Owen's types could be found, and used this as justification to designate a neotype for the Indus river dolphin (No. 623 in the Pilleri collection, which is now in the possession of the Staatliches Museum für Naturkunde Karlsruhe, Stuttgart specimen SMNH 45643). However, according to Rice (1998) this neotype has no standing in zoological nomenclature, and *P. indi* is considered to be a junior synonym of *P. minor* Owen, 1853.

## SPECIES REDESCRIPTIONS

Order Cetartiodactyla Montgelard, Catzefils and Douzery, 1997

Cetacea Brisson, 1762

Odontoceti Flower, 1867 Superfamily Platanistoidea Gray, 1863

Family Platanistidae Gray, 1846

Genus *Platanista* Wagler, 1830

***Platanista gangetica* (Lebeck, 1801)****Synonymy**

*Delphinus gangeticus* Roxburgh, 1801: p. 171, pl. 5. Junior objective synonym and junior objective homonym of *D. gangeticus* Lebeck, 1801.

*Delphinorhynchus gangeticus* Lesson, 1827: p. 406. New name combination.

*Susu platanista* Lesson, 1828: p. 440. *Nomen nudum*.

*Platanista gangeticus* Wagler, 1830: p. 35. New name combination.

*Soosoo gangeticus* Hamilton, 1837: p. 254, pl. 28. New name combination.

*Platanista gangetica* Gray, 1835: pl 24. Emendation and first use of present name combination.

**Type Specimen**

Lebeck's (1801) type specimen was a 6½ English-foot-long, adult male collected in November 1797 from the banks of the Hooghly River, close to Calcutta, India. The specimen was also illustrated in Home (1818) as plate XX, p.419 and in Van Beneden and Gervais (1880) as plate XXXI, figure 1. The type specimen was destroyed in World War II, but there is still a cast of the rostrum and part of the mandible in the Natural History Museum in the UK (No. 1884.5.3.1). The figure from Home (1818) was reprinted in Pilleri and Gihir (1971; figure 5d).

**Etymology**

This species is known as the Ganges river dolphin after the river system from which it was described. We recommend the English common name Ganges river dolphin for this species. It is known by many different local names within its range including, *Susu* (popular), *Soons/Soans/Soos* (Hindi and dialects), *Shushuk* (Bengali), *Hiho/Hihu* (Assamese), *Bhagirath*, *Socho* (Hindi/Maithili: eastern Bihar), *Shus* or *Suongsu* (Nepali), *Shishumar* (probable medieval name in Sanskrit), *Pani Suar* (name during the Mughal period).

**Diagnosis**

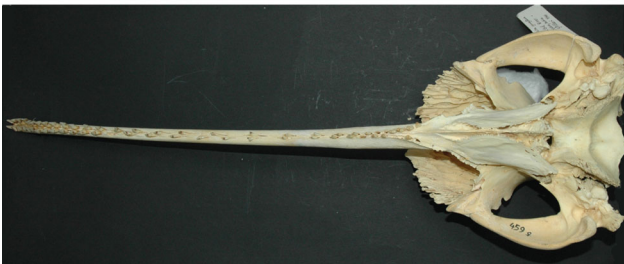
The skulls can be differentiated from those of *P. minor* by the presence of a projection at the frontal suture above the nasals and behind the maxillary crests (Figure 4). While there is some overlap in tooth counts between Indus and Ganges river dolphins, all skulls with less than 30 teeth in the upper tooth rows are Ganges river dolphins. The Ganges river dolphin has three unique mtDNA haplotypes (HAP4-6, see Braulik, Barnett, et al., 2015, GenBank accession numbers KJ629311-13) with five fixed differences separating it from the Indus river dolphin.

**Description**

Ganges river dolphins are robust dolphins with large paddle shaped pectoral flippers, a long rostrum, flexible neck, and small dorsal fin (Figures 12 and 13). Adult Ganges river dolphins are sexually dimorphic with females reaching



**FIGURE 12** Photograph of surfacing Indus River dolphin (*Platanista minor*) (top: photo credit WWF-Pakistan) and Ganges River dolphin (*Platanista gangetica*) (bottom: photo credit: Mansur/WCS Bangladesh).



**FIGURE 13** Dorsal, ventral, and lateral photos of a Ganges River dolphin skull, SMNH45648 from the Stuttgart Germany Collection.

longer lengths than males due to the longer length of the rostrum. Some animals have a small number of vibrissae on the rostrum. Ganges river dolphins are gray or grayish brown in coloration and sometimes there is a pinkish hue on the underside or around the rostrum (Figure 12). The largest female recorded was collected from the Ganges, and was 267 cm long, while the largest male was 213 cm in length (Anderson, 1879). The oldest individual recorded was a 30-year-old male (this study). Animals appear to be between 60 and 70 cm at birth (Anderson, 1879, Kasuya, 1972).

### **Distribution**

The range of the Ganges river dolphin was documented by Anderson in the 1870s (1879) and at that time the distribution included a vast network of interconnected rivers throughout India, Bangladesh and southern Nepal. The distribution extended from the Sundarbans delta, throughout the Ganges and Brahmaputra River systems and their many large and medium-sized tributaries up to the foothills of the Himalayas. The dolphin also occurred in the separate Karnaphuli-Sangu River system in southeast Bangladesh. The range remains largely as depicted by Anderson (1879), but the species has now been extirpated from some rivers, or sections of river, in the west or north of the species range, where habitat fragmentation by irrigation barrages, low water flows due to diversions, and high levels of pollution have reduced habitat viability (Sinha & Kannan, 2014).

### ***Platanista minor* Owen, 1853**

### **Synonymy**

*Platanista indi* Blyth, 1859: p. 493. Junior synonym

### **Type Specimen and Type Locality**

Owen (1853:448) described *Platanista gangetica*, var. *minor*, which was based on a skull presented by David Wallich, M.D. to the Hunterian Museum in the Royal College of Surgeons, London, in 1852 (specimen No. 2481, later renumbered as No. 2936) (Flower, 1884; Gray, 1866). The exact location of origin of the type specimen was given only as “the Indus” (Owen, 1853). Unfortunately, as with the type specimen of the Ganges river dolphin, this type specimen was destroyed during the same German bombing raid in World War II (Pilleri & Gihl, 1977).

### **Etymology**

We recommend the English common name Indus river dolphin for the species. It is known as *bhulan* in the local languages of Pakistan, and northwest India, where it occurs.

### **Diagnosis**

Indus river dolphin skulls can be differentiated from those of the Ganges river dolphin by the absence of a projection at the frontal suture above the nasals and behind the maxillary crests on the skull (Figure 4). While there is some overlap in tooth counts between Indus and Ganges river dolphins, all skulls with more than 33 teeth in the upper tooth rows are Indus river dolphins. The Indus river dolphin has three unique mtDNA haplotypes (HAP1-3, see Braulik, Barnett, et al., 2015, GenBank accession numbers KJ629309, KJ629310 & AJ554058) with five fixed differences separating it from the Ganges river dolphin.



## Description

Indus river dolphins are robust dolphins with large paddle shaped pectoral flippers, a long rostrum, flexible neck, and small dorsal fin (Figures 12 and 14). Indus river dolphins are a uniform brownish gray in coloration and sometimes there is a pinkish hue on the underside or around the rostrum (Figure 12). Some animals have a small number of vibrissae on the rostrum. The largest female Indus river dolphin recorded was 238 cm in length and the largest male was 241 cm. There is no evidence of sexual dimorphism in Indus river dolphins, but the adult sample sizes are very small (Table 2). Length at birth is around 60–70 cm.

## Distribution

The range of the Indus river dolphin was documented by Anderson (1879) in the 1870s to include the entire Indus mainstem from the delta up to the foothills of the Himalayas at Kalabagh, and all five of the large Indus tributaries: the Jhelum, Chenab, Ravi, Beas, and Sutlej (Anderson 1879). Total range of the species at the time was estimated to be approximately 3,500 km of free-flowing river (Reeves et al., 1991). Following construction of 17 irrigation barrages on the lower Indus system (starting around 1880 and continuing until approximately 1970), which fragment dolphin habitat and reduce water levels and available habitat, Indus river dolphins have suffered an 80% decline in distributional range (Braulik, Noureen, et al., 2015; Reeves et al., 1991). The vast majority of the species now occurs in approximately 690 km of the Indus mainstem between Chashma and Sukkur barrages in Sindh, Punjab and KPK Provinces of Pakistan (Aisha et al., 2017; Reeves et al., 1991). Small dolphin “populations” occur downstream of Sukkur barrage and in the Beas River, India.



**FIGURE 14** Dorsal, ventral, and lateral photos of an Indus River dolphin skull SMNH45643, the *Platanista indi* neotype (Pilleri & Gehr, 1977), from the Stuttgart Germany, Collection.



## 6 | OVERALL CONCLUSIONS

Indus and Ganges river dolphins are the sole remaining relicts of the entire Platanistoidea cetacean superfamily and thus from the perspective of evolutionary distinctiveness their conservation is of key importance. The recognition of two species of *Platanista* detailed above requires a re-evaluation of their conservation status. Both are currently listed as Endangered on the IUCN Red List and are already among the most endangered of all cetaceans. There is now an urgent need to elevate these species to a higher level of conservation concern and priority. This is especially true for the Indus river dolphin, which has declined drastically throughout most of its range due to its massive altered and degraded habitat (Braulik, Noureen et al., 2015). The Ganges river dolphin, although presently more numerous, is under great threat due to proposed and ongoing large infrastructure projects that have the potential to destroy large swaths of the most important habitat for the species (Kelkar, 2017).

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**Gill Braulik:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; writing-original draft. **Frederick Archer:** Formal analysis; visualization; writing-original draft; writing-review & editing. **Uzma Khan:** Data curation; writing-review & editing. **Mohammad Malik:** Data curation; writing-review & editing. **Ravindra Sinha:** Data curation; writing-review & editing. **Thomas Jefferson:** Methodology; writing-original draft; writing-review & editing. **Carl Donovan:** Formal analysis; writing-review & editing. **Jeff Graves:** Writing-review & editing.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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