Morphometrics of the dolphin genus *Lagenorhynchus*: deciphering a contested phylogeny

Allison Galezo[1,2] and Nicole Vollmer[1,3]

1 Department of Vertebrate Zoology, Smithsonian Institution National Museum of Natural History
2 Department of Biology, Georgetown University
3 NOAA National Systematics Laboratory

Smithsonian *National Museum of Natural History*

GEORGETOWN UNIVERSITY

Background

a b c

Recent phylogenetic studies[1-7] have indicated that the genus *Lagenorhynchus*, currently containing the species *L. obliquidens*[a], *L. acutus*[b], *L. albirostris*[c], *L. obscurus*[d], *L. cruciger*[e], and *L. australis*[f], **is not monophyletic**. These species were originally grouped together because of similarities in external morphology and coloration, but genetic studies have proposed that this grouping may not be valid.

These studies have suggested that

- *L. australis* and *L. cruciger* are sister taxa.[2-7]
- *L. obscurus* and *L. obliquidens* are sister taxa.[1-7]
- *L. australis*, *L. cruciger*, *L. obscurus*, and *L. obliquidens* belong in the subfamily **Lissodelphininae**, along with two other genera, *Lissodelphis* and *Cephalorhynchus*.[3-7]
- *L. acutus* and *L. albirostris* do not belong in the same genus as the other *Lagenorhynchus* species, or even in the Lissodelphininae subfamily. [3-7]

We sought to assess whether the skull morphology of the *Lagenorhynchus* species, as well as the morphology of species in *Lissodelphis* and *Cephalorhynchus*, reflected the results of these genetic studies.

d e f

Methods

We collected 38 skull measurements from 5 of the 6 *Lagenorhynchus* species (excluding *L. cruciger* due to a lack of samples), as well as *Lissodelphis borealis* and all 4 *Cephalorhynchus* species, totaling 106 individuals. Only mature individuals were measured. Measurements were taken using the Microscribe 3D-LX. We used the Perrin 1975[8] skull measuring scheme, with the addition of 3 novel measurements.

Cluster analysis (CA), principal component analysis (PCA), discriminant function analysis (DFA), and MANOVA statistical tests were run using R Version 3.2.1. Data were log transformed for analyses. When appropriate based on sample size, we tested for sexual dimorphism. We handled missing data in two ways: 1) deleting all variables and individuals with missing data, or 2) filling in missing data using averages from the same species. Overall clustering patterns were the same regardless of how missing data were treated, so method 2 was used during statistical analyses.

Results & Analysis

Figure 1. Phenogram from cluster analysis of dolphin skull measurements. Calculated using Euclidian distances and Ward's method.

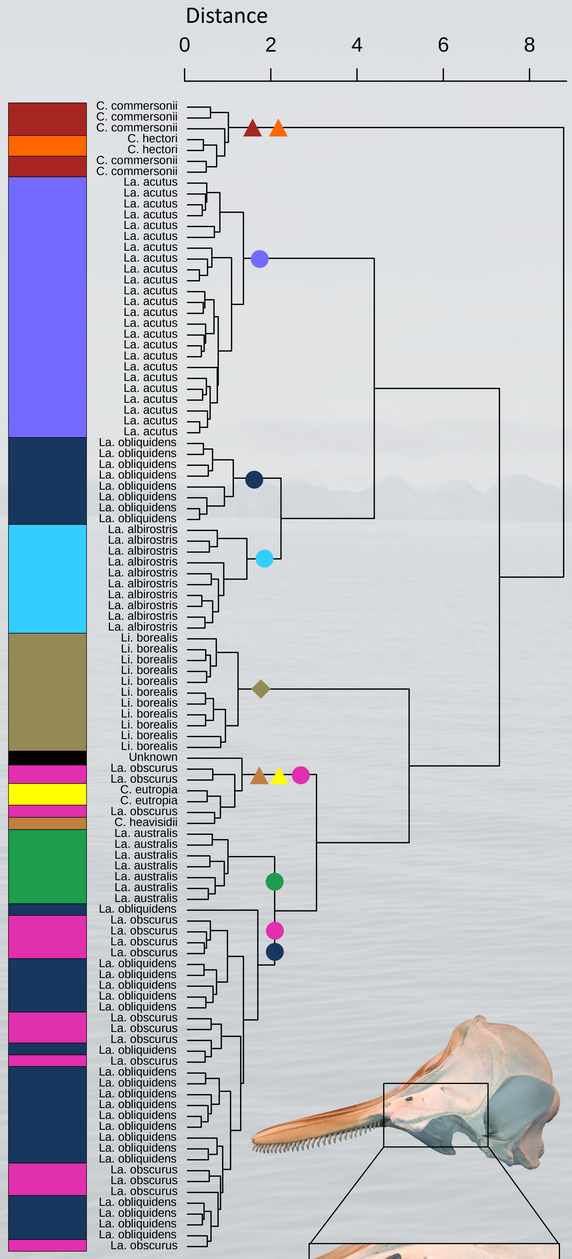

Figure 2. Species symbols key with sample sizes.

- La. acutus (24)
- La. albirostris (10)
- La. australis (7)
- La. obliquidens (28)
- La. obscurus (15)
- C. commersonii (5)
- C. eutropia (2)
- C. heavisidii (1)
- C. hectori (2)
- Li. borealis (11)
- Unknown (1)

Figure 3. PCA. Principal Component 1 (PC1) explained 59.47% of the variance in the data, and was largely a measure of skull width. PC2 (19.26%) was a measure of tooth count. Note the overlap between *La. obliquidens* ●, *La. obscurus* ●, and *La. australis* ●. All 5 *Lagenorhynchus* species ●●●●● cluster together, and are particularly isolated from *Li. borealis* ◆ and the two *Cephalorhynchus* clusters: ▲▲ & ▲▲. *La. acutus* ● and *La. albirostris* ● lie on the margins of the *Lagenorhynchus* cluster.

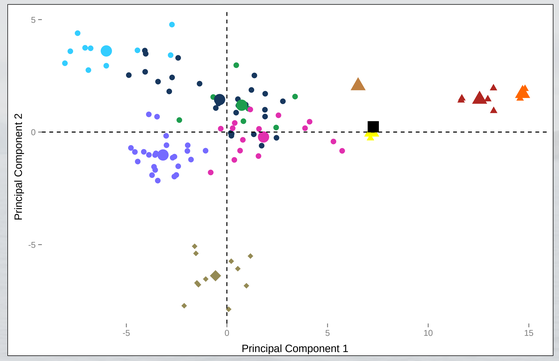

Figure 4. PCA with size correction. All variables were regressed against condylobasal length (total skull length) to correct for size. PC1 (47.35%) was dominated by supraorbital thickness, PC2 (20.48%) by lacrimal length (Fig. 5). Note the continued overlap between *La. obliquidens* ● and *La. obscurus* ●, and the shift of *La. australis* ● away from ● and ● and towards *C. hectori* ▲ and *C. commersonii* ▲. The *Lagenorhynchus* and *Cephalorhynchus* species have formed one large super-cluster, to the exclusion of *Li. borealis* ◆. *La. acutus* ● and *La. albirostris* ● lie on the margins of this super-cluster.

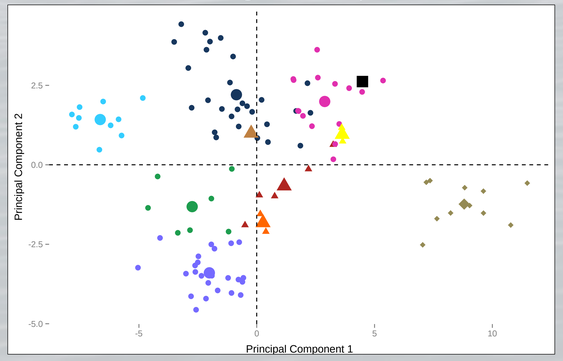

Figure 5. *Lagenorhynchus* skull. Supraorbital thickness (SOT) and lacrimal length (LL).

Discussion

- **Our morphological data support the hypothesis that the genus *Lagenorhynchus* is not monophyletic,** evident from the separation in the phenogram of *La. albirostris* and *La. acutus* from the other *Lagenorhynchus* species, and the mix of genera in the lowermost clade (Figure 1).
- Our results show that *La. obscurus* and *La. obliquidens* are very similar morphologically, which supports the hypothesis that they are closely related: they have noticeable overlap in both PCAs (Figures 3 & 4) and DFAs (not pictured) with and without a size correction, representing a wide range of skull measurements. They also cluster together in the phenogram, with the exception of 8 *La. obliquidens* individuals originating from a Southern Californian region believed to house a distinct *La. obliquidens* morphotype.[9]
- The grouping of *La. australis*, *La. obliquidens*, *La. obscurus*, *C. eutropia*, and *C. heavisidii* in the phenogram sister to *Li. borealis* supports the proposed makeup of the Lissodelphininae subfamily[4-8], but the exclusion of *C. commersonii* and *C. hectori* does not. This may be due to the exceptionally small size of *C. commersonii* and *C. hectori.* The addition of morphological data from *La. cruciger* is vital to clarifying the relationships within this subfamily because of the proposed close relationship between *La. cruciger* and *La. australis*[2-7].
- The close proximity/overlap of species clusters in the PCAs may be because they have been subject to similar evolutionary pressures, or due to the recent and rapid radiation of delphinids not giving these species ample time to accumulate great morphological differences.

Acknowledgements

We would like to thank Allen Collins for introducing Ali to the world of cnidarians, as well as John Ososky, Ana Costa, Jim Mead, and Charley Potter for sharing their insight on marine mammals. We thank Liz Cottrell and Gene Hunt, the Natural History Research Experiences (NHRE) co-directors, as well as NHRE administrator Virginia Power, for their support and guidance. A special thanks to Gene Hunt for his assistance with the PCA. This project was made possible by the National Science Foundation.

1) Cipriano, F. (1997). Antitropical distributions and speciation in dolphins of the genus Lagenorhynchus: a preliminary analysis. *Molecular Genetics of Marine Mammals Volume Special Publication*, *3*.
2) Miyazaki, N., & Shikano, C. (1997). Preliminary study on comparative skull morphology and vertebral formula among the six species of the genus Lagenorhynchus (Cetacea: Delphinidae). *Mammalia*, *61*(4), 573-587.
3) LeDuc, R. G., Perrin, W. F., & Dizon, A. E. (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Marine Mammal Science*, *15*(3), 619-648.
4) Pichler, F. B., Robineau, D., Goodall, R. N. P., Meyer, M. A., Olivarria, C., & Baker, C. S. (2001). Origin and radiation of Southern Hemisphere coastal dolphins (genus Cephalorhynchus). *Molecular Ecology*, *10*(9), 2215-2223.
5) Harlin-Cognato, A. D., & Honeycutt, R. L. (2006). Multi-locus phylogeny of dolphins in the subfamily Lissodelphininae: character synergy improves phylogenetic resolution. *BMC evolutionary biology*, *6*(1), 87.
6) May-Collado, L., & Agnarsson, I. (2006). Cytochrome b and Bayesian inference of whale phylogeny. *Molecular phylogenetics and evolution*, *38*(2), 344-354.
7) Banguera-Hinestroza, E., Hayano, A., Crespo, E., & Hoelzel, A. R. (2014). Delphinid systematics and biogeography with a focus on the current genus Lagenorhynchus: Multiple pathways for antitropical and trans-oceanic radiation. *Molecular phylogenetics and evolution*, *80*, 217-230.
8) Perrin, W. F. (1975). Variation of spotted and spinner porpoise (genus Stenella) in the eastern Pacific and Hawaii. *Scripps Institution of Oceanography*.
9) Walker, W. A., Leatherwood, S., Goodrich, K. R., Perrin, W. F., & Stroud, R. K. (1986). Geographical variation and biology of the Pacific white-sided dolphin, Lagenorhynchus obliquidens, in the north-eastern Pacific. Research on dolphins, 441, 465.

Dolphin thumbnail images © Jörg Mazur. Background image by Steve Hillebrand. Skull image by A. Galezo.

NSF REU Site, EAR-1062692