Joey LaValley

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Establishing Evolutionary Relationships between Ancient Cetaceans and Modern Odontocetes

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Abstract

The search for an accurate cetacean phylogeny has sparked many a debate. With the advent of DNA, molecular sequences can be used to do what once only comparative anatomy could accomplish. Geneticists are discovering certain clades within the cetacean phylogeny that do not exactly match previous morphological results. With aid from the latest in Tree Analysis Using New Technology (T.N.T.), we were able to combine morphological data collected in the classroom and molecular data gathered from online databases to deduce a phylogeny of 13 cetacean species, 4 extinct and 9 living. The results show how molecular and morphological characters can complement the other.

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1. Introduction

Using a combined morphological and molecular dataset, I suggest the analysis and results will be more accurate than each own its own. Comparative anatomy has its limitations. If two species resemble each other they do not necessarily have to be related. Key characters could be similar but each evolved separately than the other. For instance *Globicephala macrorhynchus* and *Delphinapterus leucas* are both larger in size than the other taxa being studied. However if we look to May-Collado and Agnarsson (2006) we see results placing the two species quite far apart on a phylogenetic tree.

This is where molecular information can be helpful. We used sequences from the 12s ribosomal mitochondrial gene and the alpha-lactalbumin gene to determine an evolutionary relationship among the taxa. Genetic information is not perfect and by adding the morphological characters we propose there will be a clearer solution. Scaling is a technique which will be applied to the quantitative morphological data. This will allow for differences in character states to be better defined.

2. Materials and Methods

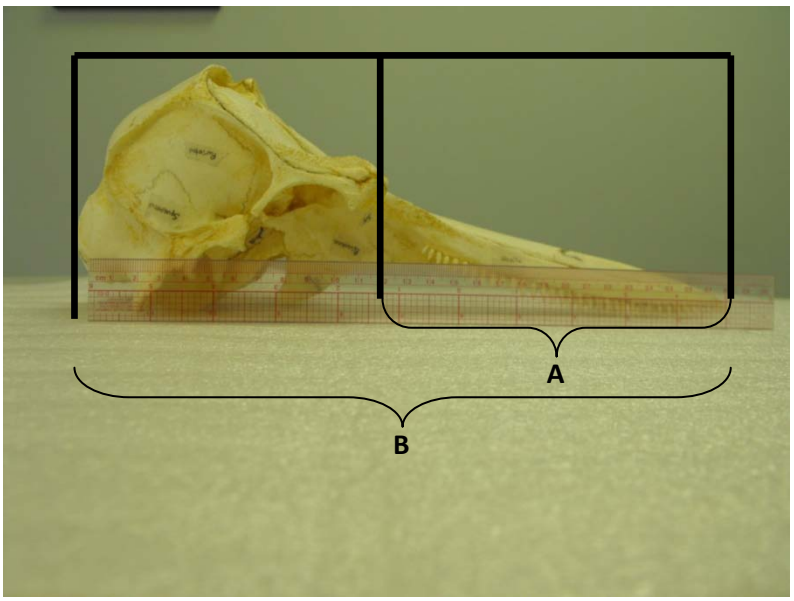
Data used in the analysis was found by two processes. The morphological data was measured from a combination of casts and skulls. Two skulls of modern Odontoceti, eight casts of modern Odontoceti and four casts of fossil cetaceans were used in defining morphological characters. The taxa are as follows: *Pakicetus, Georgiacetus vogtlensis, Xenorophus sp., Archaeodelphis patrius, Platanista gangetica, Pontoporia blainvillei, Sotalia fluviatilis, Delphinapterus leucas, Lagenorhynchus obliquidens, Lissodelphis borealis, Delphinus delphis, Tursiops truncatus* and *Globicephala macrorhynchus*. The first four taxa are our fossil casts. The last two were skulls. The measurements and their descriptions can be found following this section and in **Appendix 1**. A digital camera was used to represent each taxa and each measureable character. Microsoft Word was used to diagram the pictures. This tool was helpful in identifying each character state.

The molecular data was obtained online from the NCBI website. This database provided two molecular genes to our datasets, 12s ribosomal mitochondrial gene and Alpha-lactalbumin gene. Using a multiple sequence alignment program, ClustalW, the data was aligned so that it could be used in the T.N.T. program (Version 1.1, P. Goloboff et al). Word Pad was the application easiest to write the datasets into a format readable by T.N.T.

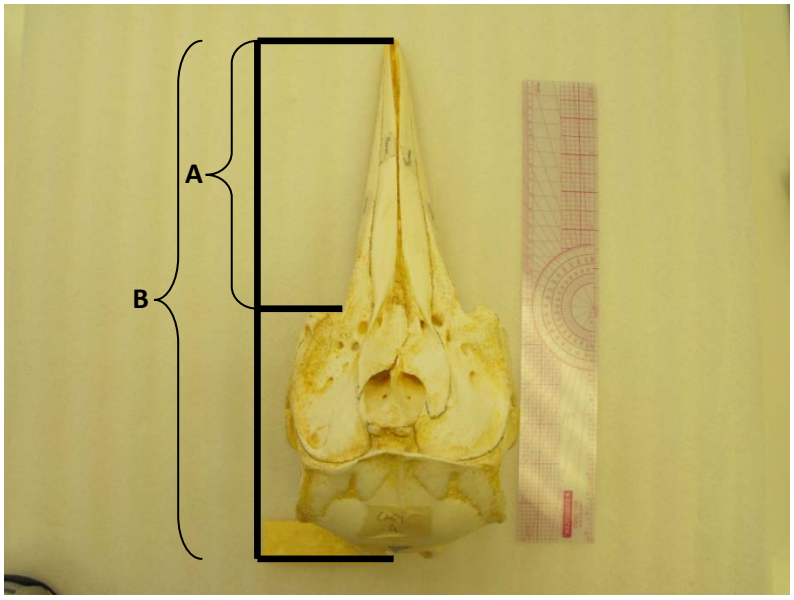
The results following **Observations** gives the trees retained from tree analysis. T.N.T. was the primary program used in the analysis of the data. There were seven datasets. Morphological data was divided into discrete and scaled; then they were combined. Molecular data for the two genes was separate and combined. Finally, all the data was combined in one large dataset containing thirteen taxa and 1057 characters.

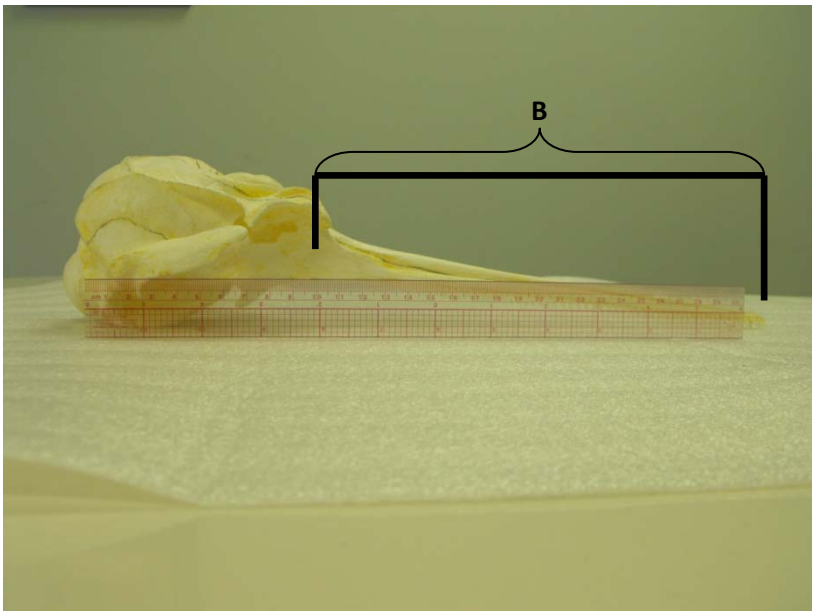
Each dataset was opened in T.N.T. and a “new technology search” was performed. Then various values of k were used in a series of implied weighting functions so as to compare changes in the trees retained. If there were multiple trees retained a strict consensus was created. Every function performed was in order to obtain better information regarding the data. To help with this, branch support was taken for each node on the three trees from the three combined datasets. This gave numerical values which show numerical evidence for certain aspects of the trees.

3. Observations

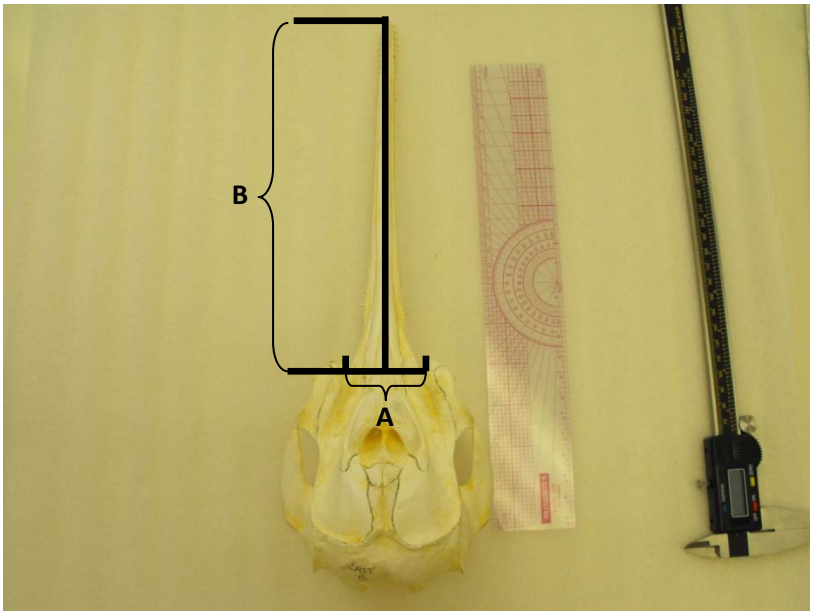


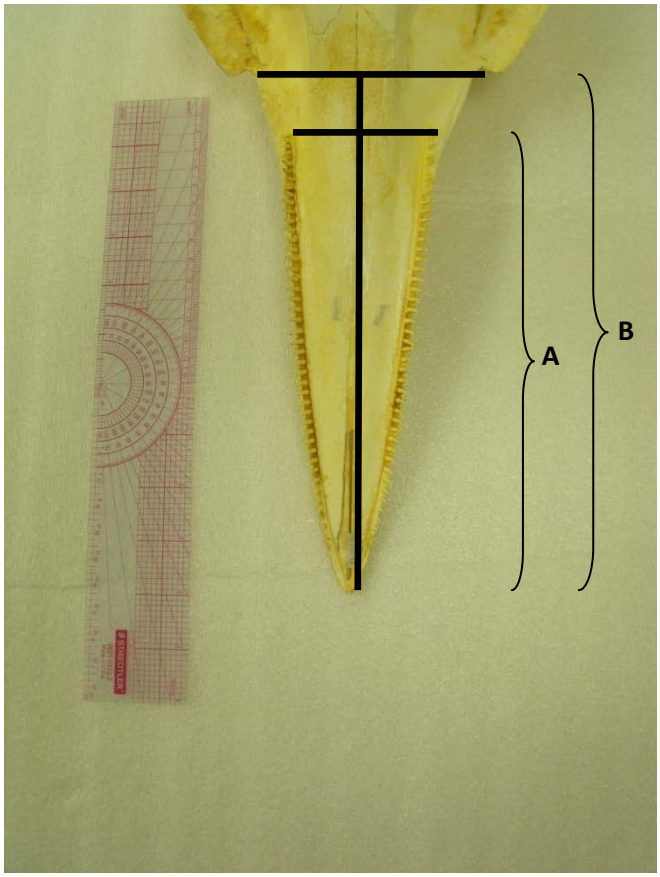
Character 1: Length of Rostrum (**A**) versus Length of Skull (**B**). Rostrum is measured from antorbital notch to anterior tip of skull. Measurement taken along the sagittal plane.





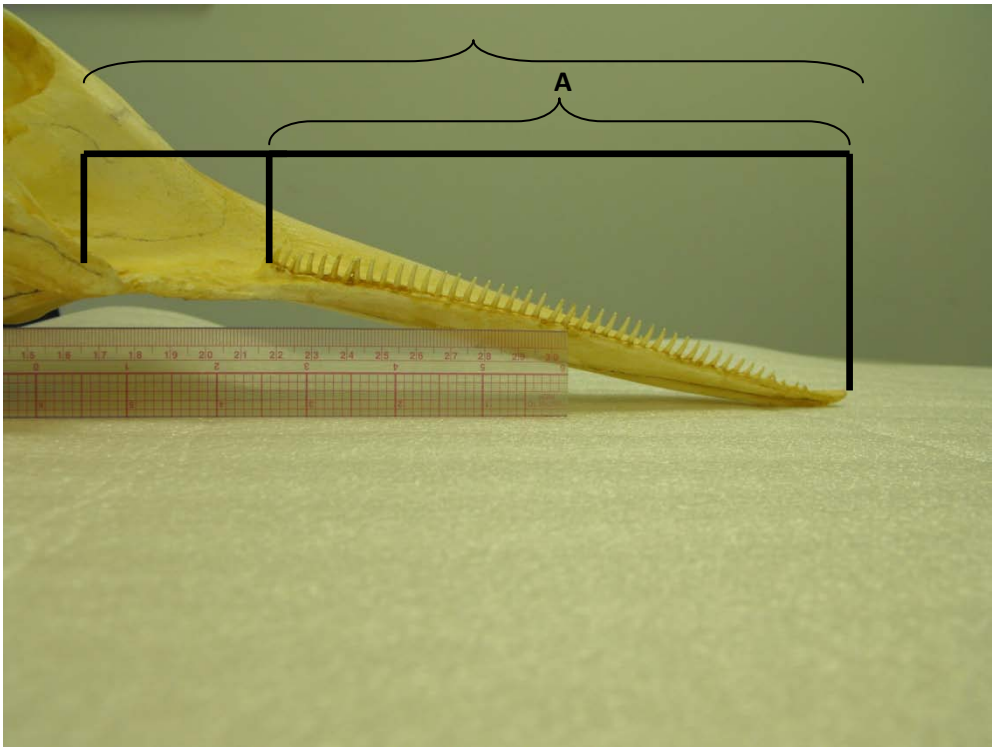
Character 2: Width of the Rostrum (**A**) versus Length of the Rostrum (**B**).

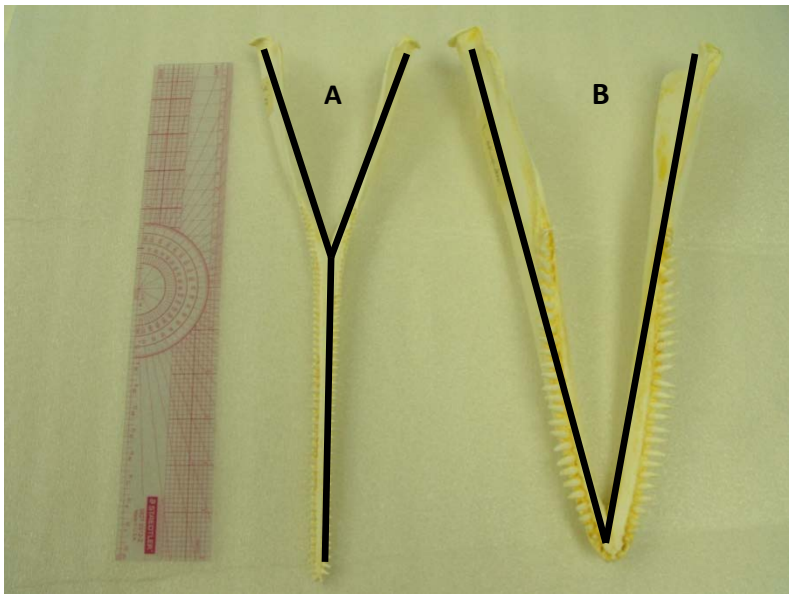




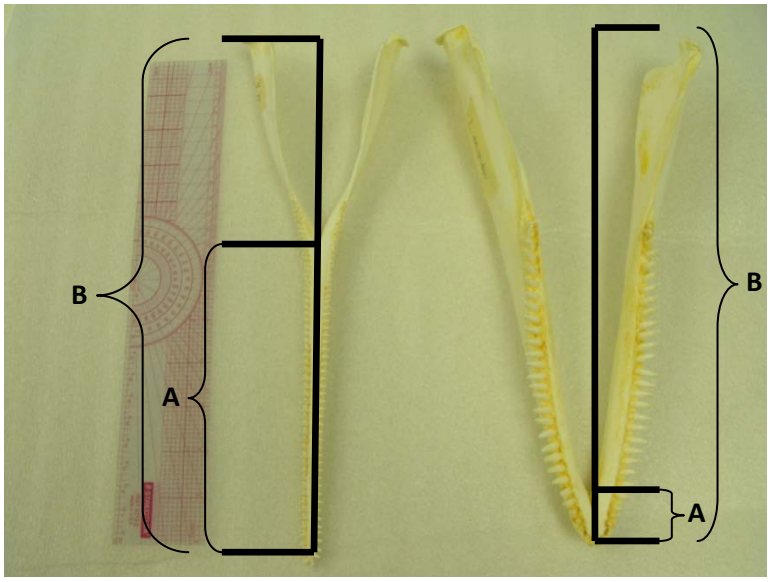
Character 3: Teeth extension on rostrum (A) versus the total length of the rostrum (B). Teeth extension is measured from most anterior point on the rostrum along the sagittal plane to the most posterior teeth.

B

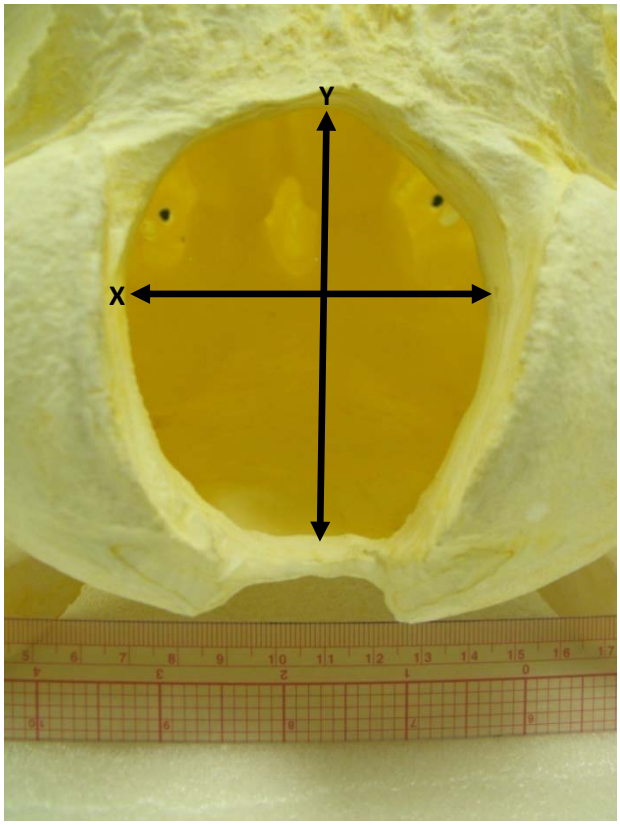




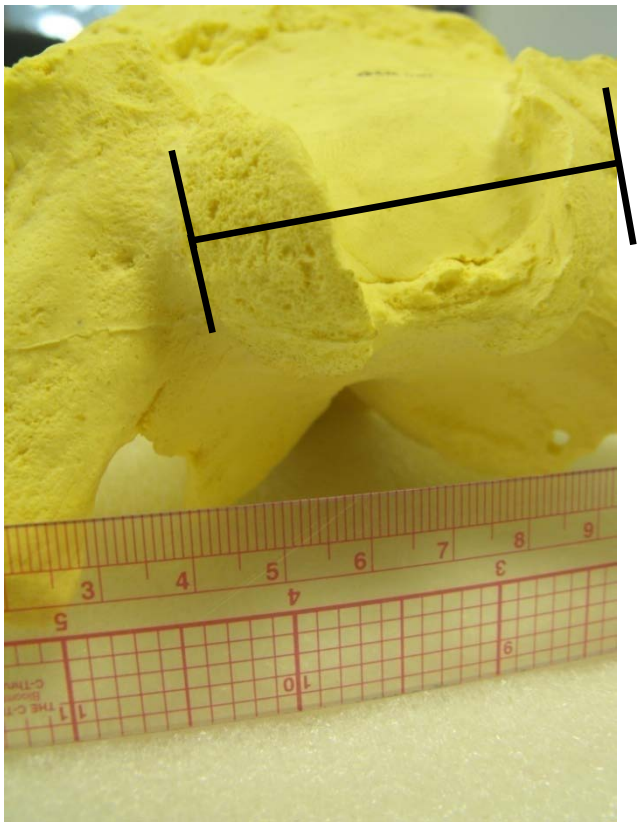
Character 5: Shape of Mandible. *Pontoporia blainvillei* (**A**) disiplays a Y-shape; *Lissodelphis borealis* (**B**) displays a V-shape.



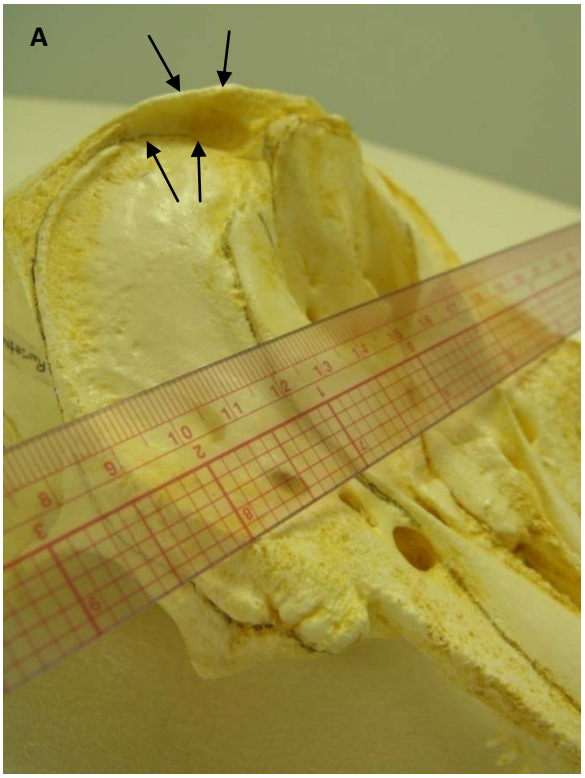
Character 6: Length of Mandibular Suture (**A**), versus Length of Mandible (**B**). Measurement taken along the sagittal plane.



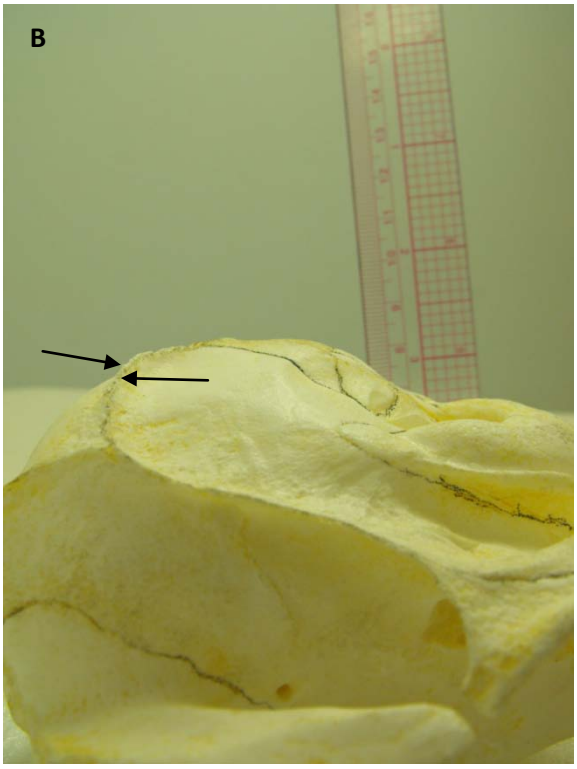
Character 7: Width (**X**) versus Height (**Y**) of Foramen Magnum.

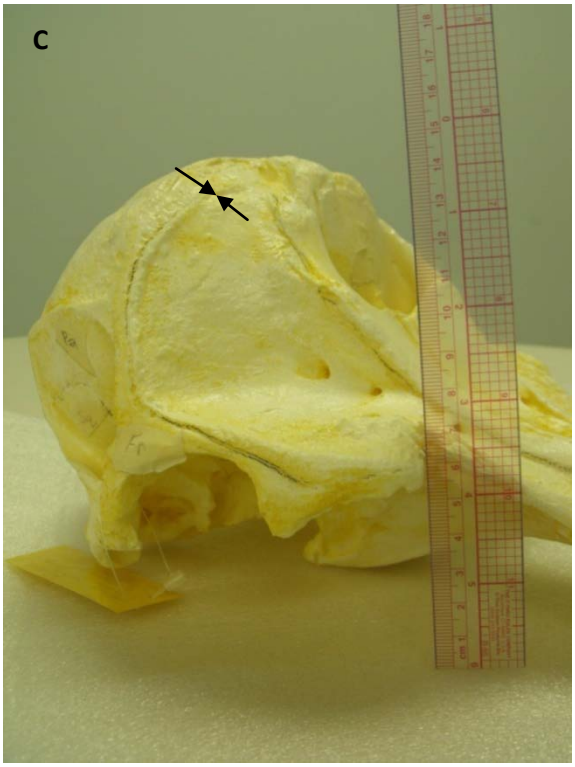


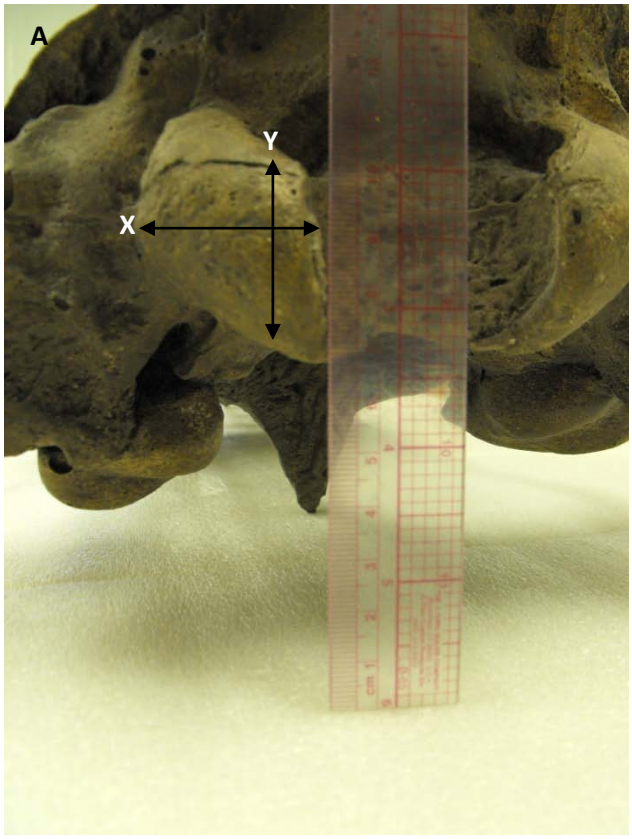
Character 8: Width Across Exoccipital Condyles. Measurement taken from most lateral point on exoccipital condyles; perpendicular to the sagittal plane. Good indicator of species size.

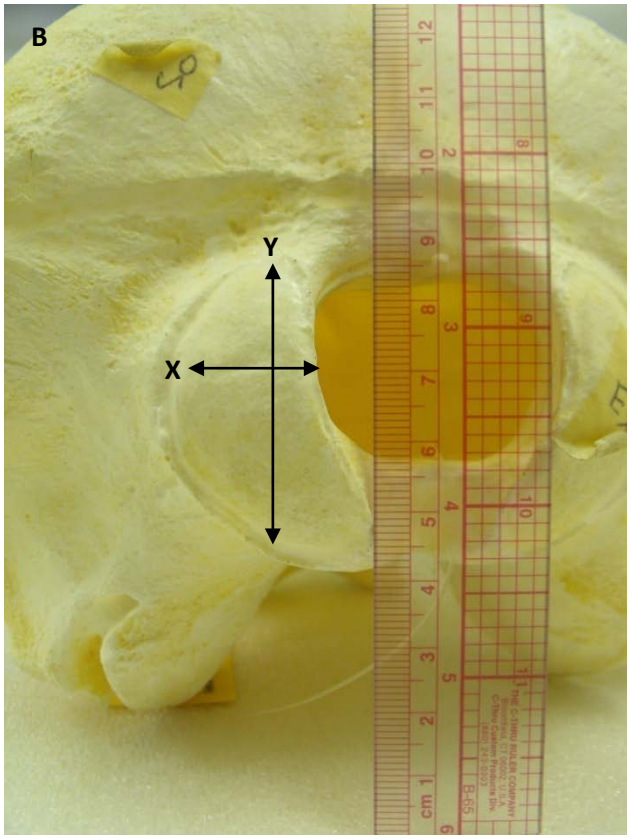


Character 10: Amount of Supraoccipital Overlap Over the Frontal. Picture **A** (*Sotalia fluviatilis*) shows a heavy overlap of the supraoccipital over the frontal. Picture **B** (*Pontoporia blainvillei*) shows a small ridge with slight overlap. Picture **C** (*Delphinus delphis*) shows no overlap of the supraoccipital over the frontal.

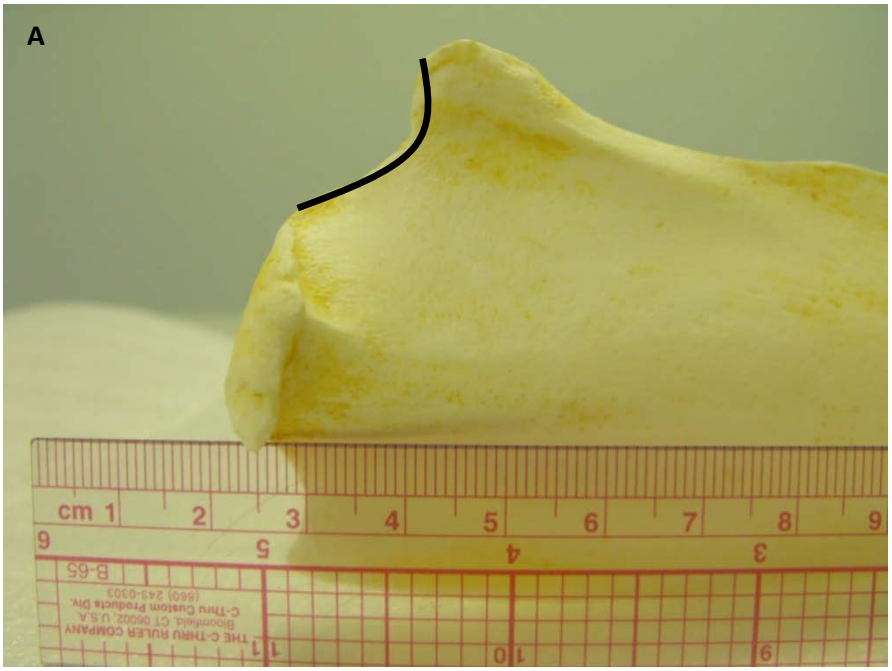


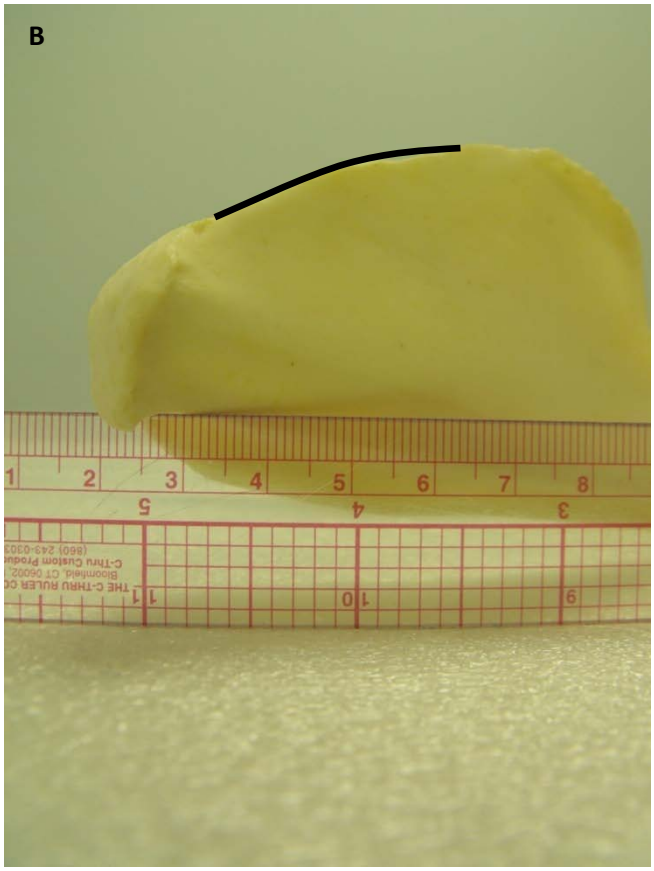




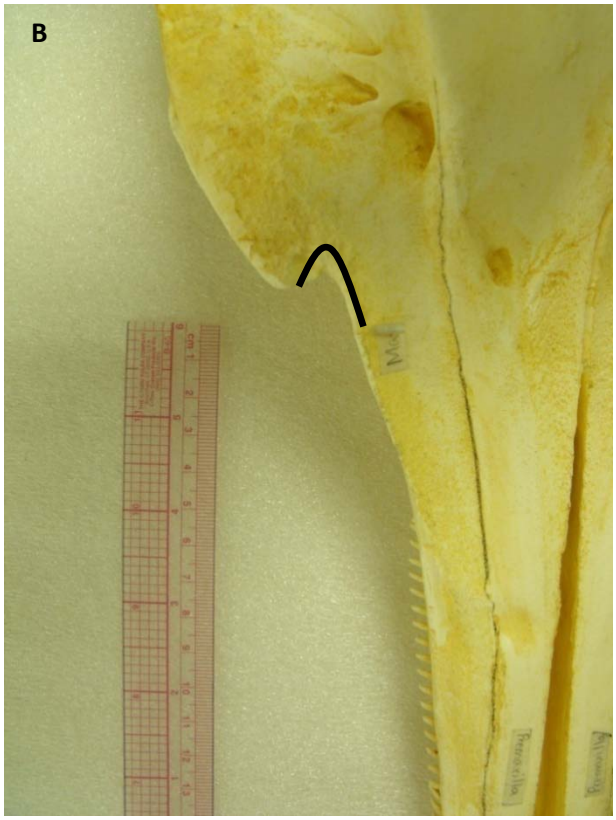


Character 11: Shape of Exoccipital Condyles. Picture **A** (*Georgiacetus vogtlensis*) shows the transverse axis greater than the dorsoventral axis. Picture **B** (*Delphinus delphis*) shows the dorsoventral axis longer than the transverse axis.

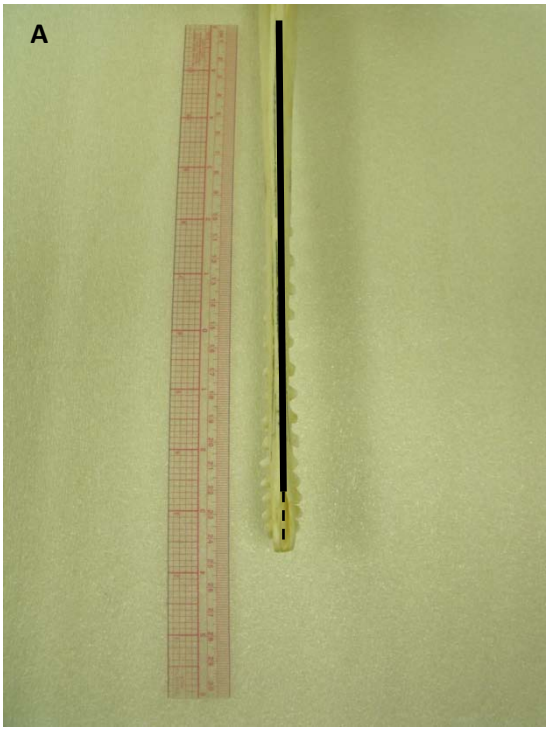




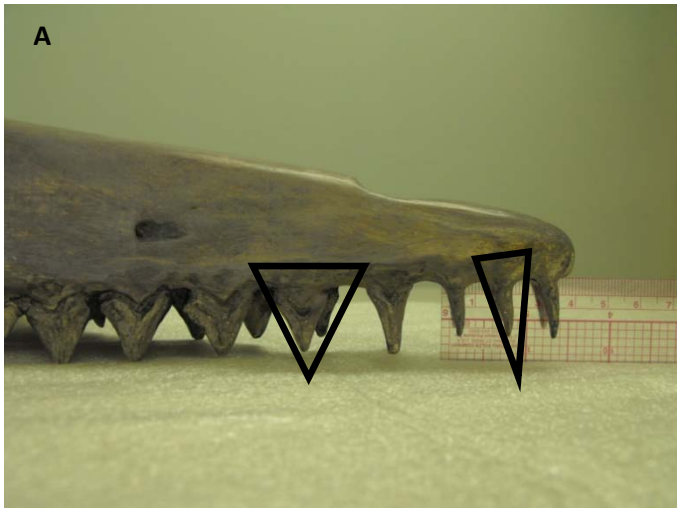
Character 12: Presence of Mandibular Notch. Picture **A** (*Lagenorhynchus obliquidens*) shows a notch in the mandible above the mandibular condyle. Picture **B** (*Platanista gangetica*) lacks the notch.

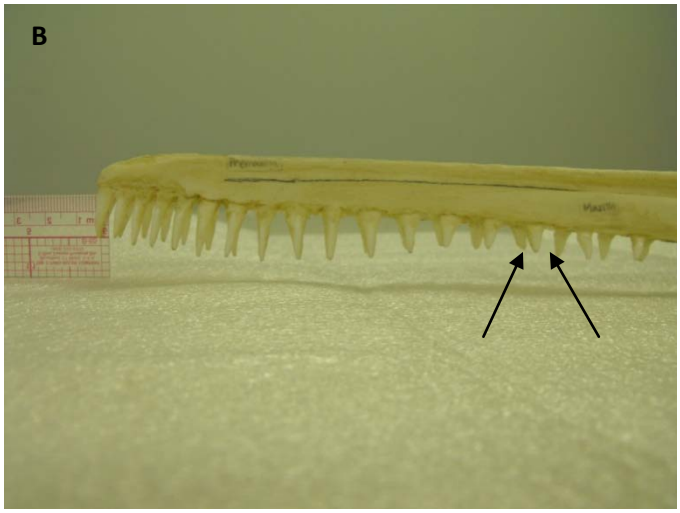


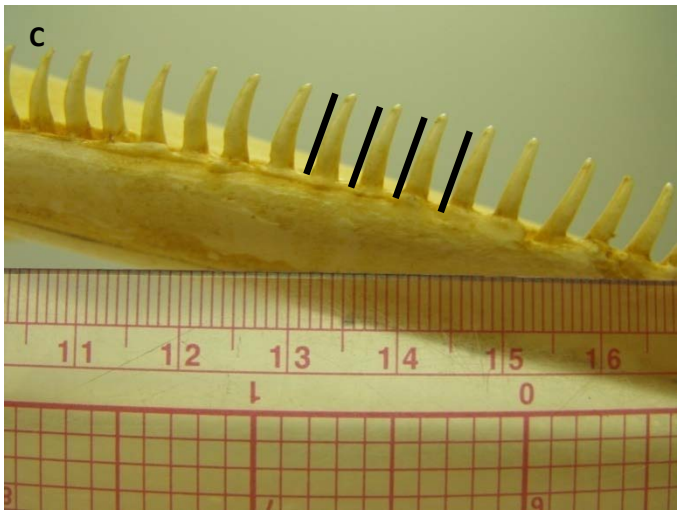
Character 13: Depth of Antorbital Notch. Picture **A** (*Delphinapterus leucas*) shows a deep antorbital notch. Picture **B** (*Lissodelphis borealis*) shows a shallow antorbital notch. Picture **C** (*Georgiacetus vogtlensis*) lacks a definitive antorbital notch.



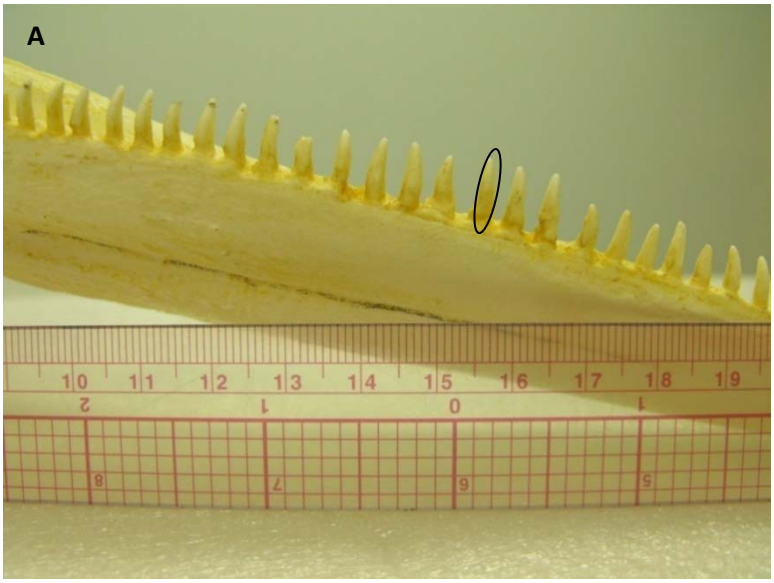
Character 14: Degree of Fusion of Premaxillae. Picture **A** (*Platanista gangetica*) shows the mesorostral canal mostly fused. Picture **B** (*Lagenorhynchus obliquidens*) shows the mesorostral canal partially fused. Picture **C** (*Globicephala macrorhynchus*) shows the mesorostral canal open. The solid lines represent fusion of the rostrum, while the dashed lines represent opening of the rostrum.



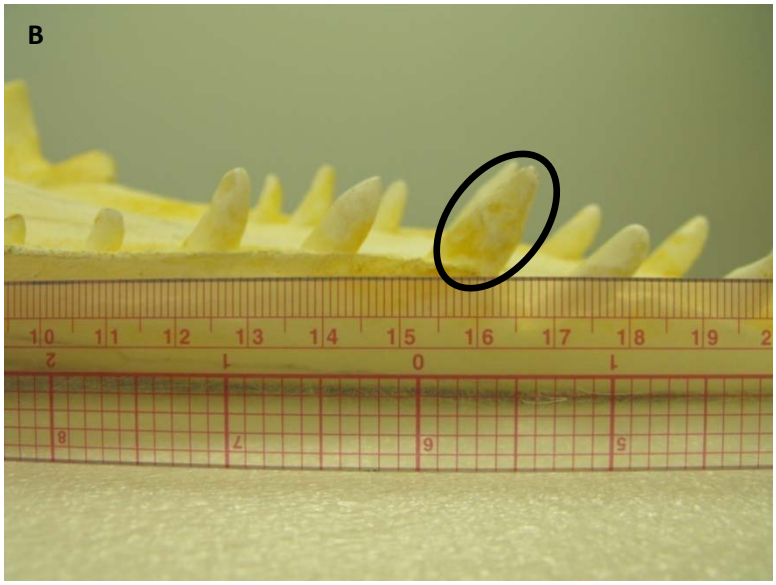


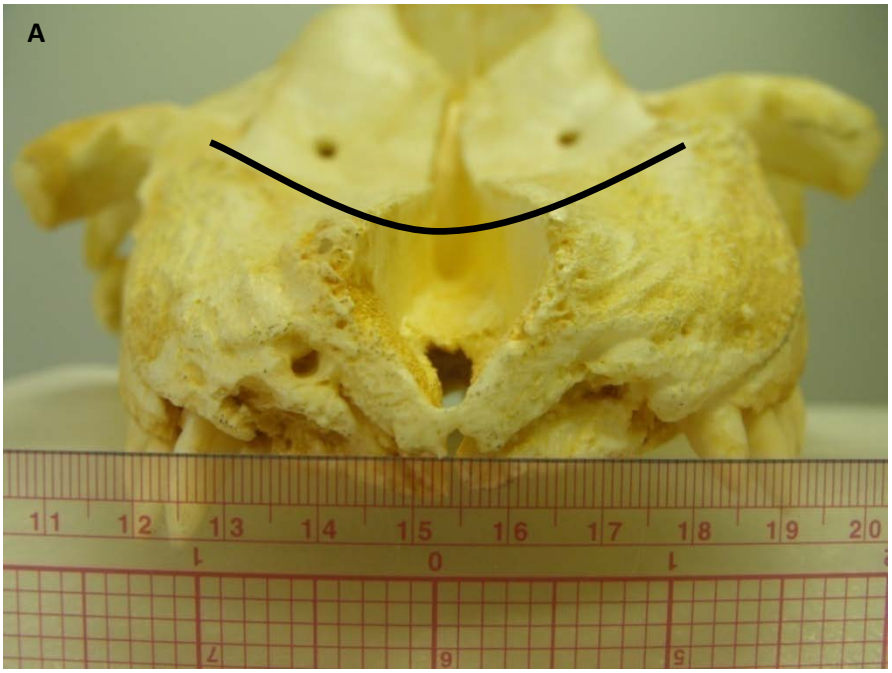


Character 15: Teeth Structure. Pictures **A** (*Pakicetus*) and **B** (*Platanista gangetica*) show variation in tooth size/shape within the individuals. Also picture **B** shows asymmetry in the tooth alignment (arrows). Picture **C** (*Lissodelphis borealis*) shows a uniform tooth structure; similarly sized, shaped, and spaced.

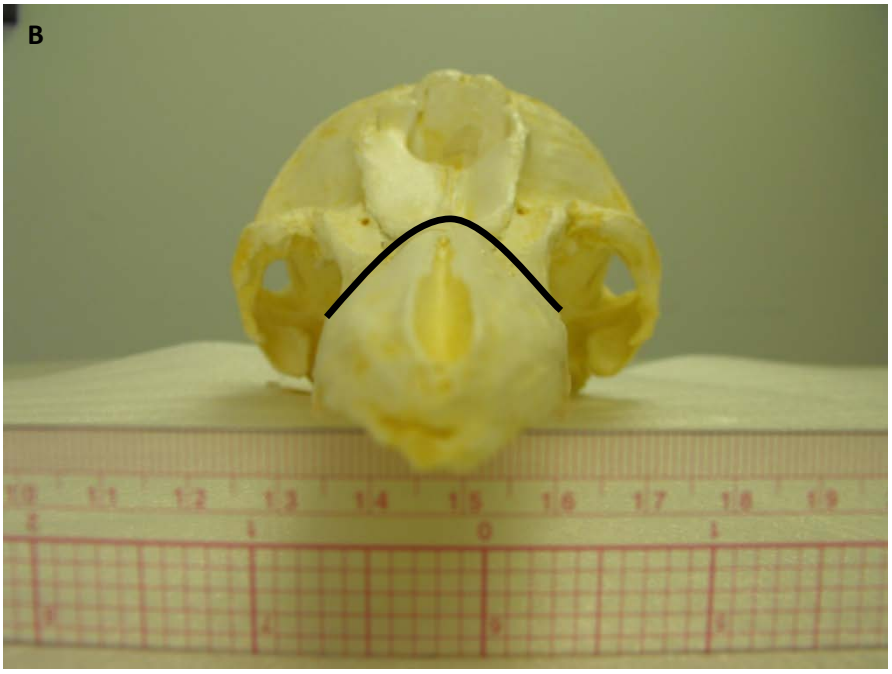


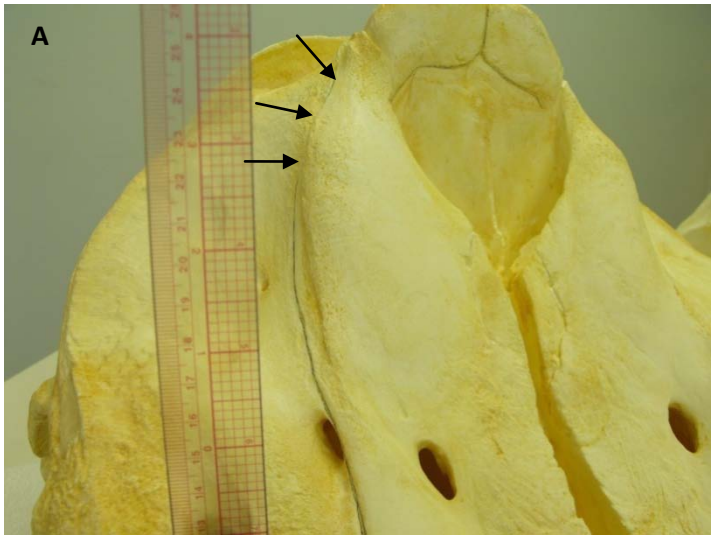
Character 16: Tooth Shape. Picture **A** (*Lagenorhynchus obliquidens*) shows thin, small peg-like teeth. Picture **B** (*Delphinapterus leucas*) shows thick, bulky teeth.

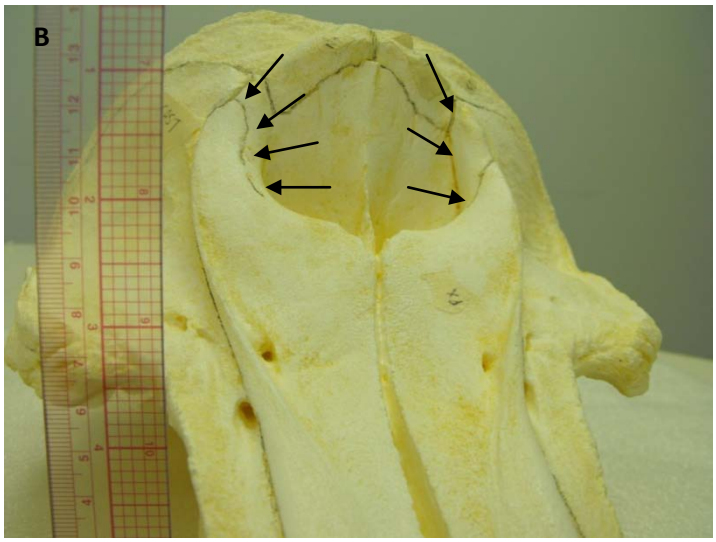


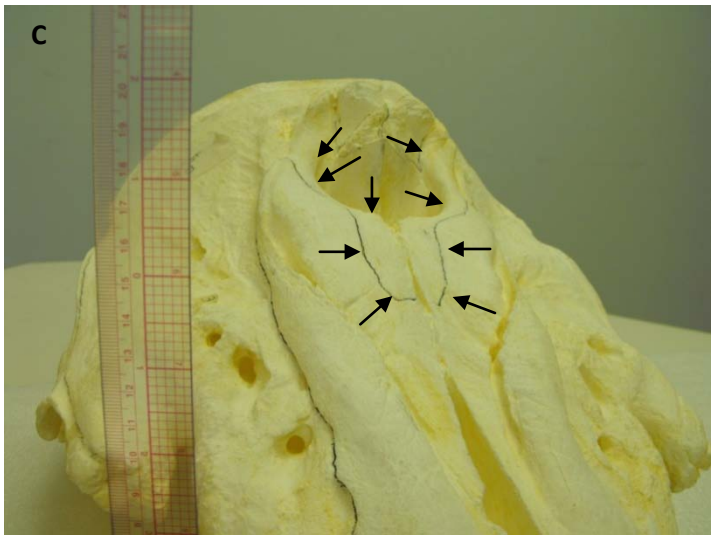


Character 17: Shape of Rostrum. Picture **A** (*Globicephala macrorhynchus*) shows a concave rostrum. Picture **B** (*Delphinus delphis*) shows a convex rostrum.

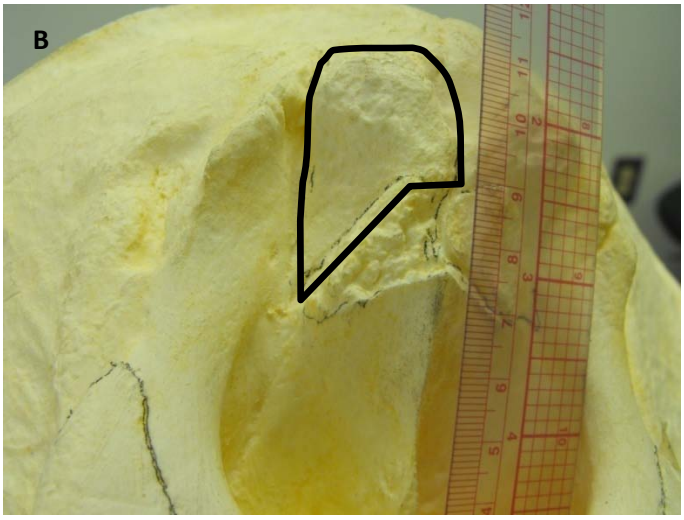




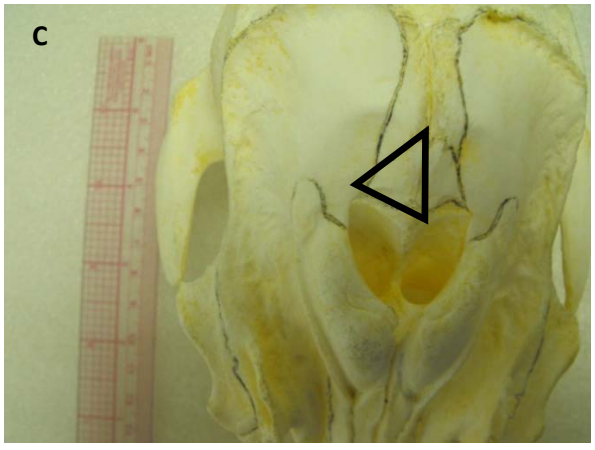


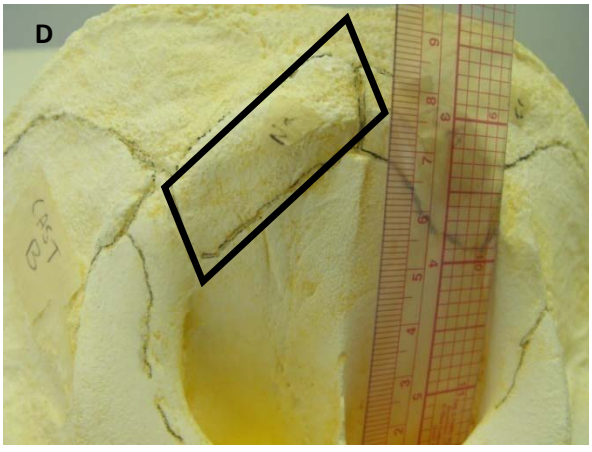


Character 18: Extension of Maxilla into External Bony Nares. Picture **A** (*Globicephala macrorhynchus*) shows no extension of the maxilla into the nasal opening. Picture **B** (*Lagenorhynchus obliquidens*) shows a little extension of maxilla into the nasal opening. Picture **C** (*Delphinapterus leucas*) shows a dramatic extension of the maxilla into the nasal opening and covering part of the premaxilla. The arrows show the extension or lack thereof.

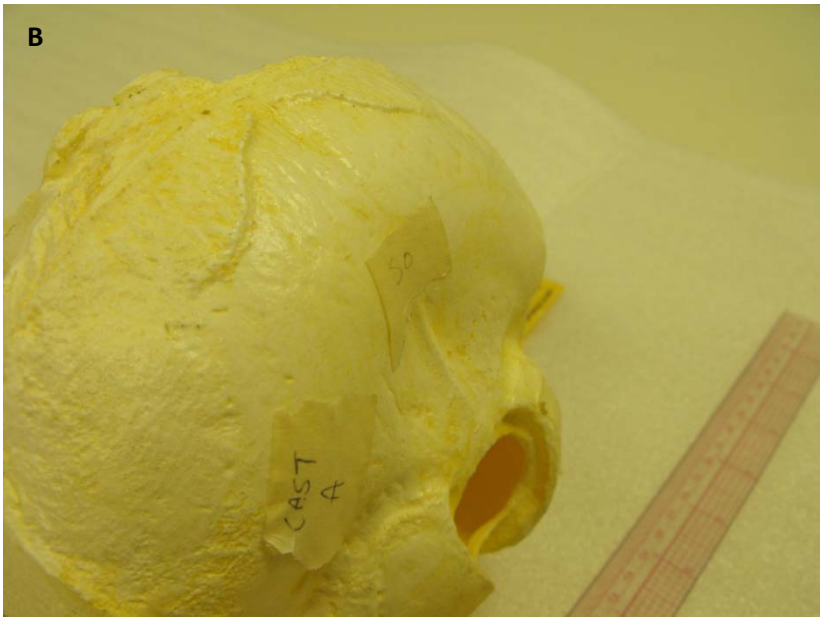


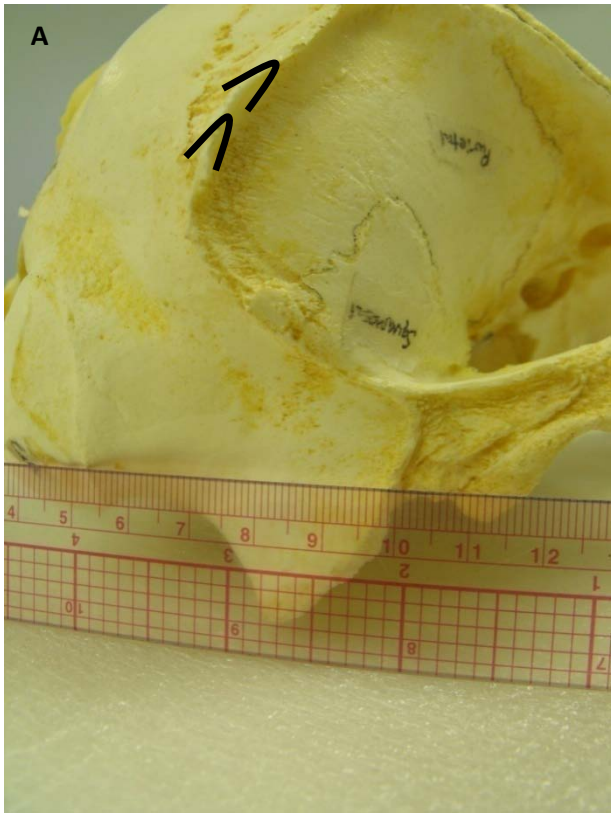
Character 19: Shape of Nasals. Picture A (*Sotalia fluiatilis*) has round nasals. Picture B (*Delphinapterus leucas*) has teardrop nasals. Picture C (*Pontoporia blainvillie*) has triangular nasals. Picture D (*Lagenorhynchus obliquidens*) has square/rectangular nasals.



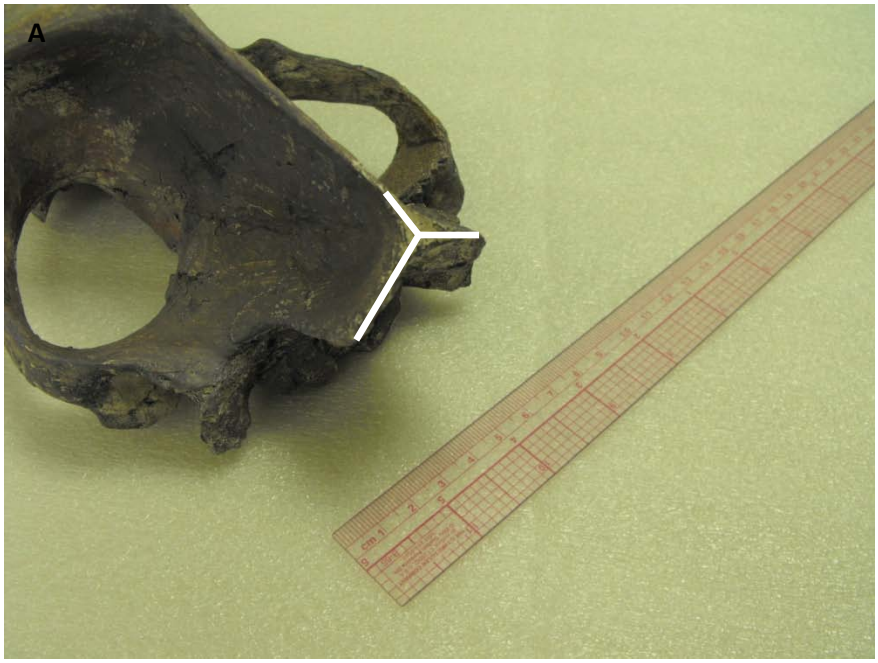


Character 20: Presence of a Sagittal Crest on the Occiput. Picture **A** (*Sotalia fluviatilis*) shows a sharp ridge on the occiput. Picture **B** (*Delphinus delphis*) shows no sagittal crest on the occiput (but a slight ridge lower on the occipital).

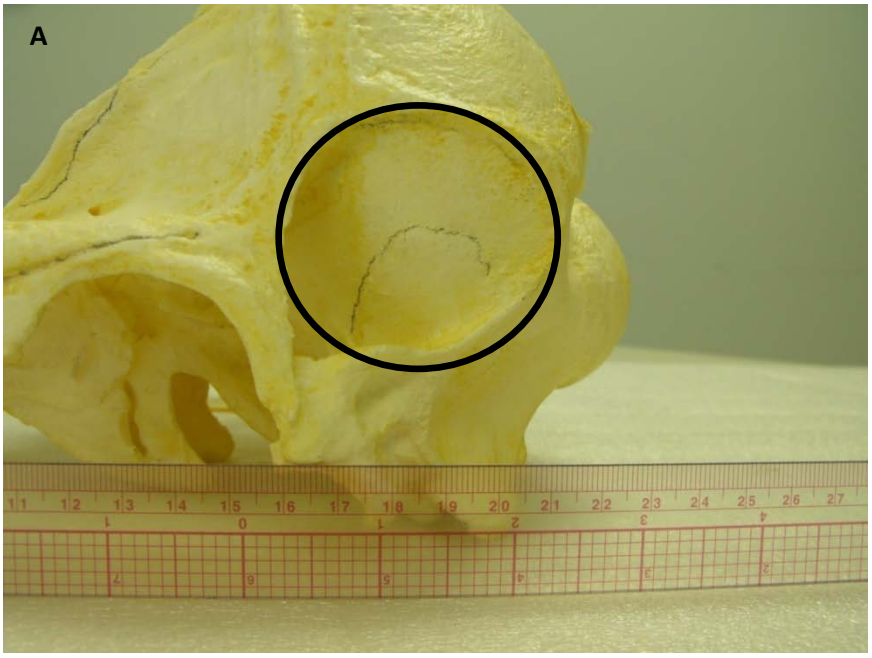




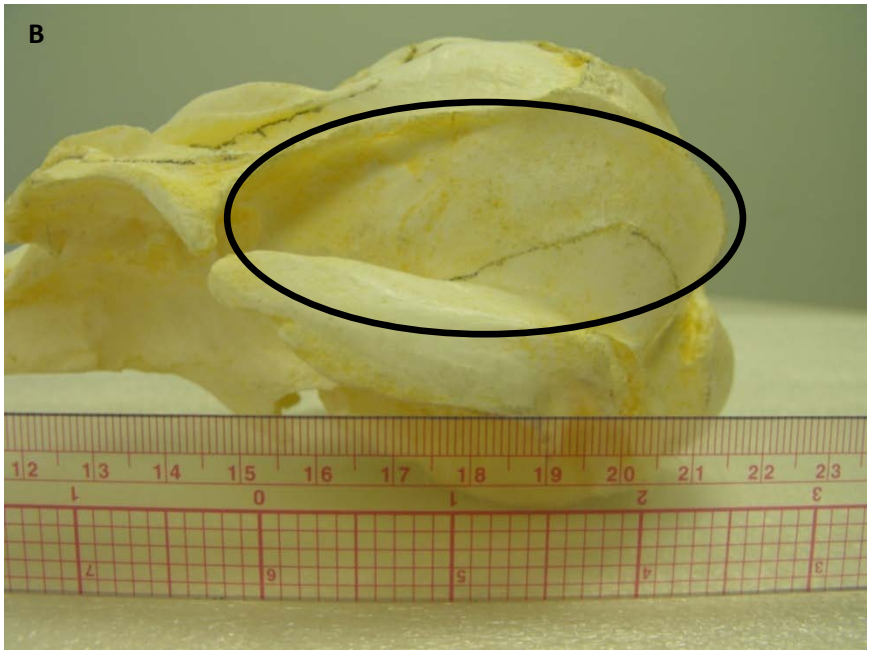
Character 21: Lamdoidal Crest. Picture **A** (*Sotalia fluviatilis*) shows a sharp ridge at the meeting of the parietal and occipital. Picture **B** (*Platanista gangetica*) shows a smooth ridge forming the lamdoidal crest.



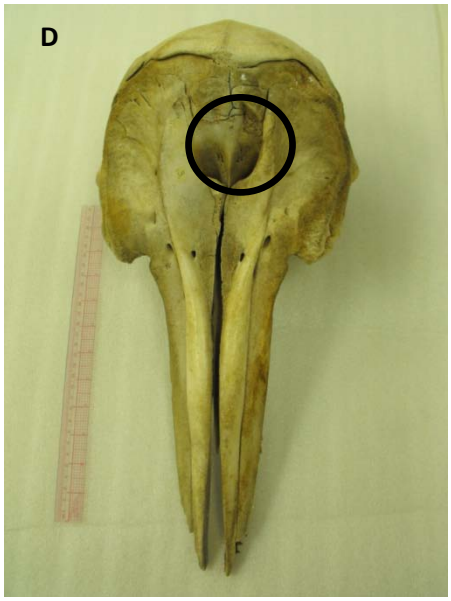
Character 22: Presence of a Nuchal Crest. Picture **A** (*Pakicetus*) shows the nuchal crest as the most posterior projection on the skull. Picture **B** (*Tursiops truncatus*) shows no sign of a nuchal crest.

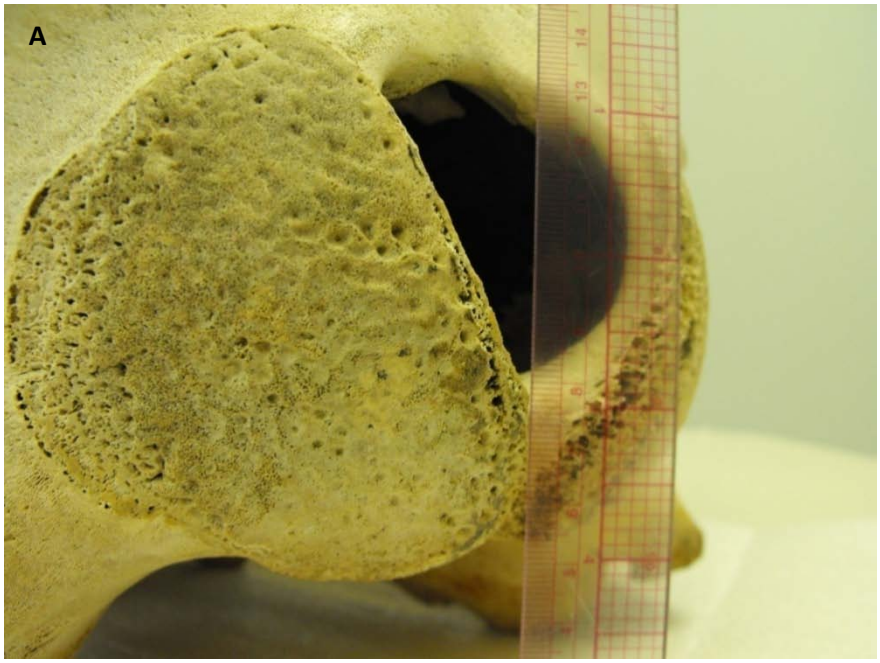


Character 23: Shape of Temporal Fossa. Picture **A** (*Delphinus delphis*) shows a round temporal fossa. Picture **B** (*Pontoporia blanvillei*) shows an elongated

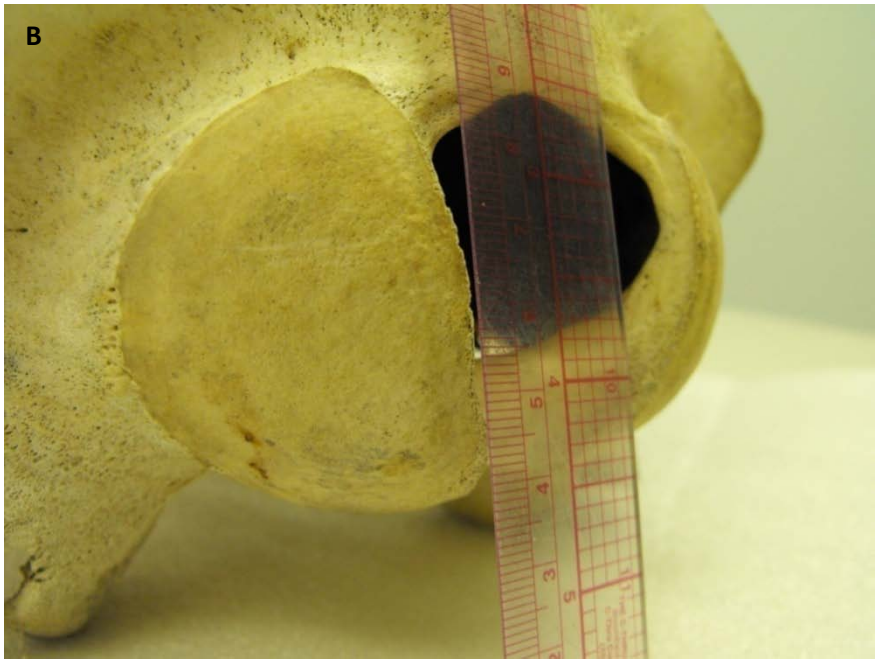


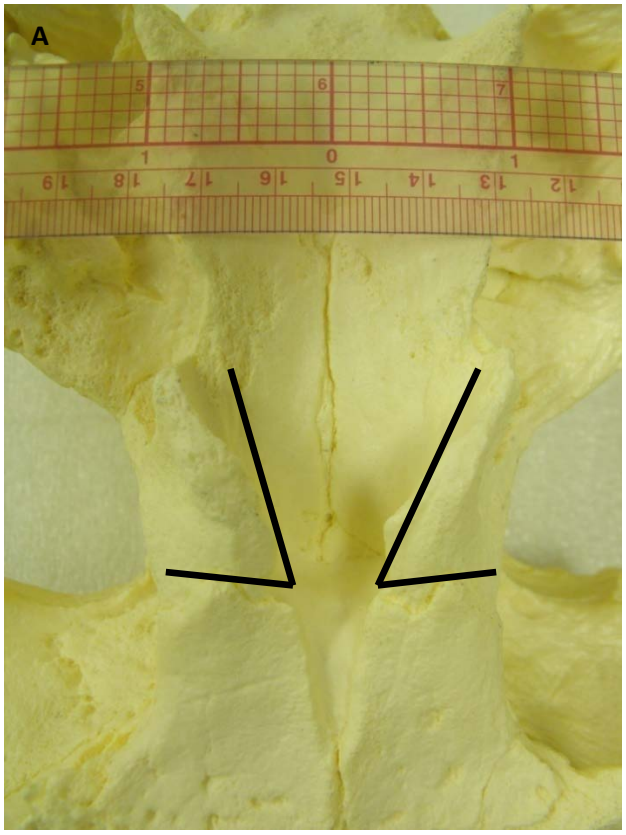
Character 24: Position of Blowhole on Rostrum. Picture **A** (*Pakicetus*) has a blowhole most anteriorly (This is speculative. The fossil used to make this cast did not have a rostrum intact). Picture **B** (*Georgiacetus vogtlensis*) has a blowhole anterior, middle. Picture C (Xenorophoid) has a blowhole posterior, middle. Picture **D** (*Tursiops truncatus*) has a blowhole posterior to the rostrum.



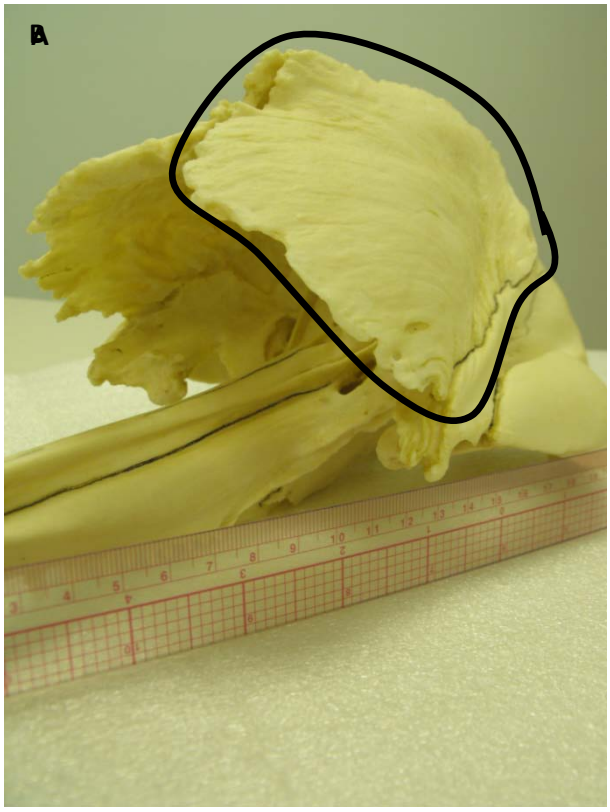


Character 26: Texture of Exoccipital Condyles. Picture **A** (*Globicephala macrorhynchus*) shows rough, pitted condyles. Picture **B** (*Tursiops truncatus*) shows smooth condyles.

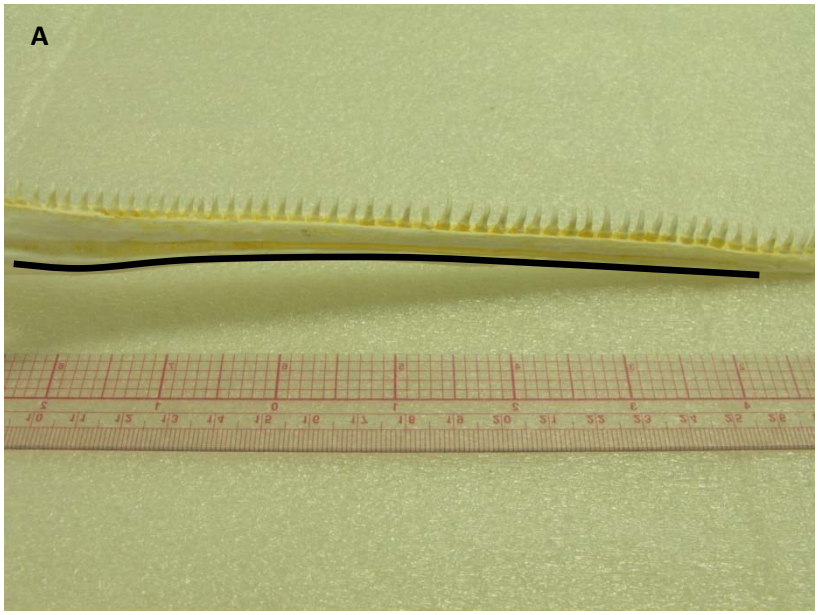




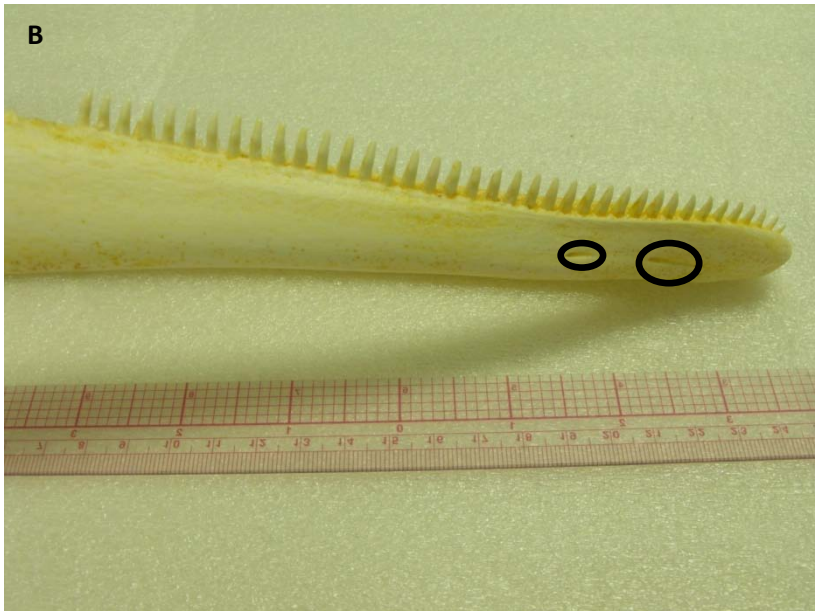
Character 28: Do Pterygoids Touch at Most Medial Part? Picture **A** (*Archaeodelphis patrius*) shows how pterygoids do not touch each other. Picture **B** (*Delphinus delphis*) shows how pterygoids do touch and fuse at most medial part.

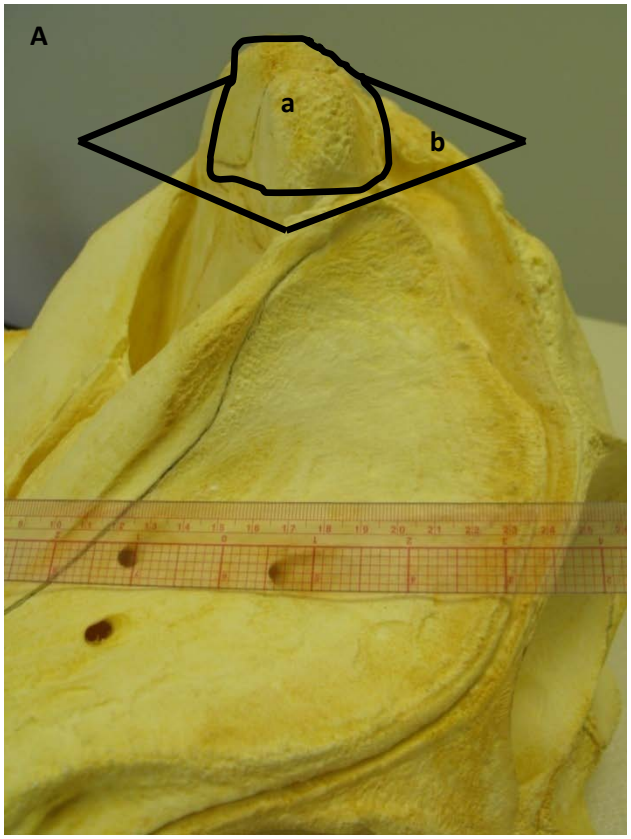


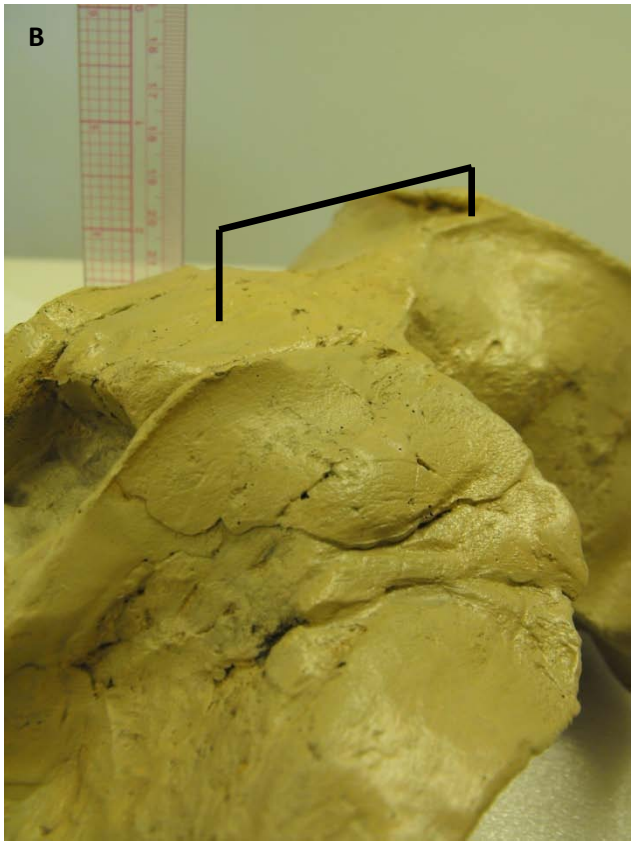
Character 29: Presence of Maxillary Crest. Picture **A** (*Platanista gangetica*) shows this. Picture **B** (*Lagenorhynchus obliquidens*) lacks this feature.



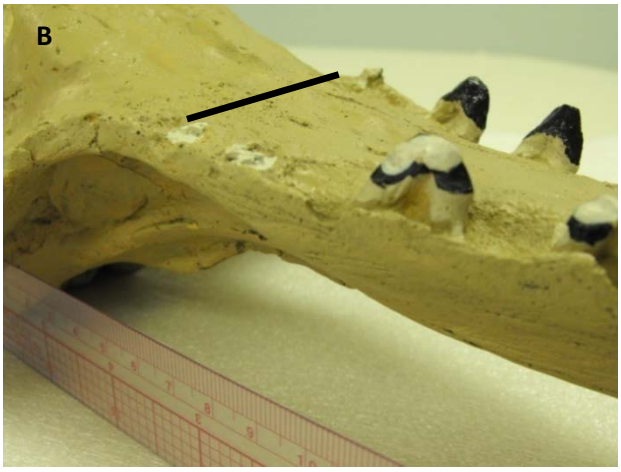
Character 30: Presence of Mandibluar Groove. Picture **A** (*Pontoporia blainvillei*) shows a groove running along the lateral side of the mandible. Picture **B** (*Lagenorhynchus obliquidens*) shows no groove, but tiny foramina (possible homologs).



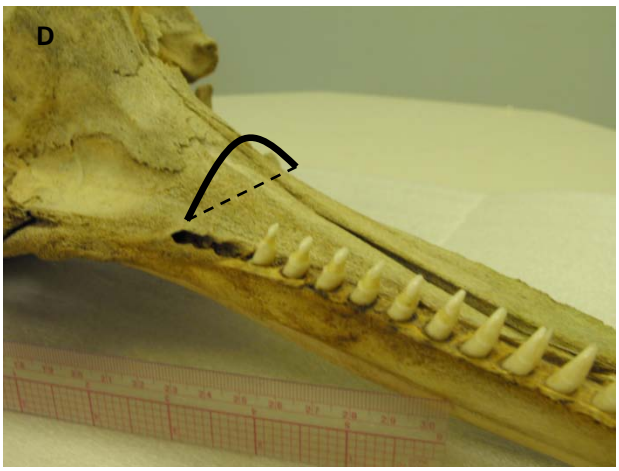


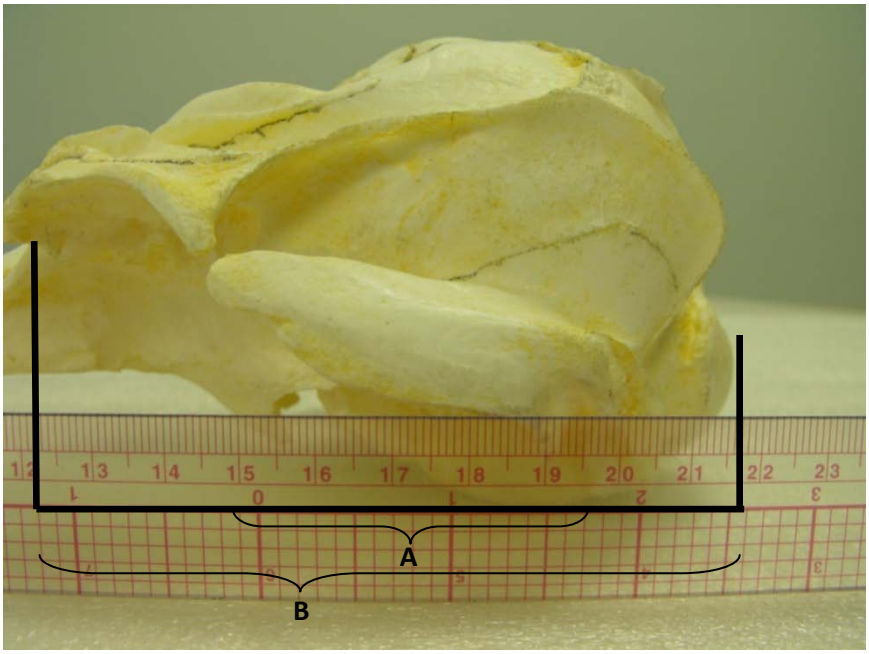


Character 33: Position of Nasals Relative to Braincase. Picture **A** (*Globicephala macrorhynchus*) shows nasals (**a**) set atop the braincase (represented as plane **b**). Picture **B** (Xenorophoid) shows the nasals positioned below the top of the braincase.



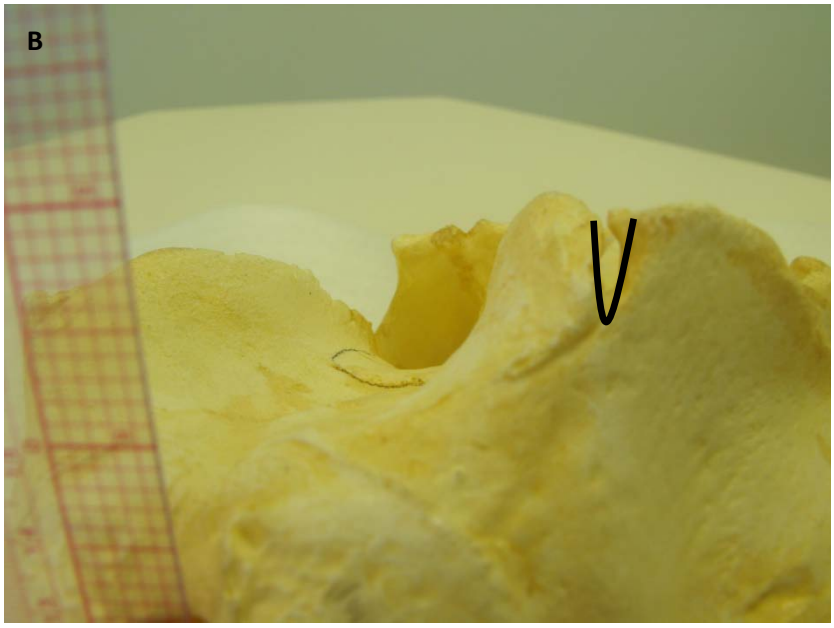
Character 34: Angle of Palate. Pictures **A** and **B**(Xenorophoid) shows the palate flat. Pictures **C** and **D** (*Tursiops truncatus*) shows the palate vaulted. Measument taken from most posterior teeth, perpendicular to the sagittal plane.

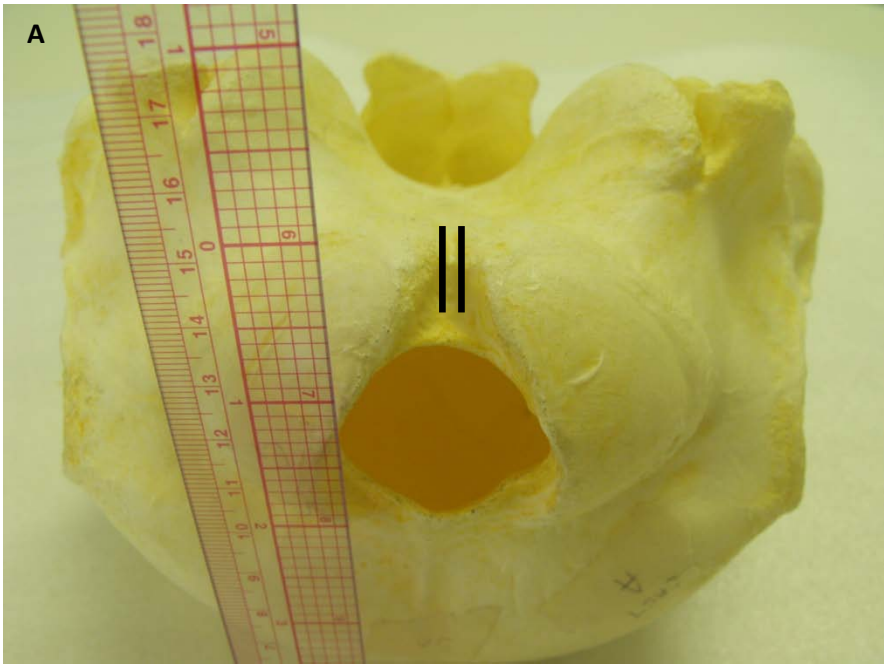




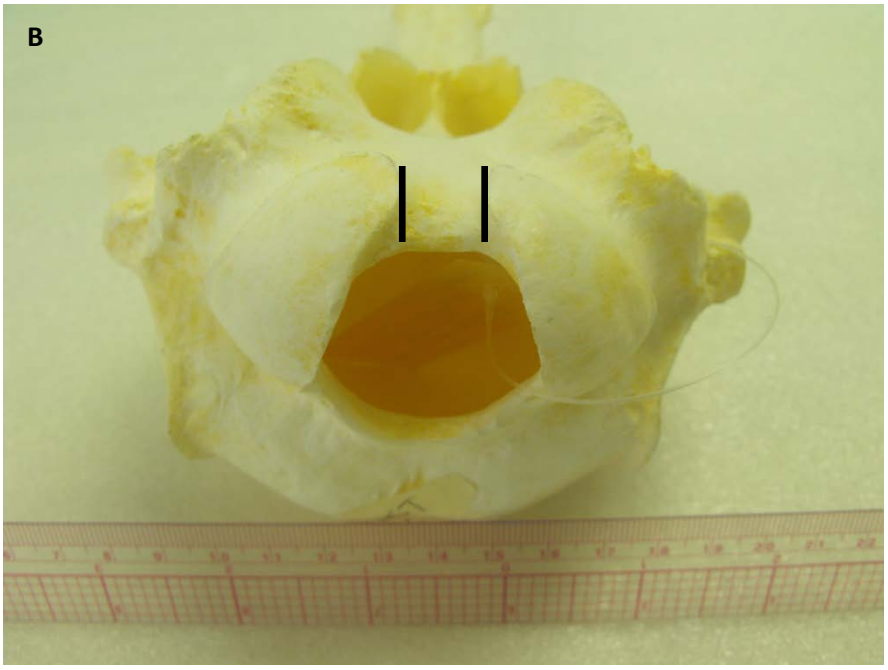
Character 35: Length of Squamosal versus Length of Skull (posterior to antorbital notch). Squamosal measured from external acoustic meatus (A). Skull measured from antorbital notch to exoccipital (B).

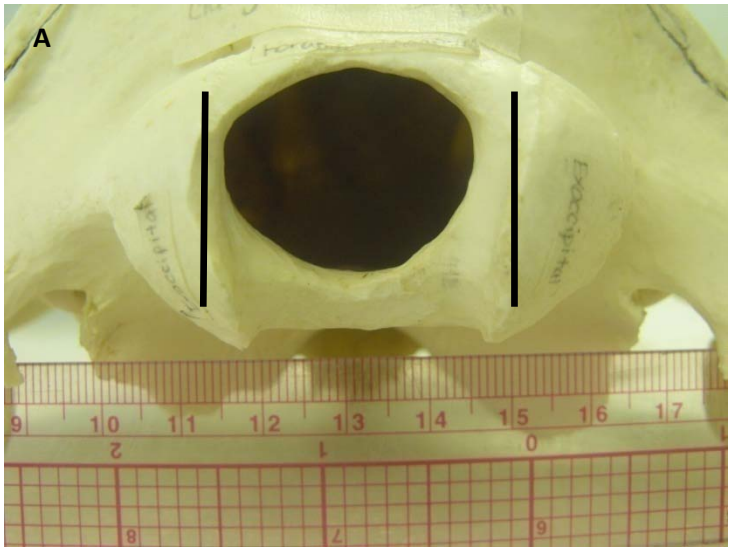
Character 36: Jugular Notch. Picture **A** (Xenorophoid) shows a wide and shallow notch (In this cast the width of the jugular notch may be partially due to damage). Picture **B** (*Lissodelphis borealis*) shows a skinny and deep notch.

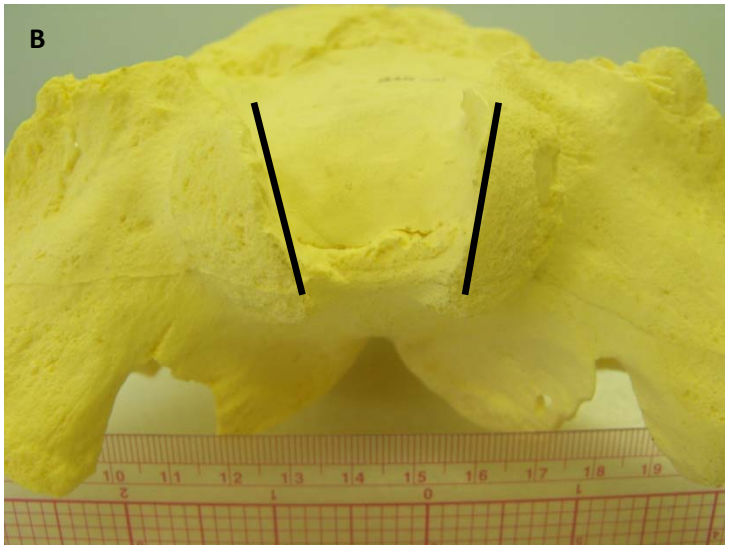


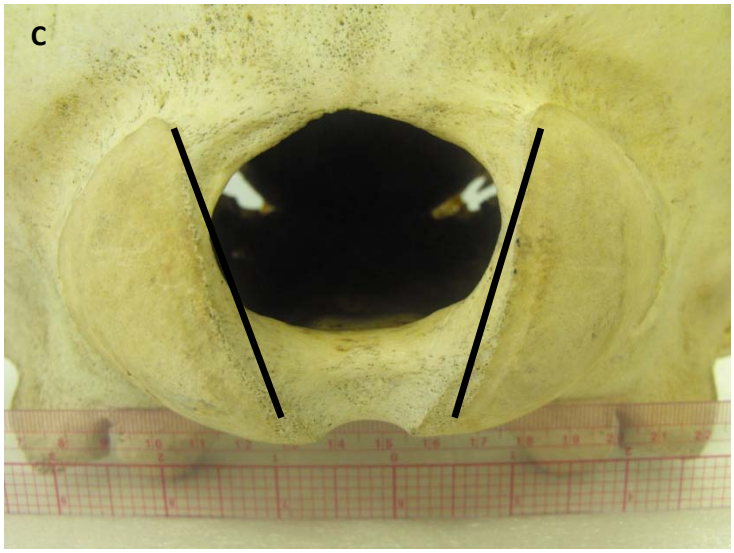


Character 37: Interconyloid Notch. Picture **A** (*Delphimus delphis*) shows a narrow space between the exoccipitals. Picture **B** (*Pontoporia blainvillei*) shows a wide notch.

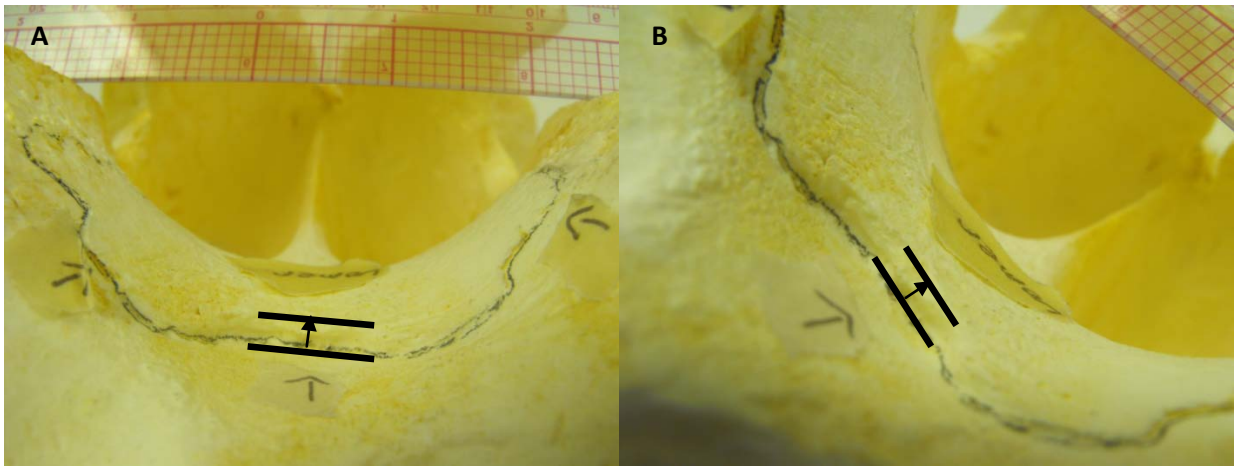




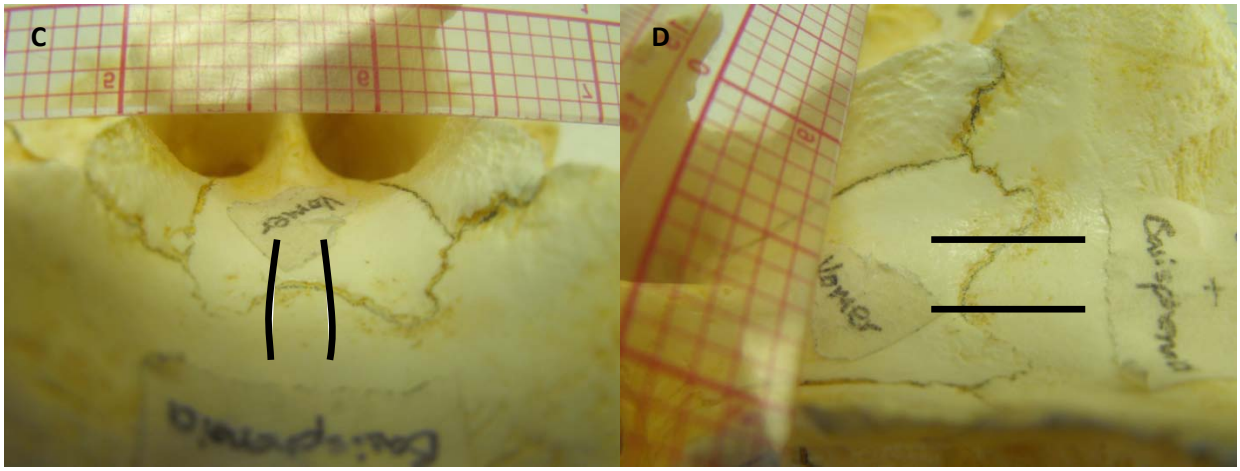


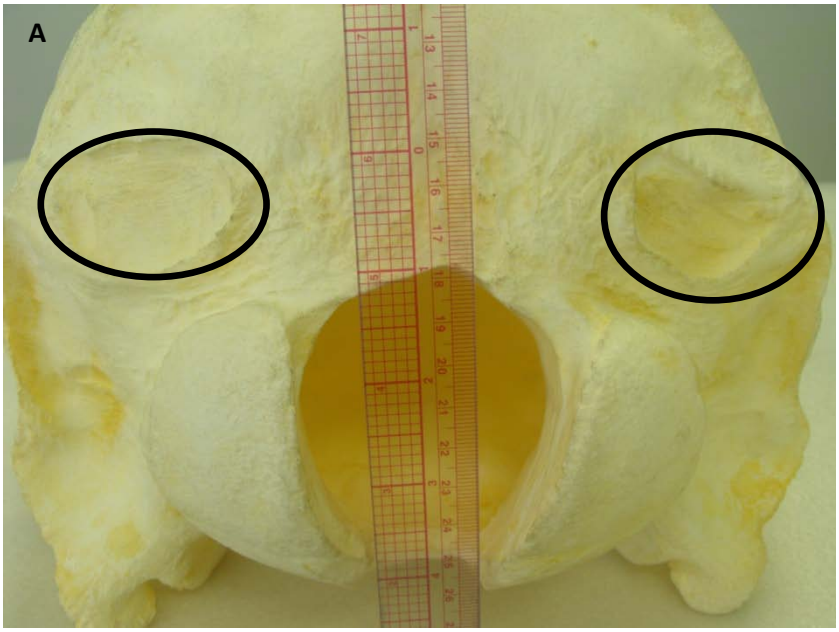


Character 38: Angle of Exoccipital Condyles. Picture **A** (*Platanista gangetica*) shows nearly parallel condyles. Picture **B** (*Archaeodelphis patrius*) shows slightly V-angled condyles. Picture **C** (*Tursiops truncatus*) shows wider angled occipitals.

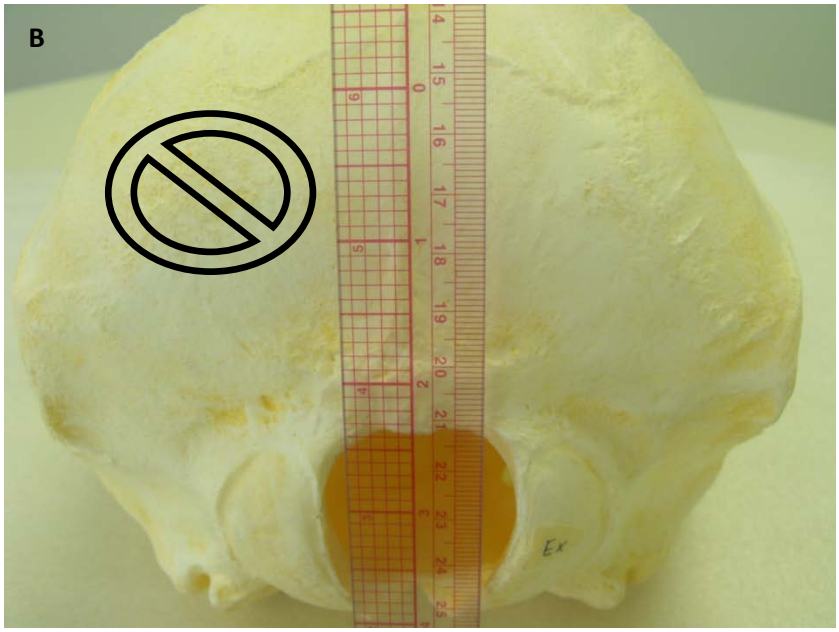


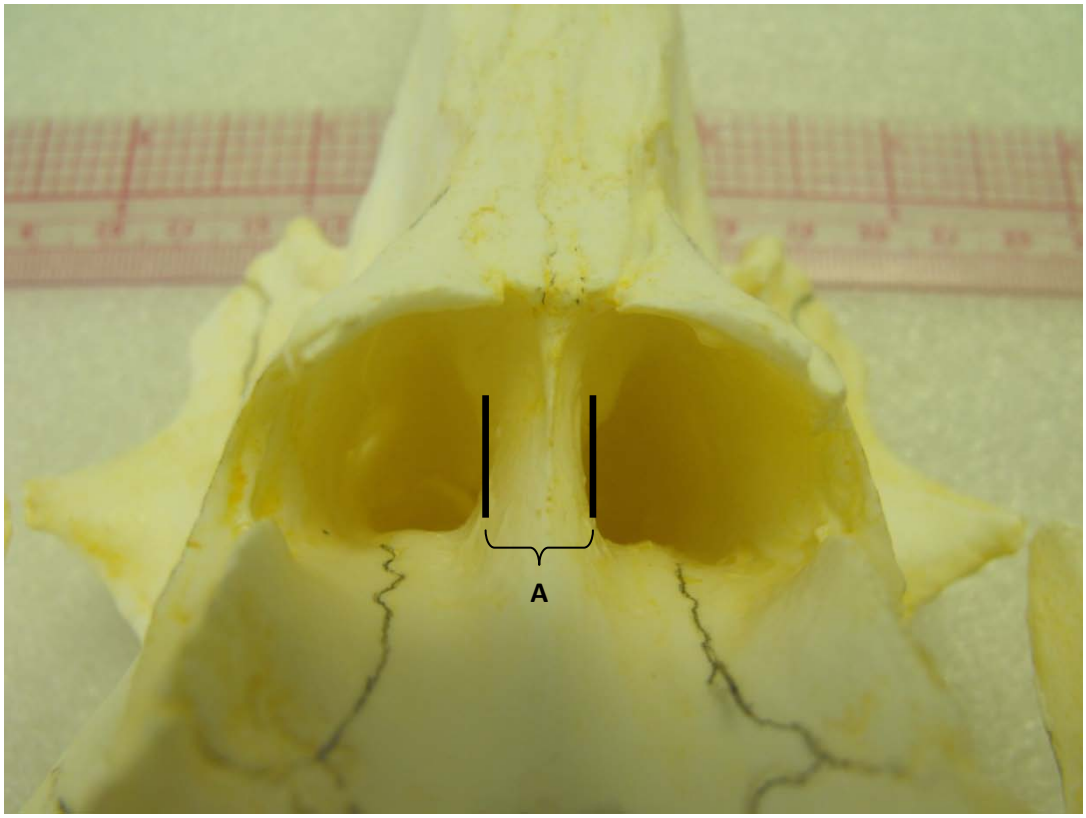
Character 39: Vomer to Basisphenoid. Pictures **A** and **B** (*Globicephala macrorhynchus*) show the vomer elevated over the basisphenoid. Pictures **C** and **D** (*Sotalia fluviatilis*) show the vomer and basisphenoid smoothly fused.



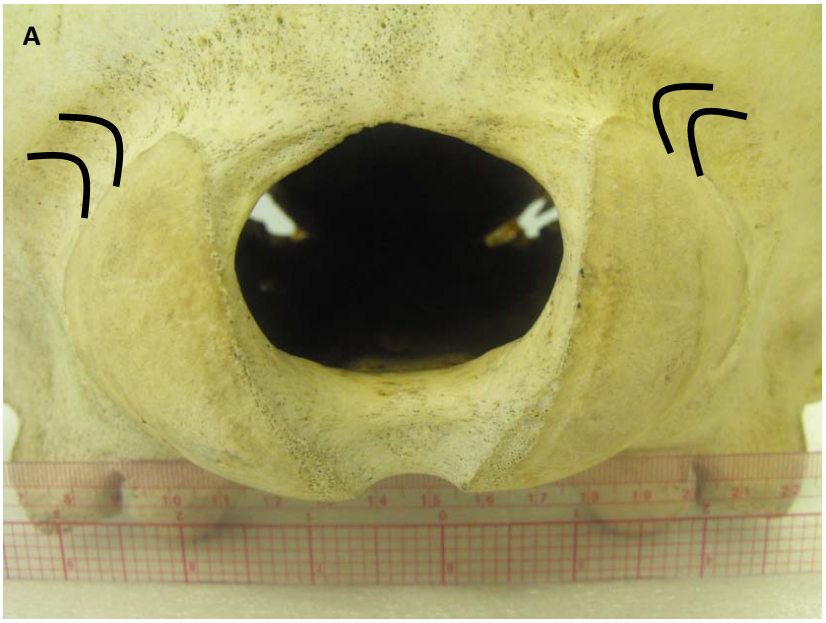


Character 40: Presence of Supraoccipital Fenestra. Picture **A** (*Delphinapterus leucas*) shows the groove. Picture **B** (*Lagenorhynchus obliquidens*) does not have this groove.

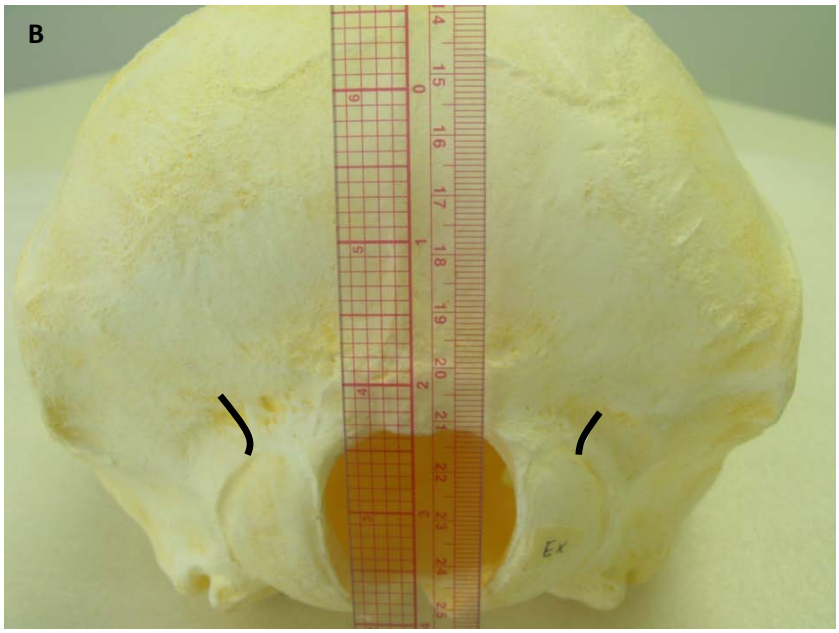


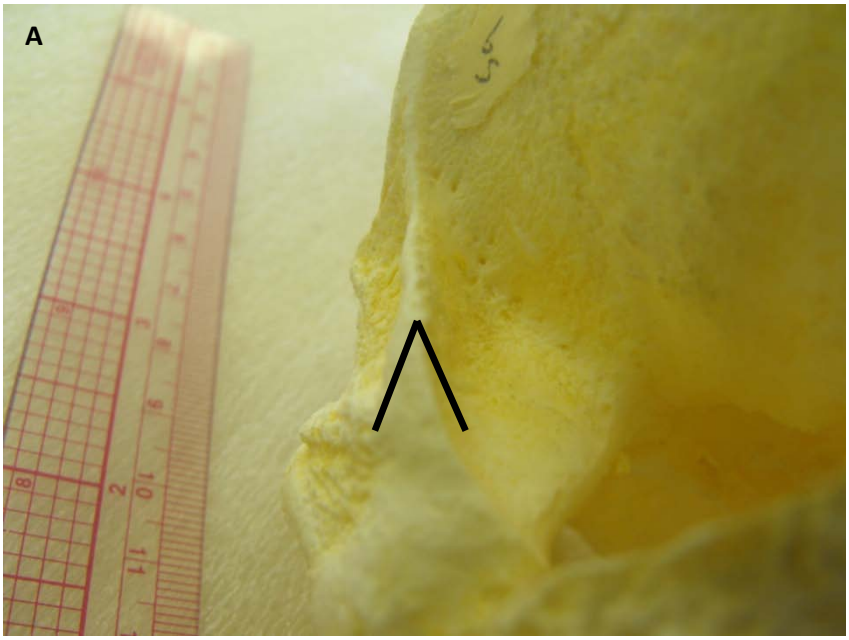


Character 41: Width of Vomerine Crest. Represented as **A** in the picture above.

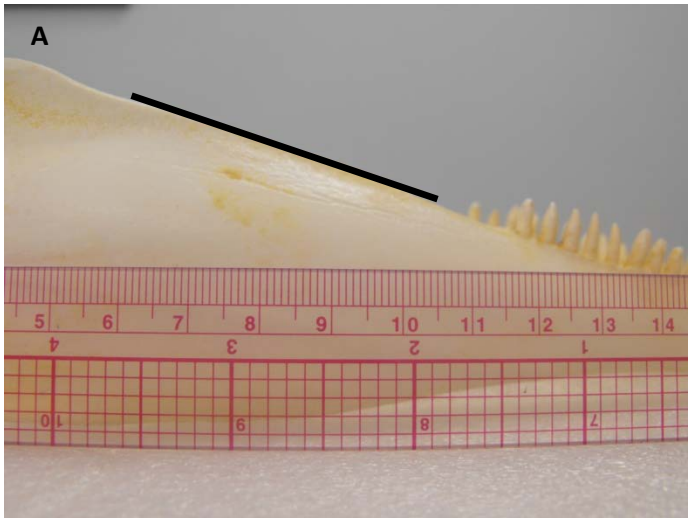


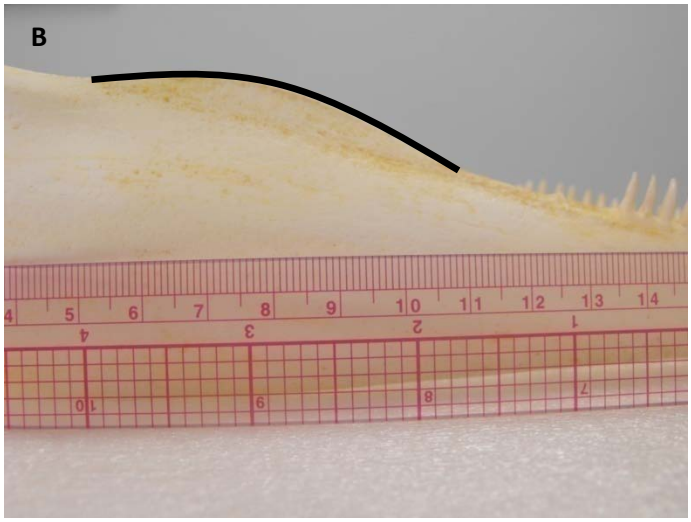
Character 42: Depth of Dorsal Condyloid Fossa. Picture **A** (*Tursiops truncatus*) shows a deep fossa above the exoccipitals. Picture **B** (*Lagnorhynchus obliquidens*) shows very little fossa above the exoccipitals.

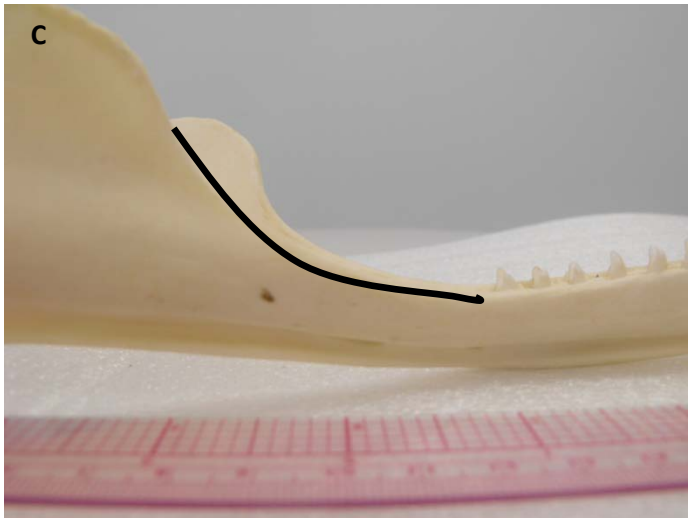




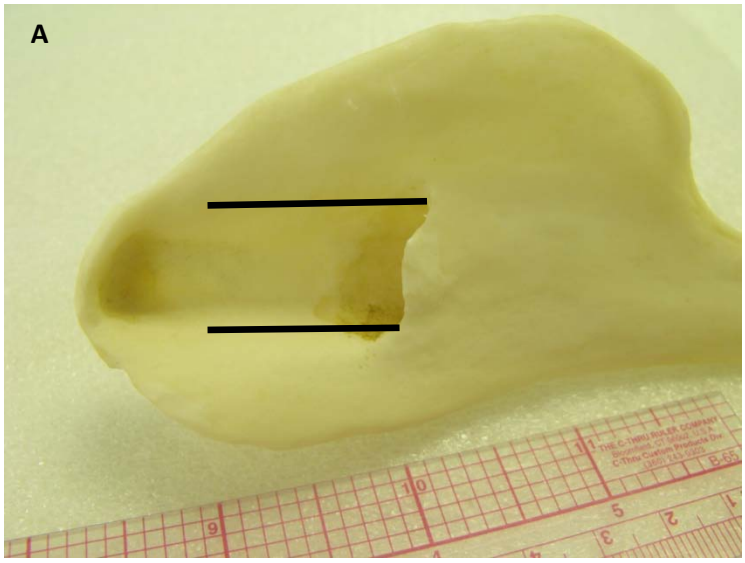
Character 43: Subtemporal Crest. Picture **A** (*Lagenorhynchus obliquidens*) shows a sharp crest. Picture **B** (*Platanista gangetica*) shows a rounded crest.

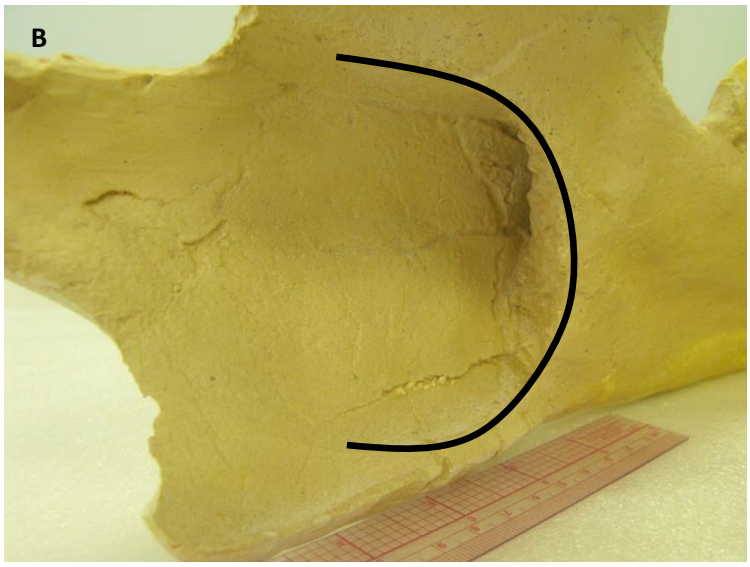


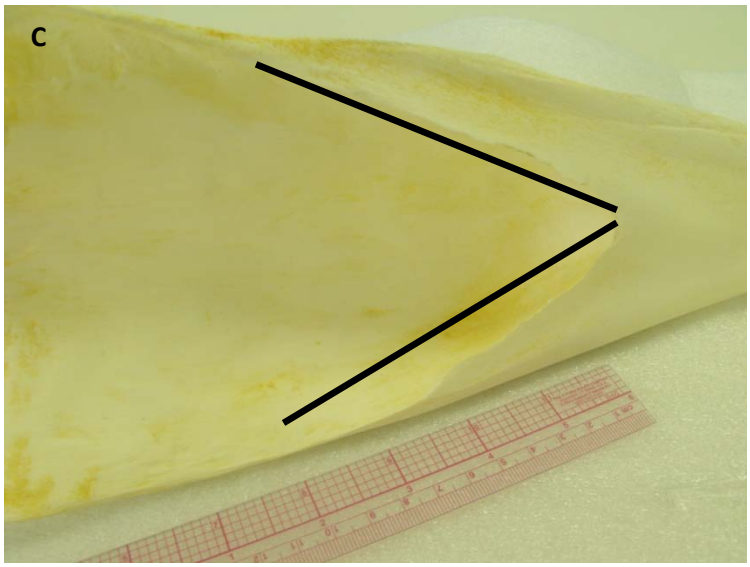




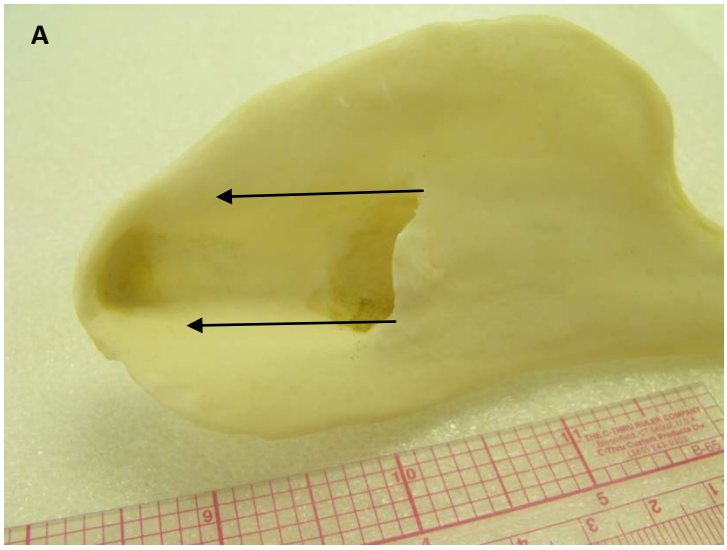
Character 44: Angle of Coronoid Ramus. Picture **A** (*Sotalia fluviatilis*) shows a flat/straight ramus. Picture **B** (*Lissodelphis borealis*) shows an arc in the ramus. Picture **C** (*Platanista gangetica*) shows a dip in the ramus.

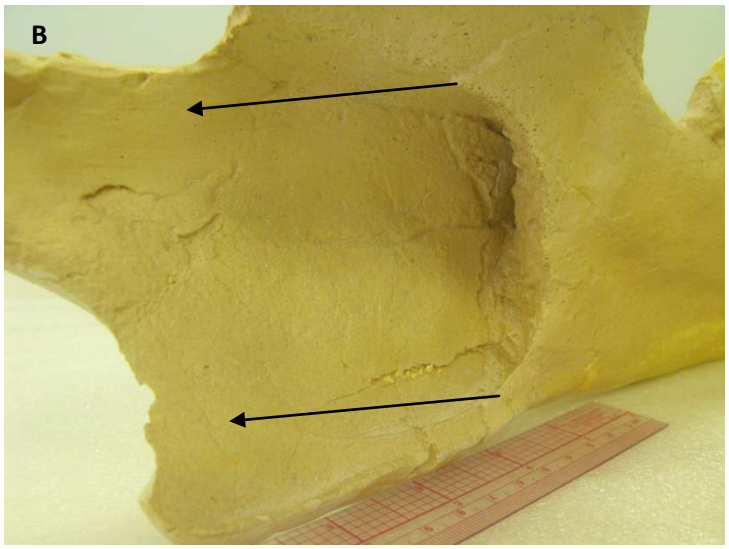


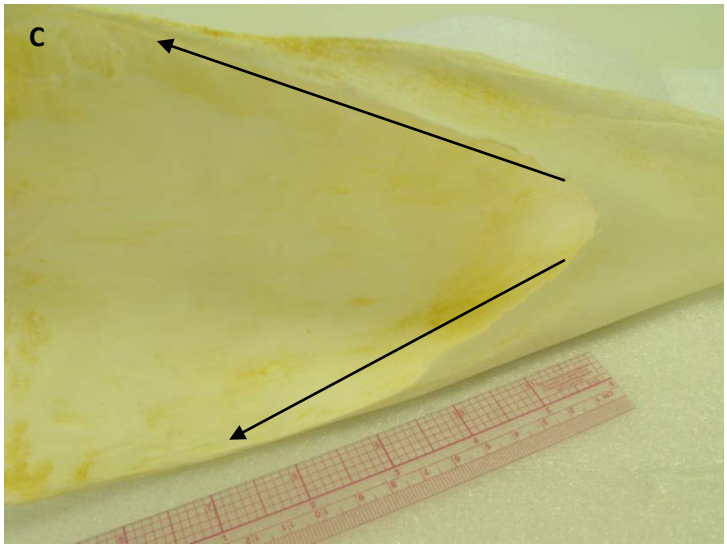




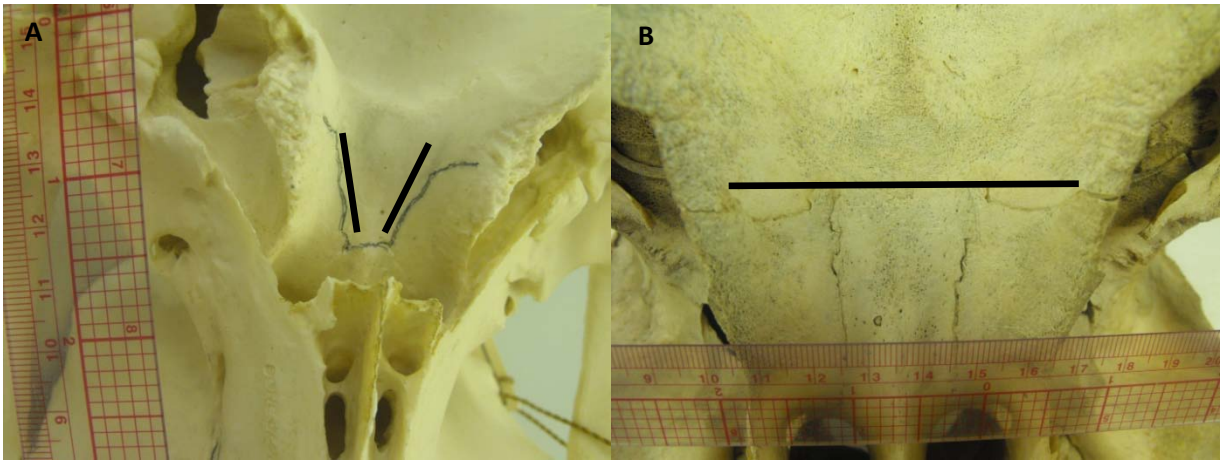
Character 45: Shape of Mandibular Foramen. Picture **A** (*Platanista gangetica*) shows the opening square shaped. Picture **B** (*Georgicetus vogtlensis*) shows the opening rounded. Picture **C** (*Globicephala macrorhynchus*) shows the opening pointed.



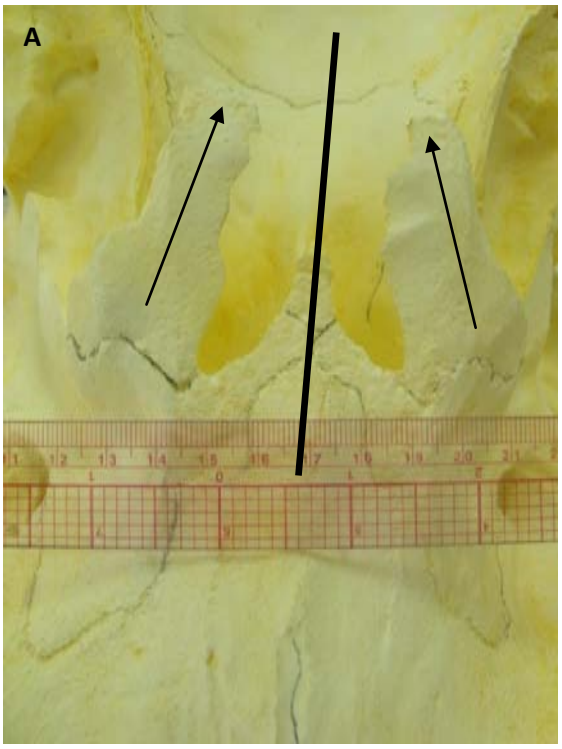




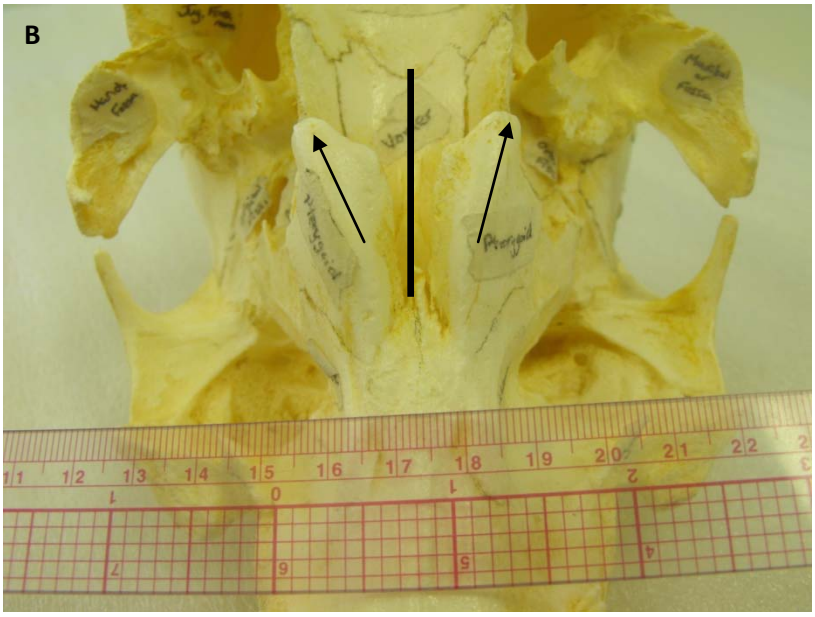
Character 46: Shape of Mandibular Fossa. Pictures **A** (*Platanista gangetica*) **B** (*Georgicetus vogtlensis*) shows the opening uniformly shaped. Picture **C** (*Globicephala macrorhynchus*) shows the opening expanding.

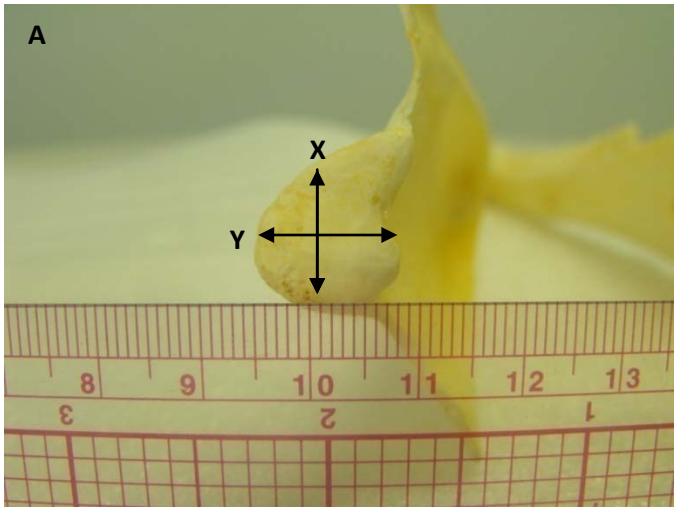


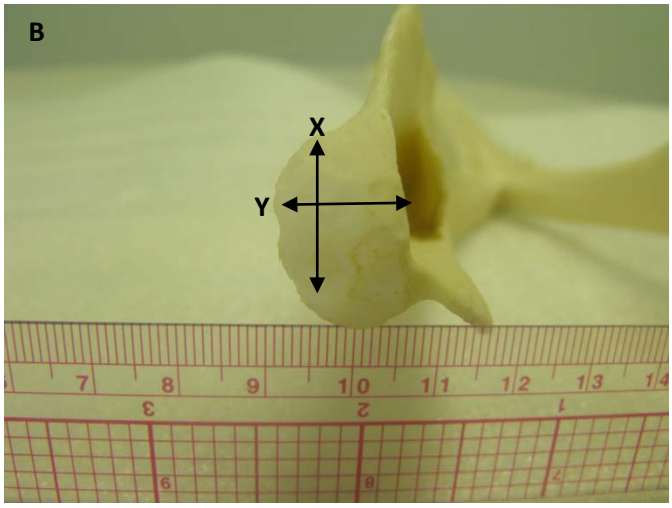
Character 47: Shape of Vomer-Basisphenoid Suture. Picture **A** (*Platanista gangetica*) shows a deeply V-shaped suture. Picture **B** (*Tursiops truncatus*) shows a straight/ square suture. Picture **C** (*Delphinaterus leucas*) shows a slightly V-shaped suture.

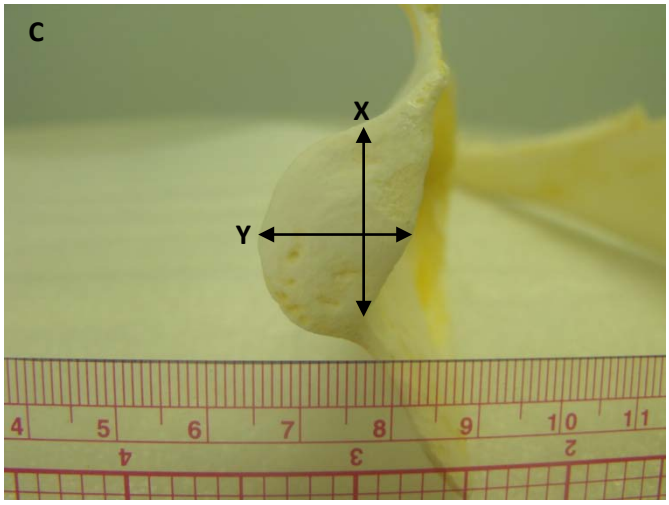


Character 48: Direction that Pterygoids Point. Picture **A** (*Delphinapterus leucas*) shows the pterygoids pointing medially. Picture **B** *(Sotalia fluviatilis*) shows the pterygoids pointing laterally.





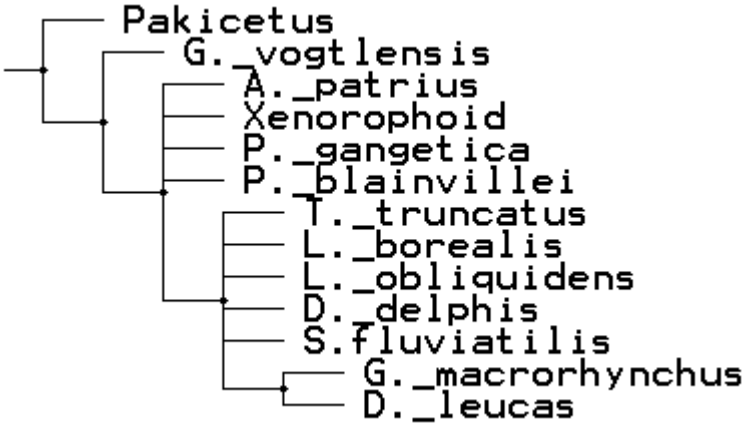




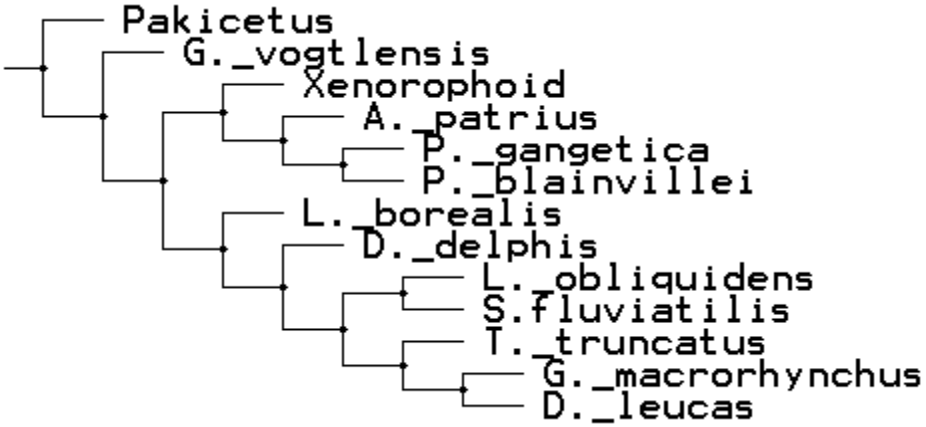
Character 49: Shape of Mandibular Condyles. Picture **A** (*Sotalia fluviatilis*) shows the horizontal axis (**Y**) longer than the vertical axis (**X**). Picture **B** (*Platanista gangetica*) shows **X** and **Y** the same length. Picture **C** (*Lagenorhynchus obliquidens*) shows **X** being longer than **Y**.

4. Results

1. Discrete Data Analysis

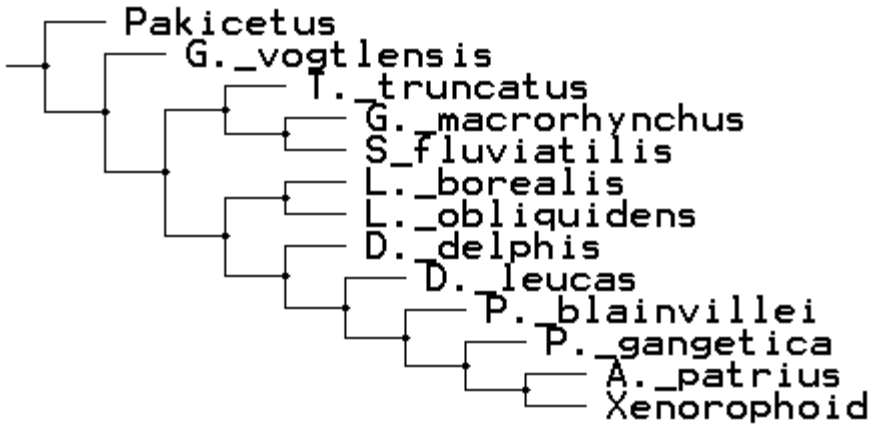


The morphological data based on the characters described in **Observations** run using discrete character states, produced eight most parsimonious trees with a fit of 132. A strict consenus (above) shows a large lack of clarity, with two unresolved bushes and a fit of 153.

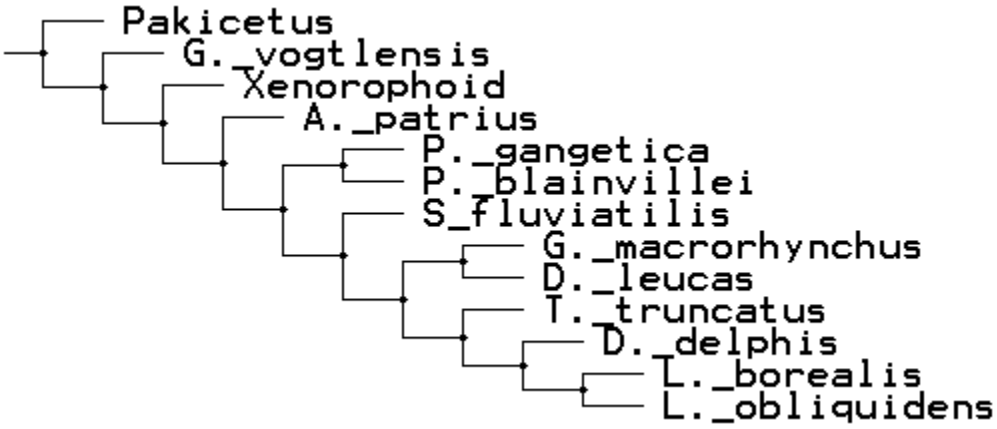


The tree above was produced with an implied weighting of 3. There is no strict consensus due to the unlikely repetition of a fit of 11.78571 that was obtained, but one clade is common to both trees. The clade of *G. macrorhynchus* and *D. Leucas* is the same and as we will see in the combined morphological analysis this clade is consistent.

2. Scaled Data Analysis

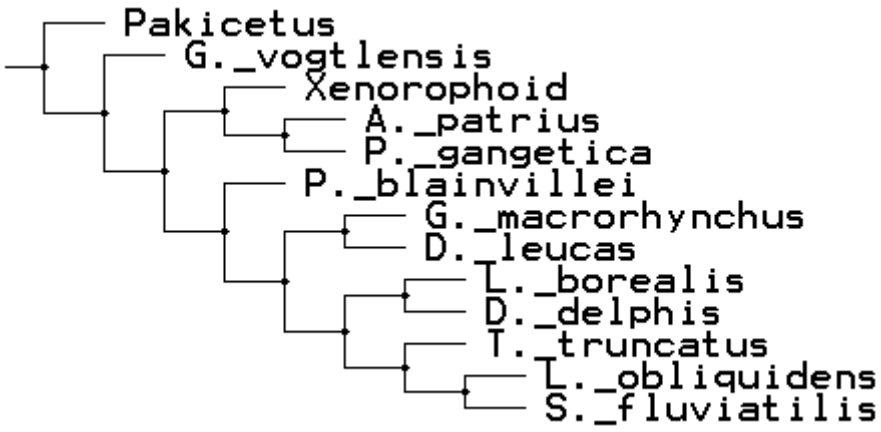


The tree above was retained from eighteen scaled characters. These characters were continuous, having more than two character states and/or quantitative measurements. The fit is 32.635. There is a rooting issue which places two taxa of fossils as the most derived on the tree. Ignoring the fossil taxa, there are two clades which show similarity to the preferred phylogenetic hypothesis by May-Collado and Agnarsson (2006). These are the clade including *L. borealis* and *L. obliquidens* as well as the clade containing *D.leucas*, *P. blainvillei*, and *P. gangetica*. These will continue to present themselves throughout the analysis.

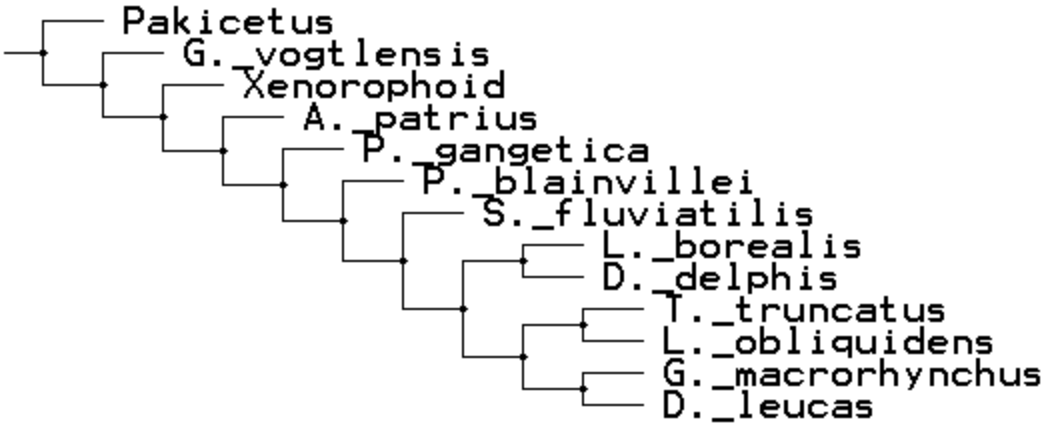


Another repetitive clade can be seen when the scaled data undergoes implied weighting (k=3, fit: 3.53776). The clade containing *G. macrorhynchus* and *D. leucas* is retained in many of the trees. As we look at the molecular data later and that of May-Collado and Agnarsson (2006) we see that these taxa are separated by many other taxa. Using the continuous morphological data is the most likely reason for this pairing. Both taxa are very similar in size and appearance, therefore when measured the resulting data is scaled similarly.

3. Combined Discrete and Scaled Data



By using continuous and discrete data combined, we see characteristics in the tree above that are also in seen in the analysis of the separate data in **1** and **2**. The clade containing *A. patrius* and *P. gangetica* reoccurs and as we will see in the overall tree clade this remains. Also the previously discussed clade with *G. macrorhynchus* and *D. leucas* is present in this tree as well as the tree below.



When an implied weighting of 3 is applied *P. gangetica* 'separates' from the fossils and the clade with *G. macrorhynchus* and *D. leucas* moves to the end of the tree. The branch support for this tree is shown below.

Branch Support for Morphological Data

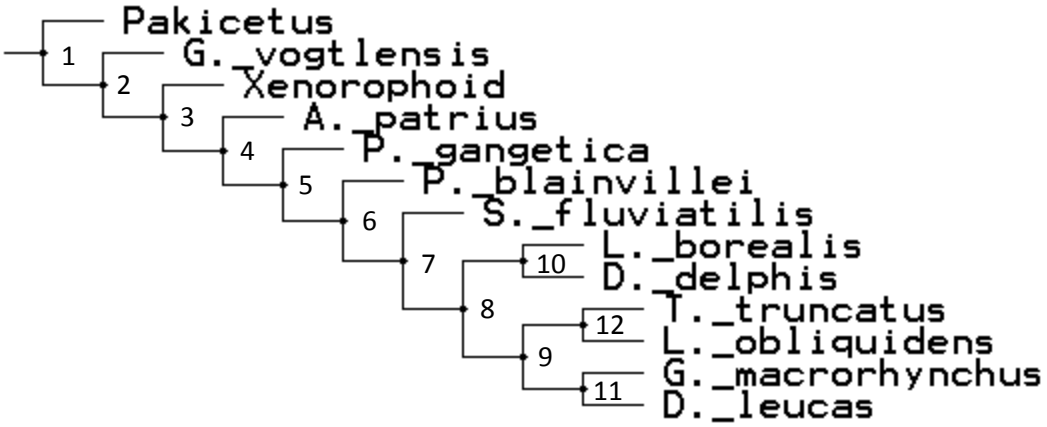


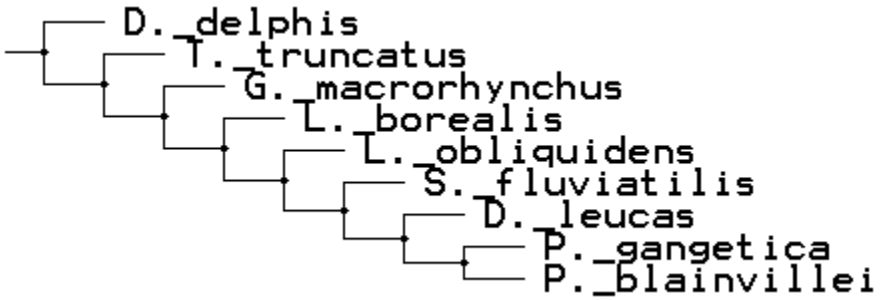
Table 1

	Best fit of tree with node	Best fit of tree without node	Branch Support
1	9.32243	9.32243	0*
2	9.32243	9.64761	0.32518**
3	9.32243	9.64761	0.32518
4	9.32243	9.47600	0.15357
5	9.32243	9.41842	0.09599
6	9.32243	9.41842	0.09599
7	9.32243	9.41842	0.09599
8	9.32243	9.36675	0.04432
9	9.32243	9.36675	0.04432
10	9.32243	9.66850	0.34607
11	9.32243	9.41842	0.09599
12	9.32243	9.32799	0.00556

*Due to the rooting of the taxa, the branch support is zero.

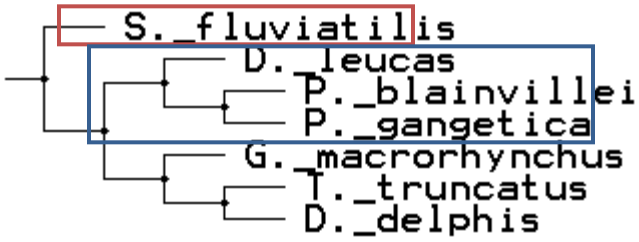
**Also due to the rooting, branch support is zero, however node 2 and 3 share the same branch and therefore have the same branch support

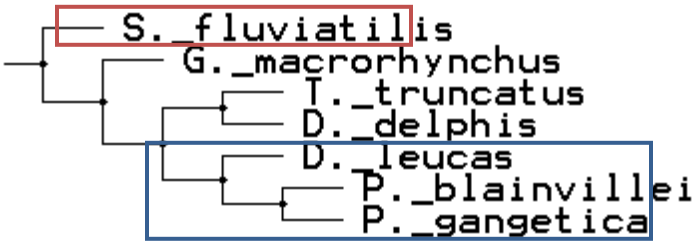
4. **12s Ribosomal Gene Analysis**

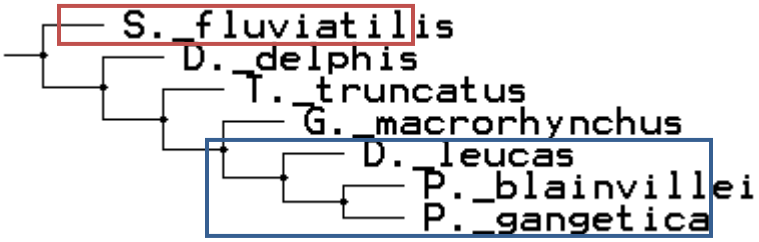


The clade seen in the unweighted scaled data anaylsis composed of *D.leucas, P. blainvillei,* and *P. gangetica* is present in this analysis as well as the ensuing analysis. The same tree is retained when implied weighting is 3, but as different k-values (1-10) are used new trees are retained each time. This shows how implied weighting can increase the differences in characters and can sometimes be uninformative.

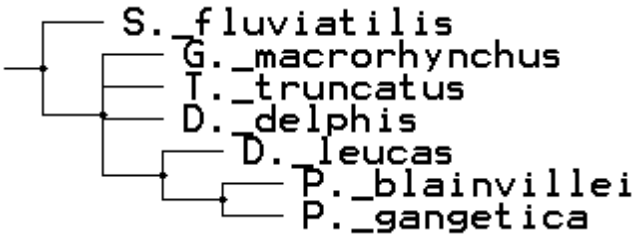
5. **Alpha-lactalbumin Gene Analysis**





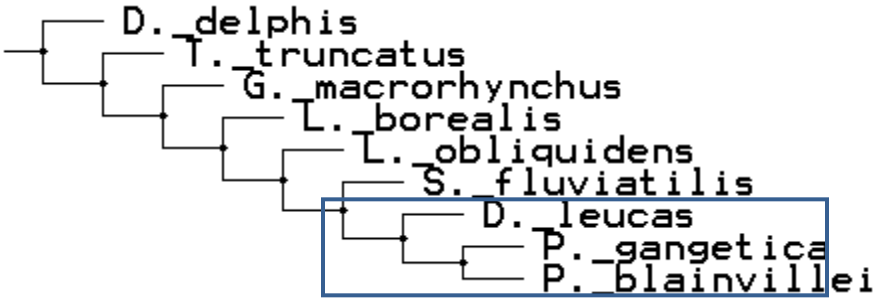


When unweighted parsimony is used, the three trees above are retained with a fit of 55. There is a rooting issue in the taxa. By default the first taxa is placed in the first position of the trees. There is a repeating clade in all three trees and the remaining taxa are grouped in an unresolved bush as seen below in the strict consensus.

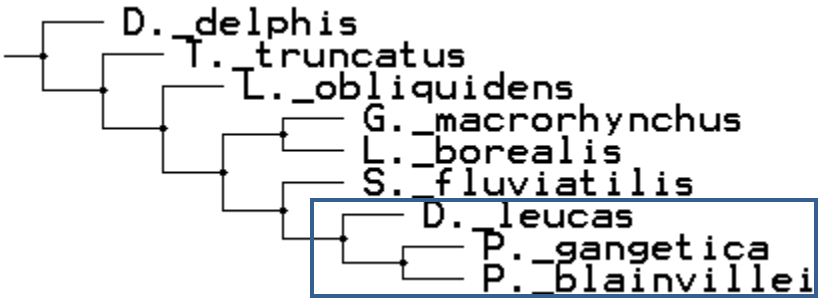


The same strict consensus is retained for an implied weighting of 3, where again three trees are retained, each with variations in the position of the three individual taxa which are included in the unresolved bush. This situation is the similar when the k-value changes. Therefore there is significant support for the clade which includes *D. leucas, P. blainvillei,* and *P. gangetica*. This also reiterates the sometimes unresolving nature of implied weighting. This is not to say implied weighting is not informative, only that for this particular dataset this method does not show information not already shown in unweighted anaylsis.

6. Combined 12s Ribosomal Gene and Alpha-lactalbumin Gene Data Analysis



By combining the molecular data we see a repeat of the same clade (highlighted in blue). An issue that may arise comes from one dataset having seven taxa while the other had nine. We would expect the two taxa, *L. borealis* and *L. obliquidens* to have less of a clear relationship with the other taxa due to the greater number of characters the other taxa share. This turns out not to be the case as the analysis shows below.



During implied weighting different k-values (1-10) were used and the same tree was retained each time. This is different than the separate gene data, where a new tree was retained each time the k-value changed. Implied weighting in this dataset shows consistency and therefore the information it contributes can be helpful. The branch support is shown on the next page.

Branch Support for Molecular Data

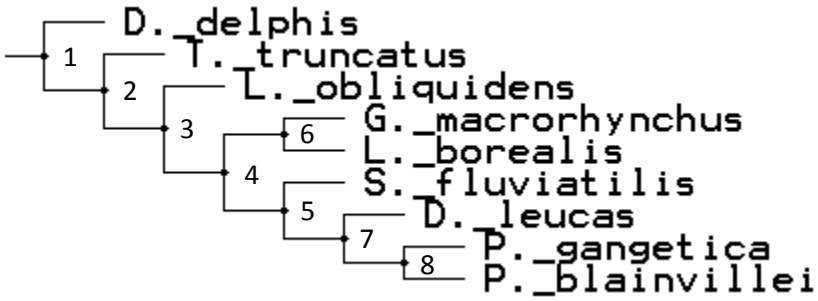
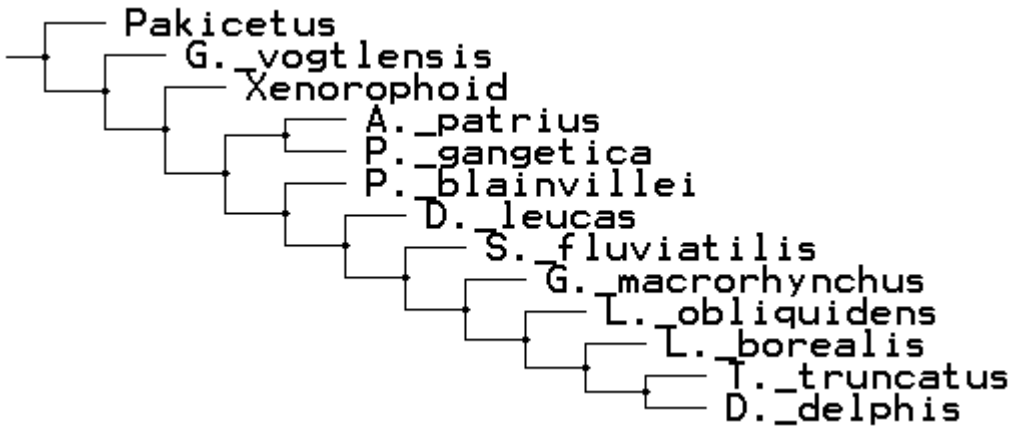


Table 2

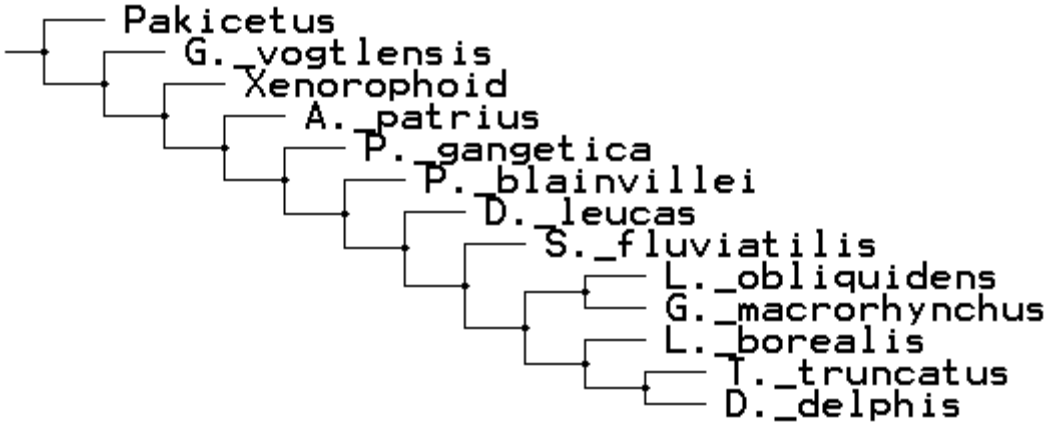
	Best fit of tree with node	Best fit of tree without node	Branch Support
1	5.30	5.30	0 *
2	5.30	5.30	0 **
3	5.30	6.10	0.80
4	5.30	5.30	0 **
5	5.30	5.55	0.25
6	5.30	5.30	0 **
7	5.30	6.45	1.15
8	5.30	6.45	1.15

*This the same rooting issue as denoted in the branch support for morphological data.
**Also a rooting issue, nodes 2, 4, and 6 would be on the same branch if there wasn't strong support for node 3 and slight support for node 5. Branch support does not seem to add much information for this dataset. However, it does show the clade including *D. leucas*, *P. gangetica*, and *P. blainvillei* being supported the most; a repetition seen throughout the results in the gene data.

7. Combine Morphological and Molecular Data Analysis



All individual datasets are combined to have 1057 characters. Since a majority of those characters are molecular we can suggest that some of the repeating patterns seen in only the morphological data analysis will be overshadowed by the sheer weight of molecular data. This is true for the clade of *G. macrorhynchus* and *D. leucas*. It is no longer in the retained tree, which has a fit of 251.797.



The tree above was retained when the k-value was 2-4 using implied weighting. However, when implied weighting was used with k-values of 5-10, the same tree, which was retained under unweighted parsimony, was retained. This shows that only very small k-values affect the outcome. For instance a high k-value, 1000, is basically the same as not using a weighting method. By having low k-values such as 4 retain the same tree, it shows that the data, unweighted, is secure or strongly supported.

Branch Support for All Combined Data

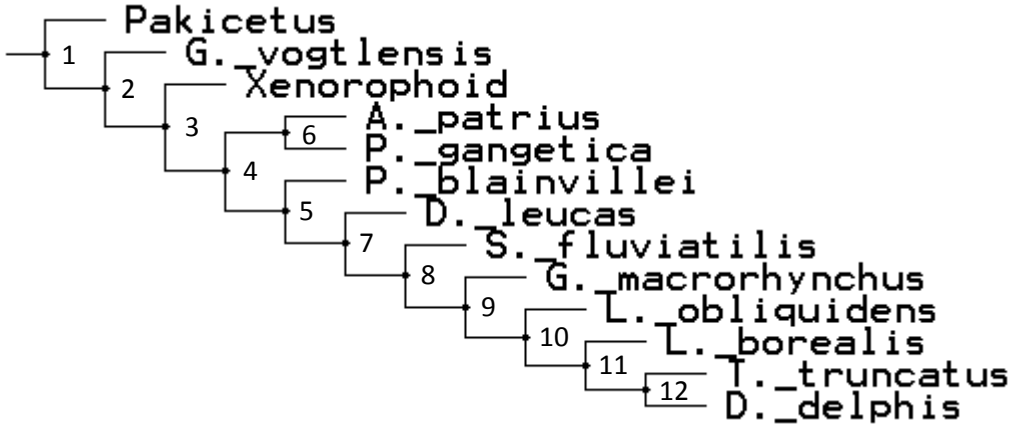


Table 3

	Best fit of tree with node	Best fit of tree without node	Branch Support
1	251.797	251.797	0*
2	251.797	251.797	1.929**
3	251.797	253.726	1.929
4	251.797	252.297	0.500
5	251.797	252.443	0.646
6	251.797	252.443	0.646
7	251.797	252.443	0.646
8	251.797	254.044	2.247
9	251.797	254.044	2.247
10	251.797	253.123	1.326
11	251.797	252.497	0.700
12	251.797	255.089	3.292

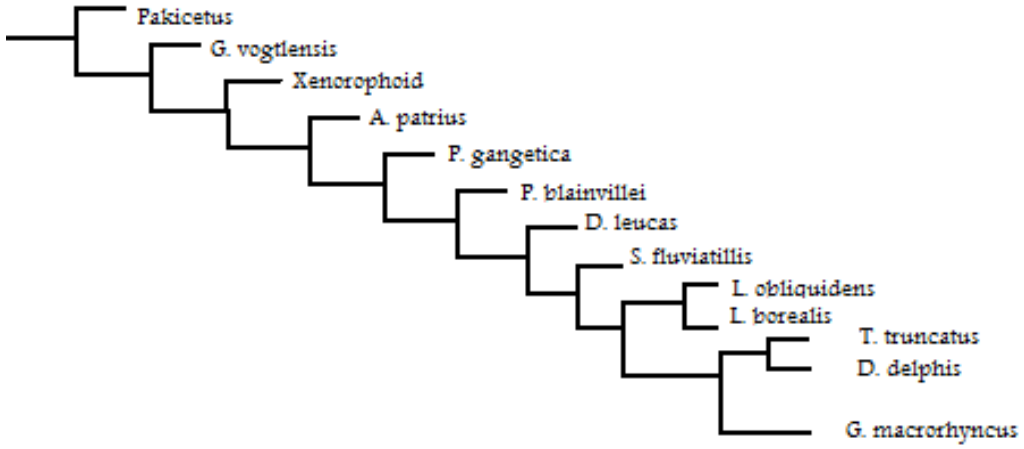
*Due to the rooting of the taxa, the branch support is zero.

**Also due to the rooting, branch support is zero, however node 2 and 3 share the same branch and therefore have the same branch support.

5. Discussion

The final phylogeny seen above, with all data combined in one dataset, does what I had thought. The phylogeny retained portions of the phylogenies formed when the morphological and molecular data were separate. The clade including *P. gangetica, P. blainvillei,* and *D. leucas* is one example that has been a common throughout the results. In the molecular data (**Table 2**) the nodes for said clade had the highest branch support. The final phylogeny also shows remnants of clades that are not very repetitive, such as grouping of *P. gangetic* and *A. patrius.* This was present in one of the earlier morphological analyses. As another example of the efficiency of combining all the data, the phylogeny does get rid of clades that are prominent in the smaller datasets. A good example is the repetition of clade containing *G. macrorhynchus* and *D. leucas* due to the two taxa's similarity, which is not present in the combined analyses.

The final phylogenetic tree can be seen two pages back. I do not feel that this is the most accurate depiction of the taxa's relationships to one another. The tree is showing new clades which were not seen in the other analyses. I have taken the steadiest relationships throughout the analyses, those that were present in both the morphological and molecular analyses. It can be seen below.



To begin with, I felt the fossils belonged first in the evolutionary relationship based on the primitive characteristics as well as knowledge gained from a visit to the Museum of Charleston, where Dr. Albert Sanders gave our class an in depth look at the evolution of fossil cetaceans. I do not think there is enough morphological evidence in this project to imply that *P. gangetica* was a direct descendent of *A. patrius* like the final analysis suggests. That is not to say it did not happen, but I do not think we have collected enough evidence to insinuate that relationship.

The clade of *D.leucas, P. blainvillei,* and *P. gangetica* is present in both morphological and molecular analyses and is also present in the final analysis. Although not as obvious as the previous clade *L. obliquidens* and *L. borealis* are seen together more with each other than with the other taxa. *T. truncatus* and *D. delphis* are paired in the final analysis and have the highest branch support of all the clades at 3.292. Both *S. fluviatilis* and *G. macrorhynchus* floated and disrupted the other relationships throughout the analyses; therefore I have placed them between the taxa to which they are most commonly adjacent.

It is important to remember we only studied nine living cetaceans. In May-Collado and Agnarsson (2006) they studied molecular data on 63 species of Cetacea. According to their results there are a number of species and branches filled in between the taxa we studied. Therefore it would be extremely difficult and unlikely to repeat their results with only 15% of their sample. This is not assuming May-Collado and Agnarsson discovered the perfect evolutionary relationships. It is simply stating the need for more taxa if a more accurate phylogenetic tree is to result.

Finally, I believe these analyses show that neither pure morphological, nor pure molecular data will result in a precise relationship map. There is a common ground between both disciplines which can yield the answers to the evolutionary puzzle.

Acknowledgements

I would like to thank Dr. Jonathon Geisler for offering a challenging course and assistance he gave throughout the course. I would also like to acknowledge Dr. Albert Sanders of the Museum of Chareston and Michael McGowen for sharing their expertise with the class. And Pablo Goloboff, Steve Farris, and Kevin Nixon for use of T.N.T.

References

May-Collado, Laura, Agnarsson, Ingi, 2006. Cytochrom *b* and Bayesian inference of whale phylogeny. Mol. Evol. 38, 344-354.

Appendix 1

Morphological Character Descriptions

1. *Length of Rostrum/Length of Skull*. Ratio: less than 0.5 (0), 0.5 to 0.6 (1), more than 0.6 (2).
2. *Width of Rostrum/Length of Rostrum*. Ratio: less than 0.3 (0), 0.3 to 0.6 (1), greater than 0.6 (2).
3. *Length of Teeth Extension/Length of Rostrum*. Ratio: less than 0.7 (0), 0.7 to 1.0 (1), greater than 1.0 (2).
4. *Teeth Count*. Less than 30 (0), 30-60 (1), more than 60 (2).
5. *Shape of Mandible*. Y-shaped (0), V-shaped (1).
6. *Length of Mandibular Suture/Length of Mandible*. Ratio: greater than 0.3 (0), less than 0.3 (1).
7. *Width/Height of Foramen Magnum*. Ratio: less than 1.0 (0), greater than 1.0 (1).
8. *Width across Exoccipital Condyles*. Less than 80mm (0), 80mm – 120mm (1), greater than 1.2 (2).
9. *Habitat*. Saline (0), fresh (1).
10. *Amount of Overlap by the Supraoccipital over the Frontal*. None (0), slightly (1), heavy (2).
11. *Shape of Exoccipital Condyles*. Transverse axis greater (0), dorsoventral axis greater (1).
12. *Presence of Mandibular Notch*. Present (0), absent (1).
13. *Depth of Antorbital Notch*. Notch absent (0), present and shallow (1), deep (2).
14. *Degree of Fusion of Premaxillae (dorsal)*. Open (0), partially fused (1), mostly fused (2).
15. *Teeth Structure*. Not uniform (0), uniform (1).
16. *Tooth Shape*. Bulky (0), peg-like (1).
17. *Shape of Rostrum along Sagittal Plane from Anterior View*. Convex (0), concave(1).
18. *Extension of Maxilla into External Bony Nares*. Dramatically (0), slightly (1), none (2).
19. *Shape of nasals*. Teardrop (0), square/rectangular (1), round (2), triangular (3), other (4).
20. *Presence of Sagittal Crest on Occiput.* Present (0), absent (1).
21. *Lamdoidal Crest.* Smooth (0), sharp (1).
22. *Presence of Nuchal Crest*. Present (0), absent (1).
23. *Shape of the Temporal Fossa*. Round (0), elongated (1).
24. *Position of Blowhole on Rostrum*. Most anterior (0), middle anterior (1), middle posterior (2), most posterior (3).
25. *Geographic Location*. Wide range (0), Arctic (1), South America (2), Pacific (3), India (4).
26. *Texture of Condyles*. Rough (0), smooth (1).
27. *Social Behavior*. Pack (0), Solitary (1).
28. *Pterygoids Touch at Most Medial Part.* No (0), yes (1).
29. *Presence of Maxillary Crest*. Absent (0), present (1).
30. *Mandibular Groove*. Present (0), not present (1).
31. *Geologic Age*. Eocene (0), Oligocene (1), recent (2).
32. *Migration Patterns*. Yes (0), no migration (1).
33. *Nasals Extend Above Braincase*. No (0), yes (1).
34. *Palate Shape*. Vaulted (0), flat (1).

35. *Length of Squamosals vs. Length of Skull Posterior to Antorbital notch.* Ratio: less than 0.2 (0), 0.2 to 0.4 (1), greater than 0.4 (2).
36. *Jugular Notch*. Skinny and deep (0), wide and shallow (1).
37. *Intercondyloid Notch*. Wide (0), narrow (1).
38. *Angle of Exoccipital Condyles from Posterior View*. Parallel (0), slightly V-shaped (1), widely V-shaped (2).
39. *Vomer to Basisphenoid*. Elevated (0), smooth/flush (1).
40. *Presence of Supraoccipital Fenestra*. Absent (0), present (1).
41. *Width of the Vomerine Crest*. Less than 8mm (0), between 8mm and 15mm (1), greater than 15mm (2).
42. *Depth of Dorsal Condyloid Fossa*. Deep (0), shallow (1).
43. *Subtemporal Crest*. Sharp ridge (0), round (1).
44. *Angle of Coronoid Ramus*. Arc (0), flat (1), dip (2).
45. *Shape of Mandibular Foramen (as it points anteriorly)*. Round (0), straight (1), pointed (2).
46. *Shape of Mandibular Fossa (as it opens posteriorly)*. Uniform (0), expanding (1).
47. *Shape of Vomer-Basisphenoid Suture*. Deep V pointing anteriorly (0), shallow V pointing anteriorly (1), square/straight running transverse (2).
48. *Direction that Pterygoids Point*. Medially (0), laterally (1).
49. *Shape of Mandibular Condyles*. Equal axes (0), horizontal axis longer (1), vertical axis longer (2).

Appendix 2

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
S. fluviatilis	1	1	1	2	1	1	1	0	0	2	1	0	1	2	1	1	0	1	2	0	1	1	0	2	2	1	0	0	1	1	2		0	0	1
D. leucas	0	2	1	0	1	1	0	2	0	0	1	0	2	1	1	0	0	0	0	1	1	1	1	2	1	0	0	0	1	1	2	0	0	1	1
G. macrorhynchus	0	2	0	0	1	1	1	2	0	2	1	0	2	0	1	0	1	2	0	1	1	1	1	2	0	0	0	0	1	1	2	0	1	1	1
D. delphis	1	1	1	1	1	1	1	1	0	0	1	0	1	2	1	1	0	1	4	1	0	1	0	2	0	1	0	1	1	1	2	1	0	0	0
P. blainvillei	2	0	1	2	0	0	0	0	0	1	1	0	2	2	1	1	0	1	3	1	1	1	1	2	2	1	1	0	0	0	2		0	1	2
L. obliquidens	0	1	1	2	1	1	1	0	0	0	1	0	1	1	1	1	1	2	1	0	0	1	0	2	3	1	0	0	1	1	2	0	0	0	1
L. borealis	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	0	2	4	0	0	1	0	2	3	0	0	1	1	1	2		0	0	0
P. gangetica	2	0	0	1	0	0	1	0	1	0	1	1	2	2	0	1	0	2	4	1	0	1	1	2	4	1		0	0	0	2	1	0	0	2
T. truncatus	1	1	1	1	1	1	1	1	0	1	1		1	0	1	1	0	1	4	0	1	1	1	2	0	1	0	0	1		2	0	0	0	1
G. vogtlensis	1	1	2		0	0	0	1	1	0	0	0	0	0	0	0	0	0	4	1	1	0	1	1		1			1	1	0		0	1	
Pakicetus								0		0	0		0		0	0				0		0	1	0		1			1		0				
Xenorophoid	1	0	1					0			1						0	2	4	1	1	1	1	2		1			1		1		0	1	2
A. patrius								0													1			2		0			1		1				

	36	37	38	39	40	41	42	43	44	45	46	47	48	49
S. fluviatilis	1	1	2	1	0	1	1	0	1	2	1	1	1	1
D. leucas	0	0	2	1	1	2	0	1	1	2	1	1	0	2
G. macrorhynchus	1	1	2	0	0	2	1	0	1	2	1	1	1	2
D. delphis	0	1	2	0	0	1	0	0	0	2	1	2		2
P. blainvillei	1	0	1	1	0	0	0	1	2	2	1	1	1	2
L. obliquidens	0	1	1	0	0	1	1	0	1	2	1	2	1	2
L. borealis	0	1	1	0	0	1	1	0	1	2	1	2	0	1
P. gangetica	0	0	0	1	0	0	1	1	2	1	0	0		2
T. truncatus	0	1	2	0	0	2	0	0				2	1	
G. vogtlensis	0	0	1		0		0	0	2	0	0		0	0
Pakicetus	1	0	2	0	0		0	0						
Xenorophoid	1	0	0	0	0	0	0	1						
A. patruis	0	0	1	1	0		1						1	

Character/Taxon Matrix of discrete data. These numbers correlate to the characters and character states listed in **Character Descriptions** and are visually shown in **Observations**. The data not measured is due to fossil/cast completeness, or the character cannot be applied to the individual.

Appendix 3

All data combined. Copied in small font in order to cut down on space. Ready for copying to WordPad and run in T.N.T.

nstates cont;

xread

'Joey LaValley'

1057 13

&[cont]

Pakicetus ? ? 0.000 ? ? 1.000 0.000 0.000 0.000

D._leucas 0.053 0.712 0.508 0.000 0.101 0.421 0.961 0.000 1.000

S._fluviatilis 0.447 0.558 0.566 0.611 0.188 0.701 0.199 1.000 0.500

G._macrorhynchus 0.000 1.000 0.000 0.000 0.012 0.684 1.000 1.000 1.000

D._delphis 0.377 0.341 0.449 0.278 0.061 0.791 0.467 0.000 0.500

P._blainvillei 0.807 0.000 0.588 1.000 0.863 0.585 0.148 0.500 1.000

L._obliquidens 0.160 0.505 0.716 0.522 0.000 0.967 0.300 0.000 0.500

L._borealis 0.324 0.403 0.447 0.311 0.068 0.694 0.352 0.500 0.500

P._gangetica 1.000 0.091 0.154 0.444 1.000 0.863 0.053 0.000 1.000

T._truncatus 0.258 0.407 0.639 0.333 ? 0.915 0.550 0.500 0.500

G._vogtlensis 0.254 0.373 1.000 ? ? 0.617 0.593 0.000 0.000

Xenorophoid 0.484 0.161 0.699 ? ? 0.000 0.256 ? ?

A._patrius ? ? ? ? ? ? 0.043 ? ?

&[cont]

Pakicetus ? ? 0.000 0.000 ? 1.000 ? ? ?

S._fluviatilis 1.000 0.500 1.000 1.000 0.103 1.000 0.295 1.000 0.500

D._leucas 0.500 0.000 1.000 1.000 0.333 1.000 0.724 1.000 0.500

G._macrorhynchus 0.000 1.000 1.000 1.000 0.256 1.000 1.000 1.000 0.500

D._delphis 1.000 0.500 1.000 1.000 0.000 1.000 0.341 1.000 1.000

P._blainvillei 1.000 0.500 1.000 1.000 0.590 0.500 0.224 1.000 0.500

L._obliquidens 0.500 1.000 1.000 1.000 0.205 0.500 0.355 1.000 1.000

L._borealis 0.500 1.000 1.000 1.000 0.000 0.500 0.326 1.000 1.000

P._gangetica 1.000 1.000 1.000 1.000 1.000 0.000 0.000 0.500 0.000

T._truncatus 0.000 0.500 1.000 1.000 0.103 1.000 0.750 ? 1.000

G._vogtlensis 0.000 0.000 0.333 0.000 ? 0.500 ? 0.000 ?

Xenorophoid ? 1.000 0.667 0.500 0.538 0.000 0.178 ? ?

A._patrius ? ? 0.667 0.500 ? 0.500 ? ? ?

&[num]

Pakicetus --0-00--0-01-1--1----100000----

S._fluviatilis 101011020110210011-001110101111

D._leucas 10101000111110001100100110111102

G._macrorhynchus 1010101011110000110111100101112

D._delphis 10101104101001011110001000001-2

P._blainvillei 001011031111211000-011010012112

L._obliquidens 10101111001031001100000100101112

L._borealis 101011041011410111-000100100102

P._gangetica 01110104101141-00010000101120-2

T._truncatus 101-1104011101001-000010000--1-

G._vogtlensis 010000041101-1--11-0100-0002000

Xenorophoid --1---041111-1--1--01100001----

A._patrius ---------1---0--1----00101---1-

&[dna]

D._delphis GCTTNGTCGTAAACTTAAATAATCCC?AAAACAAGATTATTCGCCAGAGT

T._truncatus ??????TCGTAAACTTAAATAATCCT?AAAACAAGATTATTCGCCAGAGT

L._borealis GCTTAGTCGTAAACTTAAATAGTCCT?AAAACAAGACTATTCGCCAGAGT

L._obliquidens ??????TCGTAAACTTAAATAGTCCT?AAAACAAGACTATTCGCCAGAGT

G._macrorhynchus ??????TCGTAAACTTAAATAGTCCT?AGAACAAGACTATTCGCCAGAGT

S._fluviatilis GCTTAGTCGTAAACTTAAATAGTCCC?AAAACAAGACTATTCGCCAGAGT

D._leucas ??????TCGTAAACTTAAATAGTCCTTAAAACAAGACTATTCGCCAGAGT

P._blainvillei GCTTAGTCGTAAACCCAATTGGTTCA?ATAACAAGACCATTCGCCAGAGT

P._gangetica ??????????????????????TCANAANACANGRTNAKTCGCCAGAGT

&[dna]

D._delphis ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

T._truncatus ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

L._borealis ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

L._obliquidens ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

G._macrorhynchus ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

S._fluviatilis ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

D._leucas ACTACCGGCAACAGCCCGAAACTCAAAGGACTTGGCGGTGCTTCATATCC

P._blainvillei ACTACCGGCAACAGCCTAAAACTCAAAAGACTTGGCGGTGCTTCACATCC

P._gangetica ACTACTAGCAACAGCTTAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

&[dna]

D._delphis TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA

T._truncatus TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA

L._borealis TTCTAGAGGAGCCTGTTCTATAAACGATAAACCACGATTAACCTCACCAA

L._obliquidens TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA

G._macrorhynchus TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA

S._fluviatilis TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA

D._leucas CTCTAGAGGAGCCTGTTCTGTAAACGATAAACCCCGATCAACCTCACCAA

P._blainvillei TTCTAGAGGAGCCTGTTCTATAAACGATAAACCCCGATAAACCTCACCAA

P._gangetica CTCTAGAGGAGCCTGTTCTATAATCGATAAACCCCGATCAACCTCACCAA

&[dna]

D._delphis TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA

T._truncatus TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTARAAAA

L._borealis TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA

L._obliquidens TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA

G._macrorhynchus TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA

S._fluviatilis TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA

D._leucas TCCTTGCTACCTCAGTCTATATACCGCCATCTTCAGCAAACCCTA?AAAA

P._blainvillei CTCTTGCTACTTCAGTCTATATACCGCCATCTCAAGCAAACCCTA?AAAA

P._gangetica CCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCCAGTAAG

&[dna]

D._delphis GGAACGAAAGTAAGCACAACTACTGCACGTAAAAACGTTAGGTCAAGGTG

T._truncatus GGAACGAAAGTAAGCACAACTACTRCACGTAAAAACGTTAGGTCAAGGTG

L._borealis GGAACGAAAGTAAGCACAACTATTGCACGTAAAAACGTTAGGTCAAGGTG

L._obliquidens GGAACGAAAGTAAGCACAACTATTGCACGTAAAAACGTTAGGTCAAGGTG

G._macrorhynchus GGAATGAAAGTAAGCACAACYATTGCACGTAAAAACGTTAGGTCAAGGTG

S._fluviatilis GGAATGAAAGTAAGCACAACCATTGCACATAAAAACGTTAGGTCAAGGTG

D._leucas GGAACGAAAGTAAGCACAACTATCGCACATAAAAACGTTAGGTCAAGGTG

P._blainvillei GGAATGAAAGTAAGCACAACTATCTCTCACAAAAACGTTAGGTCAAGGTG

P._gangetica GGAACGACAGTAAGCACAACTACTTTACGTAAAAACGTTAGGTCAAGGTG

&[dna]

D._delphis TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTATAATAAGAACAC

T._truncatus TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTATAATAAGAACAC

L._borealis TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTATAATAAGAACAC

L._obliquidens TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTATAACAAGAACAC

G._macrorhynchus TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTACAATAAGAACAC

S._fluviatilis TAACCTATGGGTTGGGAAGAAATGGGCTACATTTTCTATAATAAGAACAC

D._leucas TAACCTATGGGTTGGGAAGAAATGGGCTACATTTTCTATAACAAGAACAT

P._blainvillei TAACCTATGGGTTGGAAAGAAATGGGCTACATTTTCTATAACAAGAACAT

P._gangetica TAACCTATGGGATGGGAAGAAATGGGCTACATTTTCTACACTAAGAATAC

&[dna]

D._delphis CC?CTTAAACTCACACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG

T._truncatus CC?CTTAAACTCACACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG

L._borealis CC?CTTAAATTTACACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG

L._obliquidens CC?CTTAAACTTACACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG

G._macrorhynchus CC?CYTAAACTTAYACGAAAGTTTTTATGAAATCTAAAAACTAAAGGAGG

S._fluviatilis CA?CTTAAACCTATACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG

D._leucas CC?CTCAAGTCTACACGAAAGTTTTTATGAAAACTAAAAACCAAAGGAGG

P._blainvillei CCTCATAAA?TGATACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG

P._gangetica CC?TTTATACCTAAACGAAAGTTTTTATGAAATATAAAAACCAAAGGAGG

&[dna]

D._delphis ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCATGAAG

T._truncatus ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCA?????

L._borealis ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCATGAAG

L._obliquidens ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCA?????

G._macrorhynchus ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCA?????

S._fluviatilis ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCATGAAG

D._leucas ATTTAGCAGTAAATTAAGAATAGAGTGCTTAATTGAATAAGGCCN?????

P._blainvillei ATTTAGCAGTAAACTAAGAATAGAGTGCTTATTTGAACAAGGCCATGAAG

P._gangetica ATTTAGCAGTAAATTAAGAATANAGCGCTTAATTGAATAAGGCCATGAAG

&[dna]

D._delphis CACGC

T._truncatus ?????

L._borealis CACGC

L._obliquidens ?????

G._macrorhynchus ?????

S._fluviatilis CACGC

D._leucas ?????

P._blainvillei CACGC

P._gangetica CACGC

&[dna]

S._fluviatilis CTCTGCTCTTGGTGGGCATCCTGTTCCATGCCGTCCAGGCCGAACAATTA

D._leucas CTCTGCTCTTGGTGGGCATCCTGTTCCATGCCATCCAGGCAGAACAGTTA

D._delphis CTCTGCTCTTGGTGGGCATCCTGTTCCATGCCGTCCAGGCCGAACAATTG

T._truncatus ??????????GGTGGGCATCCTGTTCCATGCCGTCCAGGCCGAACAATTA

G._macrorhynchus ??????????????????????????????CCGTCCAGGCCGAACAATTA

P._gangetica ???????CTTGGTGGNCATCCTGTTCCATGCCATCCAGGCTGAACAATTA

P._blainvillei ??

&[dna]

S._fluviatilis ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG

D._leucas ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG

D._delphis ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG

T._truncatus ACAAAATGTGAGCTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG

G._macrorhynchus ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG

P._gangetica ACAAAATGTGAGTTGTTCCAGAGACTGAAAGACCTGGATGGCTATGGAGG

P._blainvillei ??

&[dna]

S._fluviatilis CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCATAC

D._leucas CGTCACTTTGCCTGAATGTGAGTTCTCTGCTATCTTGCTTTGTTCCATAC

D._delphis CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCACAC

T._truncatus CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCACAC

G._macrorhynchus CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCACGC

P._gangetica CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCATAC

P._blainvillei ?GTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCATAC

&[dna]

S._fluviatilis TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTCCTC

D._leucas TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTTCTC

D._delphis TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTTCTC

T._truncatus TTCATCTTCTTCTGTCTTCCCCACCTTTCTCTTCCTCCTCTTTTTTTCTC

G._macrorhynchus TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCGCCTCTTTTTTTCTC

P._gangetica TTCATCTTCTTCTGTCTTGCCCACGCTTCTCTTCCTCCTCTTTTTTTCTC

P._blainvillei TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTCCTC

&[dna]

S._fluviatilis TACTTTTAACTCAATTATCTAAGAATCCTCTCATCTGCTCATCTGTTTAC

D._leucas TATTTTTAACTCAGTTATCTAACAATCCTCT???????T?ATCTGTTTAC

D._delphis TACTTTTAACTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTAC

T._truncatus TACTTTTAACTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTAC

G._macrorhynchus TACTTTTAACTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTAC

P._gangetica TACTTTTAATTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTAC

P._blainvillei TACTTTTAACTCAATTATCTAGTAATCCTCTTATCTGCTCATCTGTTTAC

&[dna]

S._fluviatilis TCTTTTATTACATTTATTCACCTGTCTCTCCTTTCTCCCATTGTCTGATT

D._leucas TCTTTTATTACATTTATTCACCTATCTCTTCTTTCTCCCATTGTCTGATT

D._delphis TCTTTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGATT

T._truncatus TCTTTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGATT

G._macrorhynchus TCTTTTATTACATTTATTCACCTGTCTCTCCTTTCTCCCATTGTCTGATT

P._gangetica TCTCTTGTTACATTTATTCACCTATCTCTCCTTTTTCCCATTGTCTGATC

P._blainvillei TCTTTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGACT

&[dna]

S._fluviatilis GGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCGT

D._leucas GTTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTTG??GCCGT

D._delphis GGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCGT

T._truncatus GGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCGT

G._macrorhynchus GGTTTTT?GGAGCTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCGT

P._gangetica GTTTTTTTGGAACTCTTAATCTTATCAAGATACCCTGTGGTTG??GCCGT

P._blainvillei GTTTTAT?GGAACTCTTAATCTTATCAAGATACTCTGGGGTTGTGGCCAT

&[dna]

S._fluviatilis ATTTGGAGATTGGCTGGAGAGCCTTTTTCTGTCTG??????????TCCAC

D._leucas ATTTGGAGATTGGCTGGAGAGCCTTTTTCTGTCTG??????????TCCAC

D._delphis ATTTGGAGATTGGCTGGAGAGCCTTTTTCTGTCTG??????????TCCAC

T._truncatus ATTTGGAGATTGGCTGGAGAGCCTTTTTCTGTCTG??????????TCCAC

G._macrorhynchus ATTTGGAGATTGGCTGGAGAGCCTTTTTCTGTCTG??????????TCCAC

P._gangetica ATTTGGAGATTGGCTGGAGAGCCTTTTTCTGTTTGGGAATACAGGTCCTC

P._blainvillei ATTTGGAGATTGGTTGGAGAGCCTTTTTCTGTCTG??????????TCCAC

&[dna]

S._fluviatilis ATTTATGCTGTATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

D._leucas ATTTATGCTATATGTGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

D._delphis ATTTATGCTATATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

T._truncatus ATTTATGCTATATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

G._macrorhynchus ATTTATGCTATATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

P._gangetica ATTTATGCTATATGTGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

P._blainvillei ATTTATGCTATATGTGGACATCCCTGTGATATCTCTTTTTCATCTTTCTT

&[dna]

S._fluviatilis TCAGGGGTCTGTACCGTATTTCATACTAGTGGGTGTGACACACAAACCAT

D._leucas TCAGGGGTCTGTACCGTATTTCATACTAGTGGTTGTGACACACAAACCAT

D._delphis TCAGGGGTCTGTACCGTATTTCATACTAGTGGGTGTGACACACAAACCAT

T._truncatus TCAGGGGTCTGTACCGTATTTCATACTAGTGGGTGTGACACACAAACCAT

G._macrorhynchus TCAGGGGTCTGTACCGTATTTCATACTAGTGGTTGTGACACACAAACCAT

P._gangetica TCAGGGGTCTGTACCGTATTTCATACCAGTGGTTGTGACACACAAACCAT

P._blainvillei TCAGGGGTCTGTACCGTATTTCATACTAGTGGTTGTGACACACAAACCAT

&[dna]

S._fluviatilis AGTAAATAACAGTGACAGCACAGAATATGGACTTTTCCAGATCAATAATA

D._leucas AGTAAATAACAATGACAGCACAGAATATGGACTCTTCCAGATCAATAATA

D._delphis AGTAAATAACAATGACAGCACAGAATATGGACTTTTCCAGATCAATAATA

T._truncatus AGTAAATAACAATGACAGCACAGAATATGGACTTTTCCAGATCAATAATA

G._macrorhynchus AGTAAATAACAACGACAGCACAGAATATGGACTTTTCCAGATCAATAATA

P._gangetica AGTAAATAACAATGGCAGCACAGAATATGGACTCTTCCAGATCAATAATA

P._blainvillei AGTGAATAACAACGGCAGCACAGAATATGGACTCTTCCAGATCAATAATA

&[dna]

S._fluviatilis AAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGAC

D._leucas AAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGAC

D._delphis AAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGAC

T._truncatus AAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGAC

G._macrorhynchus AAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGAC

P._gangetica AAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGGT

P._blainvillei AAATTTGGTGCAGAGACAAGCAGATCCCTCACTCAAGGGACATCTGTGGC

&[dna]

S._fluviatilis ATC

D._leucas ATC

D._delphis ATC

T._truncatus ATC

G._macrorhynchus ATC

P._gangetica ATC

P._blainvillei ATC

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proc/;