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Evolutionary Trends from ancient Cetaceans to modern Odontocedes.

Abstract

Given the course of one semester at Georgia Southern University, 13 different species of Cetaceans were scoured for morphological characters to define the evolutionary trends. This was completed under the tutelage of Dr. Jonathan Geisler. The morphology of the different taxa was then analyzed through two programs, Winclada and TNT. Searches such as branch support and implied weighting were conducted to compare and validate the results. Molecular data for 9 of the species was introduced and analyzed both alone and then combined with the morphological data.

1. Introduction

During the 2008 fall semester at Georgia Southern University, the Dolphin Evolution Class, through the Department of Geology and Geography, had the objective of trying to define the evolutionary trend of 13 species of Cetaceans. The instructor for this course is Dr. Jonathon Geisler and the National Science Foundation is provided funds to support it (DEB-0640361 to J. Geisler). The duration of the class has been spent studying the taxonomy of the species and building a foundation of how the research and analysis should be conducted. The end result of the class consists of a final report documenting and analyzing the data collected.

Through the process of reaching the objective, the class focused on morphological characters of the skulls. Outside research into previous studies was discouraged. After obtaining a substantial amount of morphological characters, mitochondrial DNA was added in. The purpose of discouraging outside research was to allow an independent formation of an evolutionary tree. If research had been conducted prior to the research conducted in class, then students would look automatically to certain relationships between the species.

Currently there is still much debate over the relationship trends of Cetaceans and the splitting point between Odonteceti and Mysticeti. The curator of the Charleston Museum, Dr. Albert Sanders, provided the class with an in depth overview of trends in ancient Cetaceans. Many parallels have been drawn between species, and as new skeletal remains continue to be found these relationships themselves must change.

Another perplexing issue in the debate is those that stick strictly to DNA and those that focus on morphological characters. Problems will arise from only relying on one of the sources, so it would be best to combine them. Even then, interpretations may differ. Michael McGowen, a molecular biologist and Ph.D. student in California explained to the class the benefits of molecular data. There is an enormous potential data set, and the character sets are discrete. There is also the ability of having greater phylogenetic limits then when using morphology. One problem that can arise when using mtDNA is there rate of mutation since they do not always replicate accurately.

2. Materials and Methods

The morphological characters were obtained from 13 different species of Cetacean skulls. A majority of these skulls were casts, while two were actual skeletal remains. Here is a list of the species in no particular order and the type of skull:

- *Globicephala macrorhynchus* (cast and real)
- *Delphinapterus leucas* (cast)
- *Tursiops truncatus* (real)
- *Pakicetus* (cast)
- Xenorophoid (cast)
- *Georgiacetus vogtlensis* (cast)
- *Sotalia fluviatilis* (cast)
- *Platonista gangetica* (cast)
- *Pontoporia blainvillei* (cast)
- *Delphinus delphis* (cast)
- *Lagenorhynchus obliquidens* (cast)
- *Lissodelphis borealis* (cast)
- *Archeadelphis patrius* (cast)

In order to record and document our morphological characters digital cameras, calipers, and rulers were used. The digital cameras were used in to specify the character and its states, while the rulers were used as scale in the photos. The calipers provided an accurate number for the quantitative characters. Several computer programs were used in order to organize and evaluate the data: Microsoft Excel, WordPad, Microsoft Word, and Microsoft PowerPoint.

Analyzing the morphological characters was completed using two programs, one called Winclada and the other TNT (Willi Henig Society. Goloboff, Farris, and Nixon. 2008. Cladistics 24:774-786). Two different genes were used in the molecular data. One was the Alpha lactalbumin gene, which its main function is as a whey protein found in milk (Vilotte). The other, 12s, is a rhybosomial mitochondrial DNA (McGowen). NCBI provided several DNA sequences for the **alpha lactalbumin**, while the **12s** was provided in class. List of Cetacean species covered in molecular data (^ means 12s and *means alpha lactalbumin):

- *Delphinus delphis* ^*
- *Tursiops truncatus* ^*
- *Lagenorhynchus obliquidens* ^
- *Lissodelphis borealis* ^
- *Platonista gangetica* ^*
- *Pontoporia blainvillei* ^*
- *Sotalia fluviatilis* ^*

- *Globicephala macrorhynchus* ^*
- *Delphinapterus leucas* ^*

The initial research began with gathering morphological characters of the skulls in class. Both quantitative and qualitative characters were documented by digital cameras in order to allow repeatable results. 47 morphological characters have been chosen for the final character list out of the numerous ones compiled by the class. 3 other characters relating to geologic age, migratory habits, and gregariousness were compiled with the 47 morphological characters to total 50.

Of the 50 characters 47 of them were multi-state characters; this includes quantitative data that was converted into categories of 0, 1, 2, etc. These unordered and discrete characters were then run through Winclada and analyzed to produce a MPT. When using Winclada the characters were weighted as unweighted parsimony so all of the unions are equal in cost. *Pakicetus* was chosen as the out-group for all of the remaining data since recent studies have shown for him to be the least derived. Character 0 is used with all question marks to start character 1 at the position of 1. To see the character mapping of the MPT from Winclada see Appendix II.

The next objective with the 50 characters was to scale them between 0 and 1 using Microsoft Excel and then formatting it on WordPad. The qualitative characters were scaled in their raw form. Due to an error earlier, all of my characters were then run through TNT as continuous as opposed to a combination of continuous and numerical.

Robert Mcgowen demonstrated how to use and find the molecular data. Some of the molecular data was provided on a Word document, while the remaining species were found through NCBI. The molecular data for both the 12s and the alpha lactalbumin underwent a multiple sequence alignment using ClustalW. Both DNA sequences were formatted in WordPad and then analyzed in TNT. The molecular data and the scaled quantitative data were then combined and formatted in WordPad before being opened and run through TNT.

The program TNT (Tree analysis using New Technologies) has been the essential part of analyzing and comparing data. To learn more about the program and its functions look in the References under Goloboff. Through TNT the data was able to go through several different comparisons. Since the MPT (most parsimonious tree(s)) produced for each of the major data sets was one, several of the functions were unneeded. These included: majority rule tree, consensus strict tree, and an agreement sub-tree. Implied weighting and branch supports were conducted on each of the major data sets. For implied weighting the values of K used were 1, 3, 5, 7, and 10. These values were chosen since they fall in between 1 and 10, and they would provide the best results to compare whether the MPT would be susceptible to change. Branch supports were conducted on each of the clades for all the major data sets but the unordered and discrete. The major data sets include: unordered and discrete characters, scaled quantitative data, combined molecular data, and combined molecular with scaled quantitative.

3. Results

3.1 Un-scaled, all discrete (Winclada)

The cladistics analysis of the un-scaled and all discrete characters resulted in one Most Parsimonious Tree (Figure 1). The out-group, *Pakicetus*, was chosen since current data places *Pakicetus* as the least derived among the other species used. Several of the characters that validate this tree include the Geologic Age, presence of a nuchal crest, structure of the teeth, ratio of the symphasis (mandible suture) to the mandible length, and the squamosal length to the length of the skull.

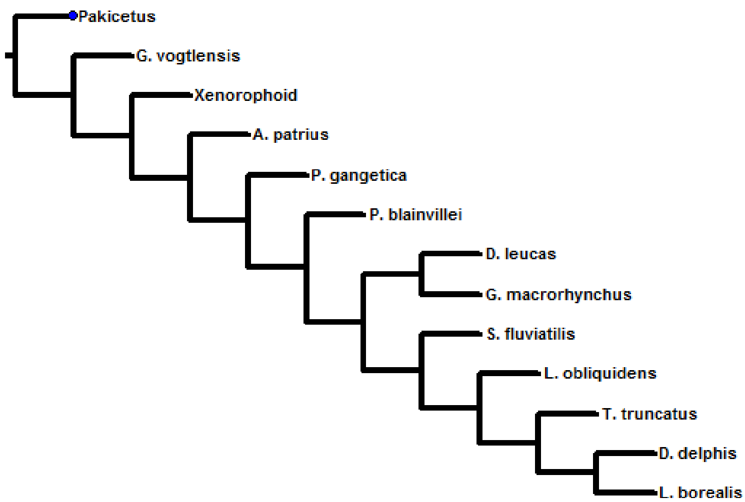

Fig. 1: MPT (Length = 151)

3.2 Scaled Quantitative Data (TNT)

The cladistics analysis of the scaled quantitative and multi-state characters through TNT produced one most parsimonious tree (Figure 2). There is only one notable difference between the unscaled discrete and the scaled quantitative data, and that is shown that *Tursiops truncatus* has regressed a branch while *Lagenorhynchus obliquidens* has progressed forward one branch.

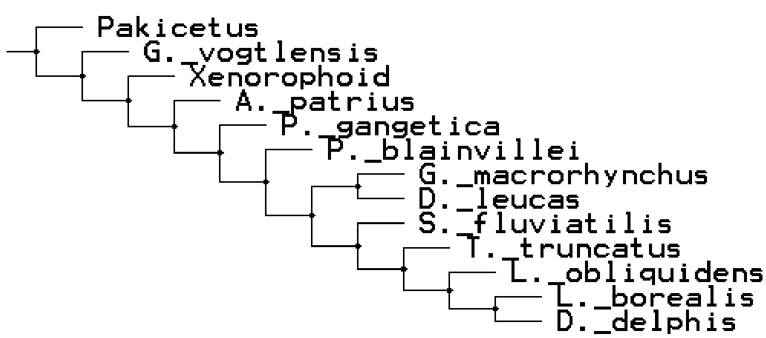

Fig. 2: MPT (Length=93.727)

Conducting a branch support on each node produced the following results (Table 1). Clade 3 with the highest branch support regressed *Archeadelphis patrius* to the same branch as *Georgiacetus vogtlensis.*

(Table 1: Note that node 1 starts with the out-group)

Clade #	Best Score	Tree Length	Branch Support	# of trees

1	93.727	N/A	N/A	N/A
2	93.727	93.727	0	1
3	93.727	96.727	3	1
4	93.727	94.727	1	1
5	93.727	95.132	1.405	1
6	93.727	95.541	1.814	1
7	93.727	94.65	0.923	1
8	93.727	95.541	1.814	1
9	93.727	95.782	2.055	1
10	93.727	94.523	0.796	1
11	93.727	94.314	0.587	1
12	93.727	94.921	1.194	1

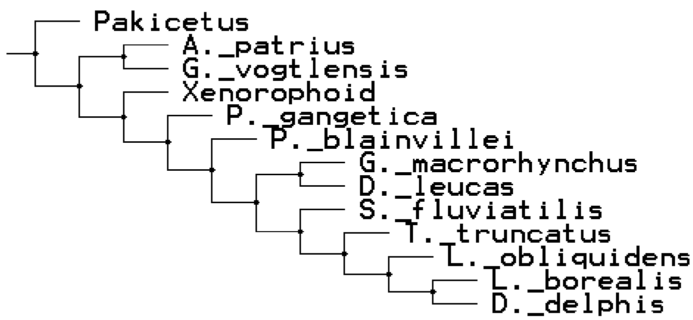

Fig. 2a: Tree Length=96.727

After conducting a branch support, several different weights were applied to see how the data would react. Several different K values between 1 and 10 were used and no change occurred to the positions of the species. The K values and there results are displayed below.

K=1
Tree Length = 19.251

K=3
Tree Length = 10.137

K=5
Tree Length=6.925

K=7
Tree Length = 5.266

K=10
Tree Length=3.876

3.3 Molecular Data (TNT)

Combining both the 12s and the alpha lactalbumin molecular data and conducting a cladistics analysis provided one most parsimonious tree (Fig. 3). Before combining the two DNA sequences, they were run individually. Alpha lactalbumin provided 3 most parsimonious trees while 12s had 1 tree. The 12s provided a similar linear progression that is provided below.

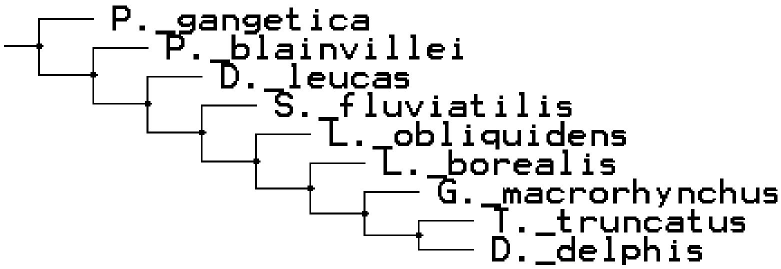

Fig. 3: MPT (Length=147)

Conducting a branch support on each node produced the following results (Table 2). Both clade 3 and 4 have a branch support of 5, though clade 3 produced 3 trees. The tree from clade 4 is below (Fig. 3a).

(Table 2: Note that node 1 starts with the out-group)

Clade #	Best Score	Tree Length	Branch Support	# of trees
1	147	N/A	N/A	N/A
2	147	147	0	1
3	147	152	5	3
4	147	152	5	1
5	147	148	1	1
6	147	147	0	1
7	147	147	0	1
8	147	151	4	1

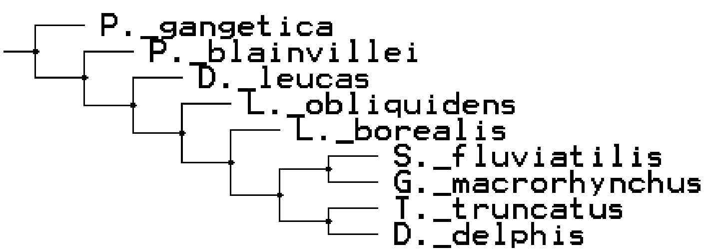

Fig. 3a: Tree Length=148

Several different weights between the values of 1 and 10 were conducted on the combined molecular data. The results from the different K values are listed below. When the weight was set at 3 the largest change occurred and is shown below in figure 3b. The other values involved branch changes from the most parsimonious tree (figure 3).

K=3
Tree Length=5.3

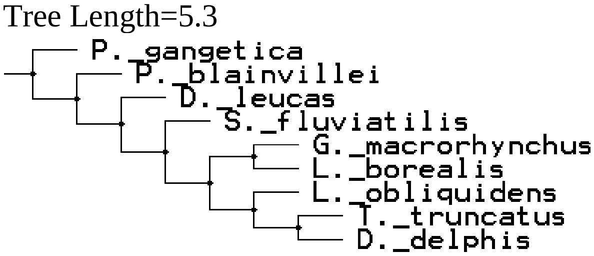

Fig. 3b

K=5
Tree Length=3.571
Change between *Globicephala macrorhynchus* and *Lagenorhynchus obliquidens*.

K=1 K=7 K=10
Tree Length=10.333 Tree Length=2.694 Tree Length=1.97
Change with *Lagenorhynchus obliquidens* moving up two branches and *Globicephala macrorhynchus* and *Lissodelphis borealis* shifting back one.

3.4 Combined Molecular Data and Scaled Quantitative Data (TNT)

Both the combined molecular data and the scaled quantitative data produced one most parsimonious tree when put through a cladistics analysis (Fig. 4). The resultant below shows a straight linear tree.

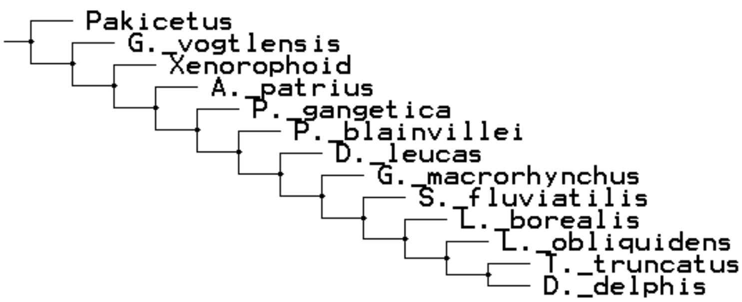

Fig. 4: MPT (Length=248.638)

Conducting a branch support on each node produced the following results (Table 3). Clade 3 had the highest branch support and grouped *Xenorophoid* and *Archeadelphis* patrius as well as *Platonista gangetica* and *Pontoporia blainvillei* (Fig. 4a). The next highest tree supported with was clade 12, and it retained the linear progression but rotated several of the species (Fig. 4b).

(Table 3: Note that node 1 starts with the out-group)

Clade #	Best Score	Tree Length	Branch Support	# of trees
1	246.638	N/A	N/A	N/A
2	246.638	248.638	2	1
3	246.638	251.128	4.49	1
4	246.638	249.128	2.49	1
5	246.638	249.224	2.586	1
6	246.638	248.959	2.321	1
7	246.638	248.959	2.321	1
8	246.638	248.959	2.321	1
9	246.638	248.748	2.11	1
10	246.638	249.364	2.726	1
11	246.638	248.941	2.303	1
12	246.638	250.083	3.445	1

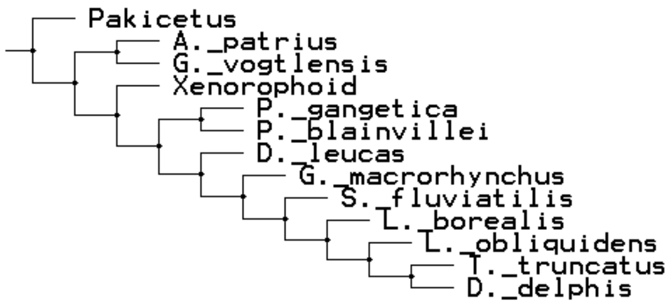

Fig. 4a: Tree Length=251.128

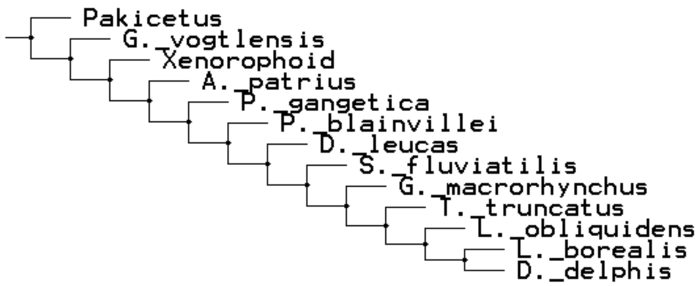

Fig. 4b: Tree Length=250.083

Several different values of K were chosen between 1 and 10 to see how implied weighting might affect the trends. Two changes occurred with a K value of 1 and 3 (Fig. 4c). The remaining K values used were 5, 7, and 10. They only produced one change that is present in Fig. 4.

K=1	K=3
Tree Length=31.054	Tree Length=16.676

Change with *Sotalia fluviatilis* and *Globicephala macrorhynchus*, and *Lagenorhynchus obliquidens* and *Lissodelphis borealis.*

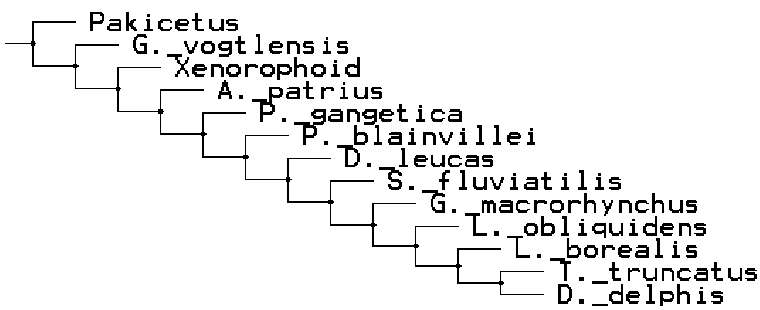

Fig. 4c

K=5	K=7	K=10
Tree Length=11.464	Tree Length=8.745	Tree Length=6.455

Change occurred with *Sotalia fluviatilis* and *Globicephala macrorhynchus;* switched branches.

4. Discussion

Having almost similar trees between both the unscaled discrete characters and the scaled quantitative characters is a little discouraging. Possibly it may be a result of having all the characters placed as continuous in TNT, or maybe there are several characters that are not independent. After *Pontoporia blainvillei* on both figures 1 and 2 the relations are not what the combined data predicts or within my assumptions. I would not have placed *Lissodelphis borealis* with *Lagenorhynchus obliquidens* as opposed to the relationships shown in the tree.

The combined molecular and scaled data tree is a straight linear progression. This is a little unexpected. The branch supports did not help resolve the situation since they produced relationships that do not seem to be very strong. Between the implied weighting at 1 and 3 and the branch support from node 12, *Sotalia fluviatilis* has regressed behind *Globicephala macrorhynchus*. This has occurred also with the molecular data and its MPT and in implied weighting. The molecular data though has two DNA sequences with one accounting for 7 species and the other for 9, so this might have resulted in producing that change.

There does not need to be any need for discussion of the molecular data by itself since it has already been studied in full detail.

Upon examining the major data sets and their MPT there is a general relationship among the trees that can be conferred. Several of the species have to be placed with a general consensus in mind because they tend to float back and forth between some of the analyses conducted. Figure 5 is a tree that has been constructed based upon examining the MPT's of the major data sets, and the other trees received from the implied weighting and branch support searches that were conducted.

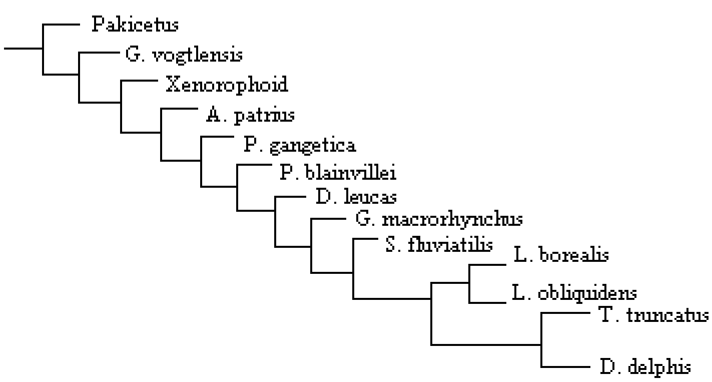

Fig. 5

In all of the trees that were examined *Delphinus delphis* is always the most derived, while Tursiops truncatus and Lissodelphis borealis alternate positions. Inspecting the trees more closely, there seems to be many relationships between *Lissodelphis borealis* and *Lagenorhynchus obliquidens*, and *Tursiops truncatus* is paired with *Delphinus delphis* more consistently and doesn't wander as much. *Pakicetus* to *Pontoporia blainvillei* hardly has any deviations throughout numerous trees. The three remaining species are much harder to place since they switched places quite often between themselves, but more often than the other two, *Delphinapterus leucas* tends to lag behind. The final decision to place *Sotalia fluviatilis* as more derived then *Globicephala macrorhynchus* came from it appearing ahead of *Globicephala macrorhynchus* in all the MPT of the major data sets. The branch supports and different K values showed that there is some discrepancy between the two but *Sotalia fluviatilis* stands to be more derived than *Globicephala macrorhynchus.*

Dr. Albert Sanders provided a broad schematic of what has been occurring to the Cetacean skulls since their primitive ancestors. Since the prehistoric ancestors of Cetaceans were aquatic then to land then back to an aquatic environment, many of the adaptations had to alter for survival. The main changes have been the progression of the nasals towards the anterior, the maxilla extending over the frontal, the supraoccipital and frontals meet while the parietals move laterally, and the lightening of the brain case. When examining these skulls, and taking into consideration the evolutionary developments, it is easy to see the order from *Pakicetus* to *Pontoporia blainvillei* in Fig. 5. After that point it becomes hard to discern the remaining development.

In order to evaluate these results it is important to compare them to other scientific data that has been completed. One study that was published in 2006 by Laura May-Collado and Ingi Agnarsson, claims their "results provide the most detailed phylogeny of Cetacea to date." Their data pool and number of taxa greatly outnumber those from the class, so in comparing the projected tree (Figure 5) to their end data result, there are some similarities.

Appendix I: Data Set

Unordered all discrete

Pakicetus -----01---0-120000-01--0000-0-0----0--00010020-0---
S._fluviatilis -20010110140-12211011101000102101110122001112011001
D._leucas -00112010230022210110100100000201100222010012111101
G._macrorhynchus -01112110031002210210110100002201121011102210111211
D._delphis -110111101000122110100010011001011-0211100002021021
P._blainvillei -20000001020012211010100000011211110202001011111001
L._obliquidens -20110110111002211111001000100101110221100101021011
L._borealis -11011110100012211111001101101101100121100101021021
G._vogtlensis -000010-0-0002010020010000-0000000000000000-10-0--0
P._gangetica -210001010001022010100000101102120-1202000110100100
Xenorophoid --00-0000-000012---1010000-0001----0--00010001-0---
A._patrius -----0----0--012-----10-100-0-1---10--0000111--0---
T._truncatus -100-11102000122112011000001011---10--0-00002021211

Scaled Quantitative Data

Pakicetus ? ? ? ? ? 0.000 0.000 ? ? ? 0.000
S._fluviatilis ? 0.611 0.566 0.281 0.188 0.203 0.130 0.103 0.447 0.295 1.000
D._leucas ? 0.000 0.508 0.712 0.101 0.961 0.327 0.333 0.053 0.724 0.750
G._macrorhynchus ? 0.000 0.000 1.000 0.012 1.000 0.120 0.256 0.000 1.000 0.750
D._delphis ? 0.278 0.449 0.341 0.061 0.467 0.084 0.000 0.378 0.341 0.000
P._blainvillei ? 1.000 0.588 0.000 0.863 0.148 0.200 0.560 0.807 0.224 0.500
L._obliquidens ? 0.522 0.719 0.504 0.000 0.300 0.017 0.205 0.160 0.355 0.250
L._borealis ? 0.311 0.447 0.403 0.068 0.352 0.134 0.000 0.324 0.326 0.000
G._vogtlensis ? 0.044 1.000 0.373 0.623 0.593 0.179 ? 0.254 ? 0.000
P._gangetica ? 0.444 0.154 0.091 1.000 0.053 0.052 1.000 1.000 0.000 0.000
Xenorophoid ? ? 0.699 0.161 ? 0.256 1.000 0.538 0.484 0.179 0.000
A._patrius ? ? ? ? ? 0.043 ? ? ? ? 0.000

T._truncatus ? 0.333 0.639 0.407 ? 0.550 0.031 0.103 0.258 0.750 0.000

Pakicetus ? 1 1 0 0 0 0 ? 0 1 ? ? 0 0 0 0 ? 0 ? 0 ? ? ? ? 0 ? ? 0 0 0 0.5 0 0 0.5 0 ? 0 ? ? ?
S._fluviatilis 0 ? 0.5 1 1 1 1 0 1 1 1 0 1 0 0 0 1 0 1 0.5 0 0.5 1 0.5 0 0.5 1 1 0 0 0.5 0.5 0.5 1 0 0.5 1 0 0 1
D._leucas 0 0 1 1 1 1 0 0.5 1 0 1 0 0 1 0 0 0 0 0 1 0 0.5 1 0 0 1 1 1 0 1 0 0 0.5 1 1 0.5 1 0.5 0 1
G._macrorhynchus 1 0 0 1 1 1 0 1 1 0 1 1 0 1 0 0 0 0 1 1 0 0.5 1 1 1 0 0.5 0.5 1 0 1 1 0.5 0 1 0.5 1 1 0.5 1
D._delphis 0 0 0.5 1 1 1 1 0 1 0 0 0 1 0 0 1 1 0 0 0.5 0 0.5 1 ? 0 1 0.5 0.5 1 0 0 0 0 1 0 1 1 0 1 1
P._blainvillei 0 0 0.5 1 1 1 1 0 1 0 1 0 0 0 0 0 0 1 0.5 1 1 0.5 1 0.5 0 1 0 1 0 0 0.5 0 0.5 0.5 1 0.5 1 0 0 1
L._obliquidens 1 0 0 1 1 1 1 0.5 1 1 0 0 1 0 0 0 1 0 0 0.5 0 0.5 1 0.5 0 1 1 0.5 1 0 0 0.5 0 0.5 0 1 1 0 0.5 1
L._borealis 0 0 0.5 1 1 1 1 0.5 1 1 0 0 1 1 0 1 1 0 0.5 0.5 0 0.5 1 0 0 0.5 1 0.5 1 0 0 0.5 0 0.5 0 1 1 0 1 1
G._vogtlensis 0 0 1 0 0.5 0 0 1 0 0 1 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0.5 0 ? 0 ? ? 0
P._gangetica 0 1 0 1 1 0 1 0 1 0 0 0 0 0 1 0 1 1 0 1 1 1 0 ? 1 1 0 1 0 0 0 0.5 0.5 0 1 0 0 0.5 0 0
Xenorophoid 0 0 0 0.5 1 ? ? ? 1 0 1 0 0 0 0 ? 0 0 0 0.5 ? ? ? ? 0 ? ? 0 0 0 0.5 0 0 0 1 ? 0 ? ? ?
A._patrius ? ? 0 0.5 1 ? ? ? ? ? 1 0 ? 1 0 0 ? 0 ? 0.5 ? ? ? 0.5 0 ? ? 0 0 0 0 0.5 0.5 0.5 ? ? 0 ? ? ?
T._truncatus 0 0 0.5 1 1 1 1 0.5 0 1 1 0 0 0 0 0 1 0 0.5 0.5 ? ? ? 0.5 0 ? ? 0 ? 0 0 0 0 1 0 1 1 1 0.5 1

Article II: Character List

1. *Total amount of teeth located on the rostrum.* Number of less than 20 (0); number of teeth greater than 20 but less than 50 (1); number of teeth greater than 50 (2). **Figure 1.**
2. *Extension of teeth along the Rostrum versus the entire length of the rostrum; the length of the Rostrum was measured from anterior end to the antorbital notch, and the extension of the teeth was measured medially without any deviation to the horizontal.* Ratio greater than 0.8 (0); ratio less then 0.8 (1). **Figure 2.**
3. *Shape of the mandible*.) Mandibles with a “Y” shape (0); mandibles with a “V” shape (1). **Figure 3.**
4. *Width of Rostrum vs. length of Rostrum.* Ratio less than 0.5 (0); ratio greater than 0.5 (1). **Figure 4.**
5. *Length of rostrum vs. length of skull (correlates to elongation of the face).* Ratio less then 0.6 (0); Ratio greater than 0.6 (1). **Figure 5.**
6. *Length of mandible suture versus length of mandible.* Ratio greater than 0.4 (0); ratio less than 0.4 (1). **Figure 6.**
7. *Shape of nasals.* Other (0); square/rectangular (1); triangular (2); tear drop (3); round (4). **Figure 7.**
8. *Shape of rostrum on dorsal side viewed in anterior view.* Convex shape (0); concave shape (1). **Figure 8.**
9. *Height of foramen magnum over width of foramen magnum.* Ratio is greater than 1 (0); ratio is less than 1 (1). **Figure 10.**
10. *Habitat of species.* Saline environment (0); freshwater (1).
11. *Maxilla extension into the external bony nares.* No extension (0); slight extension (1); dramatic extension (2). **Figure 12(a-c).**
12. *Geologic Age.* Eocene (0); Oligocene (1); Recent (2).
13. *Position of the Blowhole.* Located anteriorly on the skull(0); located between the anterior edge of the skull and the posterior edge (1); located towards the anterior edge of the skull (2); **Figure 14.**
14. *Structure of the teeth.* Varying shape and size of teeth (0); uniform shape and size (1). **Figure 15.**
15. *Shape of individual teeth.* Slim and slender (1); big and bulky (0). **Figure 16.**
16. *Condition of the mesorostral canal.* Mesorostral canal is fused to where no opening can be seen (0); mesorostral canal fuses towards the posterior (1); mesorostral canal has no fusions (2). **Figure 17.**
17. *Nuchal crest.* Present (0); absent (1). **Figure 18**
18. *Sagittal crest on the occiput; found on posterodorsal side on posterior end of the skull.* Absent (0); present (1). **Figure 20.**
19. *Lambdoidal crest.* Slight (0); sharp (1). **Figure 19**.
20. *Nasal extension height compared to braincase height.* Positioned below the braincase (0); extends above braincase (1). **Figure 21.**
21. *Shape temporal fossa in lateral view.* Elliptical shape (0); circular shape (1). **Figure 22.**
22. *Texture of the exoccipital condyles.* Smooth texture (0); uneven texture, considered bumpy and/or rough (1). **Figure 23.**

23. *Mandibular notch.* Present (0); absent (1). **Figure 24**
24. *Connection of pterygoids along saggital plane on ventral side of skull.* No apparent connection (0); connection present (1). **Figure 25**
25. *Shape of palate on the ventral side of skull.* Flat in shape (0); vaulted in shape (1).
26. *Maxillary crest.* Absent (0); present (1). **Figure 27**
27. *Occipital overlap of frontal.* No overlap (0); slight overlap (1); heavy overlap (2). **Figure 37.**
28. *Presence of the antorbital notch; found on the posterior end of the rostrum.* Absent (0); slight depth (1); deep antorbital notch (2). **Figure 33**.
29. *Squamosal length compared to length of skull.* Ratio greater than 0.4 (0); ratio less than or equal to 0.4 (1). **Figure 36.**
30. *Presence of groove on the lateral side of the mandible towards its ventral margin.* Absent (0); present (1). **Figure 32**
31. *Shape formed by the mandibular foramen; found on the medial wall of the mandible towards the posterior.* Rounded (0); pointed (1); straight (2). **Figure 30.**
32. *Projection of the mandibular fossa from its origin; found on the medial wall of the mandible towards the posterior.* Maintains a uniform planar projection to the horizontal (0); expands up to coronoid ridge and ventral side of mandible (1). **Figure 31.**
33. *Direction of pterygoid propagation.* Pterygoid propagates medially (0); pterygoid propagates laterally (1). **Figure 37.**
34. *Squamosal located below basioccipital crest.* Located above (0); located below (1). **Figure 43.**
35. *Comparison of mandibular condyle axes (differences in x and y); found on the posterior end of the mandible.* Axes are similar in length (0); transverse axis is longer than x axis (1); dorsoventral axis, x axis, is longer then horizontal axis, y axis (2). **Figure 28.**
36. *Differences in coronoid process/ridge; found on the dorsal side of the mandible towards the posterior.* Major curve (0); slight curve (1); no apparent curve (2). **Figure 29.**
37. *Intercondyloid notch; posterior end of skull on ventral side just below exoccipital condyles.* The intercondyloid notch is described as being converging wide (0); converging narrow (1); diverging (2). **Figure 34.**
38. *Pterygoid hamulus; located on the ventral side of the skull and on the lateral sides of the pterygoid.* Absent (0); present (1). **Figure 35.**
39. *Vomer to basisphenoid.* Elevated (0); smooth/flush (1). **Figure 38.**
40. *Width of Vomerine crest*. Less than 8 mm (0); between 8 mm and 15 mm (1); greater than 15 mm (2). **Figure 39.**
41. *Subtemporal crest; crest along the zygomatic process of the squamosal.* Sharp (0); round (1). **Figure 40.**
42. *Shape of Vomer-basisphenoid suture.* Deep V (0); shallow V (1); square or straight (2). **Figure 42.**
43. *Jugular notch.* Skinny and deep (0); wide and shallow (1). **Figure 44.**
44. *Intertemporal constriction.* Present (0); absent (1). **Figure 43.**
45. *Indention on supraoccipital.* No indention (0); indention present (1). **Figure 41.**

46. *Width of exoccipital condyles (size of species).* Width less than or equal to 80mm (0); width greater than 80mm and less than or equal to 120mm (1); width greater than 120mm (2). **Figure 9.**
47. *Angle of exoccipital condyles.* Parallel (0); acute V (1); wide V (2). **Figure 45.**
48. *Depth of Dorsal condyloid fossa.* Deep (0); shallow (1). **Figure 46.**
49. *Migratory.* Stationary to region (0); may migrate under conditions (1); migratory (2).
50. *Travel or hunt in herds.* Solitary to herds of less than 10 (0); herds of 10 to 100 (1); herds of 100 and larger (2).

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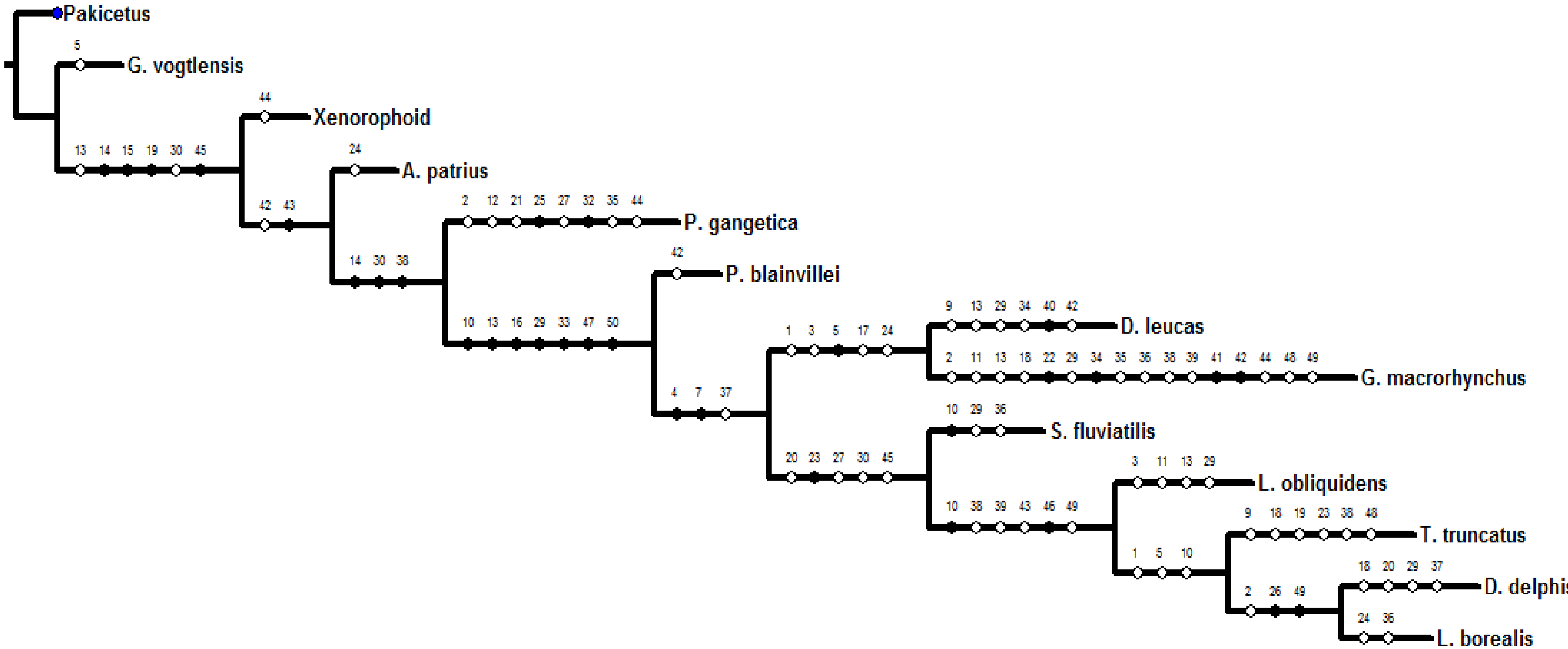
Appendix III: Character Mapping of Unordered and discrete characters



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Jake Taylor
Character States
Geol 5090
December 5, 2008

1. *Total amount of teeth located on the rostrum.* Number of less than 20 (0); number of teeth greater than 20 but less than 50 (1); number of teeth greater than 50 (2). **Figure 1.**
2. *Extension of teeth along the Rostrum versus the entire length of the rostrum; the length of the Rostrum was measured from anterior end to the antorbital notch, and the extension of the teeth was measured medially without any deviation to the horizontal.* Ratio greater than 0.8 (0); ratio less then 0.8 (1). **Figure 2.**
3. *Shape of the mandible*.) Mandibles with a “Y” shape (0); mandibles with a “V” shape (1). **Figure 3.**
4. *Width of Rostrum vs. length of Rostrum.* Ratio less than 0.5 (0); ratio greater than 0.5 (1). **Figure 4.**
5. *Length of rostrum vs. length of skull (correlates to elongation of the face).* Ratio less then 0.6 (0); Ratio greater than 0.6 (1). **Figure 5.**
6. *Length of mandible suture versus length of mandible.* Ratio greater than 0.4 (0); ratio less than 0.4 (1). **Figure 6.**
7. *Shape of nasals.* Other (0); square/rectangular (1); triangular (2); tear drop (3); round (4). **Figure 7.**
8. *Shape of rostrum on dorsal side viewed in anterior view.* Convex shape (0); concave shape (1). **Figure 8.**
9. *Height of foramen magnum over width of foramen magnum.* Ratio is greater than 1 (0); ratio is less than 1 (1). **Figure 10.**
10. *Habitat of species.* Saline environment (0); freshwater (1).
11. *Maxilla extension into the external bony nares.* No extension (0); slight extension (1); dramatic extension (2). **Figure 12(a-c).**
12. *Geologic Age.* Eocene (0); Oligocene (1); Recent (2).
13. *Position of the Blowhole.* Located anteriorly on the skull(0); located between the anterior edge of the skull and the posterior edge (1); located towards the anterior edge of the skull (2); **Figure 14.**
14. *Structure of the teeth.* Varying shape and size of teeth (0); uniform shape and size (1). **Figure 15.**
15. *Shape of individual teeth.* Slim and slender (1); big and bulky (0). **Figure 16.**
16. *Condition of the mesorostral canal.* Mesorostral canal is fused to where no opening can be seen (0); mesorostral canal fuses towards the posterior (1); mesorostral canal has no fusions (2). **Figure 17.**
17. *Nuchal crest.* Present (0); absent (1). **Figure 18**
18. *Sagittal crest on the occiput; found on posterodorsal side on posterior end of the skull.* Absent (0); present (1). **Figure 20.**
19. *Lambdoidal crest.* Slight (0); sharp (1). **Figure 19**.
20. *Nasal extension height compared to braincase height.* Positioned below the braincase (0); extends above braincase (1). **Figure 21.**

21. *Shape temporal fossa in lateral view*. Elliptical shape (0); circular shape (1). **Figure 22.**
22. *Texture of the exoccipital condyles.* Smooth texture (0); uneven texture, considered bumpy and/or rough (1). **Figure 23.**
23. *Mandibular notch.* Present (0); absent (1). **Figure 24**
24. *Connection of pterygoids along saggital plane on ventral side of skull.* No apparent connection (0); connection present (1). **Figure 25**
25. *Shape of palate on the ventral side of skull.* Flat in shape (0); vaulted in shape (1).
26. *Maxillary crest.* Absent (0); present (1). **Figure 27**
27. *Occipital overlap of frontal.* No overlap (0); slight overlap (1); heavy overlap (2). **Figure 37.**
28. *Presence of the antorbital notch; found on the posterior end of the rostrum.* Absent (0); slight depth (1); deep antorbital notch (2). **Figure 33**.
29. *Squamosal length compared to length of skull.* Ratio greater than 0.4 (0); ratio less than or equal to 0.4 (1). **Figure 36.**
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31. *Shape formed by the mandibular foramen; found on the medial wall of the mandible towards the posterior.* Rounded (0); pointed (1); straight (2). **Figure 30.**
32. *Projection of the mandibular fossa from its origin; found on the medial wall of the mandible towards the posterior.* Maintains a uniform planar projection to the horizontal (0); expands up to coronoid ridge and ventral side of mandible (1). **Figure 31.**
33. *Direction of pterygoid propagation.* Pterygoid propagates medially (0); pterygoid propagates laterally (1). **Figure 37.**
34. *Squamosal located below basioccipital crest.* Located above (0); located below (1). **Figure 43.**
35. *Comparison of mandibular condyle axes (differences in x and y); found on the posterior end of the mandible.* Axes are similar in length (0); transverse axis is longer than x axis (1); dorsoventral axis, x axis, is longer then horizontal axis, y axis (2). **Figure 28.**
36. *Differences in coronoid process/ridge; found on the dorsal side of the mandible towards the posterior.* Major curve (0); slight curve (1); no apparent curve (2). **Figure 29.**
37. *Intercondyloid notch; posterior end of skull on ventral side just below exoccipital condyles.* The intercondyloid notch is described as being converging wide (0); converging narrow (1); diverging (2). **Figure 34.**
38. *Pterygoid hamulus; located on the ventral side of the skull and on the lateral sides of the pterygoid.* Absent (0); present (1). **Figure 35.**
39. *Vomer to basisphenoid.* Elevated (0); smooth/flush (1). **Figure 38.**
40. *Width of Vomerine crest*. Less than 8 mm (0); between 8 mm and 15 mm (1); greater than 15 mm (2). **Figure 39.**
41. *Subtemporal crest; crest along the zygomatic process of the squamosal.* Sharp (0); round (1). **Figure 40.**
42. *Shape of Vomer-basisphenoid suture.* Deep V (0); shallow V (1); square or straight (2). **Figure 42.**

43. *Jugular notch.* Skinny and deep (0); wide and shallow (1). **Figure 44.**
44. *Intertemporal constriction.* Present (0); absent (1). **Figure 43.**
45. *Indention on supraoccipital.* No indention (0); indention present (1). **Figure 41.**
46. *Width of exoccipital condyles (size of species).* Width less than or equal to 80mm (0); width greater than 80mm and less than or equal to 120mm (1); width greater than 120mm (2). **Figure 9.**
47. *Angle of exoccipital condyles.* Parallel (0); acute V (1); wide V (2). **Figure 45.**
48. *Depth of Dorsal condyloid fossa.* Deep (0); shallow (1). **Figure 46.**
49. *Migratory.* Stationary to region (0); may migrate under conditions (1); migratory (2).
50. *Travel or hunt in herds.* Solitary to herds of less than 10 (0); herds of 10 to 100 (1); herds of 100 and larger (2).

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American Cetacean Society. "Fact Pack." http://www.acsonline.org/factpack/index.html (accessed on October 23, 2008).

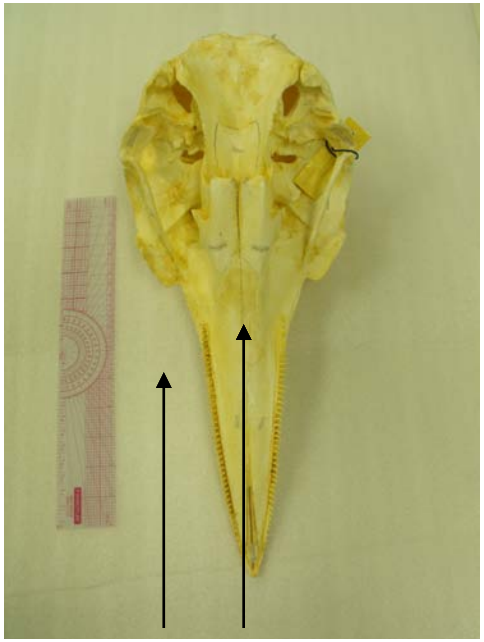
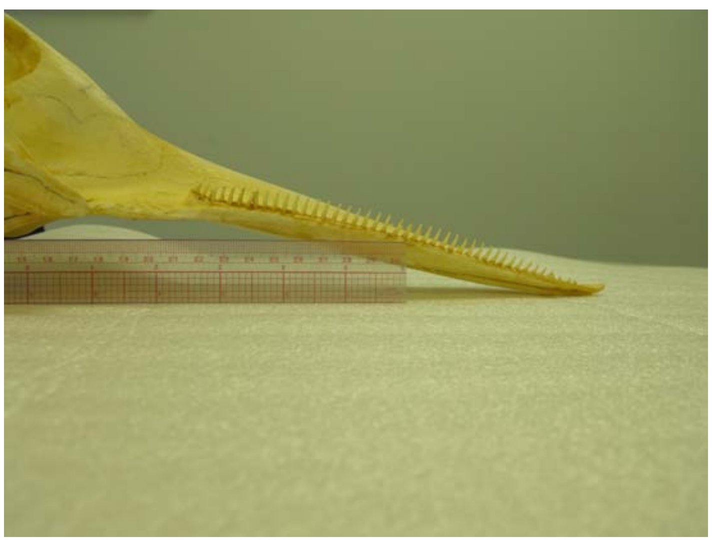


Figure 2: C.S. #2 (top and bottom) Teeth extension on the rostrum: *Lissodelphis borealis*



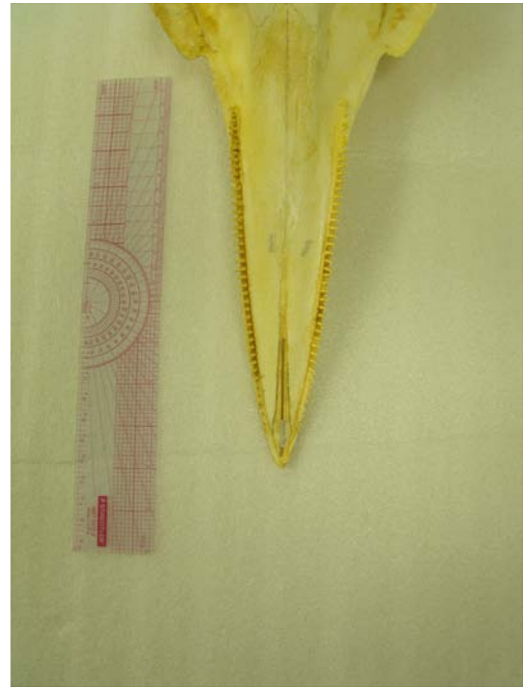


Figure 1: C.S. #1 Teeth count on Rostrum: *Lissodelphis borealis*

Figure 3: C.S. #3 Mandible shape: L *Pontoporia blainvillei* (Y) and R *Lagenorhynchus obliquidens (V)*

Figure 4: C.S.#4 Rostrum w vs. l: *Lagenorhynchus obliquidens*

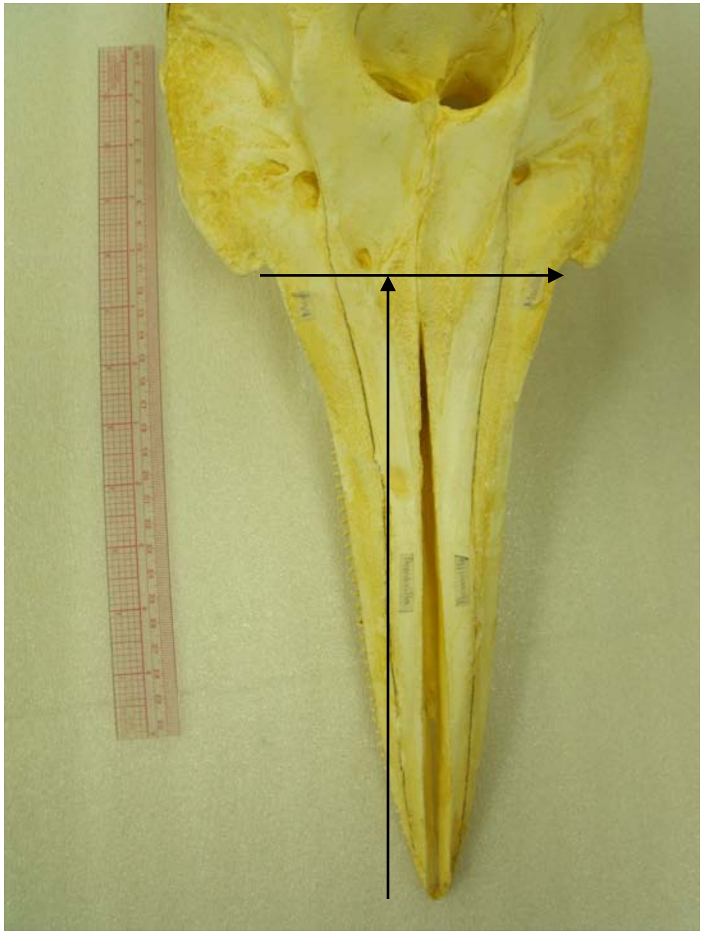


Figure 5: C.S. #5 L rostrum vs. l of skull: *Sotalia fluviatilis*

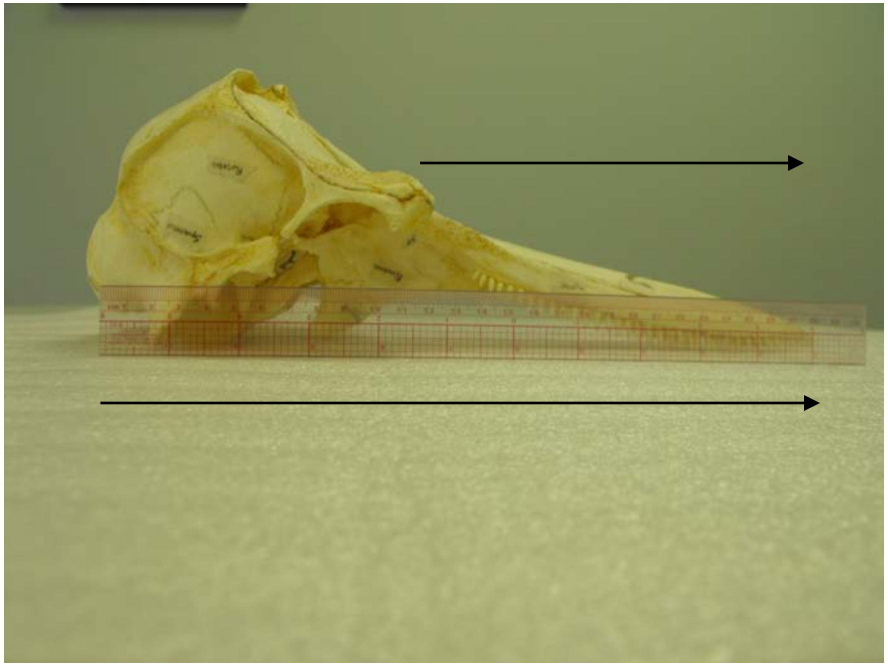
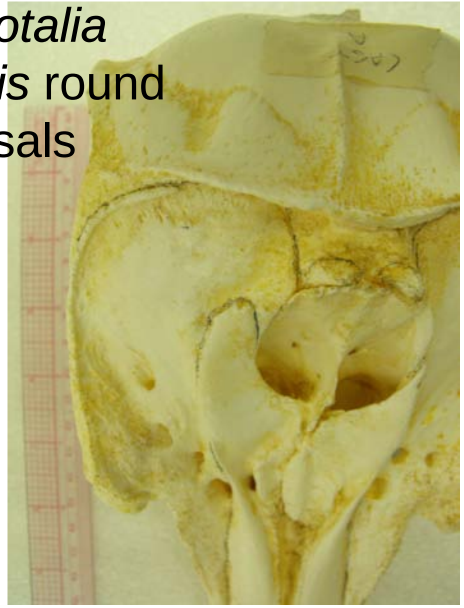
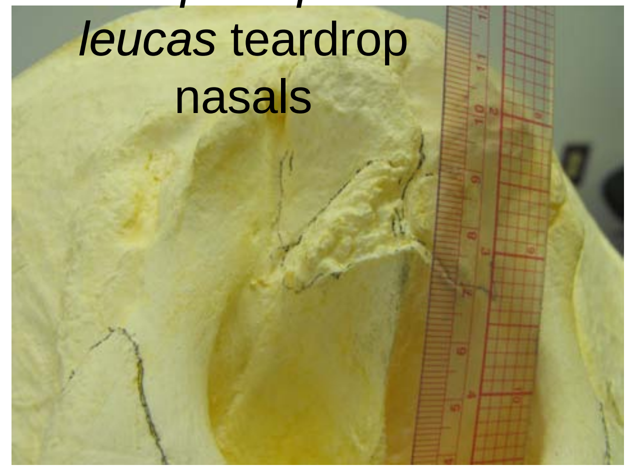


Figure 7: C.S. #7 shape of nasals

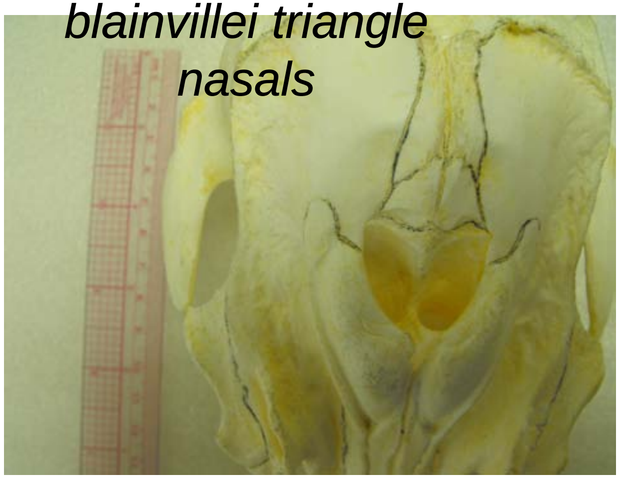
1. *Sotalia fluviatilis* round nasals



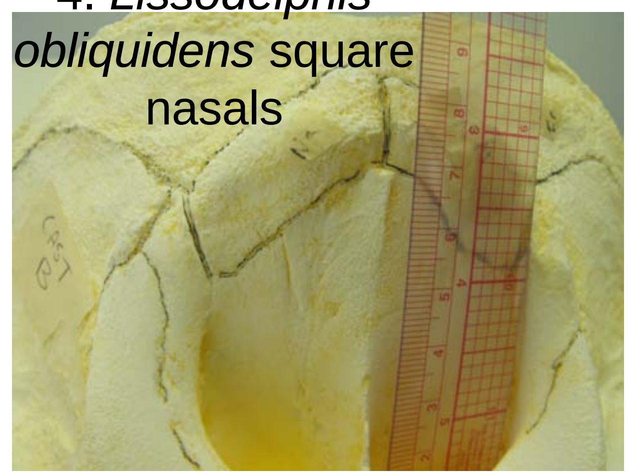
2. *Delphinapterus leucas* teardrop nasals



3. *Pontoporia blainvillei triangle nasals*



4. *Lissodelphis obliquidens* square nasals



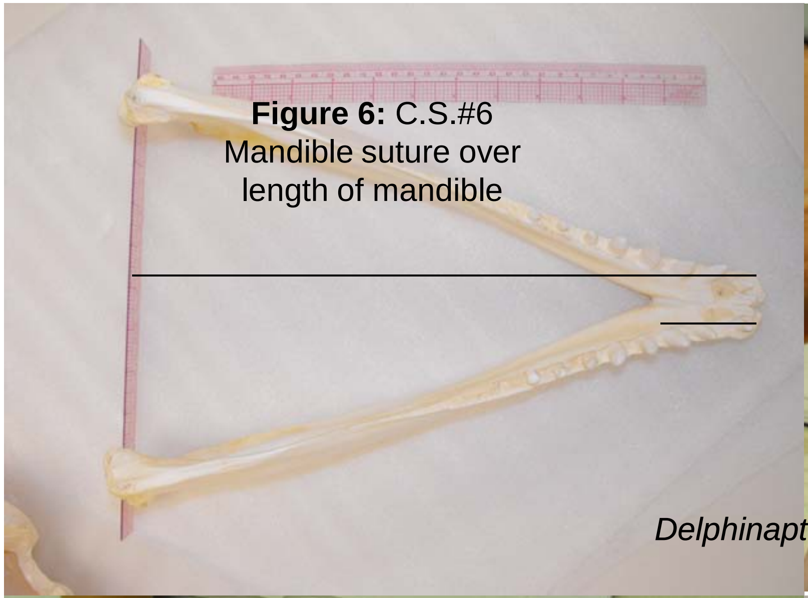


Figure 6: C.S.#6
Mandible suture over
length of mandible

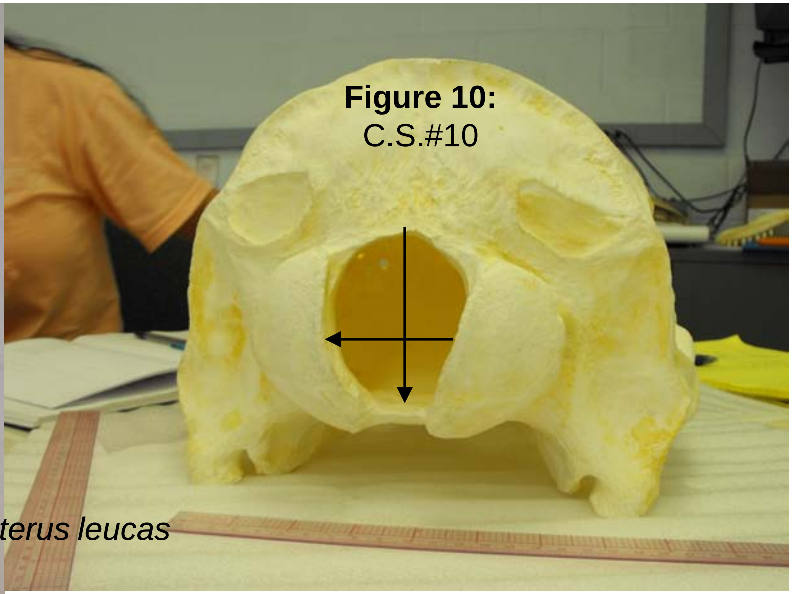
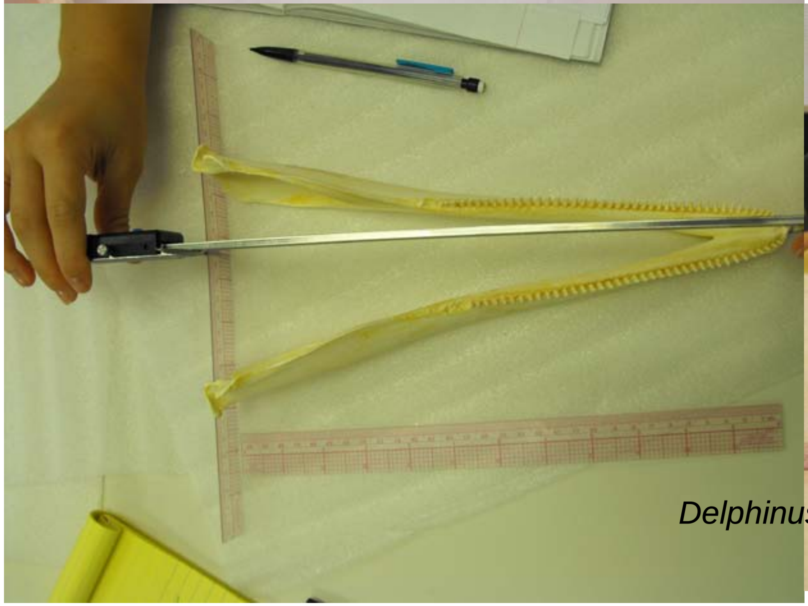
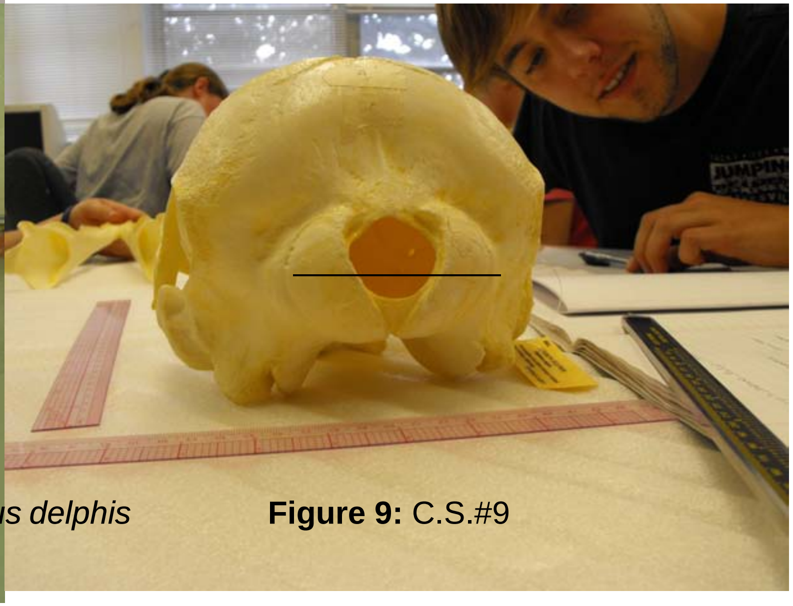


Figure 10:
C.S.#10

Delphinapterus leucas





Delphinus delphis

Figure 9: C.S.#9

Figure 8: C.S. #8 Shape of Rostrum.
Globicephala macrorhynchus

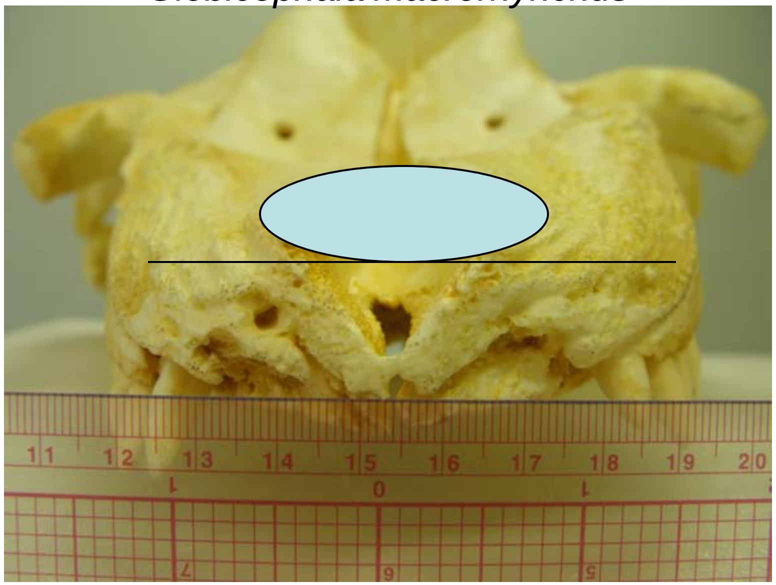


Figure 12a: C.S. #12 Mx extension to bony nares (none). *Globicephala macrorhynchus*

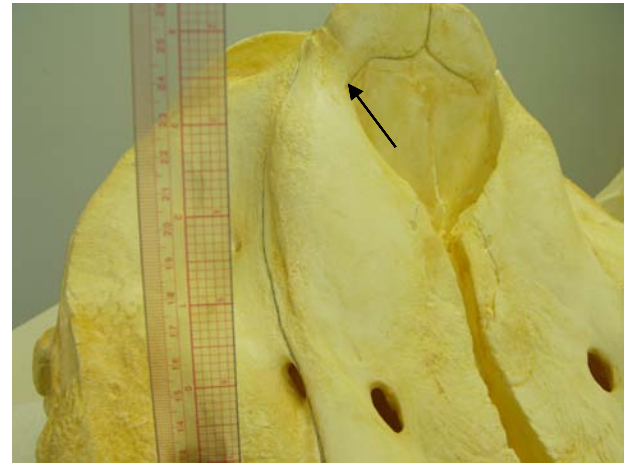


Figure 12b: C.S.#12 (slightly)
Lissodelphis obliquidens

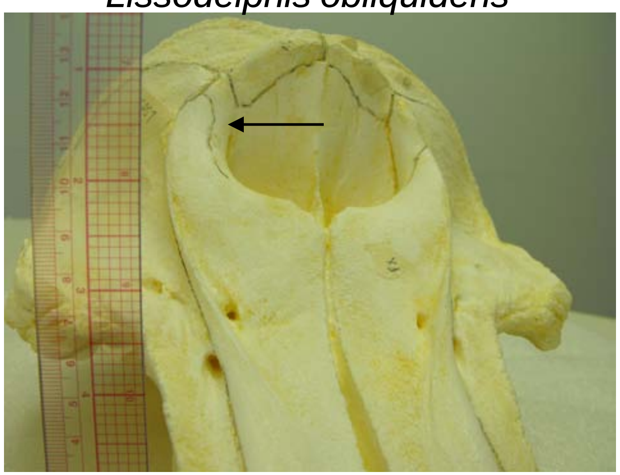


Figure 12c: C.S. #12 (dramatic)
Delphinapterus leucas

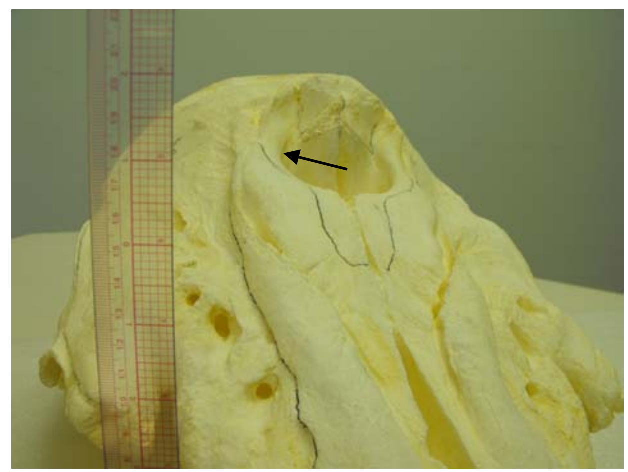
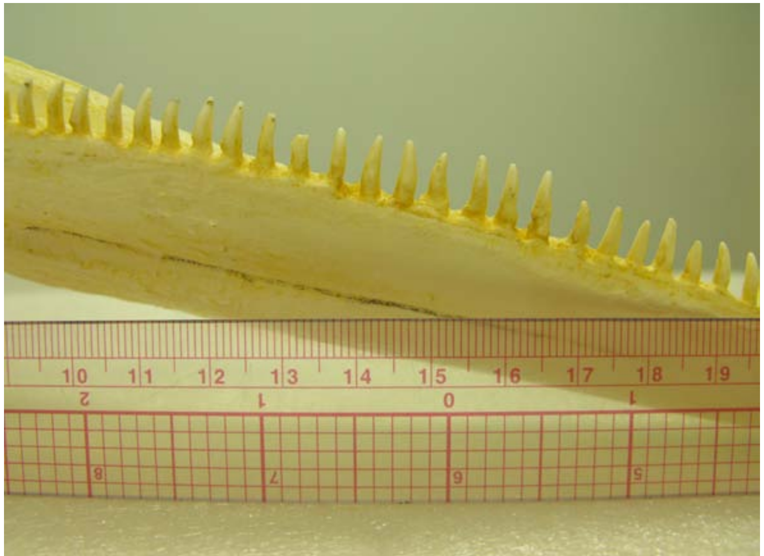




Figure 14: C.S. #14 Position of Blowhole

(top left) front *Pakicetus;* (top right) top *Tursiops truncatus* (bottom left); middle *Georgiacetus vogtlensis*



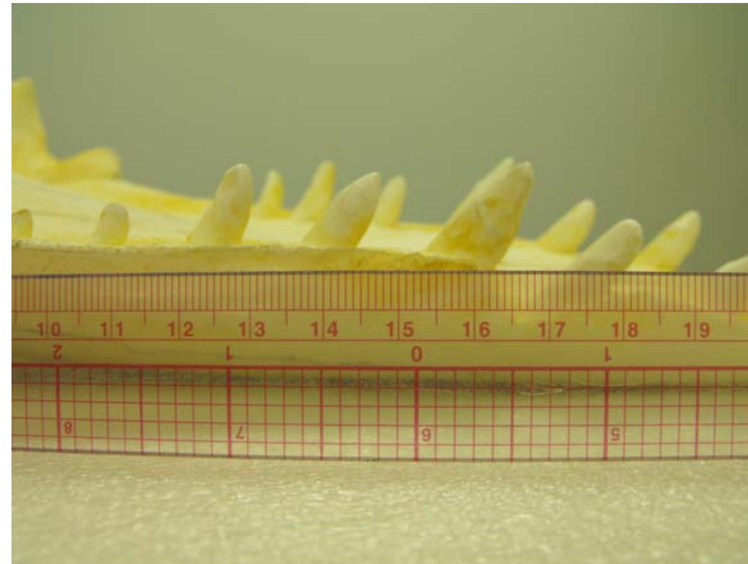
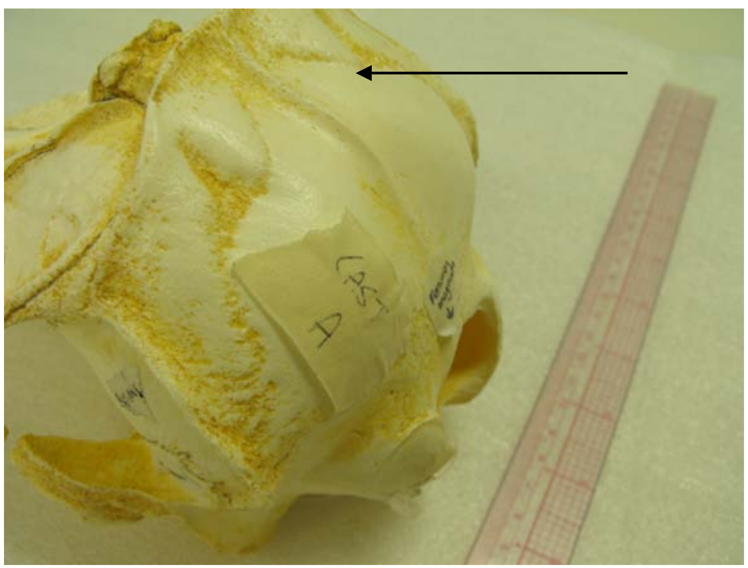


Figure 16: C.S.#16 Shape of teeth (left) slim and slender *Lagenorhynchus obliquidens* (right) big and bulky *Delphinapterus leucas*



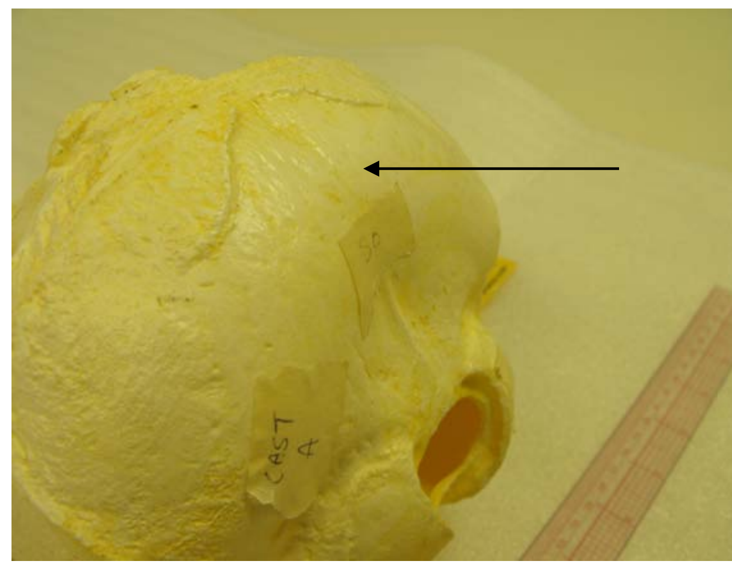
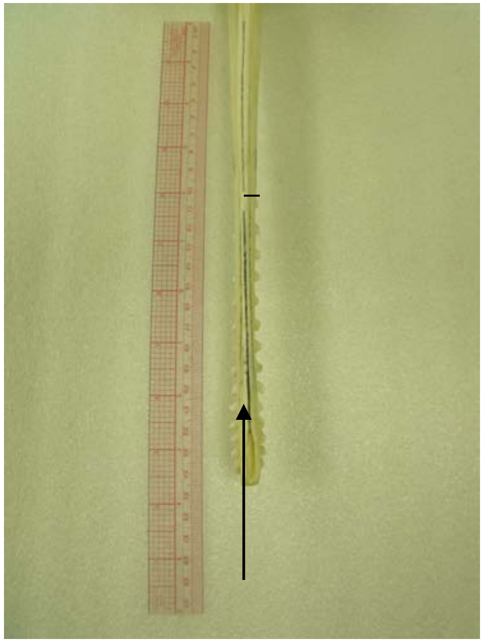


Figure 20: C.S.#20 Saggital crest on occiput (left) yes *Sotalia fluviatilis* (right) no *Delphinus delphis*



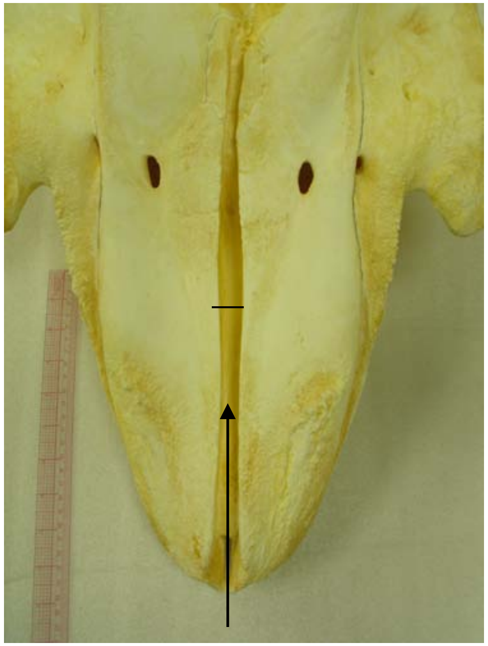


Figure 17: C.S. #17 mesorostral canal (top left) mostly fused *Platonista gangetica;* (top right) slightly fused *Lagenorhynchus obliquidens;* (bottom left) open *Globicephala macrorhynchus*

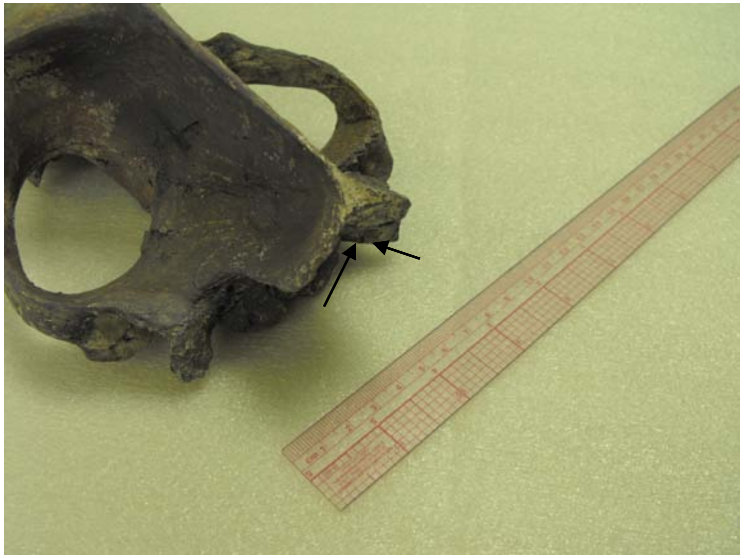


Figure 18: C.S.#18 Nuchal Crest (left) Yes *Pakicetus* (right) No *Tursiops truncatus*

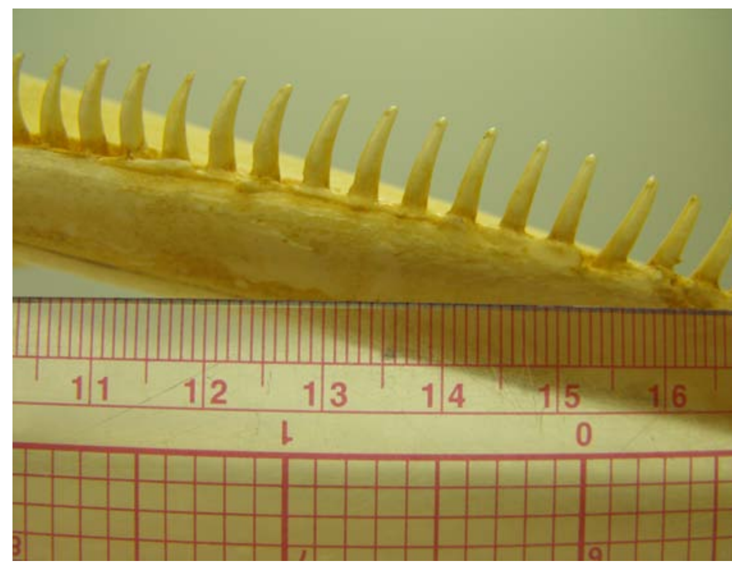


Figure 15: C.S. #15 Teeth Structure (left) Varying *Pakicetus* (right) Uniform *Lissodelphis borealis*

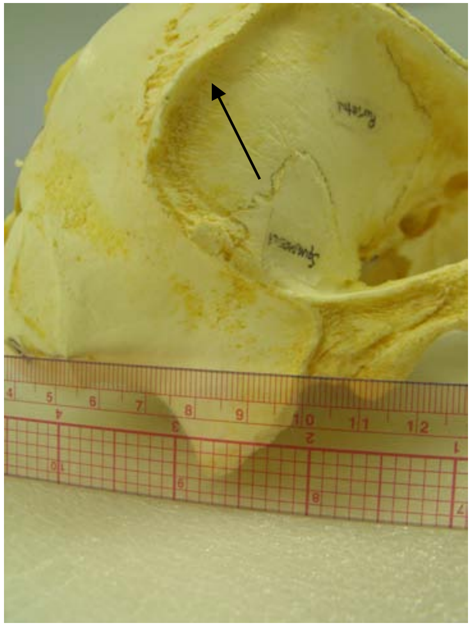
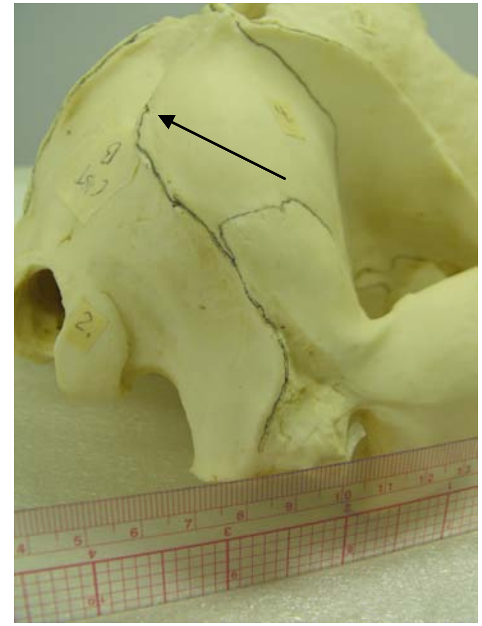


Figure 19: C.S.#19 lambdoidal crest (left) sharp *Sotalia fluviatilis;* (right) slight *Platonista gangetica*



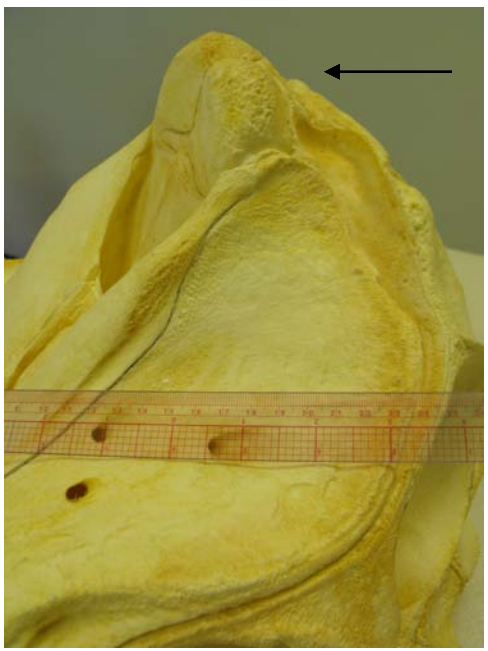


Figure 21: C.S.#21 nasal extension compared to brain case (left) above *Globicephala macrorhynchus;* (right) below *xenorophoid*

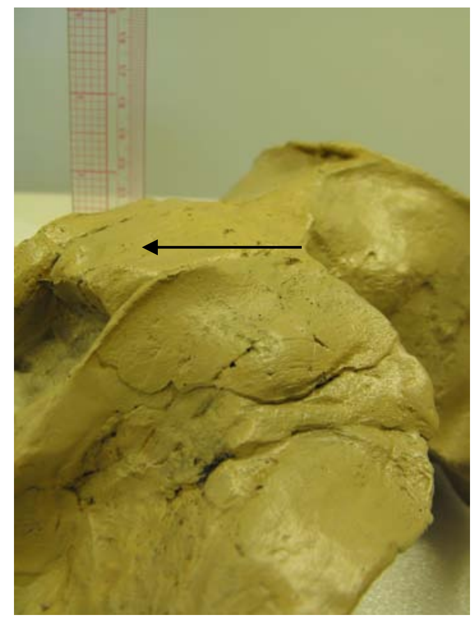
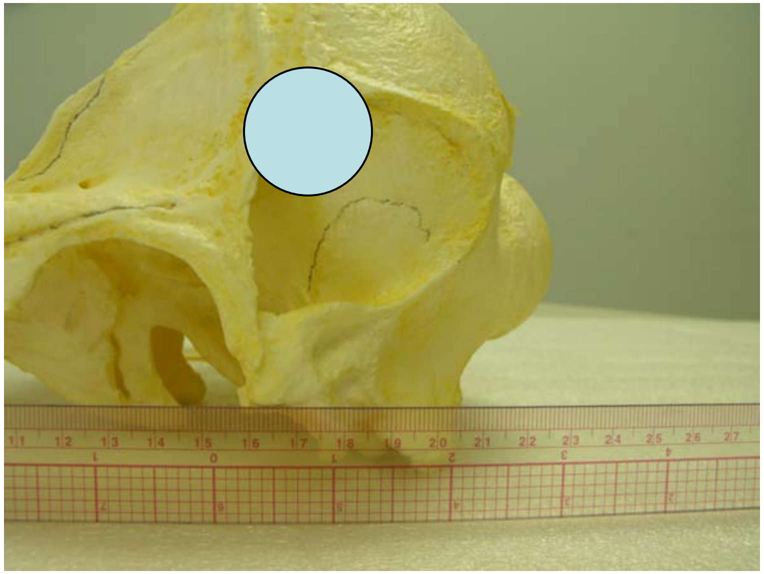


Figure 22: C.S.#22 Shape of temporal fossa (left) circular *Delphimus delphis;* (right) elliptical *Pontoporia blainvillei*



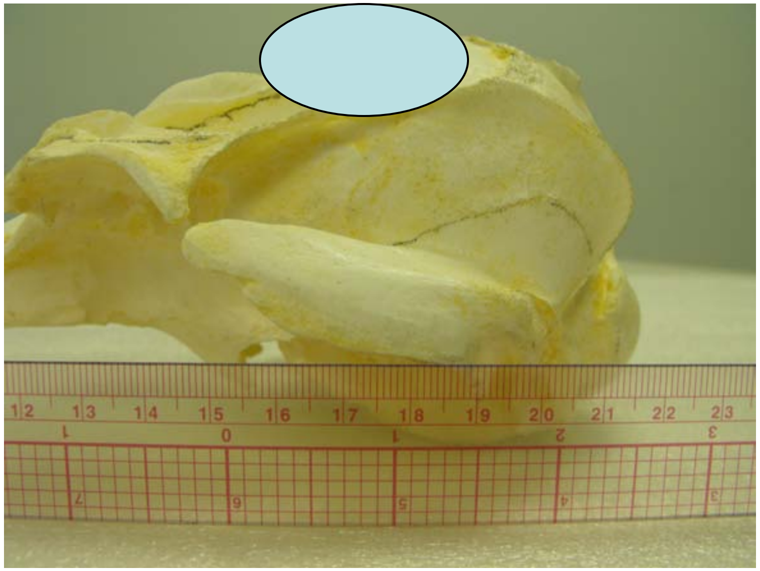
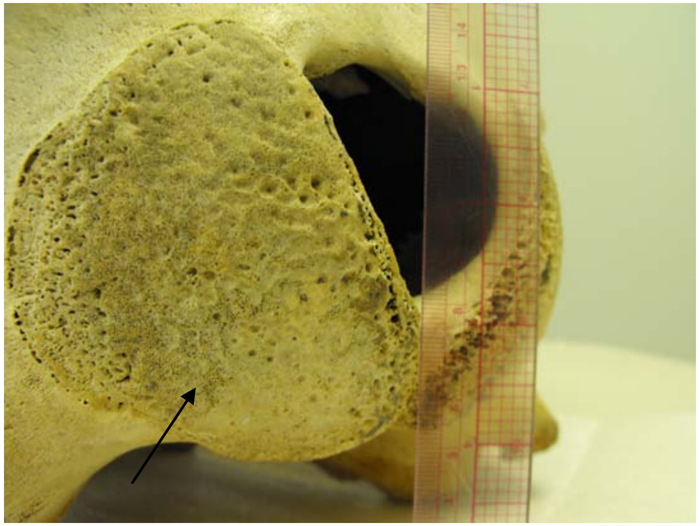
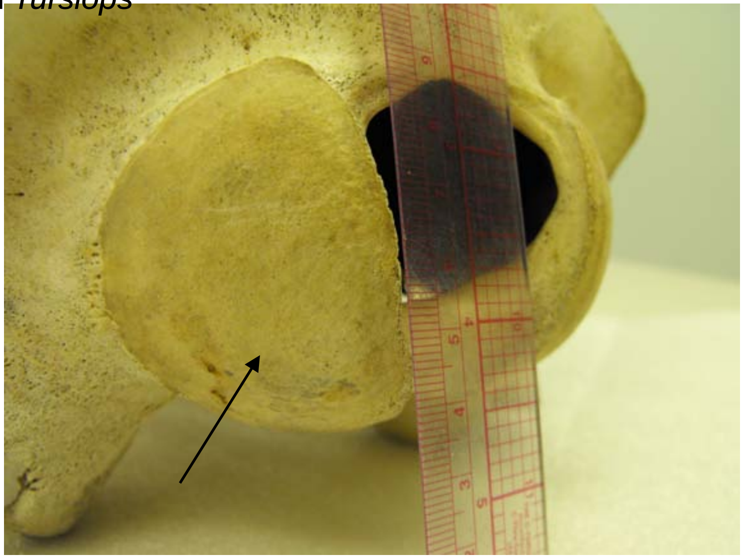


Figure 23: C.S.#23 Texture of exoccipital condyles (left) rough *Globicephala macrorhynchus;* (right) smooth *Tursiops truncatus*





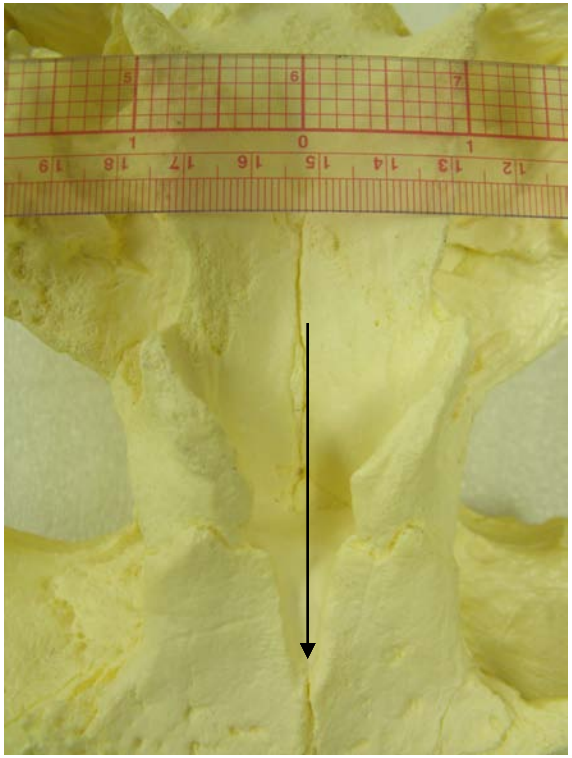


Figure 25: C.S.#25 Pterygoids meet at most medial point (left) no *Archeodelphis patrius;* (right) yes *Delphimus delphis*

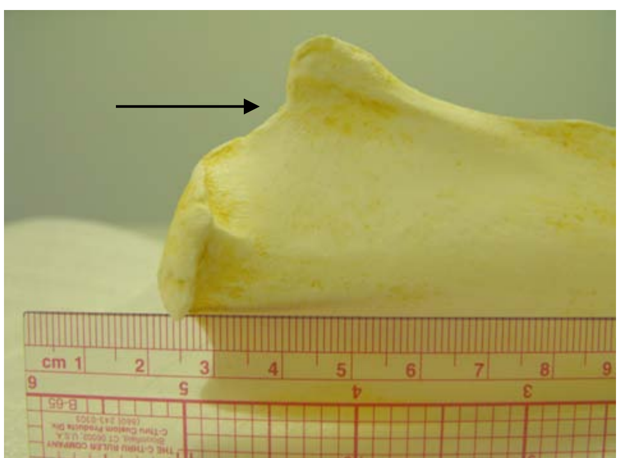


Figure 24: C.S.#24 Mandibular notch (left) yes *Lissodelphis borealis;* (right) no *Pontoporia blainvillei*

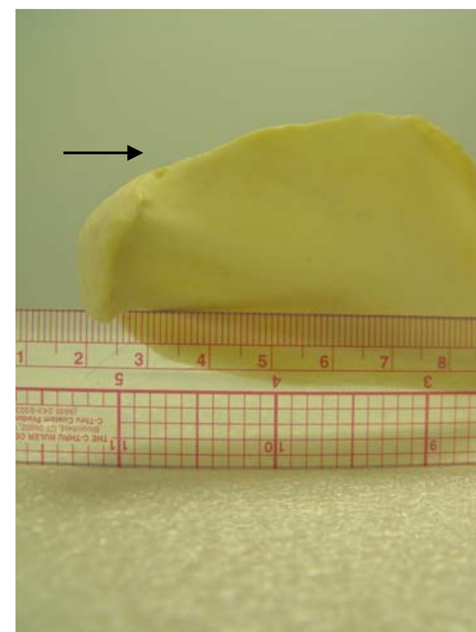


Figure 26: C.S.#26 Shape of Palate (top left) flat *Xenorophoid;* (bottom right) vaulted *Tursiops truncatus*

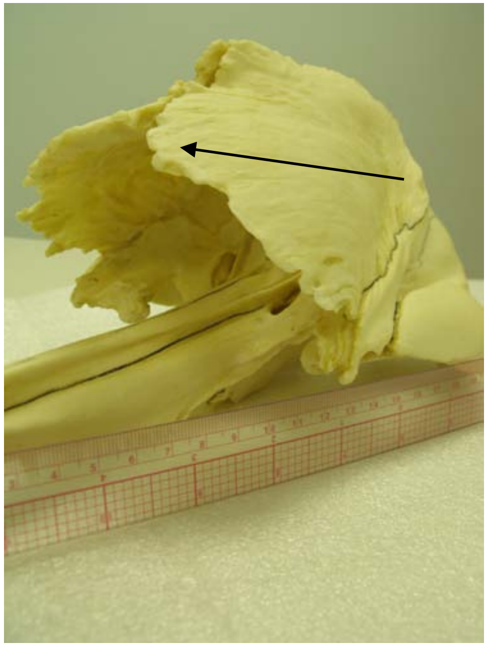


Figure 27: C.S.#27 Maxillary crest (left) yes *Platonista gangetica;* (right) no *Lagenorhynchus obliquidens*

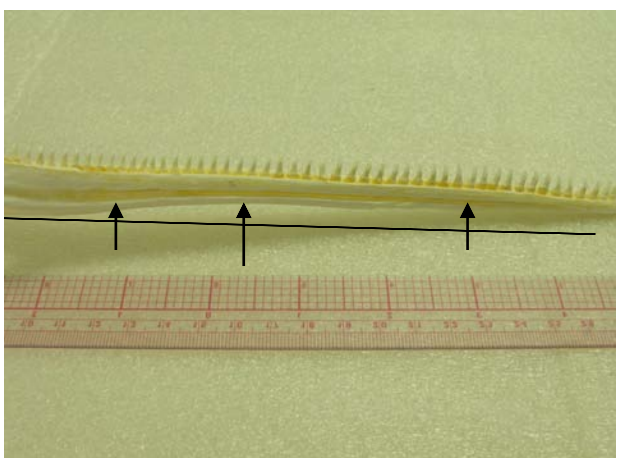
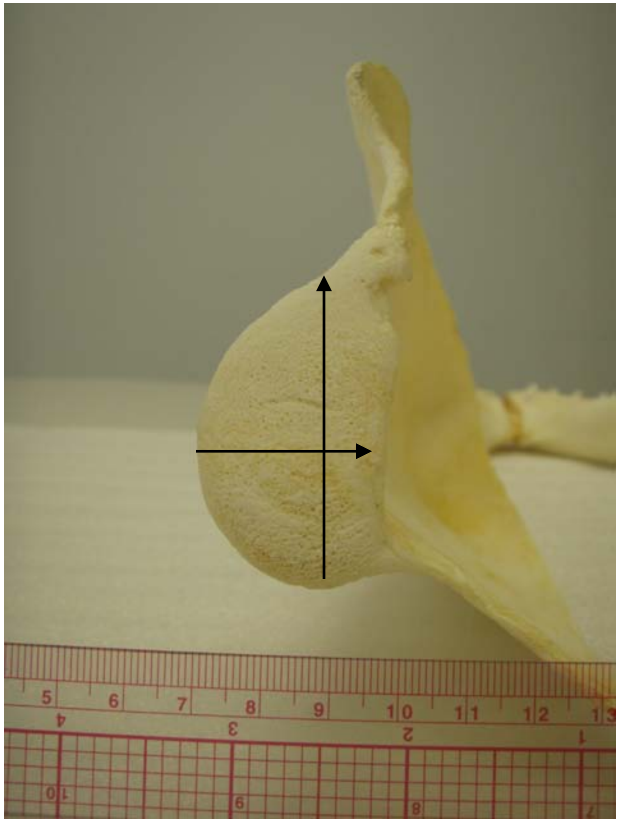
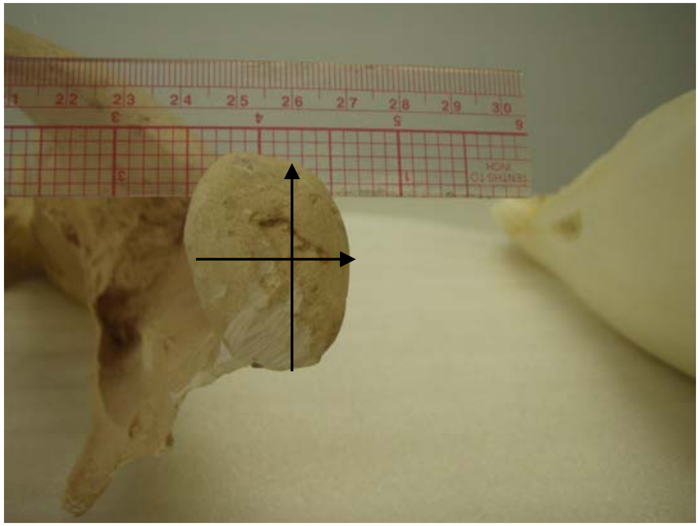


Figure 32: C.S.#32 Mandible groove (left) yes *Pontoporia blainvillei;* (right) no *Lissodelphis obliquidens*





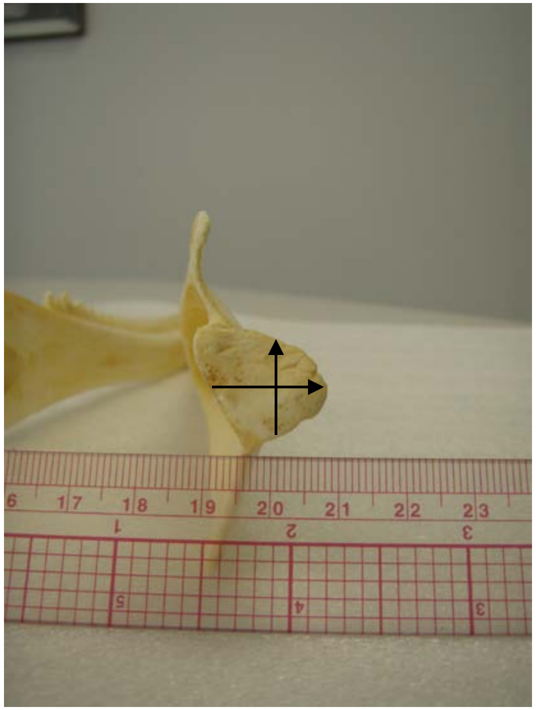
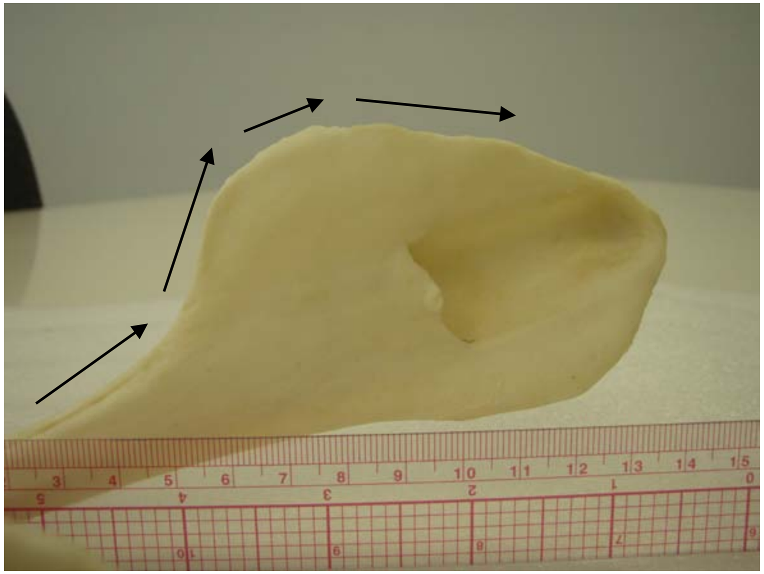


Figure 28: C.S.#28 Comparison of mandibular condyle axes (top left) vertical extended *Globicephala macrorhynchus;* (top right) even lengths *Georgiacetus vogtlensis;* (bottom right) horizontal extended *Sotalia fluviatilis*



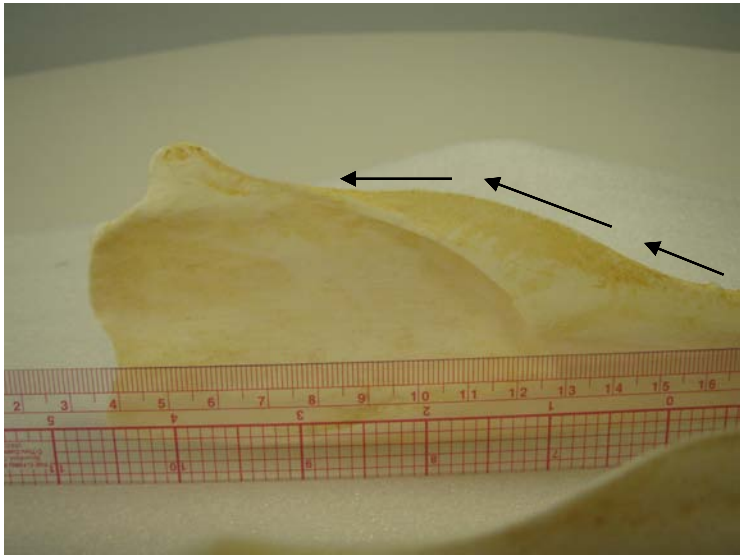
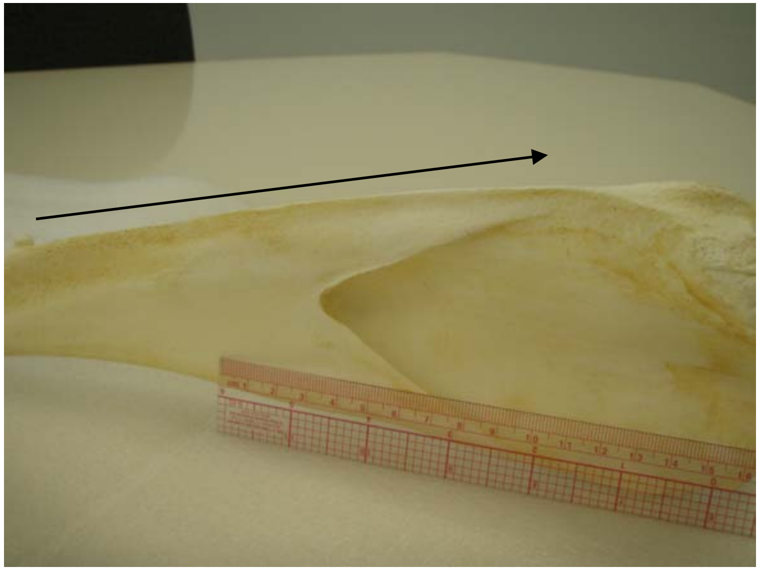
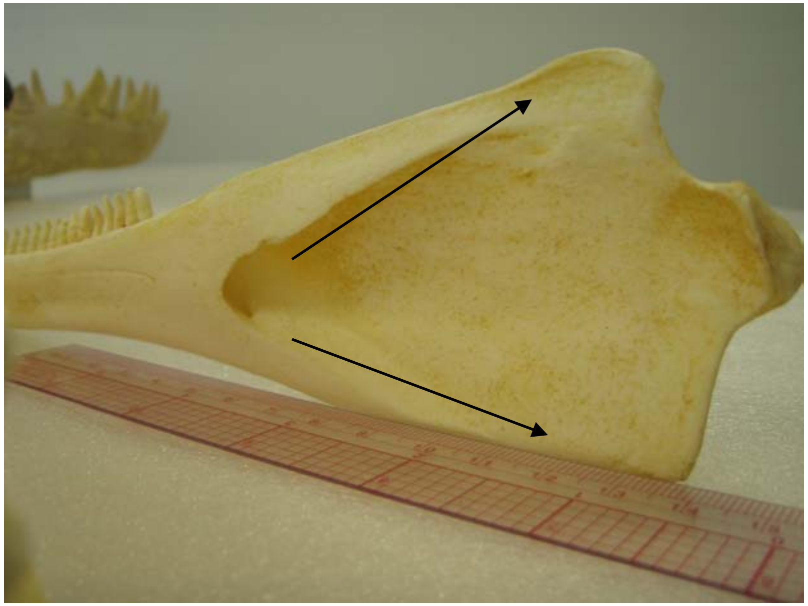


Figure 29: C.S. #29 Differences in coronoid ridge/process (top left) major curve *Platonista gangetica;* (top right) slight curve *Lissodelphis borealis;* (bottom right) no apparent curve *Delphinapterus Leucas*





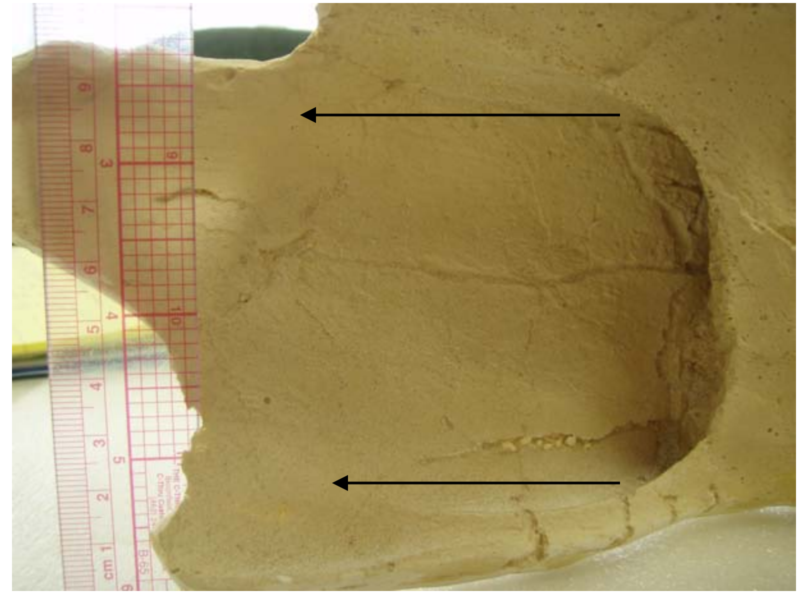


Figure 31: C.S. #31 Comparison of projection of mandibular fossa (top left) extends to coronoid ridge and bottom of mandible *Sotalia fluviatilis;* (top right and bottom left) maintains uniform parallel projection

Georgiacetus vogtlensis and *Platonista gangetica*

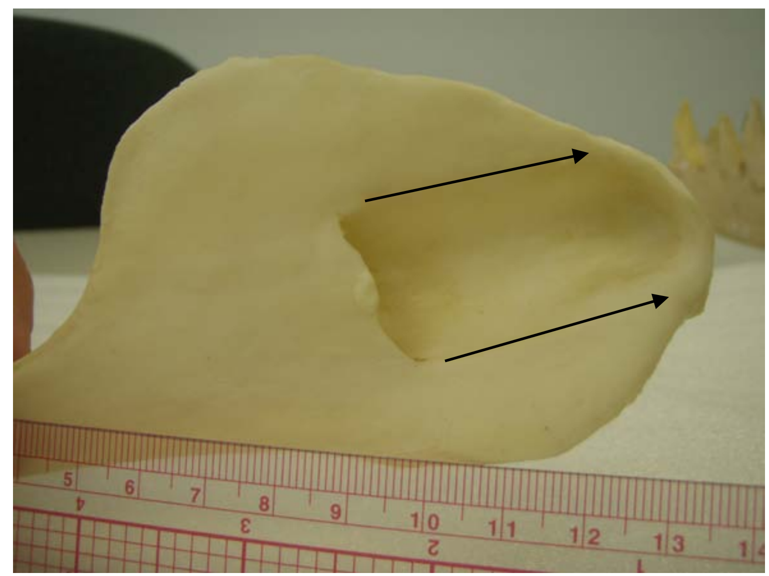
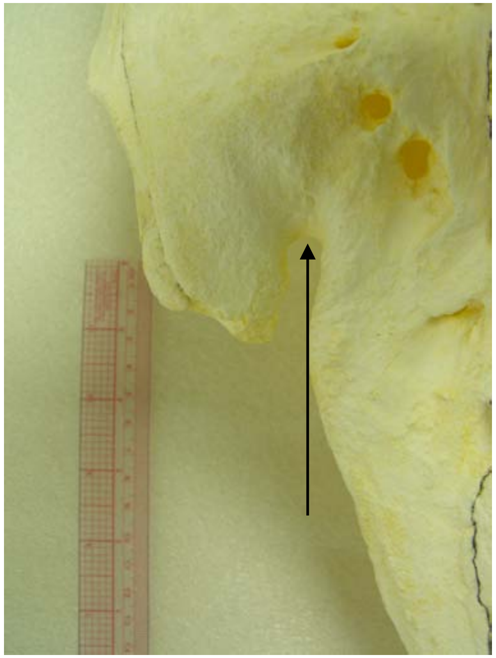
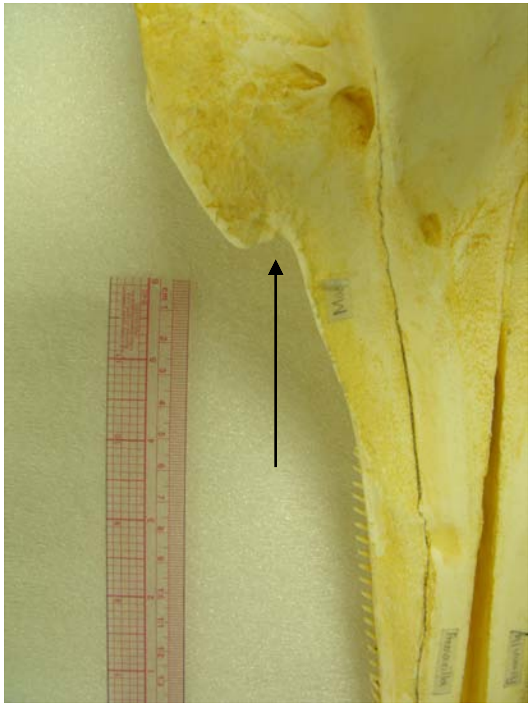


Figure 30: C.S. #30 Shape formed by mandibular foramen on medial wall (top left) pointed *Sotalia fluviatilis;* (top right) rounded *Georgiacetus vogtlensis;* (bottom right) straight *Platonista gangetica*





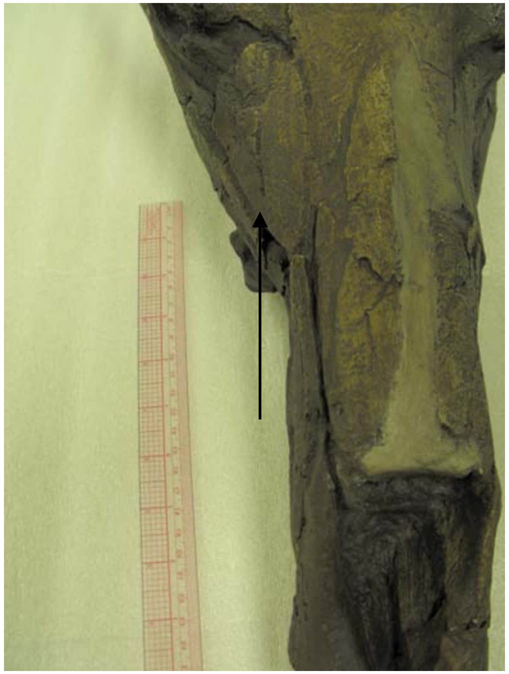


Figure 33: C.S.#33 Antorbital notch (top left) Deep *Delphinapterous leucas;* (top right) slight depth *Lissodelphis borealis; (*bottom left) absence *Georgiacetus vogtlensis*

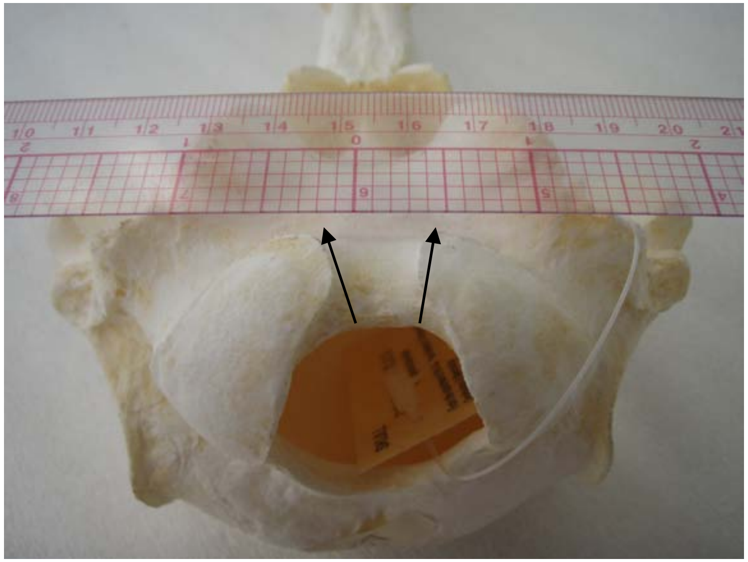


Figure 34: C.S. #34 intercondyloid notch (top left) convergent wide *Georgiacetus vogtlensis;* (top right) convergent narrow *Lissodelphis borealis;* (bottom right) divergent *Pontoporia blainvillei*

Figure 35: C.S. #35 Pterygoid hamulus (L) present *Delphinapterus Leucas;* (R) absent *Sotalia fluviatilis*

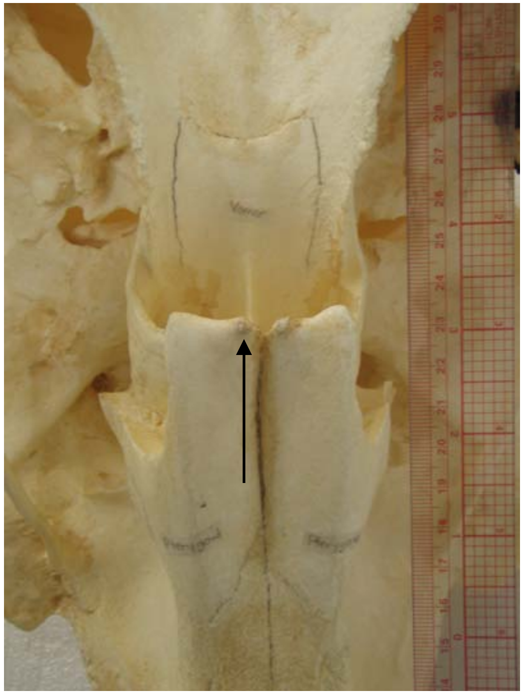


Figure 37: C.S. #33 direction of pterygoid propagation (left) laterally *Lissodelphis borealis* (right) medially *Lagenorhynchus obliquidens*

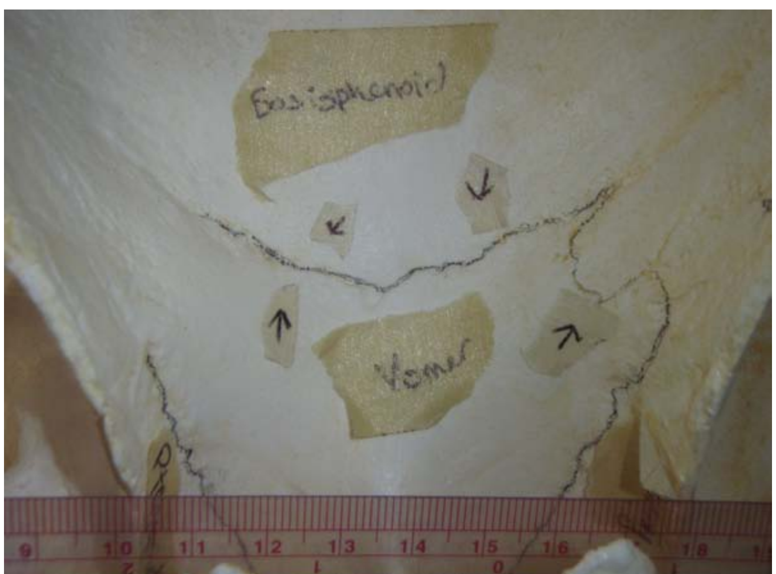
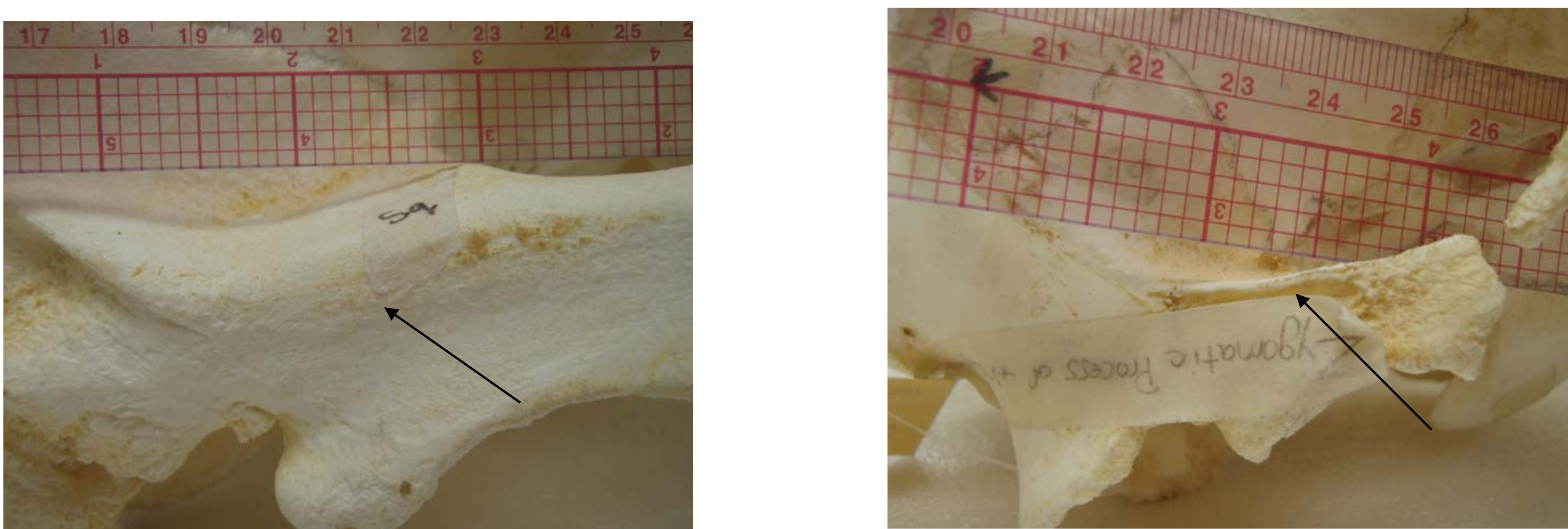


Figure 38: C.S. #39 Vomer to basisphenoid suture (left) elevated *Delphinapterus leucas* (right) smooth/flush *Globicephala macrorhynchus*

Figure 39: C.S. #40 width of vomerine crest (left) *Grampus griseus*

*specimen not used in analysis

Figure 40: C.S. #41 subtemporal crest (bottom left) round *Delphinapterus leucas* (bottom right) *Sotalia fluviatilis*



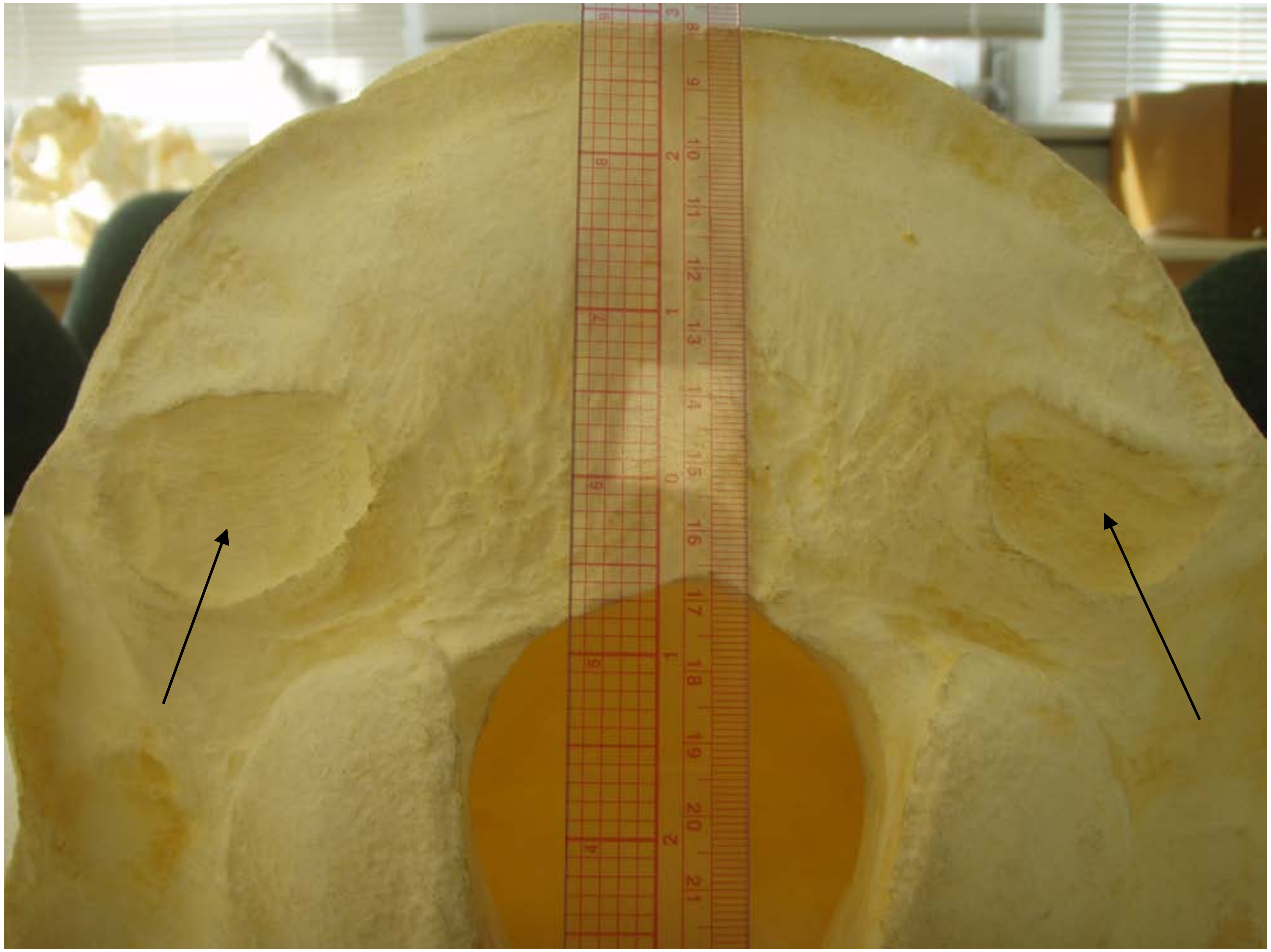


Figure 41: C.S. #41 indention on supraoccipital *Delphinapterus leucas*

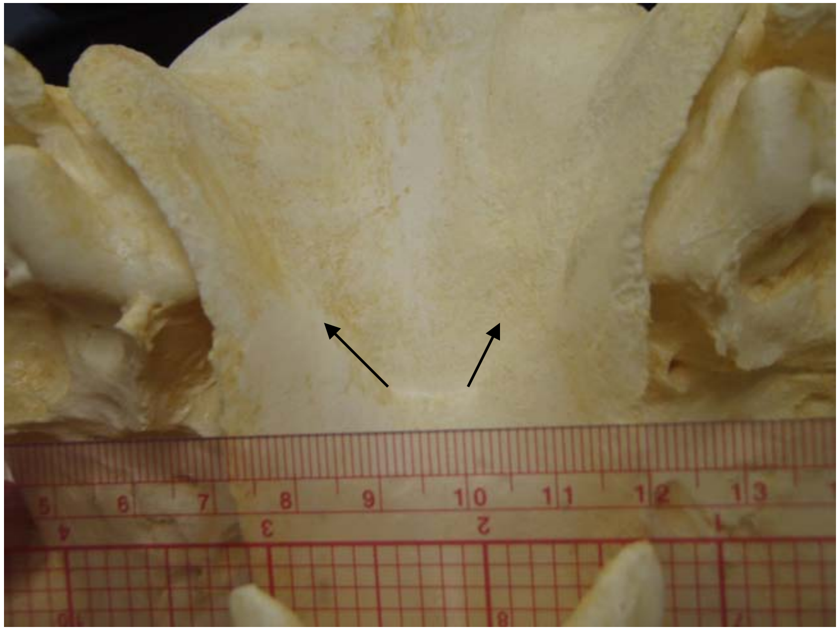


Figure 42: C.S. #42 shape of vomer suture (left) shallow V *Delphinus delphis* (bottom left) square/straight *Globicephala macrorhynchus* (bottom right) deep V *Georgiacetus vogtlensis*

Figure 43: C.S. #44
Intertemporal constriction (right) present *Georgiacetus vogtlensis (bottom)* absent *Delphinus delphis*

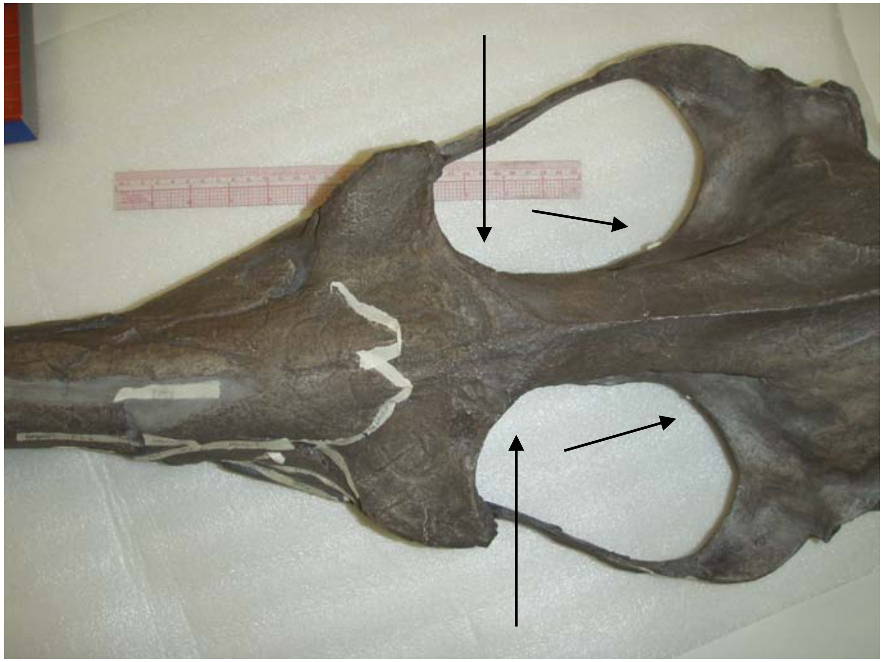


Figure 45: C.S. #47 angle of exoccipital condyles (left) *Platonista gangetica* (bottom left) *Lagenorhynchus obliquidens* (bottom right) *Delphinus delphis*

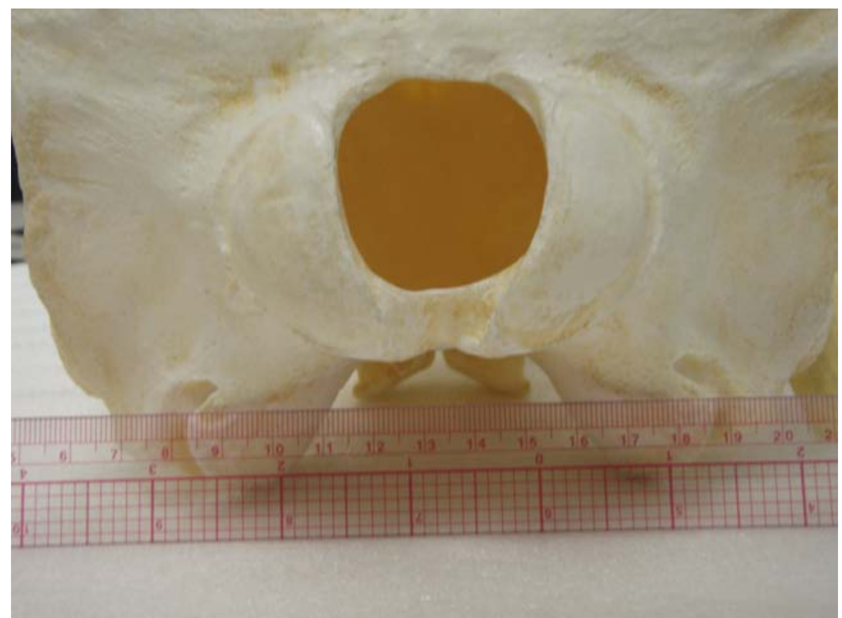


Figure 46: C.S. #48 Depth of dorsal condlyoid fossa (left) *Lissodelphis borealis* (bottom) *Delphinus delphis*