The Evolutionary Relationships of Living and Extinct Taxa of Cetacea as Determined by Cladistic Analyses of Combined Morphological and Genetic Data

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12/05/08

Abstract:

This project examined the evolutionary relationships of fifteen species of Cetacea (*Delphinapturus leucas, Delphimus delphis, Globicephala macrorhynchus, Laganorhynchus obliquidens, Lissodelphis borealis, Pepono electra, Platanista gangetica, Pontoporia blainvillei, Soltalia fluvtilis, Tursiops truncatus, Ziphius cavirostris, Archeodelphis patrius, Georgiacetus vogtlensis, Pakicetus sp*and an unnamed species of Xenorophid). The study was conducted by cladisticly analyzing a mix of morphological and genetic data. The morphological data was gathered through the examination of a set of skull casts of the fifteen species and the genetic data consisted of the aligned DNA sequences for the Twelve S (ribosomal) and the Alpha Lactalbumin genes. The data was analyzed by the TNT phylogeny program yielded a single tree with positive branch supports.

Introduction:

Cetacea are a wide and varied order of marine mammals. It is comprised of eighty three extant species (3) and approximately thirty seven extinct species – at the time of this paper – with specimens spanning the early Eocene to the late Pleistocene (1,2). Previous morphological research has determined the clade to be an offshoot of the order artiodactyl; this theory was later corroborated through the use of genetic data (4). Cetacea are divided in to the suborders Odontoceti (toothed whales) and Mysticeti (baleen whales).

All species of Cetacea have been placed in the evolutionary tree utilizing either morphology or genetics; but relatively little work has been conducted using both. This study will determine the relationship of eleven extant Odontocetes (*Delphinapturus leucas* (D.l), *Delphimus delphis* (D.d), *Globicephala macrorhynchus* (G.m), *Laganorhynchus obliquidens* (L.o), *Lissodelphis borealis* (L.b), *Pepono electra* (P.e), *Platanista gangetica* (P.g), *Pontoporia blainvillei* (P.b), *Soltalia fluvtilis* (S.f), *Tursiops truncatus* (T.t), *Ziphius cavirostris* (Z.c)) two Xenorophids (*Archeodelphis patrius* (A.p) and an unnamed species here after refered to as (Xeno)) and two Archeaocetes (*Georgiacetus vogtlensis* (G.v), *Pakicetus sp.* (Pak)) through the cladistic analysis of combined morphological and genetic data. Cladistics is a relatively recent method of determining evolutionary relationships. It is composed of the statistical analysis of the relatedness of species through the comparison of shared characters and traits.

Materials:

For the purpose of this study, museum quality replicas – cast from skulls of the California Academy of Sciences Department of Ornithology and Mammology's specimens – of D.d, D.l, G.m, L.o, L.b, P.e, P.g, P.b, and S.f were obtained from Skulls Unlimited International®. A replica of P.g skull was obtained from Bone Clones®. Skull casts of extinct species were provided by Dr. Geisler and actual skull of G.m, T.t and Z.f were provided by Georgia Southern University's Biology Department.

Photo-documentation was conducted with Fujifilms' 10 megapixial Finepix S1000fd digital cameras.

Genetic information for the Alpha Lactalbumin gene and the Twelve S ribosomal gene were provided by Michael McGowen and the National Center of Biological Information and were aligned using the ClustalW website.

Microsoft Excel and Note pad were used to organize data in to matrices. Data was analyzed using the T.N.T phylogeny program and WinClada (5).

Methods:

Data collection:

Morphological:

The sutures on the casts were traced over using number two pencils in order to facilitate observations. A list of forty nine character traits was complied through visual observation of the fifteen specimens and sorted by part of the skull. The character states for each species were then cataloged and recorded in to an Excel spread sheet then

organized in to a matrix. The character states were ordered by comparison with the common cow *Bos taurus,* because it like dolphins is an artiodactyl and the domestic dog *Canis familiaris* because early ceatea were also small carnivores.

Genetic:

The genetic data of Alpha Lactalbumin and Twelve S were gathered by searching National Center of Biological Information's catalog for genes closely matching the data provided by Michael Mc.gowlen. The results of specimens we were studying were collected and then aligned using the ClustalW website.

Analysis:

Note pad was utilized to create a data matrix containing the genetic and morphological data that could then be analyzed in WinClada and TNT. Because of the fact that information on over half the character states of the earliest member of the tree (Pakicetus) were lacking a hypothetical out-group was utilized to better root the tree. It consisted of a complete set of zeros (primitive for every morphological character state) in the matrix.

The matrix was then run through the T.N.T phylogeny program as ordered characters. Branch support was then calculated for each node of the tree.

Observations:

The following is an ordered list of the morphological traits and their character states. Traits deemed primitive are marked as "0" with more derived traits labeled consecutively. Figures for non-obvious character states are listed at the end of the paper.

Mandible

1. Shape of the mandible: V shaped (0); Y shaped (1) [Fig. 1]
2. Orientation of mandibular condyle: Horizontal (0); Vertical (1); Extremely vertical (2) [Fig. 2]
3. Orientation of angle of corinoid process with respect to sagittal plane: Posterior (0); Vertical (1) [Fig. 3]
4. Corinoid ramus: Pronounced (0); Subtle (1) [Fig. 4]
5. Mandibular groove: Absent (0); Present (1) [Fig. 5]
6. Mandibular process and mandibular ramus separate: No (0); Yes (1) [Fig. 6]
7. Angle of ventral portion of mandibular synthisis with respect to transvese plane: Angled up (0); Vertical (1); Flat (2) [Fig. 7]

Rostrum

8. Tooth structure: Varied (0); Uniform (1)
9. Molars: Present (0); Absent (1)
10. Accommodation for melon: Absent (0); Present (1) [Fig. 8]
11. Position of blowhole: Anterior end of rostrum (0); Middle of rostrum (1); Posterior end of rostrum (2)
12. Presence of antorbital notch: Absent (0); Present (1)
13. Antorbital notch: Shallow (0); Deep (1) [Fig. 9]

14. Presence of "beak" formed from premaxilla: No (0); Yes (1) [Fig. 10]

15. Presence of teeth on rostrum: Present (0), Absent (1)

Calvaria

16. Overlap of the frontals by the supraoccipitals: Absent (0); Present (1) [Fig. 11]

17. Maxillary extension into bony nares: Absent (0); Present (1) [Fig. 12]

18. Maxilla present at anterior end of blowhole between premaxilla: No (0); Yes (1) [Fig. 13]

19. Lean of blowhole: Absent (0); Present (1) [Fig. 14]

20. Nasal extension above the braincase: Absent (0); Present (1) [Fig. 15]

21. Shape of nasals: Quadrilateral (0); Round (1); Triangle (2); Other (3) [Fig. 16]

22. Nasals touch: Yes (0); No (1)

23. Nasals balanced by premaxillary process: No (0); Yes (1) [Fig. 17]

Occiput

24. Saggital crest formed from parietals: Yes (0); No (1)

25. Saggital crest formed from occiput: No (0); Yes (1) [Fig. 18]

26. Lambdoidal crest: Present (0); Absent (1)

27. Nuchal crest: Present (0); Absent (1)

28. Exoccipital condyle in line with foramen magnum: Yes (0); No (1) [Fig. 19]

29. Texture of condyles: Smoothe (0); Rough (1)

30. Occiput shape: Concave (0); Convex (1)

31. Shape of jugular notch: Wide (0); Narrow (1) [Fig. 20]

32. Exoccipital condyle flush with occiput: No (0); Yes (1) [Fig. 21]

33. Shape of occiput: T shaped (0); Round (1) [Fig. 22]

34. Shape of temporal fossae: Elongated (0); Round (1) [Fig. 23]

Lateral Side of Skull

35. Angle of temporal fossae: Horizontal (0); Angled (1) [Fig. 24]

36. Shape of zygomatic process: Boxy (0); Streamlined (1) [Fig. 25]

37. Shape of external acoustic meatis: Deep (0); Shallow (1) [Fig. 26]

38. Orintation of external acoustic meatis: Vertical (0); Angled (1)

39. Jugal position in relation to eye: Ventral (0); Medial (1)

40. Fusion of pterigoids: Present (0); Absent (1) [Fig. 27]

Ventral Side of Skull

41. Pterigoid orientation: Medial (0); Lateral (1); None (2) [Fig. 28]

42. Anterior sinus fossae extension into rostrum: Absent (0); Present (1) [Fig. 29]

43. Orientation of mandibular fossae: Perpendicular to sagittal plane (0); Angled medially (1)

44. Are mandibular fossae flush with squamosal: Yes (0); No (1)

45. Shape of ventral side of rostrum when viewed laterally: Flat (0); Curved (1)

46. Lateral side of ventral side of blowhole composed of: Pterygoid hamulus (1); Phyryngeal crest (0) [Fig. 30]

47. Shape of anterior dorsal part of vomer: Angled (1); Boxy (0) [Fig. 31]

48. Depth of basisphenoid extension into anteior dorsal part of vomer: Deep (1); Shallow (0)

49. Orintation of pathway of EAM with respect to transverse plane: Horizontal (0); Angled up (1)

Data:

The following are the matrices of morphological characters sorted by the sections of the skull.

Mandible

Character trait	1	2	3	4	5	6	7
A. *patrius*	~	~	~	~	~	~	~
D. *lucus*	0	2	0	1	0	0	0
D. *delphis*	0	1	0	0	0	1	2
G. *vogtlensis*	1	1	0	0	0	0	?
G. *macrorhynchus*	0	1	0	1	0	1?	0?
L. *obliquidens*	0	1	1	1	0	1	0?
L. *borealls*	0	0	1	1	0	1	2
Pakicetus	~	~	~	~	~	~	~
P. *electra*	0	2	0	1	0	1	0
P. *gangetica*	1	1	?	0	1	0	1
P. *blainveillei*	1	2	0	0	1	0	1
S. *fluviatilis*	0	0	0	1	0	0	0
T. *truncatus*	0	~	~	~	~	~	~
Xenorophoid	~	~	~	~	~	~	~

Rostrum

Character trait	8	9	10	11	12	13	14	15
A. *patrius*	~	~	~	2	~	~	~	~
D. *lucus*	0	1	0	2	1	1	~?	0
D. *delphis*	1	1	1	2	1	0	1	0
G. *vogtlensis*	0	1	0	1	0	NA	0	0
G. *macrorhynchus*	1	1	1	2	1	1	0?	0
L. *obliquidens*	1	1	1	2	1	0	0	0
L. *borealls*	1	1	1	2	1	0	1	0
Pakicetus	0	0	~	0	~	~	~	0
P. *electra*	1	1	1	2	1	1	1	0
P. *gangetica*	0	1	1	2	1	1	0	0
P. *blainveillei*	1	1	0	2	1	0	0	0
S. *fluviatilis*	1	1	1	2	1	0	0	0
T. *truncatus*	1	1	1	2	1	0	~	0
Xenorophoid	1	1	1	2	1	0	~	0

Calvaria

Character trait	16	17	18	19	20	21	22	23
A. *patrius*	~	?	?	0	0	0	0	0
D. *lucus*	0	1	1	1	0	2	0	0
D. *delphis*	0	0	?	1	0	3	1	0
G. *vogtlensis*	0	0	?	0	0	0	0?	0
G. *macrorhynchus*	1	0	1	1	1?	1	0	0
L. *obliquidens*	0	1	0	1	0?	0	0	0
L. *borealls*	1	1	0	1	0?	3	0	0
Pakicetus	0	~	~	~	0	~0?	~	~
P. *electra*	1	1?	1?	1	1	?	?	0
P. *gangetica*	0	1	?	1	?	?	1	1?
P. *blainveillei*	0	1	?	0	0	2	0	0
S. *fluviatilis*	1	1	0	1	1?	1	1	0
T. *truncatus*	1	1	1	1	0	1	0	0
Xenorophoid	1	?	?	0	0	0	0	0

Occiput

Character trait	24	25	26	27	28	29	30	31	32	33	34
A. *patrius*	~	~	0	~	0	0	0?	0	0	~0?	0?
D. *lucus*	1	0	0	0	0	0	1	1	0	1	0
D. *delphis*	1	1	1	1	0	0	1	1	1	1	1
G. *vogtlensis*	0	0	0	0	0	0	0	1	0	0	0
G. *macrorhynchus*	1	0	0	0	0	1	1	0	1	1	0
L. *obliquidens*	1	1	1	1	1	0	1	1	1	1	0
L. *borealls*	1	1	1	1	1	0	1	1	1	1	1
Pakicetus	0	0	0	0	0	0	0	?	0	0	0
P. *electra*	1	0	?	?	0	0	1	0	0	1	0
P. *gangetica*	1	1	0?	?	0	0	0	0	0	0	0
P. *blainveillei*	1	1	0	?	1	0	1	?	0	1	0
S. *fluviatilis*	1	0	0	0	1	0	1	0	1	1	1
T. *truncates*	1	1	0	0	1	0	1	1	1	1	0
Xenorophoid	1	1	0	0	0	0	0	?	0	0	0

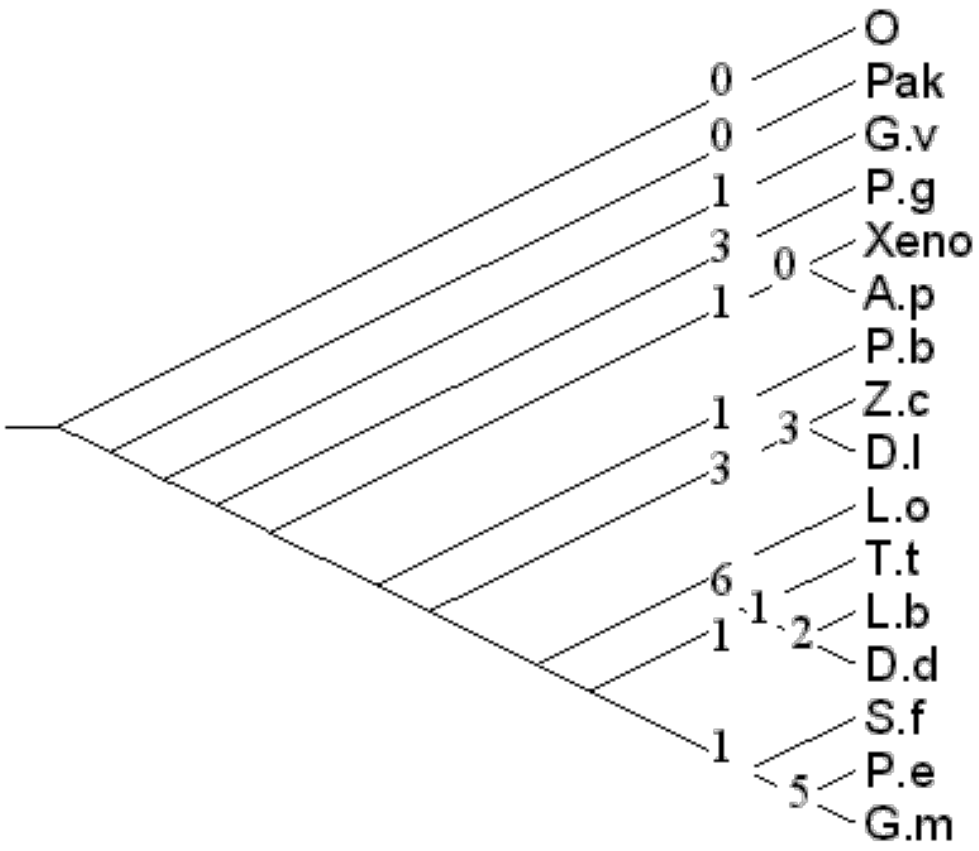
Lateral Side of Skull

Character trait	35	36	37	38	39	40
A. *patrius*	1	?	1	0	?	1
D. *lucus*	0	0	0	1	1	1
D. *delphis*	1	0	1	0	1	0
G. *vogtlensis*	1?	0	0	0	0	0
G. *macrorhynchus*	1	0	1	?	1	1
L. *obliquidens*	0	0	1	?	1	1
L. *borealls*	0	0	1	?	1	0
Pakicetus	1	0	1	0	0	?
P. *electra*	1	0	1	?	1	1
P. *gangetica*	1	1	0	0	1	0?
P. *blainveillei*	0	1	1	0	1	1
S. *fluviatilis*	1	0	1	0	1	1
T. *truncatus*	0	0	1	1	1	1
Xenorophoid	1	1	1	?	?	?

Ventral Side of Skull

Character trait	41	42	43	44	45	46	47	48	49
A. *patrius*	1	?	0	0	0?	0	?	?	0
D. *lucus*	0	0	1	0	1	0	1	0	1
D. *delphis*	1	1	1	1	1	0	0	0	0
G. *vogtlensis*	0	~	0	0	0?	?	?	?	0
G. *macrorhynchus*	1	0	1	0	1	0	0	0	1
L. *obliquidens*	1	0	1	1	1	0	1	1	1
L. *borealls*	2	0	1	1	1	0	0	0	0
Pakicetus	?	~	0	0	~	~	~?	~?	0
P. *electra*	1	0	1	0	0	?	1	0	?
P. *gangetica*	2	?	0	0	1	0	0	1	0
P. *blainveillei*	1	0	0	0	0	1	0	0	0
S. *fluviatilis*	1	0	0	1	1	0	1	0	1
T. *truncatus*	1	0	0	1	1	0	1	0	0
Xenorophoid	?	0	0	0	0	?	?	?	1

Results:



The analysis of the complete matrix through T.N.T yielded this single cladistic tree with a union length of four hundred forty one. The tree was not affected when subjected to implied weighting. Due to the fact that the program yielded only the single tree little more branch support – which is included above – could be done to assess the quality of the tree.

Discussion and Conclusion:

The morphological and genetic data melded successfully yielding a rather solid theory as to the relative evolution of the species covered in the study. As expected the Pak, G.v, A.p and Xeno evolved in chronological order (2). The P.g's placement between G.v and A.p & Xeno makes since when one considers how extremely derived the maxillary shields on the skull are and the amount of time required to evolve such adaptations. P.g's placement is also supported by its high count of primitive traits.

Considering the fact that the morphological characters comprised about three percent of our matrix, when compared to the overwhelming amount of base pairs, they were really only useful as a method of placing the species for which genetic data was unavailable. Because of the complexity of the living body and the shear number of genes involved in the minutest detail of shape in the body a method of scaling the base pairs to the morphological characters should be developed for use in future studies.

References:

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3. Insa Cassens et al.; Independent adaptation to riverine habitats allowed survival of ancient cetacean lineages Proc Natl Acad Sci U S A. 2000; 1010; 97(21): 11343–11347
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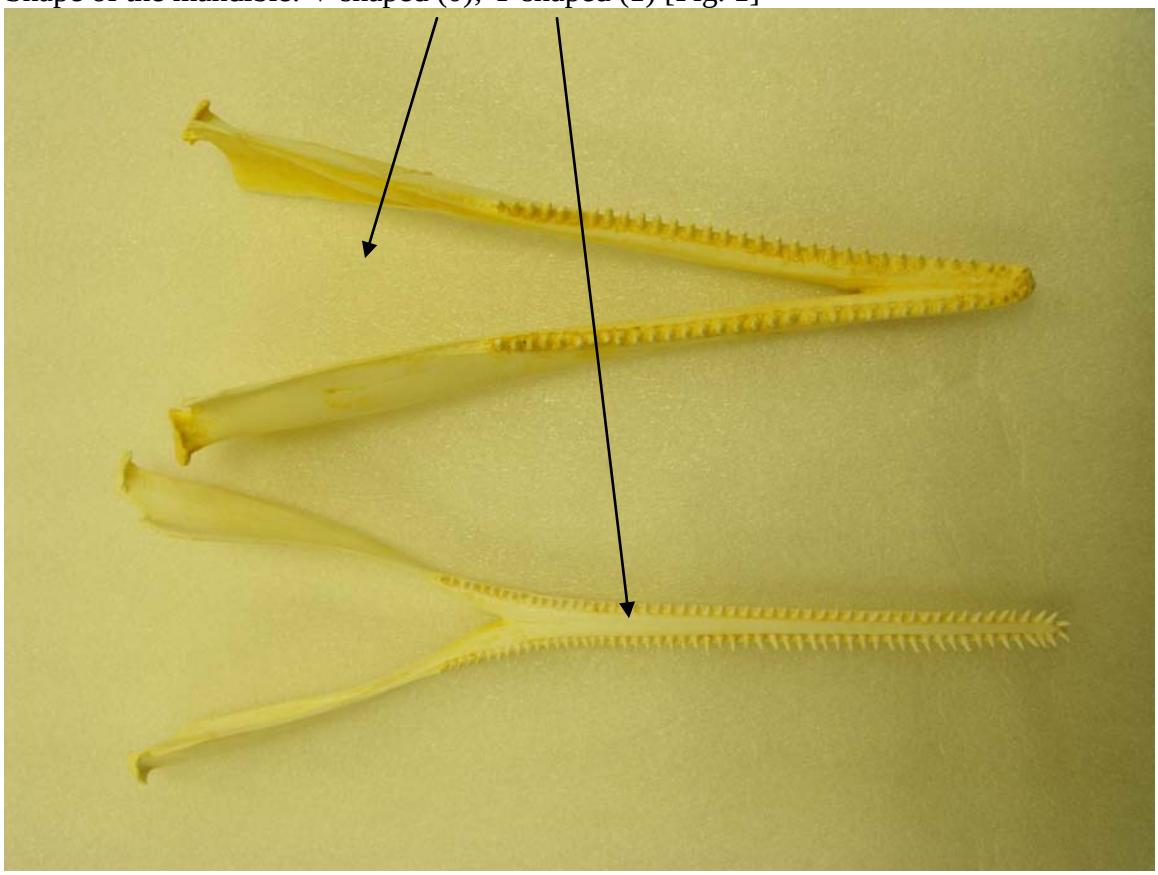
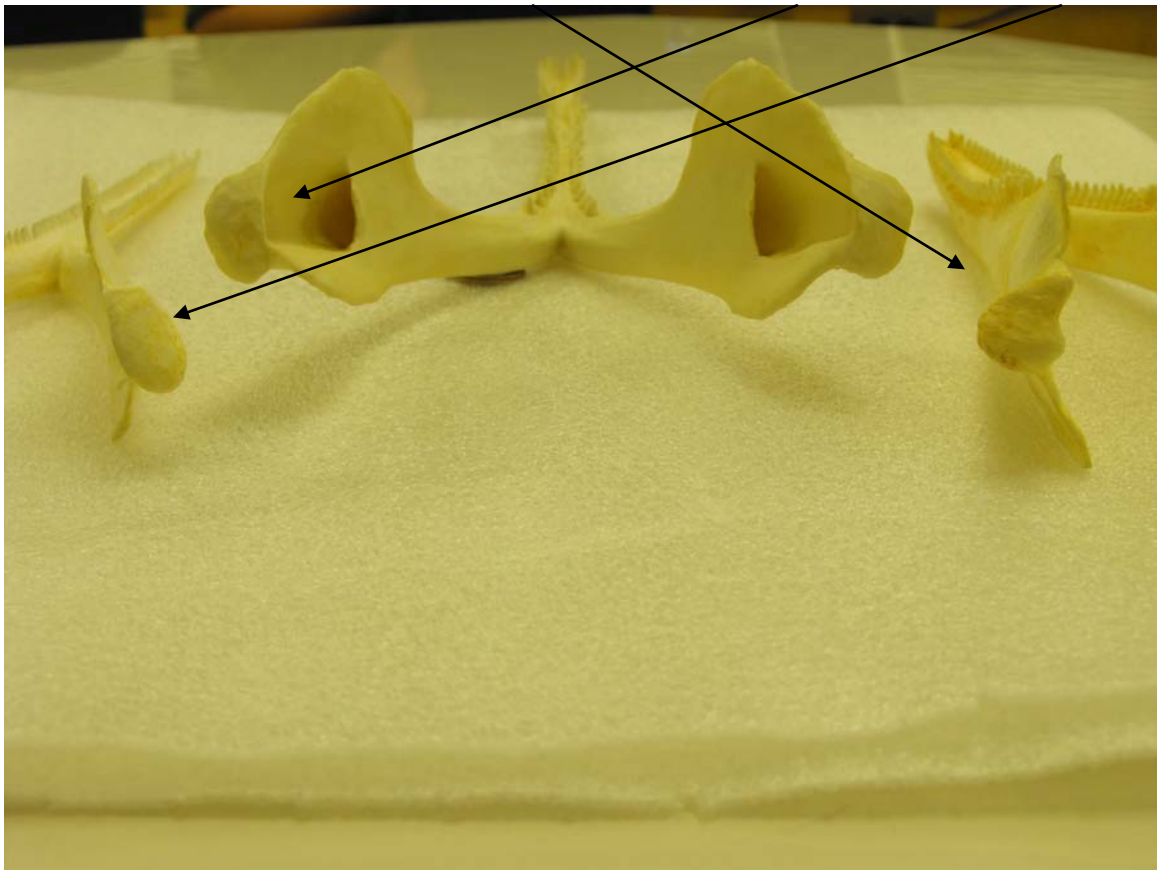
5. Cladistics, The International Journal of the Willi Hennig Society": Goloboff, P., Farris, J., & Nixon, K. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774-786.
6. WinClada: Goloboff; Farris; Nixon

Figures:

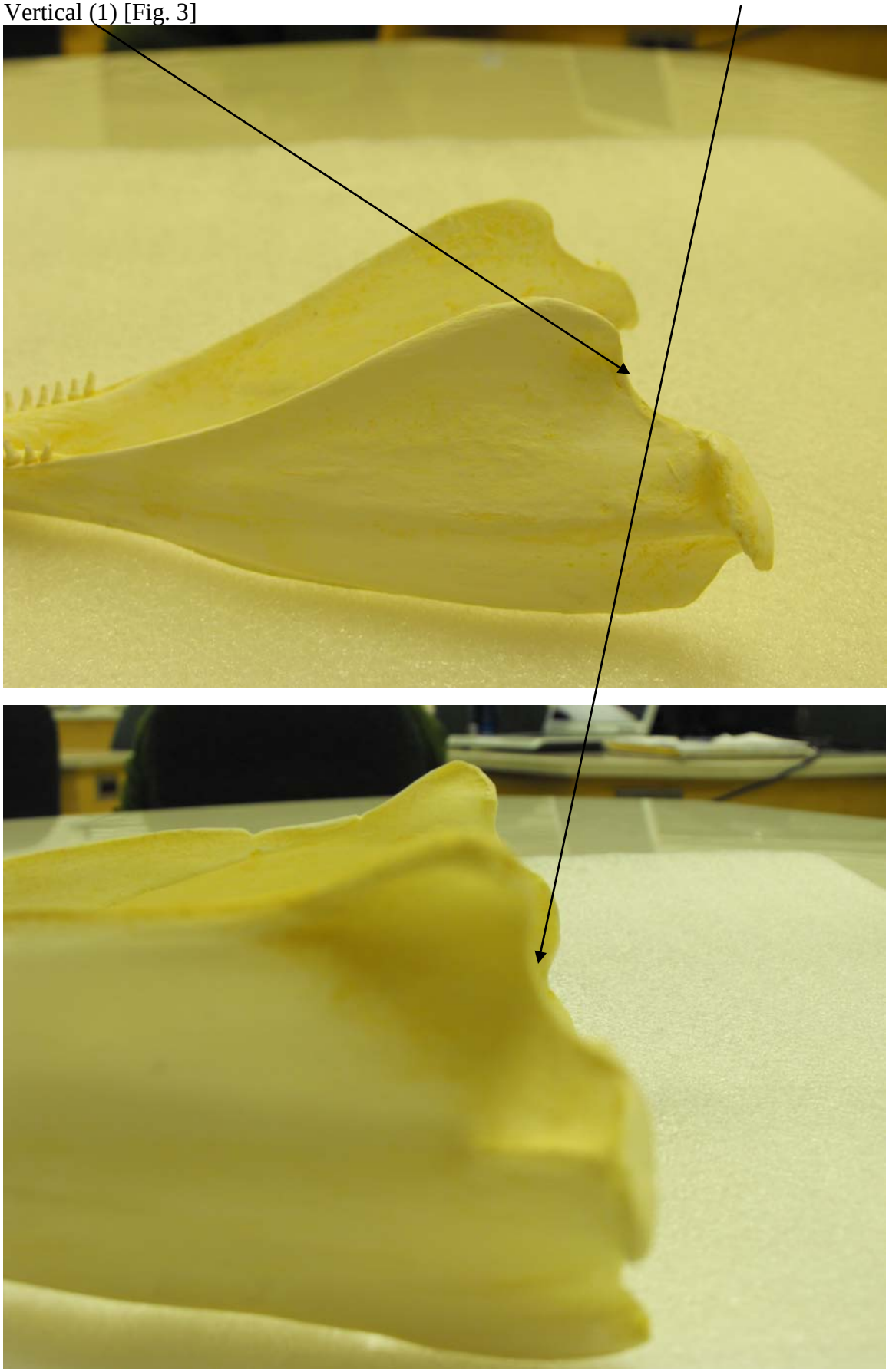
Shape of the mandible: V shaped (0); Y shaped (1) [Fig. 1]



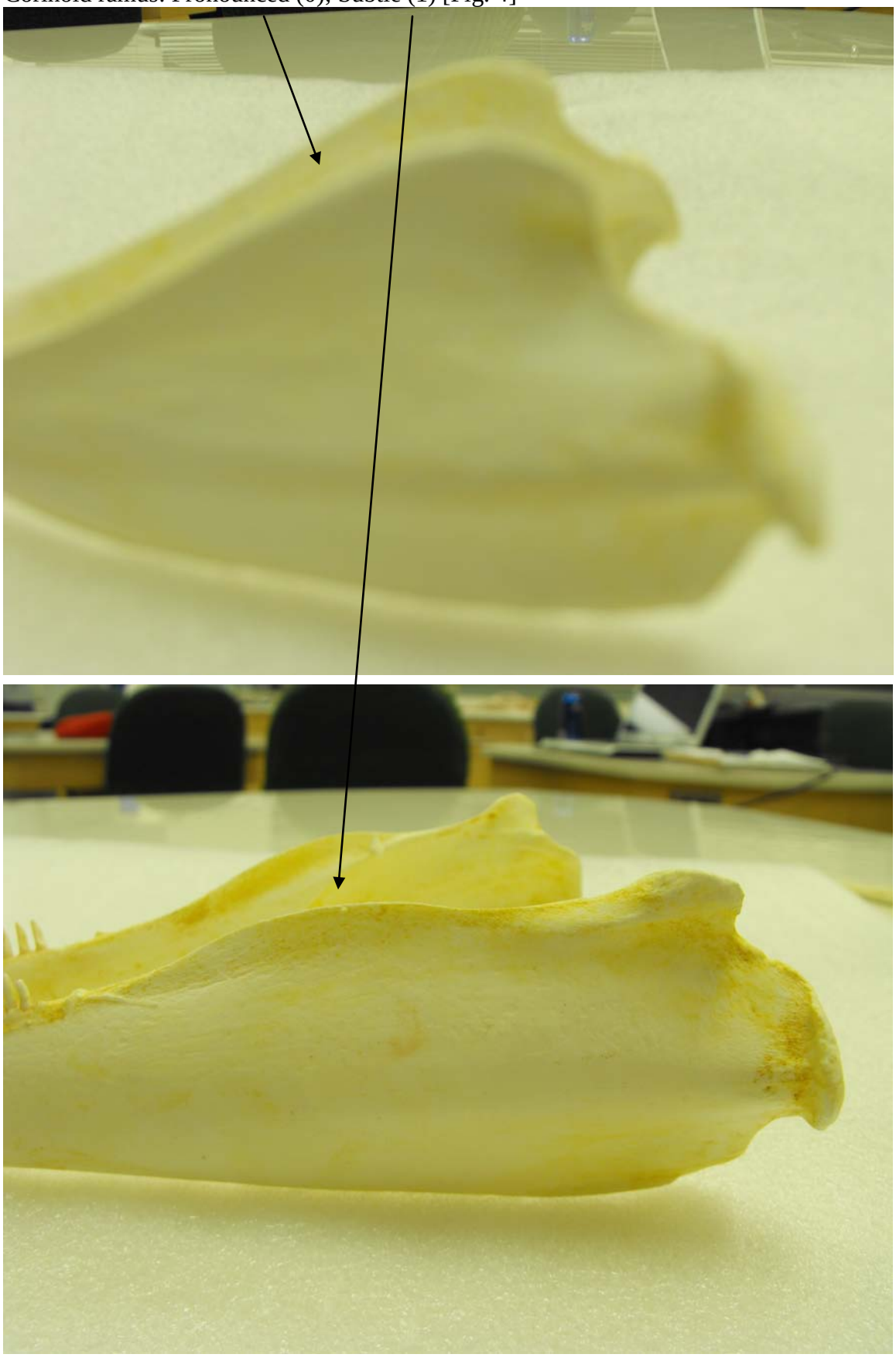
Orientation of mandibular condyle: Horizontal (0); Vertical (1); Extremely vertical(2)



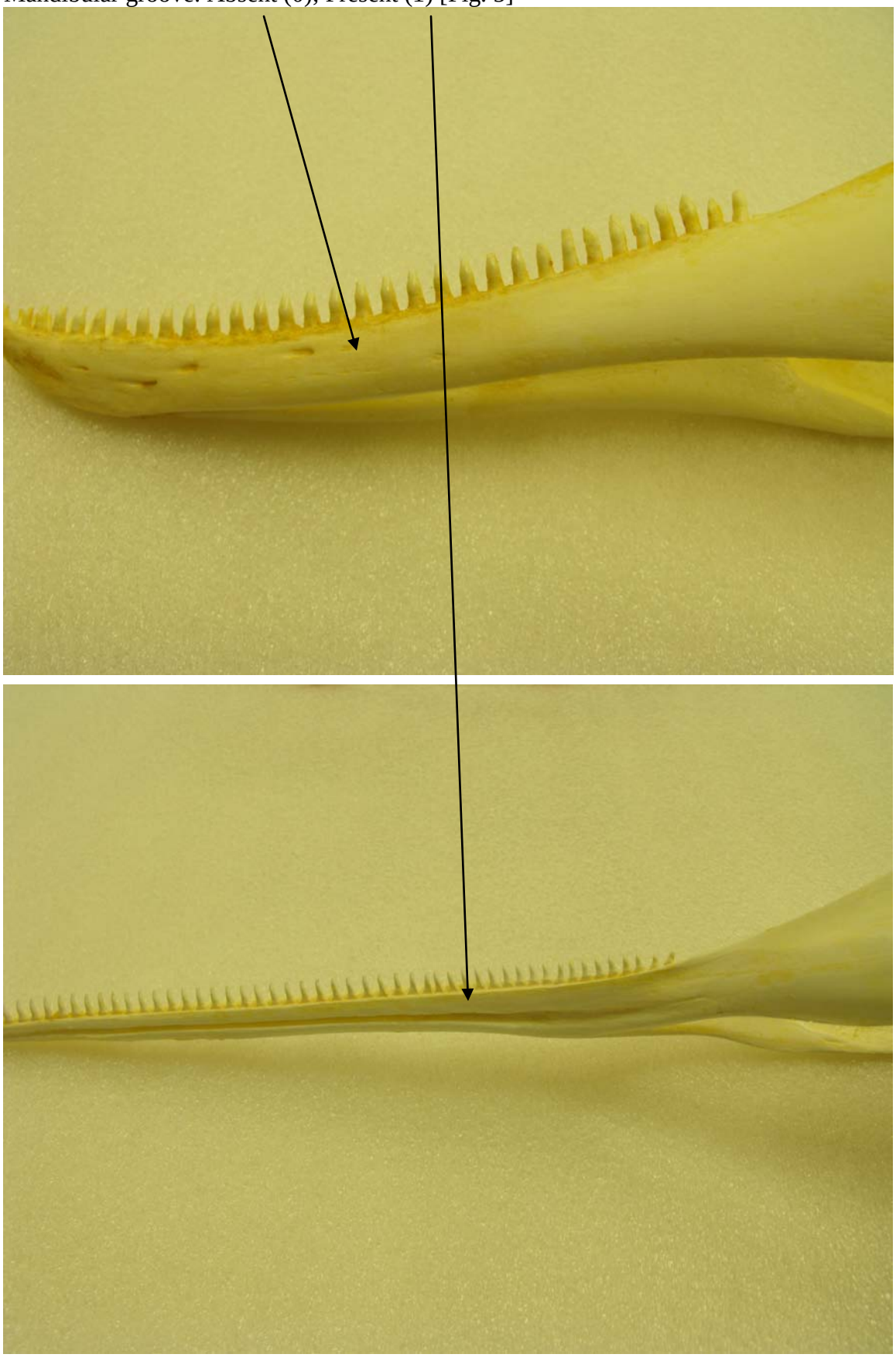
Orientation of angle of corinoid process with respect to sagittal plane: Posterior (0); Vertical (1) [Fig. 3]



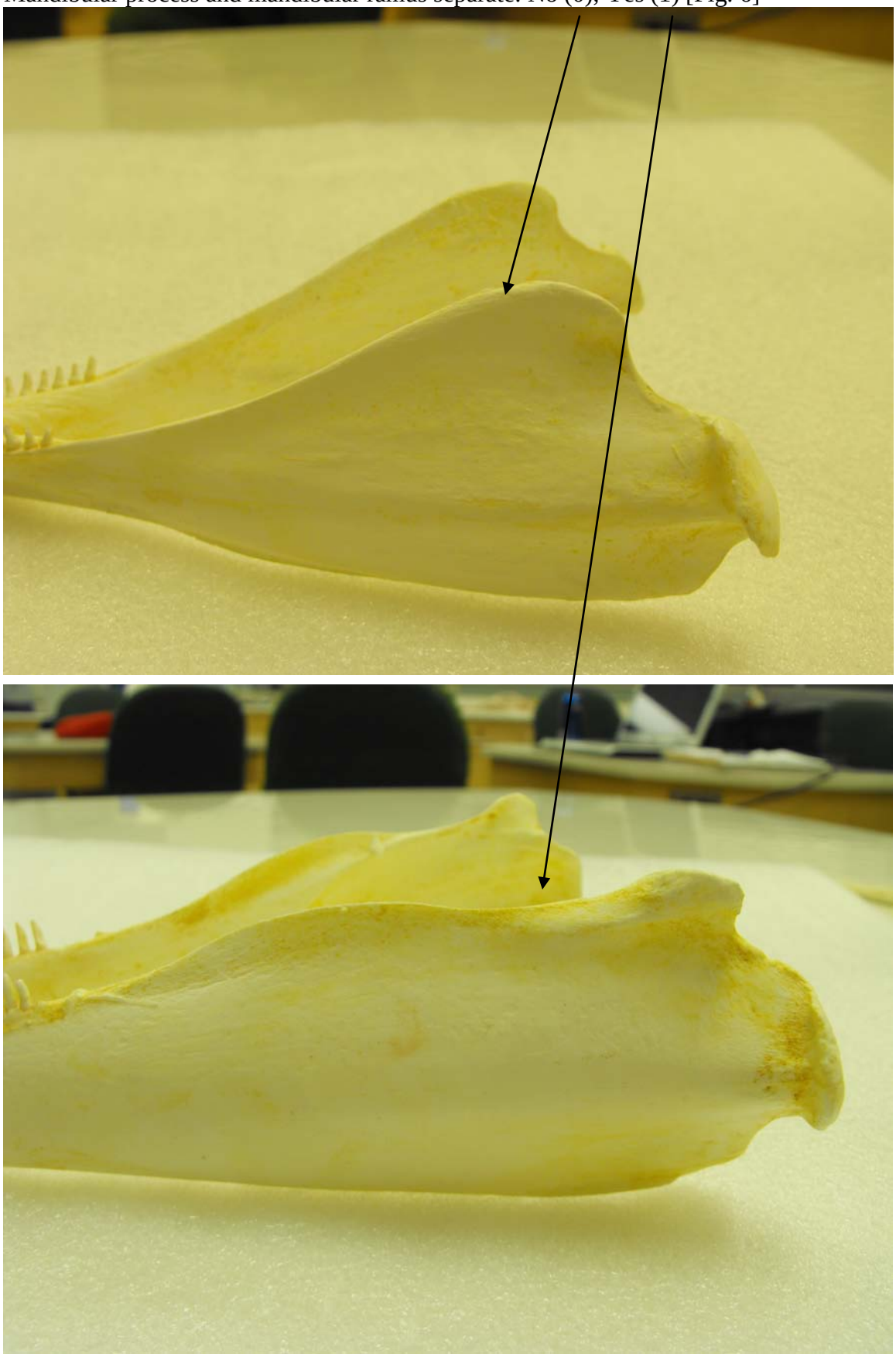
Corinoid ramus: Pronounced (0); Subtle (1) [Fig. 4]



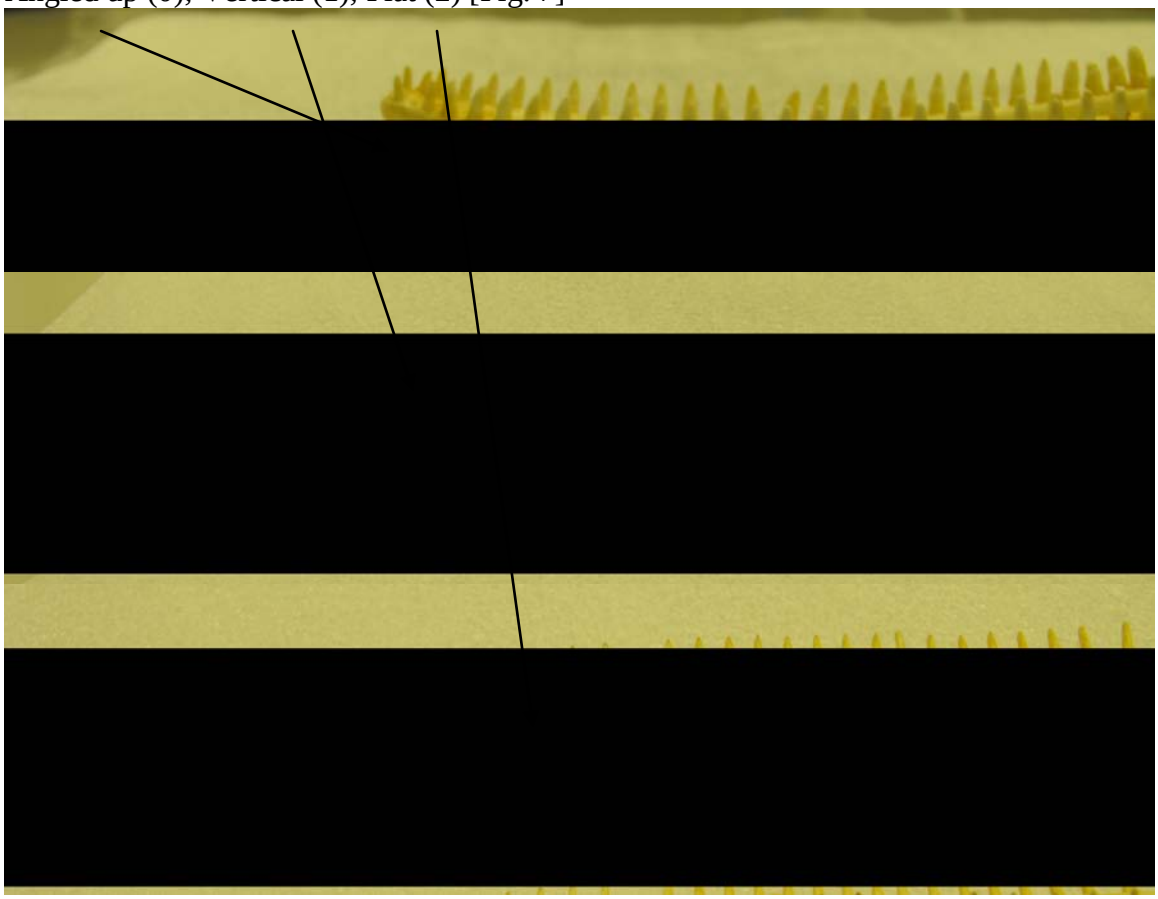
Mandibular groove: Absent (0); Present (1) [Fig. 5]



Mandibular process and mandibular ramus separate: No (0); Yes (1) [Fig. 6]

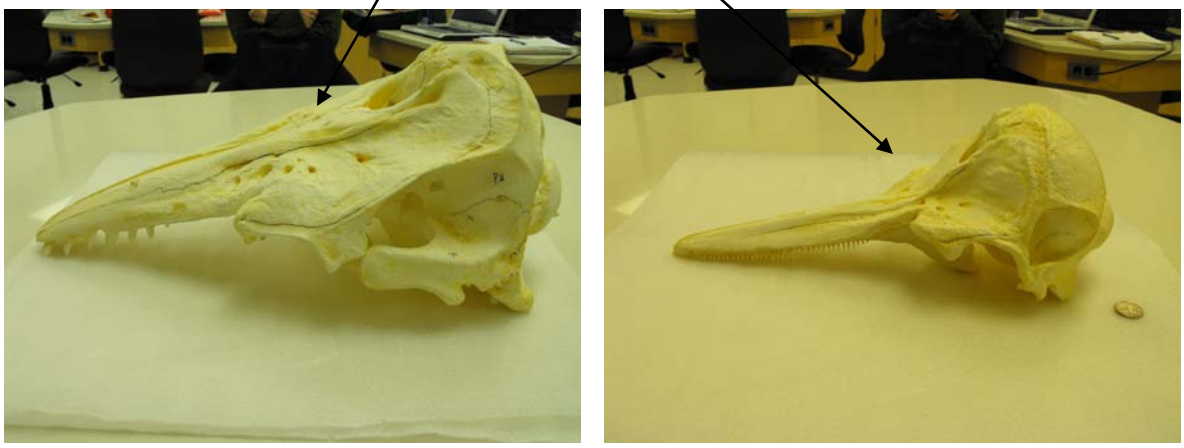


Angle of ventral portion of mandibular synthisis with respect to transvese plane: Angled up (0); Vertical (1); Flat (2) [Fig. 7]

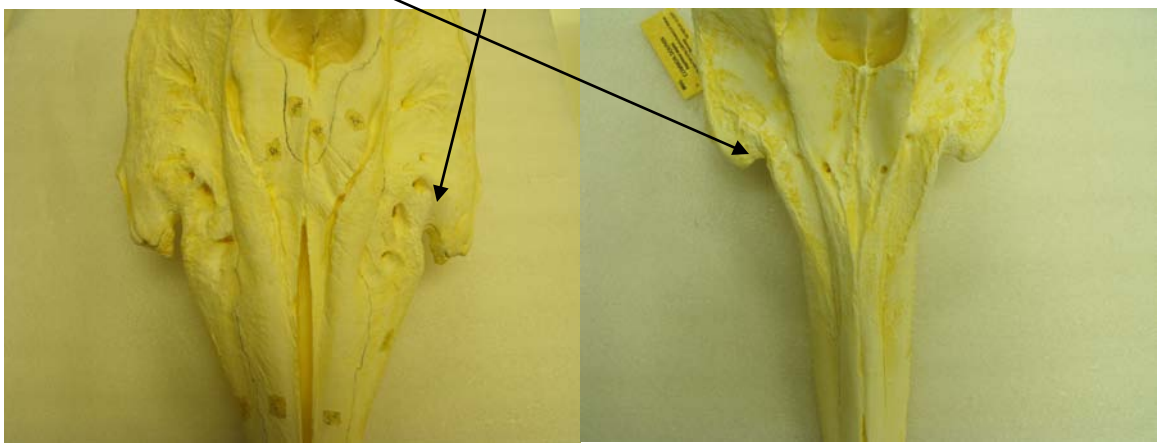


Rostrum

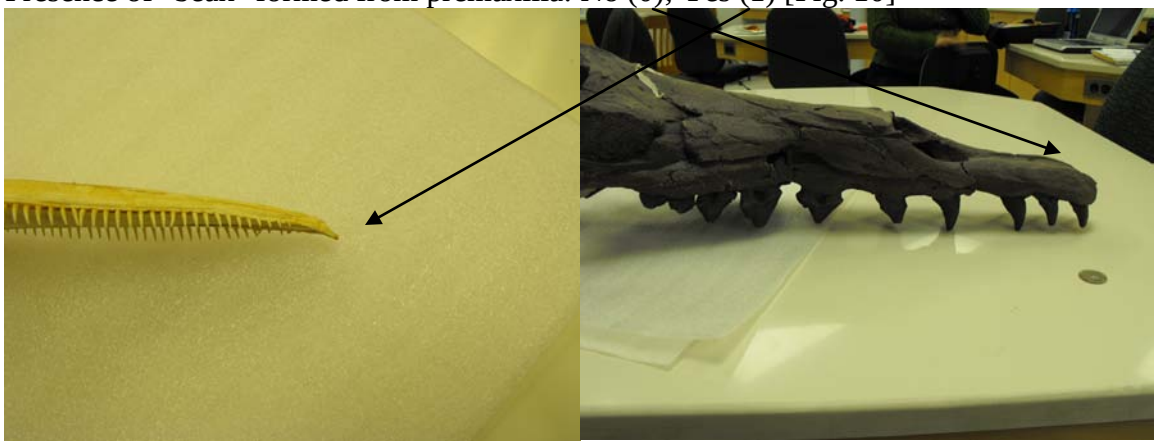
Accommodation for melon: Absent (0); Present (1) [Fig. 8]



Antorbital notch: Shallow (0); Deep (1) [Fig. 9]

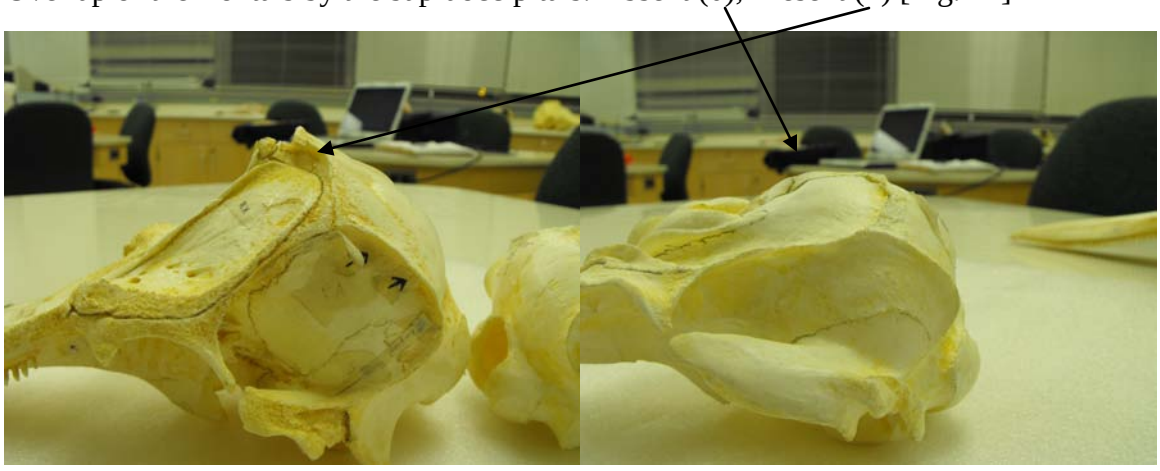


Presence of "beak" formed from premaxilla: No (0); Yes (1) [Fig. 10]

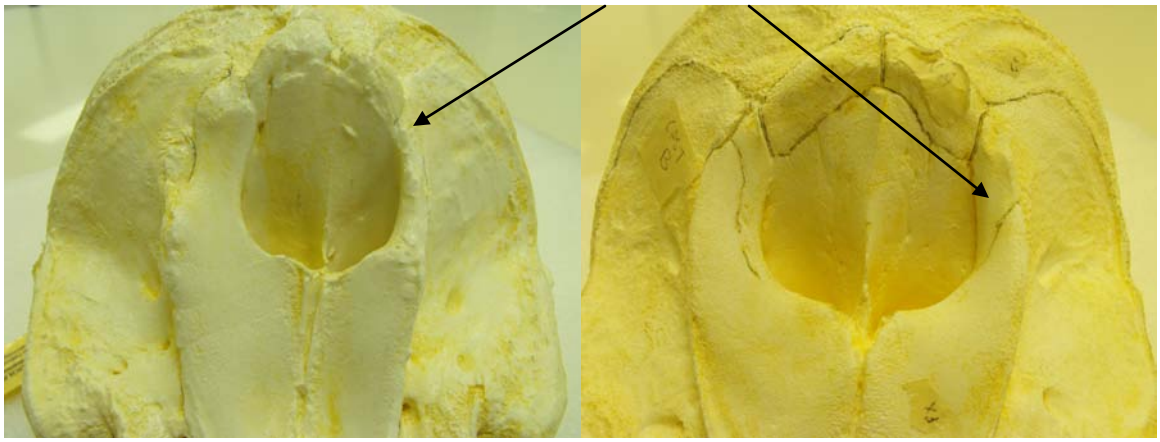


Calvaria

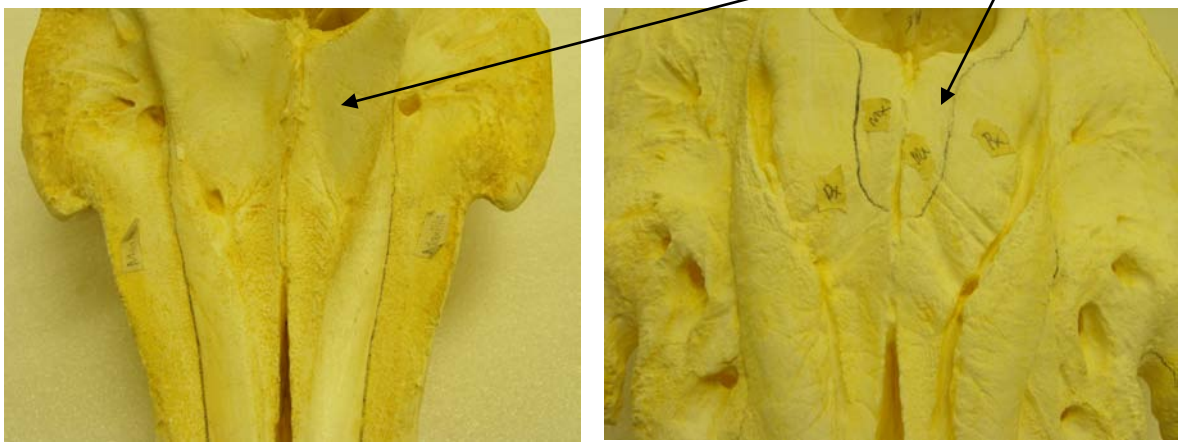
Overlap of the frontals by the supraoccipitals: Absent (0); Present (1) [Fig. 11]



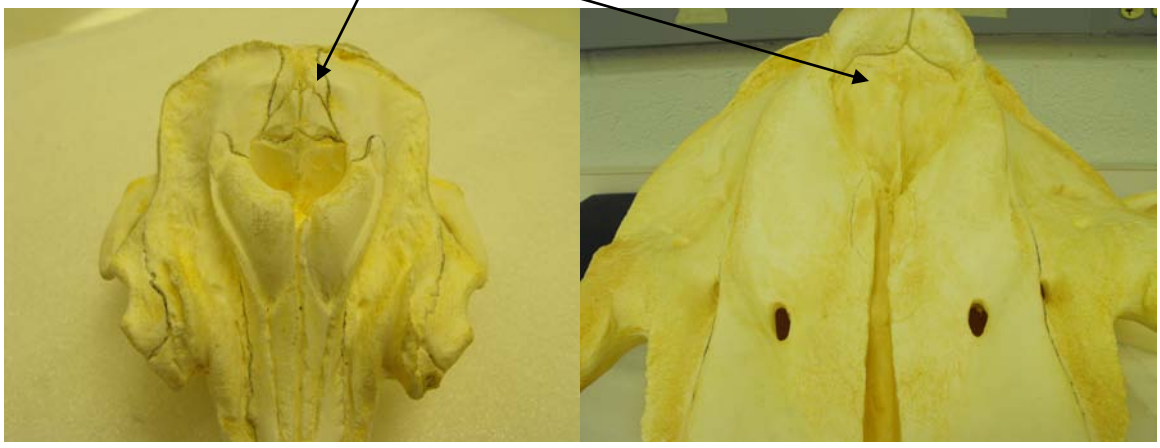
Maxillary extension into bony nares: Absent (0); Present (1) [Fig. 12]



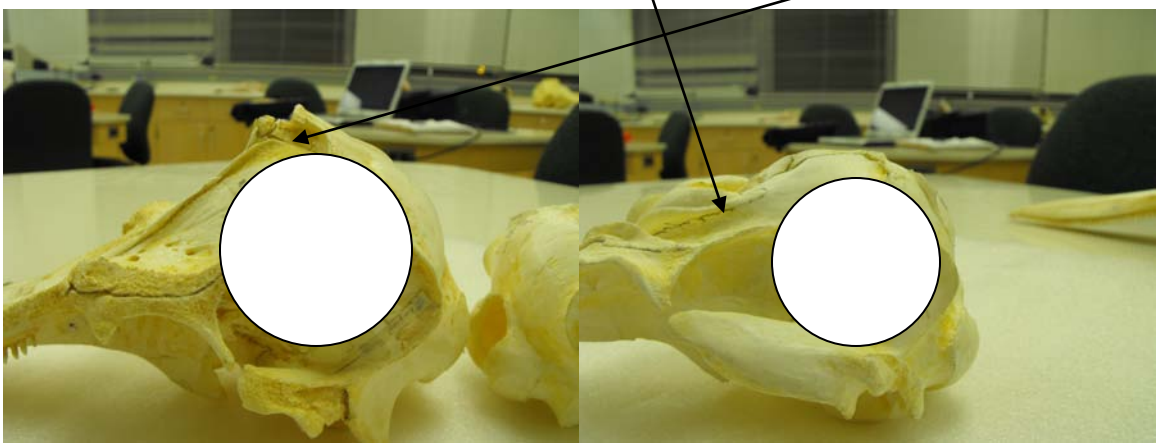
Maxilla present at anterior end of blowhole between premaxilla: No (0);Yes (1) [Fig. 13]



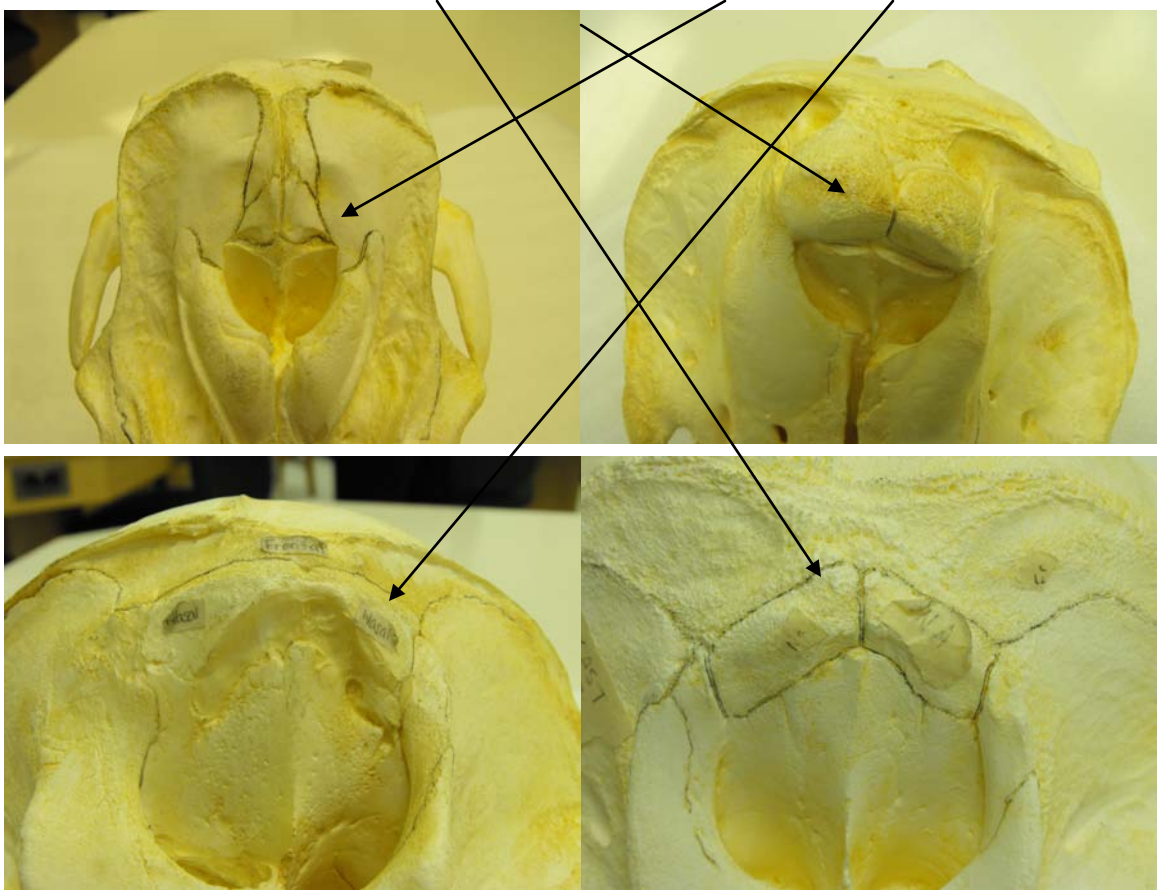
Lean of blowhole: Absent (0); Present (1) [Fig. 14]



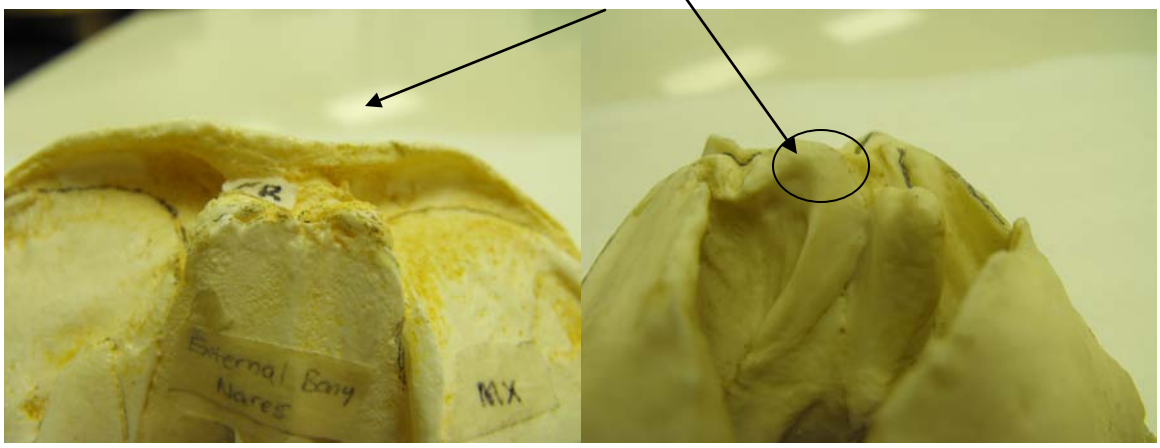
Nasal extension above the braincase: Absent (0); Present (1) [Fig. 15]



Shape of nasals: Quadrilateral (0); Round (1); Triangle (2); Other (3) [Fig. 16]

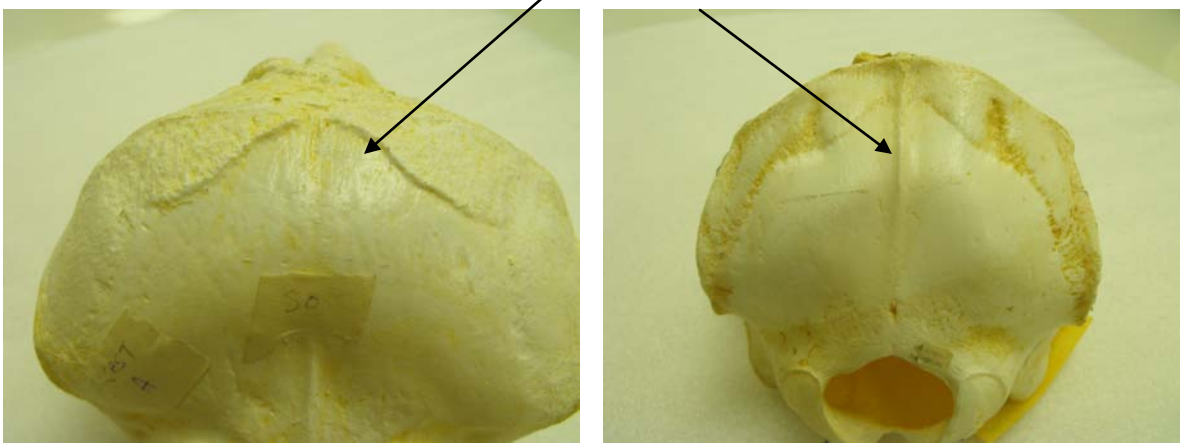


Nasals balanced by premaxillary process: No (0); Yes (1) [Fig. 17]

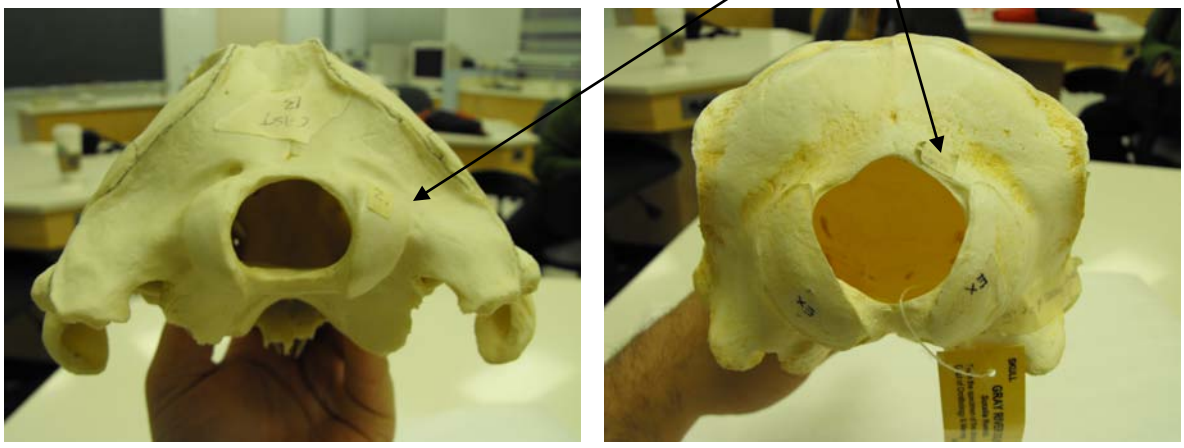


Occiput

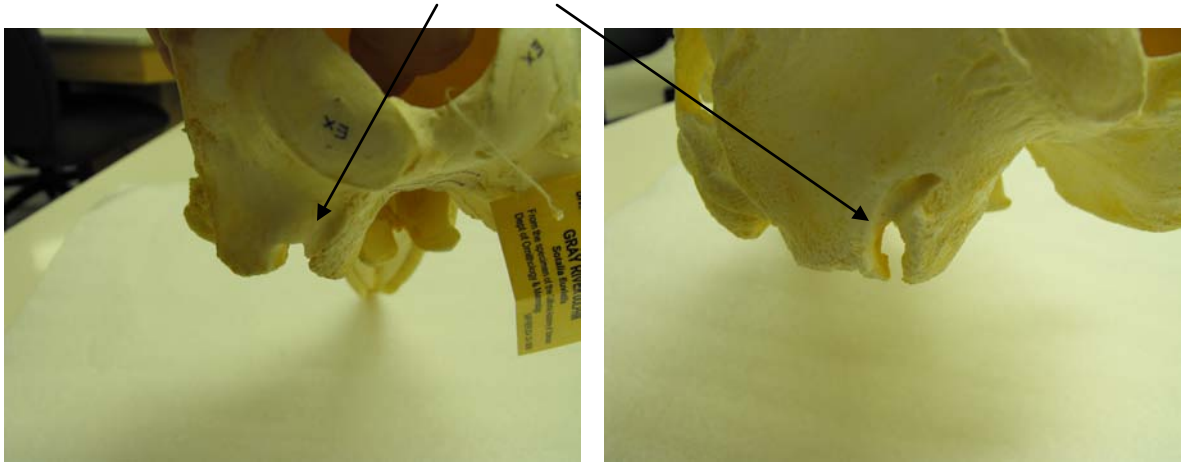
Saggital crest formed from occiput: No (0); Yes (1) [Fig. 18]



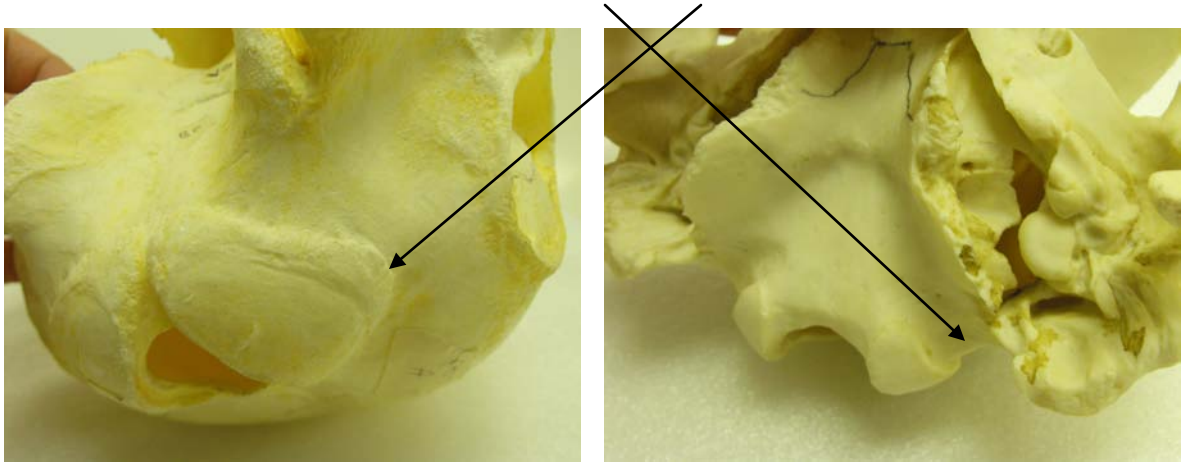
Exoccipital condyle in line with foramen magnum: Yes (0); No (1) [Fig. 19]



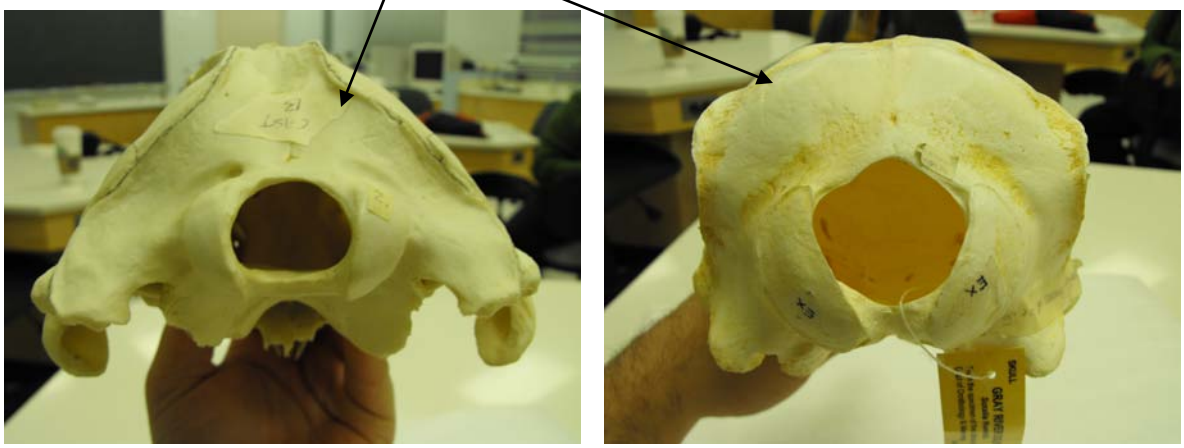
Shape of jugular notch: Wide (0); Narrow (1) [Fig. 20]



Exoccipital condyle flush with occiput: No (0); Yes (1) [Fig. 21]

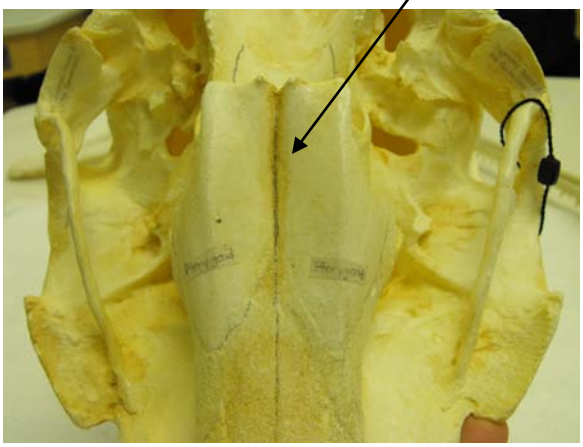


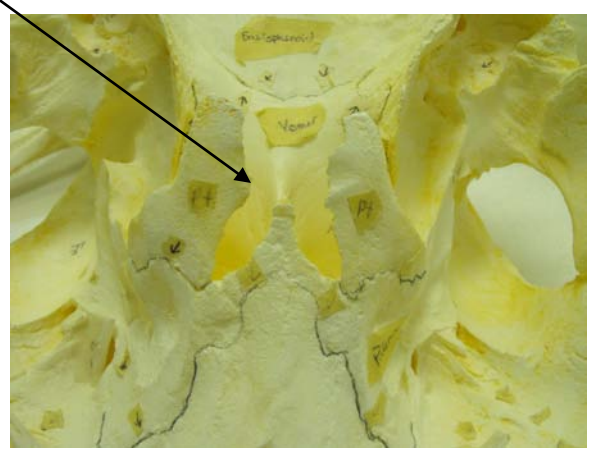
Shape of occiput: T shaped (0); Round (1) [Fig. 24]



Shape of temporal fossae: Elongated (0); Round (1) [Fig. 22]
Angle of temporal fossae: Horizontal (0); Angled (1) [Fig. 23]
Shape of zygomatic process: Boxy (0); Streamlined (1) [Fig. 24]
Shape of external acoustic meatis: Deep (0); Shallow (1) [Fig. 25]

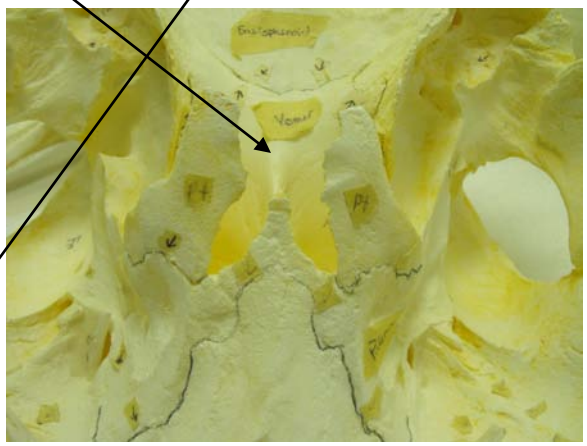
Fusion of pterigoids: Present (0); Absent (1) [Fig. 26]

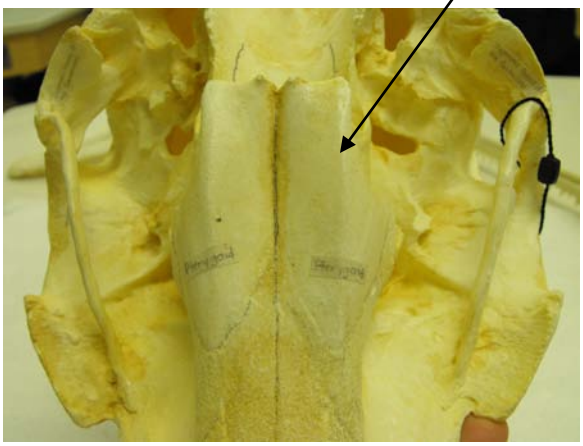




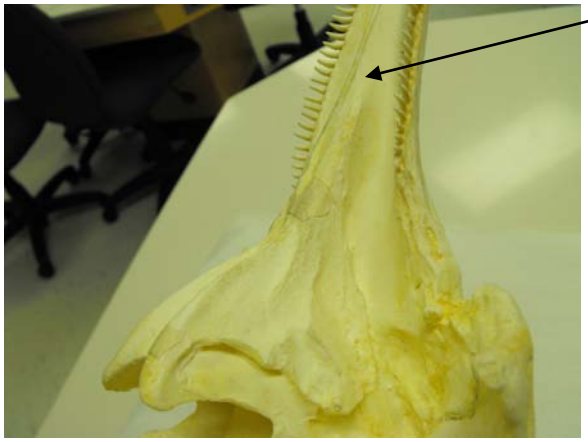
Ventral Side of Skull

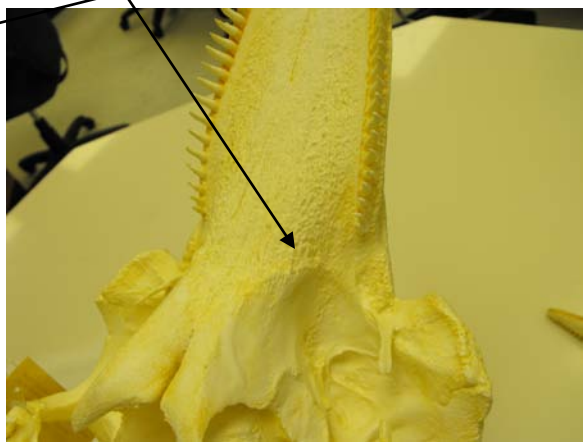
Pterigoid orientation: Medial (0); Lateral (1); None (2) [Fig. 27]



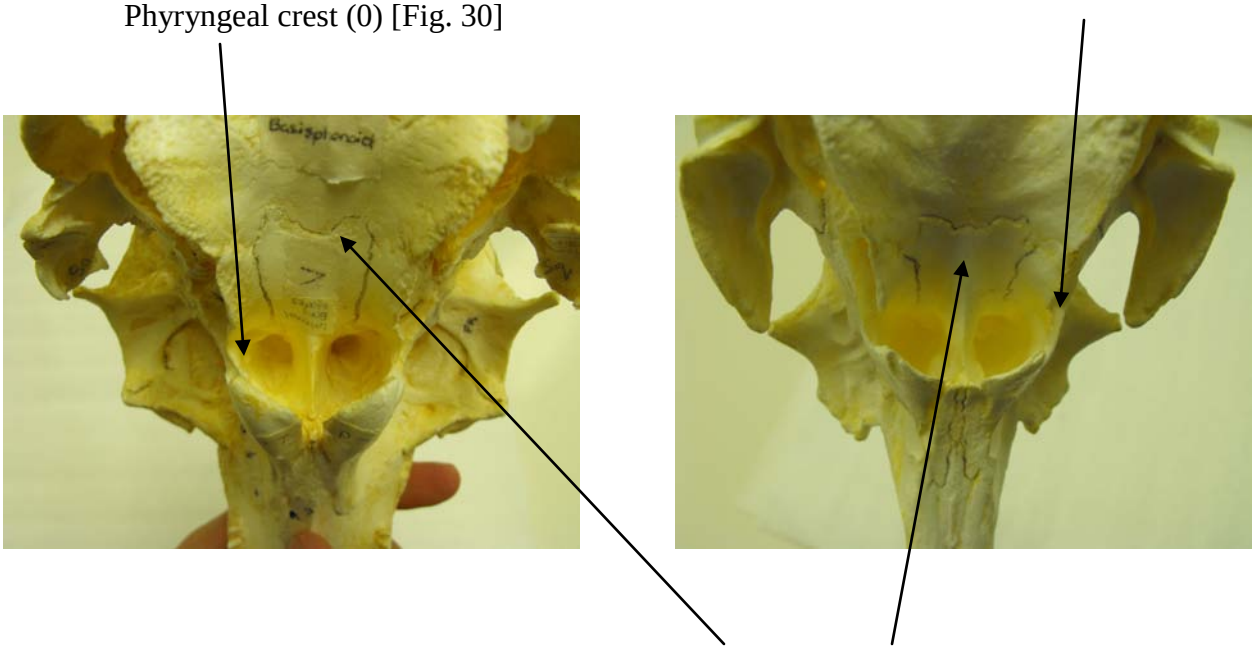


Anterior sinus fossae extension into rostrum: Absent (0); Present (1) [Fig. 28]





Lateral side of ventral side of blowhole composed of: Pterygoid hamulus (1); Phyryngeal crest (0) [Fig. 30]



Shape of anterior dorsal part of vomer: Angled (1); Boxy (0) [Fig. 31]

Apendix:

The following is a copy of the matrix, containing both morphological and genetic data, that was used for the construction of the evolutionary tree. The morphological characters appear in the same order in which the did in the observation portion of this paper.

```
nstates 32;
xread
1609 16

&[num]
O        -00000000000000000000000000000000000000000000000000
A.p      -???????????2???????00000??0?00000001?10?11?0000??0
D.l      -02010000102l1?00111020010000011010000111001010101
D.d      -0100012111210100O?1031011110011111101010111110000
G.v      -110000?01010?0000?000000000000100010000000?000???0
G.m      -0101010111211001011110010000110110101?11101010001
L.o      -0111010111210000101000011111011110001?11101110111
L.b      -0011012111210101101030011111011111001?10201110000
Pak      -???????00?0???00???00??0000000?00010100???00????0
P.e      -02010101112111011111??010??00100101012111010O?10?
P.g      -11?0101011211000l?1??11110?00000001100102?0010010
P.b      -12001011102100001?00200110?101?010011011100001000
S.f      -000100011121000110111101000101011110101110011010l
T.t      -0??????111210?011110100110010111100011111001101O0
Xeno     -???????111210?01??000001100000?000111????0000???1
Z.c      -?2?001???12100100l??011111001101000??1??????????

&[dna]
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```

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L.b      GCTTAGTCGTAAACTTAAATAGTCCT?AAAACAAGACTATTCGCCAGAGT
L.o      ??????TCGTAAACTTAAATAGTCCT?AAAACAAGACTATTCGCCAGAGT
G.m      ??????TCGTAAACTTAAATAGTCCT?AGAACAAGACTATTCGCCAGAGT
S.f      GCTTAGTCGTAAACTTAAATAGTCCC?AAAACAAGACTATTCGCCAGAGT
D.l      ??????TCGTAAACTTAAATAGTCCTTAAAACAAGACTATTCGCCAGAGT
P.b      GCTTAGTCGTAAACCCAATTGGTTCA?ATAACAAGACCATTCGCCAGAGT
P.g      ??????????????????????TCANAANACANGRTNAKTCGCCAGAGT

&[dna]
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T.t      ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC
L.b      ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC
L.o      ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC
G.m      ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC
S.f      ACTATCGGCAACAGCCCAAAACTCAAAGGACTTGGCGGTGCTTCATATCC
D.l      ACTACCGGCAACAGCCCGAAACTCAAAGGACTTGGCGGTGCTTCATATCC
P.b      ACTACCGGCAACAGCCTAAAACTCAAAAGACTTGGCGGTGCTTCACATCC
P.g      ACTACTAGCAACAGCTTAAAACTCAAAGGACTTGGCGGTGCTTCATATCC

&[dna]
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T.t      TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA
L.b      TTCTAGAGGAGCCTGTTCTATAAACGATAAACCACGATTAACCTCACCAA
L.o      TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA
G.m      TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA
S.f      TTCTAGAGGAGCCTGTTCTGTAAACGATAAACCACGATTAACCTCACCAA
D.l      CTCTAGAGGAGCCTGTTCTGTAAACGATAAACCCCGATCAACCTCACCAA
P.b      TTCTAGAGGAGCCTGTTCTATAAACGATAAACCCCGATAAACCTCACCAA
P.g      CTCTAGAGGAGCCTGTTCTATAATCGATAAACCCCGATCAACCTCACCAA

&[dna]
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L.b      TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA
L.o      TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA
G.m      TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA
S.f      TCCTTGCTACTTCAGTCTATATACCGCCATCTTCAGCAAACCCTAAAAAA
D.l      TCCTTGCTACCTCAGTCTATATACCGCCATCTTCAGCAAACCCTA?AAAA
P.b      CTCTTGCTACTTCAGTCTATATACCGCCATCTCAAGCAAACCCTA?AAAA
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L.o      GGAACGAAAGTAAGCACAACTATTGCACGTAAAAACGTTAGGTCAAGGTG
G.m      GGAATGAAAGTAAGCACAACYATTGCACGTAAAAACGTTAGGTCAAGGTG
S.f      GGAATGAAAGTAAGCACAACCATTGCACATAAAAACGTTAGGTCAAGGTG
D.l      GGAACGAAAGTAAGCACAACTATCGCACATAAAAACGTTAGGTCAAGGTG
P.b      GGAATGAAAGTAAGCACAACTATCTCTCACAAAAACGTTAGGTCAAGGTG
P.g      GGAACGACAGTAAGCACAACTACTTTACGTAAAAACGTTAGGTCAAGGTG

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L.b      TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTATAATAAGAACAC
L.o      TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTATAACAAGAACAC
G.m      TAACCTATGGATTGGGAAGAAATGGGCTACATTTTCTACAATAAGAACAC
S.f      TAACCTATGGGTTGGGAAGAAATGGGCTACATTTTCTATAATAAGAACAC
D.l      TAACCTATGGGTTGGGAAGAAATGGGCTACATTTTCTATAACAAGAACAT
P.b      TAACCTATGGGTTGGAAAGAAATGGGCTACATTTTCTATAACAAGAACAT
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L.o      CC?CTTAAACTTACACGAAAGTTTTTATGAAACCTAAAAACTAAAGGAGG
G.m      CC?CYTAAACTTAYACGAAAGTTTTTATGAAATCTAAAAACTAAAGGAGG
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L.o      ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCA?????
G.m      ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCA?????
S.f      ATTTAGCAGTAAATTAAGAATAGAATGCTTAATTGAATAAGGCCATGAAG
D.l      ATTTAGCAGTAAATTAAGAATAGAGTGCTTAATTGAATAAGGCCN?????
P.b      ATTTAGCAGTAAACTAAGAATAGAGTGCTTATTTGAACAAGGCCATGAAG
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&[dna]
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T.t      ?????
L.b      CACGC
L.o      ?????
G.m      ?????
S.f      CACGC
D.l      ?????
P.b      CACGC
P.g      CACGC
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D.d      ???TGCTCTTGGTGGGCATCCTGTTCCATGCCGTCCAGGCCGAACAATTN
S.f      CTCTGCTCTTGGTGGGCATCCTGTTCCATGCCGTCCAGGCCGAACAATTA
P.g      ???????CTTGGTGGNCATCCTGTTCCATGCCATCCAGGCTGAACAATTA
D.l      ????????????????????????????????TCCAGGCAGAACAGTTA
Z.c      ????????????????????????????????TCCAGGCTGAACAATTA
P.b      ????????????????????????????????????????????????

&[dna]
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D.d      ACAAAATGTGAGCTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG
S.f      ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG
P.g      ACAAAATGTGAGTTGTTCCAGAGACTGAAAGACCTGGATGGCTATGGAGG
D.l      ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG
Z.c      ACAAAATGTGAGTTGTTCCAGAGGCTGAAAGACCTGGATGGCTATGGAGG
P.b      ????????????????????????????????????????????????

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T.t      CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCACAC
D.d      CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCACAC
S.f      CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCATAC
P.g      CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCATAC
D.l      CGTCACTTTGCCTGAATGTGAGTTCTCTGCTATCTTGCTTTGTTCCATAC
Z.c      CGTCACTTTGCCTGAATGTGAGTTCCCTGCTATCTTGCTTTGTTCCATAC
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&[dna]
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T.t      TTCATCTTCTTCTGTCTTCCCCACCTTTCTCTTCCTCCTCTTTTTTTC?T
D.d      TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTTC?T
S.f      TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTCC?T
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D.l      TTCATCTTCTTCTGTCTTNCCCACCCTTCTCTTCCTCCTCTTTTTTTC?T
Z.c      TTCATCTT???CTATCTTNCCCACCCTTCTCTTCCTCCTCTTTTTTTCCT
P.b      TTCATCTTCTTCTGTCTTCCCCACCCTTCTCTTCCTCCTCTTTTTTCC?T

&[dna]
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G.m      CTACTTTTAACTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTA
T.t      CTACTTTTAACTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTA
D.d      CTACTTTTAACTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTA
S.f      CTACTTTTAACTCAATTATCTAAGAATCCTCTCATCTGCTCATCTGTTTA
P.g      CTACTTTTAATTCAATTATCTAATAATCCTCTTATCTGCTCATCTGTTTA
D.l      CTATTTTTAACTCAGTTATCTAACAATCCTCTTAT????????CTGTTTA
Z.c      CTACTTTTAATTCAATTATCTAATAATCCTCTTACCTGCCCATCTGTTTA
P.b      CTACTTTTAACTCAATTATCTAGTAATCCTCTTATCTGCTCATCTGTTTA

&[dna]
P.e      CTCTTTTATTACATTTATTCACCTGTCTCTCCTTTCTCCCATTGTCTGAT
G.m      CTCTTTTATTACATTTATTCACCTGTCTCTCCTTTCTCCCATTGTCTGAT
T.t      CTCTTTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGAT
D.d      CTCTTTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGAT
S.f      CTCTTTTATTACATTTATTCACCTGTCTCTCCTTTCTCCCATTGTCTGAT
P.g      CTCTCTTGTTACATTTATTCACCTATCTCTCCTTTTTCCCATTGTCTGAT
D.l      CTCTTTTATTACATTTATTCACCTATCTCTTCTTTCTCCCATTGTCTGAT
```

```
Z.c      CTCTCTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGAT
P.b      CTCTTTTATTACATTTATTCACCTATCTCTCCTTTCTCCCATTGTCTGAC

&[dna]
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G.m      TGGTTTTT?GGAGCTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCG
T.t      TGGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCG
D.d      TGGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCG
S.f      TGGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTCG??GCCG
P.g      CGTTTTTTTGGAACTCTTAATCTTATCAAGATACCCTGTGGTTG??GCCG
D.l      TGTTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTTG??GCCG
Z.c      CTGTTTTT?GGAACTCTTAATCTTATCAAGATACTCTGTGGTTG??GCCG
P.b      TGTTTTAT?GGAACTCTTAATCTTATCAAGATACTCTGGGGTTGTGGCCA

&[dna]
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P.b      TATTTGGAGATTGGTTGGAGAGCCTTTTTCTGTCTG???????????TCCA

&[dna]
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G.m      CATTTATGCTATATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCT
T.t      CATTTATGCTATATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCT
D.d      CATTTATGCTATATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCT
S.f      CATTTATGCTGTATGCGGACATCCCTGTGATATCTCTTTTTCATCTTTCT
P.g      CATTTATGCTATATGTGGACATCCCTGTGATATCTCTTTTTCATCTTTCT
```

```
D.l      CATTTATGCTATATGTGGACATCCCTGTGATATCTCTTTTTCATCTTTCT
Z.c      CATTTATGCTATATGTGGACATCCCCGTGATATCTCTTTTTCATCTTTCT
P.b      CATTTATGCTATATGTGGACATCCCTGTGATATCTCTTTTTCATCTTTCT

&[dna]
P.e      TTCAGGGGTCTGTACCGTATTTCATACTAGTGGTTGTGACACACAAACCA
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T.t      TTCAGGGGTCTGTACCGTATTTCATACTAGTGGGTGTGACACACAAACCA
D.d      TTCAGGGGTCTGTACCGTATTTCATACTAGTGGGTGTGACACACAAACCA
S.f      TTCAGGGGTCTGTACCGTATTTCATACTAGTGGGTGTGACACACAAACCA
P.g      TTCAGGGGTCTGTACCGTATTTCATACCAGTGGTTGTGACACACAAACCA
D.l      TTCAGGGGTCTGTACCGTATTTCATACTAGTGGTTGTGACACACAAACCA
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&[dna]
P.e      TAGTAAATAACAACGACAGCACAGAATATGGACTTTTCCAGATCAATAAT
G.m      TAGTAAATAACAACGACAGCACAGAATATGGACTTTTCCAGATCAATAAT
T.t      TAGTAAATAACAATGACAGCACAGAATATGGACTTTTCCAGATCAATAAT
D.d      TAGTAAATAACAATGACAGCACAGAATATGGACTTTTCCAGATCAATAAT
S.f      TAGTAAATAACAGTGACAGCACAGAATATGGACTTTTCCAGATCAATAAT
P.g      TAGTAAATAACAATGGCAGCACAGAATATGGACTCTTCCAGATCAATAAT
D.l      TAGTAAATAACAATGACAGCACAGAATATGGACTCTTCCAGATCAATAAT
Z.c      TAGTAAATAACAATGGCAGCAAAGAATATGGACTCTTCCAGATCAATAAT
P.b      TAGTGAATAACAACGGCAGCACAGAATATGGACTCTTCCAGATCAATAAT

&[dna]
P.e      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGA
G.m      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGA
T.t      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGA
D.d      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGG
S.f      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGG
```

```
P.g      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGG
D.l      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGG
Z.c      AAAATTTGGTGCAGAGACAACCAGATCCCTCACTCAAGGGACATCTGTGG
P.b      AAAATTTGGTGCAGAGACAAGCAGATCCCTCACTCAAGGGACATCTGTGG

&[dna]
P.e      CATC??????????????????????????????????????????????
G.m      CATC??????????????????????????????????????????????
T.t      CATC??????????????????????????????????????????????
D.d      CATCTCCTGTGACAGTGAGTGACCACTTTTACCATGTTCCTGTGTTTTAT
S.f      CATCTCCTGTGACAGTGAGTGACCACTTTTACCATGTTCCTGTGTTTTAT
P.g      TATCTCCTGTGACAGTGAGTGACCACTTTTACCATGTTCCTCTGTGTTTT
D.l      CATCTCCTGTGACAGTGAGTGACCACTTTTACCATGTTCCTGTGTTTTAT
Z.c      CATCTCCTGTGAAAGTGAGTGACCACTTTTACCATGTTCCTGTGTTTTTT
P.b      CATCTCCTGTGACAGTGAGTGACCACTTTTACTATGTTCTTGTGTTTTTT

&[dna]
P.e      ????????????????????????????????????????????????
G.m      ????????????????????????????????????????????????
T.t      ????????????????????????????????????????????????
D.d      TGGAGCCTATTCCTGGGATAATCTCCTTTTTTGGCGTCAAGCACACCTCT
S.f      TGGAGCCTATTCCTGGGATAATCTCCTTTTTTGGCGTCAAGCACACCTCT
P.g      TGGATCCTACTCCTGGGATAATCTCCTTTATTGGTGTCAAGCGCACCTCT
D.l      TGGAGCCTACTCCTGGGATAATCTCCTTTTTTGGCGTCATGCGCACCTCT
Z.c      TGGAGCCTACTCCTGGGATAATCTCCTTTTTTGGCATCAAGCGCACCTCT
P.b      TGAAGCCTACTCCTGGGGTAATCTCCTTTTTTGGCGTCAAGCGCACCTCT

&[dna]
P.e      ????????????????????????????????????????????????
G.m      ????????????????????????????????????????????????
T.t      ????????????????????????????????????????????????
D.d      AACTTCACTGCCTTGGACGCCACATCAACTGTGGGACTTCAACTGATAGT
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S.f      AACTTCACTGCCTTGGACGCCACATCAACTGTGGGACTTCAACTGATAGT
P.g      AACTTCACTGCCTTGGACGCCACATCAACTGTGGGACTTCAATTGATAGT
D.l      AACTTCACTGCCTTGGACGCCACATCAACTGTGGGACTTCAATTGATAGT
Z.c      AACTTCACTGCCTTGGATGCCACATCAACTGTGGGACTTCAATTGATAGT
P.b      AACTTCACTGCCTTGGACGCCACGTCAGCTGTGGGACTTCAATGGATTGT

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
D.d      ACTGAGTAAGAGGCTGTTAGAATTTTTCATTATCACCAAATCCCCAGACA
S.f      ACTGAGTAAGAGGCTGTTAGAATTTTTCATTATCACCAAATCCCCAGACA
P.g      ACTGAGTAAGAGGCTGTTAGAATTTTTCATTATCACCAAATCCCCAGACA
D.l      ACTGAGTAAGAGGCTGTTAGAATTTTTCATTATCACCAAATCCCCAGACA
Z.c      ACTGAGTAAGAGGCTGTTAGAATTTTTCATTATCACCAAATCCCCAGACA
P.b      ACTGAGTAAGAGGCTGTTAGAACTTTTCATTATCACCAAATCCCCAGACC

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
D.d      GTCCCTTAAAGTTCACGCGTAGATGATTTGAACTGTTTGGGGATCTTGAA
S.f      GTCCCTTAAAGTTCACGCGTAGATGATTTGAACTGTTTGGGGATCTTGAA
P.g      GTCCCTTAAAGTTCACGGGTAGATGATCTGAGCTGTTTGGGGATCTTGAA
D.l      GTCCCTTAAAGTTCACGCGTAGATGATTTGAACTGTTTGGGGATCTTGAA
Z.c      GTCCCTTAAAGTTCACGGGTAGATGATCTGAGCTGTTTGGGGATCTTGAA
P.b      GTCCCTTAAAGTTCACAGGTAGATAATCTGAGCTGTTTGGGGATCTTGAA

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
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D.d      GTCTAGTACCCTGCATTTTCAGAGTAAATCAGTTGATGAAGTTGATAATT
S.f      GTCTAGTACCCTGCATTTTCAGAGTAAGTCAGTTGATGAAGTTGATAATT
P.g      GTCTAATACCCTGCATTTTCAGAGTAAGTCAGTTGATGAAGTTGATAATT
D.l      GTCTAATACCCTGCATTTTCAGAGTAAGTCAGTTGATGAAGTTGATAATT
Z.c      GTCTAATACCCTGCATTTTCAGAGTAAGTCAGTCGATGAAGTTGATAATT
P.b      GTCTAATACCCTGCATTTTCAGAGTAAGTCAGTGGATGAAGTTGATAATT

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
D.d      CTTCTAGAGATGCCCCCAGAGAAGCGAAGGGAGTCCTTACCTAGGGGGAG
S.f      CTTCTAGAGATGCCCCCAGAGAAGCGAAGGGAGTCCTTACCTAGGGGGAG
P.g      CTTCTAGAGAGGCCCCCAGAGAAGCGAAGGGAGTCCTTACCTAGGGGGAG
D.l      CTTCTAGAGATGCCCCCAGAGAAGCGAAGGGAGTCCTTACCTAGGGGGAG
Z.c      CTTCTAGAGATGCCCCCAGAGAAGTGAAGGGAGTCCTTACCTAGGGGGAG
P.b      CTTCTAGAGATGCCCCCAGAGAGGCGAAGGGAGTCCTTACCTAGGGGGAG

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
D.d      GCATTATTGTACTGGATTTATCATATAGAAAGGCAACAGGCATAAGCCTC
S.f      GCATTATTGTACTGGGTTTATCATATAGAAAGGCAACAGGCATAAGCCTC
P.g      GCATTATTGTATTGGATTTCTCATATAGAAAGGCAACAGGCATAAGCCTC
D.l      GCATTATTGTACTGGATTTATCATATAGAAAGGCAACAGCATAAGCCTCT
Z.c      GCATTACTGTACTGGATTTCTCATATAGAAAGGCAACAGCATAAGCCTCT
P.b      GCATTATTGTACTGGATTTCTCATATAGAAAGGCAACAGGCATAAGCCTC

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
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T.t      ??????????????????????????????????????????????????
D.d      TAGACCAAAGAAGGACCAGGCAAGAGGGGAACTCACTACCTTTCTGGGTA
S.f      TAGATCAAAGAAGGACCAGGCAAGAGGGAAACTCATTACCTTTCTGGGTA
P.g      TAGATCAGAGAAGGACCAGGCAAGAGGGAAACTCATTACCTTTCTGGGTA
D.l      AGATCAAAGAAGGACCAGGCAAGAGGGAAACTCATTACCTTTCTGGGTAA
Z.c      AGATCAGAGAATGACCAGGCAAGAGGGAAACTCATTACCTTTCTGGGTAA
P.b      TAGATCAAAGAAGGGCTAGGCAAGAGGGAAACTCATTACCTTTCTGGGTA

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
D.d      ATACTTAGCTCTCTCATTTTTCCCCCTGTAACTCCTGCCAGAGTTCCTGG
S.f      ATACTTAGCTCTCTCATTTTTCCCCCTGTAACTCCTGCCAGAGTTCCTGG
P.g      ATACTTAGCTCTCTCATTTTTCCCTCTGTAACTCCTGCCAGAGTTCCTGG
D.l      TACTTAGCTCTCTCATTTTTCCCCCTGTAACTCCTGCCAGAGTTCCTGGA
Z.c      TACTTAGCTCTCTCATTTTTCCCCCTGTAACTCCTGCCAGAGTTCCTGGA
P.b      ATACTTAGTTCTCTCATTTTCCCCCCTGTAACTCCTGCCAGAGTTCCTGG

&[dna]
P.e      ??????????????????????????????????????????????????
G.m      ??????????????????????????????????????????????????
T.t      ??????????????????????????????????????????????????
D.d      ATGATGACCTTACTGATGACATTATGTGTGTCAAGAAGATTCTGGATAAT
S.f      ATGATGACCTTACTGATGACATTATGTGTGTCAAGAAGATTCTGGATAAT
P.g      ATGATGACCTTACTGATGACATTATGTGTGTCAAGAAGATTCTG??????
D.l      TGATGACCTTACTGATGACATTATGT??????????????????????
Z.c      TGACGACCTTACTGATGACATTATGT??????????????????????
P.b      ACGATGACCTTACTGATGACATTATGTGTGTCAA?????????????????

&[dna]
P.e      ????
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G.m      ????
T.t      ????
D.d      GTAG
S.f      GTAG
P.g      ????
D.l      ????
Z.c      ????
P.b      ????


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