東海大學生命科學系碩士論文

台灣灰鯨類化石形態及親緣關係研究

Morphology and Phylogenetic Relationships of Gray Whale-Like Fossils From Taiwan

研究生：蔡政修

Cheng-Hsiu Tsai

指導教授：林良恭

Dr. Liang-Kong Lin

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終於走到這一步了，雖然還有很多後續的工作需要進行，但，至少有一部份的成果可以呈現。

在這研究當中，最要感謝的人，當然是提供這兩件重要化石標本的人。這兩件標本分別由大地博物館館長--陳濟堂館長和一位悲愴且華麗（取自侯老師七十回顧展的名稱）的藝術家--侯立仁老師所提供。如果沒有這兩件標本，現在的我，還不知該何去何從...在此獻上我最大的敬意。

當然，對我親愛的家人也是要獻上最大的感謝，包含我母親、過世的父親、哥哥、爺爺、奶奶、叔叔及姑姑們、及所有照顧我的親戚們（族繁不及備載）。長期以來，他們不會多加過問我到底在做些什麼事情，讓我可以自由自在、無憂無慮地去追求我所喜愛的研究及各式各樣的事物。在此，將我多年來的初步研究成果獻給不計任何辛勞、代價扶養我長大成人的親人們。

野生動物實驗室的林良恭老師及自然科學博物館的張鈞翔研究員是我這研究的主要指導老師，在此也要感謝他們對我不厭其煩地指導、給我研究上的想法、建議等等。野生動物實驗室、東海生命科學系和科博館的大家（同樣地，族繁不及備載，雖然好像不太適合用在這裡）給我在生活上的幫助、討論等。還要感謝從以前到現在都還持續有連絡的好友們，在我心情低落的時候陪我天南地北的亂聊一通、或陪我發發牢騷。

要完成古生物學的研究，少不了要檢視許多的現生及化石標本。在此，要感謝每一個我所到過的博物館，讓我可以順利地檢視各個博物館所藏的標

本。台中科博館地質組與動物組、台南菜寮化石博物館、台灣博物館、台南大地博物館、嘉義市立文化中心、屏東海洋生物博物館、日本福井縣恐龍博物館、日本北海道足寄化石博物館、日本北海道天塩川歷史資料館、日本滋賀縣琵琶湖博物館、紐西蘭奧塔哥博物館等等。

最後，可以開始寫”致謝”的話，當然是已經經過了口試這一階段。除了兩位主要的指導老師（林良恭老師及張鈞翔研究員），還有台大周蓮香老師、科博館姚秋如研究員和系上的林仲平老師在口試時所給的建議、指出此研究需改進的地方、還有後續的研究方向等等，讓目前的研究更加的完善。

謝謝在我生命中留下痕跡的每一個人！

摘要

本研究針對兩件從台灣與澎湖間的海底所打撈的海洋哺乳動物化石頭骨進行形態及親緣關係研究。依據形態特徵，如上枕骨（supraoccipital）的突起、副枕突（paroccipital process）指向後方和上枕骨邊界成直線等，都說明了這兩件化石標本可能屬於鬚鯨亞目（Mysticeti）內灰鯨科（Eschrichtiidae）的物種。為確認本研究之兩件化石標本於鬚鯨亞目的親緣關係，在鬚鯨亞目的七個科（包含十四個物種、兩件新發現的化石標本）進行比對及分析，其中這七個科包含了鬚鯨亞目四個現生科，Balaenopteridae（六種）、Balaenidae（兩種）、Neobalaenidae（一種）、Eschrichtiidae（兩種）和三個已滅絕的科，Aetiocetidae（一種）、Eomysticetidae（一種）、Cetotheriidae（一種）。使用三十六個頭骨形態特徵，利用簡約法則（Parsimony analysis）和貝氏方法 （Bayesian analysis），將各個物種取得的特徵資料進行分析，本研究之兩件新發現的化石標本和另兩種灰鯨（現生種 *Eschrichtius robustus*、化石種 *Eschrichtioides gastaldii*）歸為同一類群，證實這兩件化石頭骨標本為灰鯨科的物種無異。從親緣地理的角度來看，這兩件新發現的化石標本較接近現生種 *Eschrichtius robustus*，而不是目前只有在地中海地區發現的化石種 *Eschrichtioides gastaldii*，因此在本研究暫定這兩件化石標本為 *Eschrichtius* sp.。另一部分，探討灰鯨科和鬚鯨亞目其它科的親緣關係，本結果支持了灰鯨科和已滅絕的 Cetotheriidae 親緣關係較接近。

ABSTRACT

Two extraordinary partial posterior skulls dredged from sea bottom between Taiwan and Penghu Islands were recognized and presented in this study. According to the morphological characters, such as paired tuberosities on the supraoccipital, paroccipital processes pointed posteriorly, and lateral border of supraoccipital straight etc., these two fossil skulls could be assigned into eschrichtiids (gray whale) of Mysticeti. To confirm the phylogenetic relationships between these two newly-discovered fossil specimens and species of Mysticeti, four extant families (Balaenopteridae, Balaenidae, Neobalaenidae, and Eschrichtiidae) and three extinct families (Aetiocetidae, Eomysticetidae, and Cetotheriidae) are included in this study. Thirty-six characters from these two partial skulls are selected and the compiled data collecting from each species were performed with parsimony and Bayesian analyses which both reconstruct the phylogenetic relationships. This result showed that these two skulls are grouped with living gray whale (*Eschrichtius robustus*) and one extinct species (*Eschrichtioides gastaldii*) which is a newly-established genus and species of Eschrichtiidae. From the phylogeographic perspective, these two specimens probably are closer to extant species, *Eschrichtius robustus,* rather extinct species, *Eschrichtioides gastaldii,* found around Mediterranean region only and therefore they were assigned to *Eschrichtius* sp. provisionally. Furthermore, this study also discussed the interrelationship among Mysticeti and the result supported the closer relationship of Eschrichtiidae and Cetotheriidae.

INTRODUCTION

The fossil record which is telling life’s epic provides the direct evidence for extinct life and therefore has greatly predominated over the considerations of evolutionary patterns and processes (Norell and Novacek, 1992). It could be analogized to a movie recording the history of life through geological deep time. The widespread concern, however, is that only a tiny fraction of life history are fossilized and furthermore dug out to be visible in the world. Nonetheless, the fossil record still remains crucial to understand the branching events of the tree of life.

The fossil record of Cetacea (whales, dolphins and porpoises) could be dated back to Eocene which is more than fifty million years (Fordyce, 2008). Based on fossils from near shore to deep ocean marine strata and occasionally freshwater sediments, at least more than five hundred cetacean species are discovered, described and named (Uhen, 2011). Cetacean fossil remains are unearthed from nearly well-preserved skeletons to single elements which are usually un-diagnostic bones (Fordyce and Muizon, 2001). Of these remains, specimens with skull elements are the most useful and important in doing classification and systematic research. Other bones, such as limb and vertebrate elements, could also been used at times (Kazár and Bohaska, 2008).

Cetacea, a mammalian order, comprises three suborders, extinct Archaeoceti, extant Mysticeti and Odontoceti. By earlier researchers, such as Thompson (1890), Miller (1923), Yablokov (1964) etc., they held the opinion that order Cetacea is a non-monophyletic evolutionary group, but with compiling great deal of evidence from fossil record and molecular data, modern scientists strongly believed that Cetacea is a monophyletic evolutionary group which Odontoceti and Mysticeti are descended from the family Basilosauridae in the suborder, Archaeoceti (Fordyce, 2008; Uhen, 2004, 2010). The two extant suborders, Mysticeti and Odontoceti, are widely regarded as strictly monophyletic groups separately from morphological characters (Geisler and Sanders, 2003) and molecular data (Xiong *et al*., 2009), though previous studies once doubted the phylogenetic relationship between Mysticeti and Odontoceti (Milinkovitch *et al*., 1993, 1994), which proposed the odontocete family Physeteridae (sperm whales) is the sister group to Mysticeti instead of other odontocetes based on mitochondrial genes.

The suborder, Odontoceti, consists of seventy to eighty living species according different taxonomists in the ten families, Physeteridae, Kogiidae, Ziphiidae, Delphinidae, Phocoenidae, Monodontidae, Platanistidae, Iniidae, Pontoporiidae, and Lipotidae. Based on molecular data, anatomy evidence, and fossil records, all indicate that Odontoceti is a monophyletic group (Nikaido *et al*., 2001; Geisler and Sanders, 2003). The oldest known odontocete is the early Oligocene *Simocetus rayi*, which was unearthed from the sediment around 32 million years ago (Fordyce, 2002). The diagnostic osteological features for odontocetes from the earliest fossil record to extant species, especially in the skull, include a large supraorbital process that overlaps the maxilla; a large facial fossa that houses dorsal infraorbital foramina; premaxillary sac fossa anterior to the nares; premaxillary foramina; premaxillary sulci; a periotic that is excluded from the floor of the braincase; and the presence of a middle sinus etc. (Miller, 1923; Fordyce, 2008; Uhen, 2010).

The other extant suborder, Mysticeti, is composed of less living species than odontocetes around thirteen to fourteen species in the four families, Balaenidae, Neobalaenidae, Balaenopteridae, and Eschrichtiidae. From molecular data, anatomy evidence, and fossil records, all show that Mysticeti is a monophyletic group (Fordyce, 2008; Uhen, 2010). The oldest known mysticete is the late Eocene *Llanocetus denticrenatus*, which was from the deposit about 34.2 million years ago (Mitchell, 1989). The diagnostic osteological characters for mysticetes from the earliest fossil record to extant species, particular in the skull, are relatively large rostrum with thin edges and a smoothly concave and usually broad lower surface; main bone in the rostrum, such as vomer, premaxilla, and maxilla, generally sutured loosely with each other; loose sutures between lacrimal and frontal and the preorbital part of the maxilla; maxilla extending towards the orbit, forming a prominent infraorbital plate below the frontal; mandible joints by ligaments at a short symphysis etc. (Miller, 1923; Fordyce, 2008).

Many mammalian fossils are dredged from the sea bottom between Penghu Islands and Taiwan which is named as Penghu Channel. Shikama *et al*. (1975) recognized this locality as Penghu-Tainan Fauna from the representative species, *Palaeoloxodon naumanni* and considered it having relationship with Late Pleistocene fauna in Japan. Kao (1982) described more fossil remains from this sea bottom, including *Equus ferus przewalskii*, *Elaphurus menzierianus* and *Bubalus youngi*. After comparing these new material with other fauna from China, Kao (1982) concluded that these new material are connected with the northern fauna in China instead with the fauna in Tainan during Pleistocene age, therefore, he suggested the faunal name proposed by Shikama *et al*. (1975) should be revised as Penghu Fauna. From Penghu Fauna, a wealth of terrestrial mammalian fossils are recorded since Shikama *et al*. (1975) and Kao (1982). Ho *et al*. (1997) and Tseng and Chang (2007) reported the carnivores and *Crocuta crocuta ultima* respectively; Ho *et al*. (2008) and Ho *et al*. (2010) documented the herbivores, *Cervus* and *Equus* respectively.

However, deficiently known whale fossils have been discovered in Taiwan. Tan (1937) began to research marine mammal fossils and uncovered delphinid vertebrae in Houlong Township, Miaoli County and Chochen Township, Tainan County. During excavation in the search for petroleum near Chutung Township, Hsinchu County, several balaenopterid fossil specimens were discovered, including one of a new species, *Balaenoptera taiwanica*, and reports were published by the staff of the Taiwan Petroleum Exploration Division (TPED) of the Chinese Petroleum Corporation (CPC) (Meng, 1961; Huang, 1965, 1976; Chiu, 1972). The bottom of the sea between Taiwan and Penghu Islands, named Penghu Channel contains numerous mammalian fossils, mainly terrestrial remains which have been found during the trawling operations of fishermen (Gao, 1982). Among these mammalian fossils, one nearly complete delphinid skull and cervical vertebrae was dredged from Penghu Channel and assigned to *Globicephala macrorhynchus* (Chang, 1996). From Yuanli Township, Miaoli County, a well-preserved specimen including the skull, teeth, cervical vertebrae, dorsal vertebrae and ribs was assigned to a new species of the name *Pseudorca yuanliensis* (Chang and Cheng, 1998).

In present study, two fossil skulls which were dredged from sea bottom between Taiwan and Penghu Islands (Fig. 1) were investigated. These two fossil specimens could be ascertained that both of these two fossil skulls belong to cetaceans due to the special modification in the arrangement of the cranial bones which is a unique characteristic named as telescoping in this order, Cetacea. Furthermore, Miller (1923) in his masterpiece clearly distinguished two different types of cranial modifications in Cetacea, stating "in one type (toothed cetacean) the entire proximal portion of the maxillary passes up over the frontal and backward to approach or meet the supraoccipital at a level behind the orbit; laterally it spreads out over the expanded supraorbital wing of the frontal. Backward motion of anterior elements is the most obvious feature of this first process. In the other type (baleen cetacean) the broad outer part of the hinder maxillary border projects obliquely downward and backward under the anterior margin of the great supraorbital wing of the frontal, while the narrow inner part fits closely into the body of the frontal on the upper surface of the forehead; the upper surface of the expanded supraorbital wing of the frontal is thus left bare. As though further backward progress of the maxillary were rendered difficult by this double interlocking of maxillary and frontal, telescoping is chiefly accomplished by forward extension of the occipital and parietal to and beyond the median orbital level. Forward motion of posterior elements is the most obvious feature of this second process." From this evident diagnostic feature, these two partial posterior skulls in this study represent the second modification process of telescoping discussed by Miller; hence both of them belong to the suborder, Mysticeti (baleen whales).

The telescoping condition comprehensibly deciphers the higher taxonomic status of these two newly-discovered specimens. Here, furthermore, the purpose of this study is to explore the taxonomic status and phylogenetic positions of two undetermined fossil mysticete skull dredged from sea bottom between Taiwan and Penghu Islands. In addition to taxonomic issue, their phylogenetic relationships among extant and extinct mysticetes are also discussed.

MATERIALS AND METHODS

NMNS-F051728 (Fig. 2, 3, 4, 5)

This specimen was dredged from the sea bottom between Taiwan and Penghu Islands by fishermen when performing the trawling operations. Preserved element of this specimen is the posterior portion of the skull, including occipital condyle, exoccipital, supraoccipital, basioccipital, basisphenoid, damaged squamosal, parietal, and partial frontal, etc. The specimen is now in collection at the National Museum of Natural Science (NMNS) in Taichung City, Taiwan.

LFMM-W-001 (Fig. 6, 7, 8, 9)

This specimen was also dredged from the sea bottom between Taiwan and Penghu Islands by fishermen when performing the trawling operations. The preserved element of this specimen is to a great extent similar to NMNS-F051728. It is also remaining posterior portion of the the skull, including occipital condyle, exoccipital, supraoccipital, basioccipital, basisphenoid, broken squamosal, parietal, and limited frontal, etc. This specimen is at present deposited at a private museum, Land Fossil and Mineral Museum (LFMM) in Tainan City, Taiwan.

TAXON SAMPLING

Taxa sampling were intended to encompass the diversity of the suborder of Cetacea, Mysticeti. The ingroup comprised fourteen taxa in the five families, including extinct *Cetotherium rathkei* in the Cetotheriidae; extant *Balaenoptera acutorostrata, Balaenoptera omurai, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera edeni* and *Megaptera novaeangliae* in the Balaenopteridae; extant *Balaena mysticetus* and *Eubalaena glacialis* in the Balaenidae; extant *Caperea marginata* in the Neobalaenidae; extant *Eschrichtius robustus* and extinct *Eschrichtioides gastaldii* in the Eschrichtiidae; and two newly-discovered specimens, NMNS-F051728 and LFMM-W-001. Two outgroups, *Aetiocetus polydentatus* and *Eomysticetus whitmorei*, were chosen to be the representative of toothed mysticete and early toothless mysticete respectively in the analysis.

The Cetotheriidae has been a messy receptacle for fossil species that could not fit into the modern edentulous families or the tooth-bearing mysticetes clade. In the course of pouring species into Cetotheriidae, more than 100 species have been assigned to Cetotheriidae without solid confirmation mostly. Hence, only a species, *Cetotherium rathkei* sensu stricto, is incorporated for the phylogenetic analysis. Among Balaenopteridae included, *Balaenoptera omurai* was involved in this study in spite that it is a newly-erected extant species, but a commonly-accepted species (Wada *et al.,* 2003; Sasaki *et al., 2006*). As for eschrichtiids, the only extant species, *Eschrichtius robustus*, and the extinct species, *Eschrichtioides gastaldii*, which was recently described as a new genus and species in the Eschrichtiidae from Italy by Bisconti (2008) were included in the analysis. Two more new genera and species in the Eschrichtiidae were also established lately, *Archaeschrichtius ruggieroi* (Bisconti and Varola, 2006) and *Gricetoides aurorae* (Whitmore and Kaltenbach, 2008), but regrettably they could not be analysed in this study while performing phylogenetic analyses due to the poorly-preserved condition of these two holotype, *Archaeschrichtius ruggieroi* only preserving incomplete left mandible, and *Gricetoides aurorae* mainly partial posterior skull. The taxon list in this study referred to appendix 1.

MORPHOLOGICAL CHARACTER SELECTION

The design of the data matrix for this study was in the main constrained by the preservation of these two newly-discovered specimens, NMNS-F051728 and LFMM-W-001 that both preserved the posterior portion of the skull, and thus the morphological character selection was gathered from the posterior part of the skull. While this character selection is likely to suffer from the limited region of the skull to choose characters, it is to some extent still feasible to implement these phylogenetic analyses via this restricted area because the posterior skull, such as basicranium, denotes the conservative region through the skull evolution.

Before examining these two specimens, a particular concern needs to be noted. From the sutures between each bone, such as suture between occipital and parietal, these sutures are not yet fused tightly, therefore these detached bones indicated that they both are immature individuals, in other words, juvenile specimens.

Two characters are emphasized with particular concern. The first, character 9, scores the absence or presence of paired tuberosities on the supraoccipital. This feature generally was regarded as the synapomorphy of eschrichtiids, but the problem is that for a long time the Eschrichtiidae is a monotypic clade, therefore a specific character should be put to the level of family, genus, or species rendering questionable (Ichishima *et al*., 2006). Here, I include this character, the paired tuberosities on the supraoccipital, into the phylogenetic analysis that no researcher in the literature utilized this so-called unique character (when writing this thesis, a recent publication also included this character into phylogenetic analysis (Marx, 2011)). The second concern lies on the character one. The character one, the anterior tip of supraoccipital, was modified from Bisconti (2008). The point is that among several coding for this character is unclear. The round-shaped was divided into three categories, merely round, narrow and round, and wide and round. Intuitively, the first code for round is a redundant coding, therefore, it was discarded in this study.

Each of the thirteen ingroup and outgroup taxa were coded for the thirty-six morphological characters. The coding for each taxon listed in appendix 2 and the morphological characters listed in appendix 2. Originally, I chose more than fifty morphological characters from posterior skull, but several of these chosen features could not be observed from NMNS-F051728 and LFMM-W-001. As a consequence, some of these morphological characters were deleted from the dataset. However, there still exists question mark in the dataset of coding NMNS-F051728 and LFMM-W-001 (character 15, 23, 25, 28, and 29). Repeating the analyses with same settings only removing these question marks both in the NMNS-F051728 and LFMM-W-001 shows the stability of final results (Fig. 10 and 11). Therefore these morphological characters were kept in the dataset. Of the thirty-six morphological characters, one is original in the phylogenetic analysis while the remaining characters are from previous morphological studies (Geisler and Sanders, 2003; Steeman, 2007; Bisconti, 2008; Kimura and Hasegawa, 2010). Twenty-five characters were binary while twelve were multistate, and all of these character were treated unordered and unweighted.

PHYLOGENETIC ANALYSIS

In this study, two methods for phylogenetic reconstruction were conducted. Before performing the analyses, MacClade 4.06 (Maddison and Maddison, 2003) was used to enter and edit the morphological matrix. The data matrix was analyzed using parsimony and Bayesian methods which both were used to reconstruct phylogeny. In the parsimony method to reconstruct phylogeny, PAUP 4.0b10 (Swofford, 2002) was executed while the Bayesian method, using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001).

To find the most parsimonious trees, tree search in the program, PAUP, was set to be heuristic search with the following settings. Tree bisection and reconnection (TBR) was chosen in the branch-swapping options. From the stepwise-addition options, holding one tree at each step and one thousand random replications were assigned. After the end of the heuristic search, performing the resampling method, bootstrap, showed the support of each split.

In the Bayesian method, morphological data was performed using the Mk model which was developed by Lewis (2001). This model assumed that the character are varied. Variation in rates of change among characters used gamma distribution. Analyses were conducted searches of ten million generations, sampling every hundred generations. When the value of average standard deviation of split frequencies and potential scale reduction factor come to around 0.001 and 1 respectively, the analyses would be suspended. After the analyses, it is necessary to discard 25% of the samples obtained during each run. This 25% discards was for parameter values while the information of the tree and the branch length have different burn-in settings. Therefore, it is required to give 25% discards again. To choose the better model in the analyses, Bayes factor was calculated to represent the favored model. The value between three and twelve is positive; greater than twelve is strong and more than one hundred and fifty is very strong. At the end of the analyses, it would output a cladogram with the posterior probability values for each split to show the clade credibility.

BRANCH SUPPORT

The quantification of the support for certain each branch or specifically each clade has shifted to have great concern of the phylogenetic research. The common measures used are nonparametric bootstrap values (Efron, 1979; Felsenstein, 1985), jackknife values (Farris et al., 1996), Bremer support (Bremer, 1988, 1994), and Bayesian posterior probability value (Rannala and Yang, 1996; Huelsenbeck et al., 2001).

In this study, to evaluate the reliability of phylogenetic trees reconstructed by parsimony analysis and Bayesian method, nonparametric bootstrap value and posterior probability value are computed to estimate the branch support for these two phylogenetic inferences respectively.

RESULTS

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

CETARTIODACTYLA Montgelard, Catzeflis and Douzery, 1997

CETACEA Brisson, 1762

PELAGICETI Uhen, 2008

NEOCETI Fordyce and de Muizon, 2001

MYSTICETI Flower, 1864

ESCHRICHTIIDAE Ellerman and Morrison-Scott, 1951

ESCHRICHTIUS Gray, 1864

ESCHRICHTIUS sp.

Description

Skull. The preserved element of these two specimens are the posterior portion of the skull. The incomplete specimens are composed of occipital condyle, exoccipital, supraoccipital, basioccipital, basisphenoid, broken squamosal, parietal and partial frontal etc. The anterior portion is totally missing in these two specimens and thus the characteristics of maxilla, premaxilla and the vomer could not be observed. Also one of the major feature of eschrichtiid member, disproportionately large nasals, could not be examined as well. From the unfused sutures between each bone, such as suture between occipital and parietal, and the skull size, both indicate that these two specimens are juvenile specimens.

Supraoccipital. It is part of the occipital shield which is comprised of supraoccipital and exoccipital. The most prominent feature on the supraoccipital of these two specimens, NMNS-F051728 and LFMM-W-001, is the paired tuberosities which is considered as a critically diagnostic character of eschrichtiid members. As described by Andrews (1914), “The supraoccipital presents three deep concavities, and on the superior portion two prominent and peculiar rugosities. These are undoubtedly homologous with the similar processes just under the lambdoid crest on the supraoccipital of dogs and other mammals, where the rectus capitis posterior major and minor muscles, which assist in raising the snout, are attached. Their development, and the presence of similar rugosities below upon the basisphenoid and basioccipital bones, are probably correlated with the fact that the cervical vertebrae are all free, and the neck is somewhat less abbreviated than in other large cetaceans thus allowing greater movement of the head.” The major distinction of these two specimens from extant gray whale, *Eschrichtius robustus*, and extinct species, *Eschrichtioides gastaldii*, lies in the anterior tip of supraoccipital which represented as pointed-shape in NMNS-F051782 and wide and squared in LFMM-W-001 respectively, whereas it is narrow and square in *Eschrichtius robustus* and narrow and round in *Eschrichtioides gastaldii.*

Exoccipital. It is the ventral part of the occipital shield with the occipital condyle. From dorsal view, the paroccipital processes of the exoccipital, in these two specimens, NMNS-F051728 and LFMM-W-001, both projects posteriorly and laterally and thus an obvious curve line is noticeable from occipital condyle connecting to posterior portion of paroccipital process. This feature is prominently pronounced among eschrichtiid clade, and it seems more conspicuous in juvenile individuals, such as these two newly-discovered specimens. As these animals grow, this curve line between occipital condyle and paroccipital process probably becomes less salient. These two specimens, NMNS-F051728 and LFMM-W-001, both have large occipital condyle which stands for a characteristic of the gray whales. But this feature seems likely reducing the relative ratio to the skull width through growing up (Ichishima *et al*., 2006).

Basioccipital/Basisphenoid. These two bones form the ventral border of cranium. Usually, they are firmly fused together barely observing the suture between these two bones, whereas it still could be slightly discriminated the boundary of basioccipital and basisphenoid from these two juvenile specimens, NMNS-F051728 and LFMM-W-001. The absence or poorly developed of the rectus capitus anticus muscle fossa, which is probably homologous to the rectus capitus ventralis of the dog (Evan, 1993) and its function highly likely is to move the head ventrally (Schulte and Smith, 1918), in the eschrichtiids is observed in these two specimens as well.

Parietal. It is the anterior cover for the cranium anteriorly to the occipital shield. The parietal *per se* is rather featureless to some extent, but the suture with frontal shows a useful distinction for eschrichtiids from other mysticetes. This suture is rather straight and vertical in eschrichtiids, whereas it is curve line, to some degree, like a S-shaped curvature from anterior through posterior part in balaenopterids. These two specimens, NMNS-F051728 and LFMM-W-001, both clearly exhibit this characteristic partly because of the unfused suture between parietal and frontal.

Squamosal. In both specimens, NMNS-F051728 and LFMM-W-001, the zygomatic processes of squamosal are damaged heavily, though the preservation of this bone in LFMM-W-001 is better than in NMNS-F051728. In ventral view, the external acoustic meatus is visible in both sides of NMNS-F051728 and only left side of LFMM-W-001 because of the missing of the postglenoid process of squamosal which originally should cover the partial portion of the external acoustic meatus ventrally. The squamosal was once considered as a diagnostic character for rorqual and gray whale clade (Ichishima *et al*., 2006), but recently it was broadened its coverage to include the neobalaenids (Marx, 2011). However, whether this feature could be used to be a synapomorphy for the new clade, Eschrichtiidae/Balaenopteridae/Neobalaenidae, still need further confirmation due to the indeed absence of the squamosal cleft in the extinct species of eschrichtiids, *Eschrichtioides gastaldii* (personal communication with Bisconti).

PHYLOGENETIC ANALYSIS

Parsimony Analysis

The parsimony analysis resulted in forty-six equally most parsimonious trees that are sixty-eight steps in length. The fifty-percent majority-rule consensus tree of the forty-six most parsimonious trees was presented to show grouping patterns (Fig. 10). The numbers divided by the slash on the node indicate the frequency of occurrence of each node from the different trees and bootstrap values respectively. The tree topology resolution was only to the family level, not to the genera or species level. However, two families could not be separated in this analysis, Balaenidae and Neobalaenidae. From the consensus tree of the forty-six most parsimonious trees, five major group could be identified, the outgroup *Aetiocetus polydentatus* and *Eomysticetus whitmorei*; family Cetotheriidae, *Cetotherium rathkei*; family Eschrichtiidae, *Eschrichtius robustus* and *Eschrichtioides gastaldii,* plus two new specimens NMNS-F051728 and LFMM-W-001; family Balaenopteridae, *Balaenoptera acutorostrata, Balaenoptera omurai, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera edeni,* and *Megaptera novaeangliae*; family Balaenidae and Neobalaenidae, *Balaena mysticetus, Eubalaena glacialis* and *Caperea marginata*.

These two new specimens, NMNS-F051728 and LFMM-W-001, are nested together with *Eschrichtius robustus* and *Eschrichtioides gastaldii* which both are members of the mysticete family, Eschrichtiidae. The representative species, *Cetotherium* rathkei*,* in the extinct family, Cetotheriidae, is the sister taxon of *Eschrichtius robustus, Eschrichtioides gastaldii,* NMNS-F051728, and LFMM-W-001.

Bayesian Analysis

From the Bayesian analysis, the resulting tree topology (Fig. 11) is relatively similar to the parsimony result. The numbers on the node indicate the posterior probability values for the support of each branch. The tree topology resolution, same as parsimony result, was only to the family level. However, in the Bayesian analysis, not only Balaenidae and Neobalaenidae collapsed, but also Cetotheriidae which was grouped with members of Eschrichtiidae. Four major branches could be recognized in this analysis, the outgroup *Aetiocetus polydentatus* and *Eomysticetus whitmorei*; *Cetotherium rathkei, Eschrichtius robustus, Eschrichtioides gastaldii,* plus two new specimens NMNS-F051728 and LFMM-W-001; family Balaenopteridae, *Balaenoptera acutorostrata, Balaenoptera omurai, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera edeni,* and *Megaptera novaeangliae*;

family Balaenidae and Neobalaenidae, *Balaena mysticetus, Eubalaena glacialis* and *Caperea marginata*.

Two distinctions in the Bayesian analysis recognized were the position of *E. glacialis* and *C. rathkei* in the cladogram. In the branch grouping Balaenidae and Neobalaenidae, the Bayesian result differed from the parsimony result which badly placed *Caperea marginata* with *Balaena mysticetus*, but excluding the other member in the Balaenidae, *Eubalaena glacialis*. On the other hand, the Bayesian result grouped Balaenidae and Neobalaenidae altogether, a bush-like branch.

The other difference between these two analyses located in the Cetotheriidae-Eschrichtiidae clade. Parsimony analysis left the member of Cetotheriidae, *Cetotherium rathkei*, as a independent lineage, however, in the Bayesian result, *Cetotherium rathkei* was put into the eschrichtiid clade with *Eschrichtius robustus, Eschrichtioides gastaldii* and two newly-discovered specimens, NMNS-F051728 and LFMM-W-001.

DISCUSSIONS

Geological Age

The geological age of the sediment of Penghu Channel is known from the fauna comparison between Penghu Channel and south China. From this biogeographical study, Kao (1982) concluded that the specimens from Penghu Channel belonged to late Pleistocene or early Holocene. The species studied by Kao were terrestrial mammals, such as *Equus ferus przewalskii, Elaphurus menzierianus,* and *Bubalus youngi*. Different from Kao's study (1982), Tseng and Chang (2007) described new material of hyaenid, *Crocuta crocuta ultima*, discovered from Penghu Channel as well, but put the occurrence of these specimens as late Middle Pleistocene after comparing with *Crocuta crocuta ultime* living in China during middle to late Middle Pleistocene. These studies indicate that the geological age of fossil vertebrates from Penghu Channel lived in different period, revealing that these fossils dredged from the sea bottom of Penghu Channel represent repeated migration events from whether China or Japan to Taiwan because of the alternating glaciation and interglaciation from the Late Pliocene through Pleistocene which greatly changed the topography and allowed animals roaming around Taiwan. However, the NMNS-F051728 and LFMM-W-001 are marine mammals, differing from previous studies (Kao, 1982; Tseng and Chang, 1996) which mainly discussed the geological age of Penghu Channel by terrestrial mammals.

Two hypotheses could be erected to probe into this fossil assemblage including terrestrial and marine fossils. The first, intuitively, considered that these fossil animals with totally different life style (land environment versus marine habitat) discovered from the same locality lived in discrete periods during the alternating glaciation and interglaciation since Late Pliocene that shaped the topography of Taiwan Strait significantly. During glaciation period, the so-called “land bridge” between Taiwan and China was formed for land animals to move between Taiwan and China, whereas for the time of interglaciation Taiwan Island and mainland China was separated by Taiwan Strait which would prevent the interchange of animals between these two localities. The problem confronted by this hypothesis is that it is hard to determine what kind of species or which population found from Penghu Channel fossilized in which event due to several cycle of glaciation and interglaciation occurring in Pleistocene. The second hypothesis allows the fossilization of terrestrial and marine mammals at the same period, because this idea concerns the topographic feature of Taiwan Strait. The average depth of Taiwan Strait is less than 60 meters (Peng, 2003). The isobath line of Taiwan Strait plainly indicates the submarine terrace plunging down deeper in the South China Sea which is south to Penghu Channel. Therefore, this area could form an estuary for cetaceans to strand on this locality, and on the other hand the present region of Penghu Channel or slightly north to it still is the land environment for terrestrial mammals moving around this area during the period of sea level falling down. The potential locality of fossilization for terrestrial and marine mammals is abutting plus the possible floating buried carcasses when sea level arose to place the land and marine mammals together.

As discussed above, the specific age of these two eschrichtiid specimens is indeterminable yet. Here I put these two eschrichtiid mysticetes as the Pleistocene provisionally in a broader scale.

Phylogenetic positions

From both parsimony analysis and Bayesian method, two newly-discovered specimens, NMNS-F051728 and LFMM-W-001, are placed with living species and extinct species in the Eschrichtiidae, *Eschrichtius robustus* and *Eschrichtioides gastaldii* respectively. The difference of this clade between these two results is the relationship with *Cetotherium rathkei.* In the parsimony analysis, *Cetotherium rathkei* was the sister group of two eschrichtiid members and two newly-discovered specimens, whereas *Cetotherium rathkei* was grouped with *Eschrichtius robustus, Eschrichtioides gastaldii,* NMNS-F051728 and LFMM-W-001, forming a bush-like branch.

Two prominent and peculiar tuberosities on the supraoccipital were observed from these two newly-discovered specimens which represented their close relationship with *Eschrichtius robustus* and *Eschrichtioides gastaldii.* The thick and extending paroccipital process towards posterior part to the extent of the nuchal crest is the shared character by these two new specimens, *Eschrichtius robustus, Eschrichtioides gastaldii* and *Cetotherium rathkei.* Two characters, having strong and massive tubercle on the basioccipital and massive, squared, or triangular shape of basioccipital process, possessed by *Eschrichtius robustus, Eschrichtioides gastaldii*, NMNS-F051728, LFMM-W-001, *Cetotherium rathkei* and *Eomysticetus* *whitmorei.* Among these chosen characters, the prominent and peculiar tuberosities on the supraoccipital was crucial to resolve these two incomplete newly-discovered specimens. From the emended diagnosis of Eschrichtiidae by Bisconti and Varola (2006), the robust bilateral prominence in the anterolateral surface of the supraoccipital is a main diagnostic feature which formed a strong attachment area for neck muscle.

The anterior tip of supraoccipital varies among taxa. These two newly-discovered specimens, NMNS-F051728 and LFMM-W-001, are designated as pointed and wide and squared respectively which differ from *Eschrichtius robustus* and *Eschrichtioides gastaldii.* The shape of anterior tip of supraoccipital in *Eschrichtius robustus* is narrow and squared, whereas it is narrow and round in *Eschrichtioides gastaldii. Eschrichtioides gastaldii* differs from *Eschrichtius robustus*, NMNS-F051728 and LFMM-W-001 in having lateral borders of supraoccipital continuously concave and parietal exposure on the dorsal wall of the skull. From dorsal view, the anteriormost point of the supraoccipital lies in transverse line with space between posterior edge of skull anterior edge of the floor of squamosal fossa in *Eschrichtius robustus* and LFMM-W-001, whereas it situates in line with space between anterior edge of the floor of squamosal fossa and the anterior tip of zygomatic process of squamosal in *Eschrichtioides gastaldii* and NMNS-F051728. The dorsal condyloid fossa is absent in *Eschrichtius robustus* and *Eschrichtioides gastaldii*. However, this character is observable both in these two newly-discovered specimens, NMNS-F051728 and LFMM-W-001.

From the discussions above, these two fossil specimens, NMNS-F051728 and LFMM-W-001, represented close relationships with members in the Eschrichtiidae, *Eschrichtius robustus* and *Eschrichtioides gastaldii.* The differences among these taxa are recognizable, however, these two specimens, NMNS-F051728 and LFMM-W-001, belonged to juvenile individuals, judging from size and the evident sutures between bones. Therefore, it is necessary to be prudent before deciding their taxonomical positions based on incomplete juvenile specimens. The significant dissimilarity among these taxa is the shape of anterior tip of supraoccipital and consequently the further effort would be to discriminate the variations of the shape of anterior tip of supraoccipital among individuals and the ontogenic variations from juvenile to adult individuals in *Eschrichtius robustus*.

Phylogenetic Relationships among Mysticeti

The phylogenetic relationships among Mysticeti have been greatly discussed in many articles (Geisler and Luo, 1996; Kimura and Ozawa, 2002; Sanders and Barnes, 2002; Geisler and Sanders, 2003; Dooley et al., 2004; Bisconti, 2005, 2007a, 2007b, 2008, 2010; Demere et al., 2005, Demere and Berta, 2008; Bouetel and de Muizon, 2006; Fitzgerald, 2006; Steeman, 2007; Kimura and Hasegawa, 2010; Bosselaers and Post, 2010). Each study has its foundation to support varying tree topologies. By and large, these studies on the phylogenetic relationships among Mysticeti for eschrichtiid perspective, could predominantly be categorized into three main hypotheses: (1) eschrichtiids are clustered with cetotheres (Bisconti, 2007a, 2007b, 2008, 2010; Steeman, 2007; Bosselaers and Post, 2010); (2) eschrichtiids are most closely relating to balaenopterids (Arnason et al., 1992; Geisler and Luo, 1996; Kimura and Ozawa, 2002; Dooley et al., 2004; Bisconti, 2005; Demere et al., 2005, 2008; Fitzgerald, 2006; Kimura and Hasegawa, 2010); and (3) eschrichtiids form a sister group of balaenids (Sanders and Barnes, 2002; Bouetel and de Muizon, 2006).

As mentioned above, parsimony analysis and Bayesian method conducted in this study indicate that eschrichtiids are greatly relating to cetotheres (hypothesis 1), although this clade is moderately supported by the bootstrap value in parsimony analysis and posterior probability value in Bayesian analysis. However, these two results differed in the status of *Cetotherium rathkei*, which formed a independent lineage in the parsimony analysis, but was grouped into the eschrichtiids as a unresolved grouping in the Bayesian method. These two results differed from two clade. One was the eschrichtiid-cetothere relationship, and the other was the balaenid-neobalaenid grouping. The other major difference between these two results is the higher relationship among Mysticeti, balaenopterid-balaenid clade in parsimony analysis but eschrichtiid-cetothere-balaenopterid clade in Bayesian method. Here I divided into three superfamilies to further discussions.

CETOTHERIOIDEA. The superfamily, Cetotherioidea, recently proposed by Steeman (2007) could reinforce the results of this study which rendered the merged group of eschrichtiids and cetotheres, to different extent cluster in each analysis. One formed a sister-group relationship and the other produced a bush-like lineage. Steeman (2007) put Cetotheriidae, Eschrichtiidae, and another two specimens which were described as ‘*Mesocetus’ argillarius* Roth, 1978*,* and ‘*Cetotherium’ megalophysum* Cope, 1895 respectively into this superfamily, Cetotherioidea. This superfamily was erected mainly by V-shaped posterior extension of the rostral processes, X-shaped skull vertex and narrow, posteriorly constricted nasals (but this character reversed in Eschrichtiidae). Unfortunately, these three characters could not be observed in NMNS-F051728 and LFMM-W-001 due to the preserved condition of specimens. However, from the selected character dataset in this study, this superfamily was supported by other features, thick and extending paroccipital process noticeably posterior to the extent of the nuchal crest, far and posterior position of posterolateral corner of exoccipital relative to postglenoid process of squamosal, and possible small exposure of interparietal on the dorsal wall of the skull.

From early studies (Andrews, 1914; Winge, 1921; Miller, 1923; Kellogg, 1928), Eschrichtiidae was considered closely relating to Cetotheriidae. Furthermore, Andrews (1914) even stated that the characters of the eschrichtiid skull are derivable from those of the cetotheres. Although several recent cladistic studies (Geisler and Luo, 1996; Kimura and Ozawa, 2002; Dooley et al., 2004; Bisconti, 2005; Demere et al., 2005, 2008; Fitzgerald, 2006; Kimura and Hasegawa, 2010) suggested that eschrichtiids should be clustered with balaenopterids. The Eschrichtiidae-Cetotheriidae clade is still highly supported by other cladistic analyses (Bisconti, 2007a, 2007b, 2008, 2010; Steeman, 2007; Bosselaers and Post, 2010) from following features, presence of the thick and extending paroccipital process posterior to the extent of the nuchal crest, far and posterior position of posterolateral corner of exoccipital relative to postglenoid process of squamosal, possible small exposure of interparietal on the dorsal wall of the skull, the unique morphology of the mandibular joint, and the narrow mandibular condyle. No mandibular remain was found from NMNS-F051728 and LFMM-W-001 and therefore unable to compare these unique characters of mandibular morphology between eschrichtiid-cetothere clade.

In spite of the conflict literatures pertaining to phylogenetic position of Eschrichtiidae, on the whole, Eschrichtiidae and Cetotheriidae have several synapomorphic characters and represent close relationship between these two families. Consequently, it is reasonable to erect a superfamily, Cetotherioidea, to unite Eschrichtiidae and Cetotheriidae.

BALAENOPTEROIDEA. The superfamily, Balaenopteroidea, was characterized by such following features, postglenoid process far lateral to, and approximately anterodorsally aligned with, the exoccipital process and long and narrow auditory meatus sulcus (Steeman, 2007). In this study, the balaenopteroid clade was clustered with balaenoids in parsimony analysis, whereas grouped with eschrichtiid-cetothere clade in Bayesian method. The branch support of varying pattern showed moderate value in both analyses, 51 for balaenopteroid-balaenoid clade in parsimony analysis and 55 for balaenopteroid-eschrichtiid-cetothere clade in Bayesian method. However, from Steeman's study (2007), the presence of Cetotherioidea-Balaenopteroidea clade was pointed out by several characters, such as roughened dorsal surface of pars cochlearis, low transverse processes on the atlas, broad and shallow glenoid process, anteriorly displaced coronoid process of the mandible with a relatively narrow base, and square cervical centra. On the contrary, the relationship between balaenopteroids and balaenoids is quite distant from skull morphology internally and externally, having narrower and much arched rostrum, longer baleen plates, and lacking ventral grooves etc. in typical balaenids. Therefore, the result of Bayesian analysis represented higher reliable phylogenetic relationship at superfamily level.

BALAENOIDEA. *Balaena mysticetus* was clustered with *Caperea marginata*, but excluding *Eubalaena glacialis* in the PAUP analysis. From the Bayesian result, *Balaena mysticetus, Eubalaena glacialis,* and *Caperea marginata* formed a bush-like clade. This could reflect close relationship between Balaenidae and Neobalaenidae, and therefore Brandt (1873) established a superfamily, Balaenoidea to includes these two families. Many evident characters could support this superfamily, such as supraoccipital shield approaching anterior to the posterior edge of the supraorbital process of the frontal, supraorbital process extending posterolaterally, straight and short nasals, occipital condyles levelling with the skull, compressed bulla dorsoventrally, reduced mandibular foramen, twisted distal end of the mandible, and fused cervical vertebrae completely. Because the focus of this study was the two newly-discovered specimens which were referred to eschrichtiid mysticetes and their phylogenetic relationship is significantly farther to eschrichtiid species and therefore no much discussion was on this clade.

The Record of Fossil Eschrichtiidae

Cope (1867) described a new species, *Eschrichtius cephalus*, on the basis of partial skull, mandibles, limb bones and vertebrae from Calvert Formation in Maryland during the Middle Miocene. Cope (1890) transferred the generic status from *Eschrichtius* to *Cetotherium* without solid reasons. After comparing with the genus, *Balaenoptera*, recent studies concluded that this specimen is closer related to *Balaenoptera* rather to *Eschrichtius* or *Cetotherium* (Kellogg, 1968; Barnes and McLeod, 1984; Weems and Edwards, 2007)

Eschrichtius davidsonii was erected as a new species according to a fragment mandible found from San Diego Formation, San Diego, California by Cope (1872). The age of this specimen was under debate. In his original report, Cope considered the locality of the mandible dug out was Miocene age but Bowers (1889) regarded the sediment as Pleistocene age. Several studies, however, confirmed this marine sediment belonging to Pliocene age (Gillette, 1975; Demere, 1983; Domning and Demere, 1984). Cope's original generic assignment to *Eschrichtius* was obviously erroneous due to the large coronoid process of the mandible which *Eschrichtius* does not possess this character (Barnes, 1976). Later, Cope (1890) put this species into the genus, Balaenoptera, and Barnes and McLeod (1984) and Demere (1986) agreed this generic point, although these two articles held different opinions on the species level.

A stock of vertebrae was originally assigned to the genus, *Megaptera* (Cope, 1868a), however, he later put these specimens to *Eschrichtius* (Cope, 1869), then to *Cetotherium*, and to *Siphonocetus* finally (Cope, 1895). Sadly, these specimens which were assigned together to holotype and referred specimens of a single species were from at least two different mysticetes and different localities, Maryland and Virginia States (Kellogg, 1968). Furthermore, Kellogg (1968) stated that the species was invalid due to the undiagnosable holotype and referred material.

On the basis of a cervical vertebra from Miocene age of Virginia, Cope (1868a, 1868b) assigned this specimen to *Eschrichtius leptocentrus* owing to having a large neural canal, but later (Cope, 1890) he transferred it to *Cetotherium* without supportive discussion. Barnes and McLeod (1984) declared that this species was invalid due to the incomplete material to form a solid species.

Balaena mysticetoides, originally proposed by Emmons (1858) based on an earbone, was then transferred generic rank to *Eschrichtius* by Cope (1875), but later he put it in the *Cetotherium* (Cope, 1890). Unfortunately, in the original description, Emmons did not disclose the location for this specimen, therefore the unavailable reexamination and poor figure provided by Emmons made further study impossible. Barnes and McLeod (1984) asserted it *nomen dubium*.

Cope (1870a, 1870b) proposed a new species, *Eschrichtius polyporus*, based on two fragmentary mandibles from North Carolina. He shifted the generic status to *Cetotherium* without statement (Cope, 1890). Without clear characteristics to define this species, it was regarded as *nomen vanum*, which denotes the name that has no scientific description (Barnes and McLeod, 1984).

Leidy (1851) established a species, *Balaena prisca*, which was based on a fragmentary mandible dug out from Virginia, but Cope (1868a, 1868b) mentioned this specimen using different generic status, *Balaenoptera*, and then transferred it to another genus, *Eschrichtius* (Cope, 1869). In spite of that Leidy (1869) agreed to this generic assignment (to *Eschrichtius*), Cope (1890) used the new synthesis, *Cetotherium priscum*, for this specimen. Coincidentally, this scientific name was occupied by other material assigned by Eichwald (1840). Subsequently, Cope (1895) assigned this mandibular fragment as the holotype of a new genus, *Siphonocetus*. Kellogg (1968) regarded this assignment by Cope (1895) as erroneous and invalid lacking enough comparative study with other mysticete mandibles from Calvert Formation.

A fragmentary mandible and a collection of vertebrae were originally described and assigned to a new species, *Balaenoptera pusilla*, by Cope (1868c). Then he transferred the generic status to *Eschrichtius* (Cope, 1868a) and to *Cetotherium* (Cope, 1890). The type material, fragmentary mandible, which was lost and the unidentifiable vertebrae rendered this species invalid. Kellogg (1968) clearly announced that this name should be ignored and discarded.

In 1983, Repenning reported the fossil remain of *Eschrichtius* sp. near Teshekpuk Lake of northern Alaska. Repenning did not mention what kind of material was found, however through the personal communication, Barnes and McLeod (1984) revealed that the element which was assigned to *Eschrichtius* sp. by Repenning was a partial rostrum from Late Pleistocene. Unfortunately, in the personal communication between Repenning and Barnes and McLeod, Repenning also declared that the specimen was no longer available which made this discovery dubious.

A excavation report from Pliocene Yotsukura Formation of Japan in 1989 published a fossil whale which was identified as an eschrichtiid mysticete. From the highly arched skull, triangular tympanic bulla, and the shape of scapula etc., the specimen actually is an balaenid mysticetes (Ichishima *et al*., 2006).

A great amount of poorly preserved postcranial material, including seven cervicals, seven thoracics, nine lumbars, eighteen caudals, chevron bones, pelvis, radius, ulna, and ribs etc., was assigned to the Eschrichtiidae by Kimura (1992) from Horokaoshirarika Formation in Japan. In spite of a fairly large number of fossil remains left, lacking the diagnostic component, such as skull, renders this specimen questionable (Ichishima *et al*., 2006).

In Hachinohe City of Japan, Oishi *et al*. (2001) assigned a posterior lumbar and a caudal vertebrae to Eschrichtiidae. From the morphological features of vertebrae, such as the orientation of transverse processes of vertebrae, the material possessed the characters which only are observed in the gray whale in extant baleen whales, however, this trait have also been described in the other fossil mysticete, *Otradnocetus virodovi*, by Mchedlidze (1984). As reviewed by Ichishima *et al*. (2006), the validity of this feature using to confirm the species needed through comprehensive comparisons of vertebral morphology among mysticetes, including extant and fossil species.

The material discussed above were invalid or needed further study to confirm their taxonomical position in the Eschrichtiidae. Until a well-preserved skull and postcranial skeletons were unearthed from San Pedro

Sand of Los Angeles in Late Pleistocene, there were no undoubted fossil record of eschrichtiids. Barnes (1976) mentioned this find in brief, and Barnes and McLeod (1984) put this discovery forward into science officially with detailed description. On the basis of the nearly complete fossil skull, they observed no evident osteological differences from extant *Eschrichtius robustus*, and consequently they assigned this first accepted fossil gray whale as *Eschrichtius* cf. *E. robustus*. The unambiguous characters possessed by *Eschrichtius robustus* could been recognized in this fossil skull, such as large nasal bones, paired tuberosities on the supraoccipital, large and posteriorly pointed paroccipital processes, and large occipital condyles etc.

An oldest fossil record of modern gray whale genus, *Eschrichtius*, was recovered from Yuchi Formation of Teshio Town, Hokkaido, Japan, near the boundary of Pliocene and Pleistocene described by Ichishima *et al.* (2006). The preserved material of this specimen included posterior skull, both periotics, fragmentary tympanic bullae, broken axis, thoracic vertebrae, left scapula, humerus, radius, ulna, carpal, metecarpals and ribs. However, from the unfused epiphyses of the long bones, clearly observed sutures among bone elements of skull, and the skull size, the whole skeletons should belong to a juvenile specimen. It is, therefore, needed to treat the taxonomical position of this new material prudently before the morphological differences regarded at the generic, specific, or intraspecific level in the Eschrichtiidae were better recognized. As a consequence, Ichishima *et al*. (2006) designated the Teshio whale as *Eschrichtius* sp. circumspectly. They also indicated a fossil whale which was not identified as an eschrichtiid mysticete could be assigned to Eschrichtiidae found in Akishima City, Tokyo, Japan, originally unveiled from a report of Akishima Chigaku Kenkyukai in 1966. This specimen possessed the following features, the less-telescoped skull, the proportionally large nasal, the ascending process of the maxilla much narrower than the premaxilla from dorsal view, the ventroposteriorly pointed postorbital process of the frontal, and the relatively slender zygomatic process of the squamosal (all of the above mentioned characteristics are observed by Ichishima at National Science Museum, Tokyo), which are representative traits of Eschrichtiidae.

On the basis of following emended diagnosis on mandible of Eschrichtiidae, presence of the satellite process parallel to the coronoid process but separated from it by a wide sulcus, continuously arched dorsoventrally, mylohyoidal concavity present in the medial side, Bisconti and Varola (2006) subsumed an incomplete left mandible into Eschrichtiidae and established a new genus and species, *Archaeschrichtius ruggieroi*, based on this imperfect material. In the context, they pinpointed it is inappropriate to create a new taxa according to an incomplete specimen. The new combination diagnoses for Eschrichtiidae modified by Bisconti and Varola (2006) are still needed further confirmation to substantiate the validity of this new genus and species and the diagnostic characters for differentiating generic or species level in the Eschrichtiidae because the remain of fossil eschrichtiid species were so incomplete to make a well-founded judgment.

A new genus and species, *Gricetoides aurorae,* of Eschrichtiidae was named based on a partial posterior part of cranium by Whitmore and Kaltenbach (2008). Whitmore and Kaltenbach pointed out that the features shared by *Gricetoides aurorae* and *Eschrichtius robustus* are the same as the descriptions for *Eschrichtius robustus* by Winge (1921): “The articular surface for the lower jaw on the squamosal is not pushed out especially far downward and backward, and, when seen from beneath, has not entirely covered the mastoid or pushed the exoccipital very far backward. Bony palate relatively not strongly lengthened behind. The basioccipital on the whole is only to a slight degree shaped to accommodate the larynx and gullet.” Whitmore and Kaltenbach described that *Gricetoides aurorae* differs from *Eschrichtius robustus* by having posterior side of postglenoid process almost vertical and entirely anterior to external auditory meatus, rounded vomer anteriorly and forming sharp ridge posteriorly, and palatines extending posteriorly only to a point anterior to transverse process of squamosal. However, only basal portion of posterior cranium was preserved, the main features of eschrichtiids, such as paired tuberosities on the supraoccipital and shape of anterior tip of supraoccipital, are unobservable.

A specimen previously described as *Balaenoptera gastaldii* by Portis (1885) was recently reassigned to Eschrichtiidae and established a new genus and species, *Eschrichtioides gastaldii* by Bisconti (2008). Demere *et al* (2005) also questioned the taxonomical status of '*Balaenoptera' gastaldii* and supposed that that specimen represented a new genus of basal eschrichtiid. From following characters, laterally bowed dentary, higher coronoid process of the dentary, straight rostrum in lateral view, smaller nasal narrower interorbital constriction, rounded and lower satellite process and less dorsally located groove for the mental ligament, Bisconti (2008) discriminated this specimen from other eschrichtiid members, *Eschrichtius* and *Archaeschrichtius.*

From the brief review on fossil eschrichtiids above, fossil specimens of modern gray whale discovered in Hokkaido, Japan and California, United States, and fossil genera of Eschrichtiidae, *Archaeschrichtius* and

Eschrichtioides found in Italy and *Gricetoides* in United States are widely accepted in evolutionary history of eschrichtiid lineage.

Paleobiological Perspective

Two fossil eschrichtiid specimens, NMNS-F051728 and LFMM-W-001, were discovered by fishermen when performing trawl operations from Penghu Channel. The preserved condition of two partial posterior skulls revealed that the discovery site could be near fossilized place, not trundling from elsewhere because if the fossil specimen processes this kind of rolling movement, the protruding processes would not remain intact, such as the paroccipital processes. In addition, the unfused cranial suture evidence suggested that these two specimens are juvenile individuals. From the measurement data (Table. 1), the distance between the left and right paroccipital processes is 481 and 439 mm in NMNS-F051728 and LFMM-W-001 respectively. Comparing with the oldest fossil of living genus *Eschrichtius,* HMT-F-1, found in Hokkaido, Japan, the distance between left and right paroccipital processes of these two specimens, NMNS-F051728 and LFMM-W-001, in Taiwan both are smaller than HMT-F-1 (540 mm) that Ichishima and his colleagues utilized the the size of living gray whale (LACM 54549) and the growth pattern of gray whale calf in captivity (Sumich et al., 2001) to come to an educated guess about the age of HMT-F-1, probably about thirty weeks after birth. The width across paroccipital processes of both specimens in Taiwan is shorter than the measurement recorded of HMT-F-1, strongly indicating that both NMNS-F051728 and LFMM-W-1 are younger than HMT-F-1. From the size difference between Taiwan and Japan specimens, the age of NMNS-F051718 and LFMM-W-001 could be lower than half year.

Observing the migration behavior and reproductive cycle of modern gray whales could infer the meaning of finding of these two fossil eschrichtiid specimens. The north migration of living gray whale from breeding grounds to feeding grounds could be recognized as two phases (Jones and Swartz, 2008). The first phase to leave the breeding grounds is from late January through March, mainly newly pregnant females, adult females and males, and then juveniles whereas the second phase to begin the journey could be adjourned until April or May, primarily mothers and new-born calves. The prolonged stay in the breeding area allows new-born calves to strengthen and rapidly grow in order to cope with the north migration (Jones and Swartz, 2008).

Combining the information discussed above, the occurrence of fossil eschrichtiid mysticetes from the Penghu Channel indicates the early history of western North Pacific population of eschrichtiids. Modern gray whales along western North Pacific coast is now a near extinct population and their mating and winter calving grounds still have not fully determined. Up to date evidence suggests that gray whales traverse the East China Sea into the

South China Sea to tropical waters off southeastern China at least as far south as Hainan in winter (Jones and Swartz, 2008). Although the establishment of their migration route and calving areas needs more evidence not only from fossil specimens but paleo-environments which could interpret the change of climate along the western coast of North Pacific, these two newly new-born eschrichtiid specimens found from the Penghu Channel could outline their mating and calving grounds using fossils. However, the problem here is the specific designation for these two fossil eschrichtiid specimens was undetermined although they clearly belonged to eschrichtiid mysticetes. The detailed relationship between these two newly-discovered specimens and modern gray whales, *Eschrichtius robustus,* needs further examination focusing on morphological characteristics of juvenile individuals.

CONCLUSIONS

In this study, two fossil specimens were described. After morphological comparisons and phylogenetic analyses, these two partial posterior skulls could be ascertained belonging to eschrichtiid mysticetes. The taxonomic status belonging to modern gray whales or different eschrichtiid species is still an open question till the variation degree among juvenile individual of *Eschrichtius robustus* could be elucidate thoroughly to decipher the difference between two fossil specimens and modern gray whales. The phylogenetic analyses further confirm the relationship between Eschrichtiidae and Cetotheriidae which could be regarded as a superfamily, Cetotherioidea. This result and other recent studies (Bisconti, 2007, 2008, 2010; Steeman, 2007; Bosselaers and Post, 2010) resurrected the viewpoint that eschrichtiids are more closely related to cetotheres than other mysticetes proposed by early researchers (Andrews, 1914; Winge, 1921; Miller, 1923; Kellogg, 1928).

The presence of two juvenile fossil eschrichtiid specimens in the Late Pleistocene from the Penghu Channel shows that the migration route and behavior and calving ground of eschrichtiid mysticetes along the western north Pacific coast possibly could be unravelled when paleo-environment data become accessible.

REFERENCES

Andrews, R. C. 1914. Monographs of the Pacific Cetacea. I. The California gray whale (*Rhachianectes glaucus* Cope). Its history, habits, external anatomy, osteology and relationships. Memoirs of the American Museum of Natural History 1: 227-287.

Arnason, U., S. Gretarsdottir and B. Widegren. 1992. Mysticete (baleen whale) relationships based upon the sequence of the common cetacean DNA satellite. Molecular Biology and Evolution, 9: 1018-1028.

Barnes, L. G. 1976. Outline of eastern North Pacific fossil cetacean assemblages. Systematic Zoology 25: 321-343.

Barnes, L. G. and S. A. McLeod. 1984. The fossil record and phyletic relationships of gray whales. p. 3-32. *In* M. L. Jones, S. L. Swartz, and S. Leatherwood (eds), The Gray Whale: *Eschrichtius robustus*. Academic Press.

Bisconti, M. 2005. Skull morphology and phylogenetic relationships of a new diminutive balaenid from the Lower Pliocene of Belgium. Palaeontology 48: 793-816.

Bisconti, M. 2007a. Taxonomic revision and phylogenetic relationships of the rorqual-like mysticete from the Pliocene of Mount Pulgnasco, northern

Italy (Mammalia, Cetacea: Mysticeti). Palaeontographia Italica 91: 85-108.

Bisconti, M. 2007b. A new basal balaenopterid whale from the Pliocene of northern Italy. Palaeontology 50: 1103-1122.

Bisconti, M. 2008. Morphology and phylogenetic relationships of a new eschrichtiid genus (Cetacea: Mysticeti) from the Early Pliocene of northern Italy. Zoological Journal of the Linnean Society 153: 161-186.

Bisconti, M. 2010. A new balaenopterid whale from the Late Miocene of the Stirone River, northern Italy (Mammalia: Cetacea: Mysticeti). Journal of Vertebrate Paleontology 30: 943-958.

Bisconti, M. and A. Varola. 2006. The oldest eschrichtiid mysticete and a new morphological diagnosis of Eschrichtiidae (gray whales). Rivista Italiana Di Paleontologia E Stratigrafia 112: 447-457.

Bosselaers, M. and K. Post. 2010. A new fossil rorqual (Mammalia: Cetacea: Balaenopteridae) from the Early Pliocene of the North Sea, with a review of the rorqual species described by Owen and Van Beneden. Geodiversitas 32: 331-363.

Bouetel, V. and C. de Muizon. 2006. The anatomy and relationships of *Piscobalaena nana* (Cetacea: Mysticeti), a Cetotheriidae s.s. from the Early Pliocene of Peru. Geodiversitas 28: 319-395.

Bowers, S. 1889. An abstract of a letter regarding the finding of the remains of fossil vertebrates in Ventura, California. American Geologist 4: 391-392.

Brandt, J. F. 1873. Untersuchungen über die fossilen und subfossilen cetaceen Europa's. Mémoires de L'Académie Impériale des Sciences de Saint-Petersbourg, Series 7, 20: 1-372.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795-803.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295-304.

Chang C. H. 1996. The first fossil record of a short-finned pilot whale (*Globicephala macrorhynchus*) from the Penghu Channel. Bulletin of National Museum of Natural Science 7: 73-80.

Chang, C. H. and Y. N. Cheng. 1998. Extraordinary fossil records of Cetacea from Pleistocene in Taiwan. The Ryukyu Islands Symposium 26, p. 85.

Chiu, H. T. 1972. Occurrence of whale bone fossils in Taiwan. Acta Geologica Taiwan 15: 23-26.

Cope, E. D. 1867. Descriptions of *Eschrichtius cephalus, Rhabdosteus latiradix, Squalodon atlanticus,* and *S. mento.* Proceedings of the Academy of Natural Science of Philadelphia 19: 131-132.

Cope, E. D. 1868a. Second contribution to the history of the Vertebrata of the Miocene period of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 184-194.

Cope, E. D. 1868b. An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 19: 138-157.

Cope, E. D. 1868c. Extinct Cetacea from the Miocene bed of Maryland. Proceedings of the Academy of Natural Sciences Philadelphia 20: 159-160.

Cope, E. D. 1869. Third contribution to the fauna of the Miocene period of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 21: 6-13.

Cope, E. D. 1870a. Remarks on *Eschrichtius polyporus, Hypsibema crassicauda, Hadrosaurus tripos,* and *Polydectes biturgidus.* Proceedings of the Academy of Natural Sciences of Philadelphia 21: 191-192.

Cope, E. D. 1870b. Fourth contribution to the history of the fauna of the Miocene and Eocene periods of the United States. Proceedings of the American Philosophical Society 11: 285-294.

Cope, E. D. 1872. On an extinct whale from California. Proceedings of the Academy of Natural Sciences of Philadelphia 24: 29-30.

Cope, E. D. 1875. Synopsis of the vertebrata whose remains have been preserved in the formations of North Carolina. p. 29-52. *in* W. C. Kerr, Report of the Geological Survey of North Carolina. Josiah Turner, Raleigh.

Cope, E. D. 1890. The Cetacea. American Naturalist 24: 597-616.

Cope, E. D. 1895. Fourth contribution to the marine fauna of the Miocene period of the United States. Proceedings of the American Philosophical Society 34: 135-155.

Cope, E. D. 1895. The phylogeny of the whalebone whales. American Naturalist 29: 572-573.

Demere, T. A. 1983. The Neogene San Diego Basin: a review of the marine Pliocene San Diego Formation. p. 187-195. *in* D. K. Larue and R. J. Steel, (eds), Cenozoic Marine Sedimentation, Pacific Margin, U. S. A. Society of Economic Paleontologists and Mineralogists, Pacific Section. Los Angeles, California.

Demere, T. A. 1986. The fossil whale, Balaenoptera davidsonii (Cope 1872), with a review of other Neogene species of Balaenoptera (Cetacea: Mysticeti). Marine Mammal Science 2: 277-298.

Demere, T. A. and A. Berta. 2008. Skull anatomy of the Oligocene toothed mysticete *Aetiocetus weltoni* (Mammalia: Cetacea): implications for mysticete evolution and functional anatomy. Zoological Journal of the Linnean Society 154: 308-352.

Demere, T. A., A. Berta and M. R. McGowen. 2005. The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. Journal of Mammalian Evolution 12: 99-143.

Domning, D. P. and T. A. Demere. 1984. New material of *Hydrodamalis cuestae* (Mammalia: Dugongidae) from the Miocene and Pliocene of San Diego County, California. Transactions of the San Diego Society of Natural History 20: 169-188.

Dooley, A. J., N. C. Fraser and Z. X. Luo. 2004. The earliest known member of the rorqual -- Gray whale clade (Mammalia: Cetacea). Journal of Vertebrate Paleontology 24: 453-463.

Efron, B. 1979. Bootstrap methods: Another look at the jackknife. The Annals of Statistics 7: 1-26.

Eichwald, C. E. 1840. Beschreibung einiger Knochen des *Ziphius priscus.* Die Urwelt Russlands 2: 25-53.

Emmons, E. 1858. Palaeontology. Report of the North Carolina Geological Survey 15: 193-212.

Evans, H. E. (1993). Miller's Anatomy of the Dog. Third ed., W. B. Saunders, Philadelphia.

Farris, J. S., V. A. Albert, M. K. Allersjo, D. Lipscomb, and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99-124.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783-791.

Fitzgerald, E. M. G. 2006. A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. Proceedings of the Royal Society B: Biological Sciences 273: 2955-2963.

Fordyce, R. E. 2002. *Simocetus rayi* (Odontoceti, Simocetidae, new family); a bizarre new archaic Oligocene dolphin from the eastern North Pacific. Smithsonian Contributions to Paleobiology. 93: 185-222.

Fordyce, R. E. 2008. Neoceti. p. 758-763. *In* W. F. Perrin, B. G. Wursig, and J. G. M. Thewissen (eds), Encyclopedia of Marine Mammals. Academic Press.

Fordyce, R. E. and C. de Muizon. 2001. Evolutionary history of cetaceans: a review. p. 169-223. *In* J. M. Mazin and V de Buffr'enil (eds), Secondary Adaptation of Tetrapods to Life in Water. M¨unchen, Germany: Verlag Dr. Friedrich Pfeil

Geisler, J. H. and Z. X. Luo. 1996. The petrosal and inner ear of *Herpetocetus* sp. (Mammalia: Cetacean) and their implications for the phylogeny and hearing of archaic mysticetes. Journal of Paleontology 70: 1045-1066.

Geisler, J. H. and A. E. Sanders. 2003. Morphological evidence for the phylogeny of Cetacea. Journal of Mammalian Evolution 10: 23-129.

Gillette, D. D. 1975. Catalogue of the type specimens of fossil vertebrates, Academy of Natural Sciences, Philadelphia. Introduction and Part 1: Marine mammals. Proceedings of the Academy of Natural Sciences of Philadelphia 127: 63-66.

Ho, C. K., G. Q. Qi, and C. H. Chang. 1997. A preliminary study of late Pleistocene carnivore fossil from the Penghu Channel, Taiwan. Annual of Taiwan Museum 40: 195-224.

Ho, C. K., G. Q. Qi, and C. H. Chang. 2008. A preliminary study of late Pleistocene megafauna *Cervus* sp. from the Penghu Channel, Taiwan. Journal of the National Taiwan Museum 61: 1-16.

Ho, C. K., G. Q. Qi, and C. H. Chang. 2010. A preliminary study of late Pleistocene megafauna *Equus* sp. from the Penghu Channel, Taiwan. Journal of the National Taiwan Museum 63: 85-104.

Huang, T. Y. 1965. A new species of a whale tympanic bone from Taiwan, China. Transactions and Proceedings of the Palaeontological Society of Japan 61: 183-187.

Huang, T. Y. 1976. Second discovery of a whale tympanic bone from Taiwan, China. Petroleum Geology of Taiwan 13: 193-199.

Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754-755.

Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and J. P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294: 2310-2314.

Ichishima, H., E. Sato, T. Sagayama and M. Kimura. 2006. The oldest record of Eschrichtiidae (Cetacea: Mysticeti) from the Late Pliocene, Hokkaido, Japan. Journal of Paleontology 80: 367-379.

Jones, M. L. and S. L. Swartz. 2008. Gray whale, *Eschrichtius robustus.* p. 503-511. *In* W. F. Perrin, B. G. Wursig, and J. G. M. Thewissen (eds), Encyclopedia of Marine Mammals. Academic Press.

Kao, C. W. 1982. The Penghu fauna. Journal of Marine Science 27: 123-132. (in Chinese, with English abstract)

Kazár, E. and D. J. Bohaska. 2008. Toothed whale (Mammalia: Cetacea: Odontoceti) limb bones of the Lee Creek mine, North Carolina. Virginia Museum of Natural History Museum Special Publication 14: 271-324.

Kellogg, R. 1928. The history of whales - their adaptation to life in the water. The Quarter Review of Biology 3: 174-208.

Kellogg, R. 1968. Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia. 5. Miocene Calvert mysticetes described by Cope. Bulletin of the United States National Museum 247: 103-132.

Kimura, M. 1992. The study of the fossil whale from Shintotsukawa Town. Koukoku Press, Sapporo, 56 p. (In Japanese)

Kimura, T. and Y. Hasegawa. 2010. A new baleen whale (Mysticeti: Cetotheriidae) from the earliest Late Miocene of Japan and a reconsideration of the phylogeny of cetotheres. Journal of Vertebrate Paleontology 30: 577-591.

Kimura, T. and T. Ozawa. 2002. A new cetothere (Cetacea: Mysticeti) from the Early Miocene of Japan. Journal of Vertebrate Paleontology 22: 684-702.

Leidy, J. 1851. Descriptions of two fossil species of *Balaena, B. palaeatlantica* and *B. prisca.* Proceedings of the Academy of Natural Sciences of Philadelphia 5: 308-309.

Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Journal of the Academy of Natural Sciences, Philadelphia 2: 1-472.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50: 913-925.

Madison, W. P. and D. R. Madison. 2003. MacClade 4: Analysis of phylogeny and character evolution. Version 4.06 Sunderland, MA Sinauer Associates.

Marx, F. G. 2011. The More the Merrier? A Large Cladistic Analysis of Mysticetes, and Comments on the Transition from Teeth to Baleen. Journal of Mammalian Evolution 18: 77-100.

Mchedlidze, G. A. 1984. Fossilized whale from the Miocene deposits in the environs of the village of Otradnaya (Northern Caucasus). Metsniereba Press, Tbilisi.

Meng, C. Y. 1961. The first well preserved fossil bones discovered from Taiwan. Shih Yu Tung Hsin 120: 2-4. (in Chinese)

Milinkovitch, M. C., G. Orti, and A. Meyer. 1993. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. Nature 361: 346-348.

Milinkovitch, M. C., A. Meyer, and J. R. Powell. 1994. Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. Molecular Biology and Evolution 11: 939-948.

Miller, G. S. 1923. The telescoping of the cetacean skull. Smithsonian Miscellaneous Collections 76: 1-70.

Mitchell, E. D. 1989. A new cetacean from the late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. Canadian Journal of Fisheries and Aquatic Sciences 46: 2219-2235.

Nikaido, M., F. Matsuno, H. Hamilton, R. L. Brownel, Y. Cao, W. Ding, Z. Zuoyan, A. M. Shedlock, R. E. Fordyce, M. Hasegawa, and N. Okada. 2001. Retroposon analysis of major cetacean lineages: the monophyly of toothed whales and the paraphyly of river dolphins. Proceedings of the National Academy of Sciences 98: 7384-7389.

Norell, M. A. and M. J. Novacek. 1992. The fossil record and evolution: comparing cladistic and paleontological evidence for vertebrate history. Science 255: 1690-1693.

Oishi, M., H. Fujii, and S. Tagusari. 2001. Pliocene cetaceans from Shiriuchimachi, Hachinohe City, Northeast Japan (Part. 2). Research Report of the “Fossil Hachinohe Whales”. 2: 7-22. Hachinohe Children’s Science Museum.

Peng, F., Y. Ye, G. Pan, and X. Qi. 2003. Major features of topography, geology, and crustal stability in the Taiwan Strait: A scientific approach to the problem of the Taiwan Strait Tunnel Project. Marine Georesources and Geotechnology, 21: 121-138.

Portis, A. 1885. Catalogo descrittivo dei Talassoterii rinvenuti nei terreni terziari del Piemonte e della Liguria. Memorie della Reale Accademia della Scienze di Torino 37: 247-365.

Rannala, B. and Z. Yang. 1996. Probability distribution of molecular evolutionary trees: A new method of phylogenetic inference. Journal of Molecular Evolution 43: 304-311.

Repenning, C. A. 1983. New evidence for the age of the Gubik Formation Alaskan North Slope. Quaternary Research 19: 356-372.

Roth, F. 1978. *Mesocetus argillarius* sp. n. (Cetacea, Mysticeti) from Upper Miocene of Denmark, with remarks on the lower jaw and echolocation system in whale phylogeny. Zoologica Scripta 7: 63-79.

Sanders, A. E. and L. G. Barnes. 2002. Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 3: Eomysticetidae, a new family of primitive mysticetes (Mammalia: Cetacea). Smithsonian Contributions to Paleontology 93: 313-356.

Sasaki T., M. Nikaido, S. Wada, T. K. Yamada, Y. Cao, M. Hasegawa, and N. Okada. 2006. Balaenoptera omurai is a newly discovered baleen whale that represents an ancient evolutionary lineage. Molecular Phylogenetic and Evolution 41:40–52.

Schulte, H. von W., and Smith, M. de F. (1918). The external characters, skeletal muscles, and peripheral nerves of *Kogia breviceps* (Blainville). Bulletin of the American Museum of Natural History 38: 7–72.

Shikama, T., H. Otsuka, and Y. Tomida. 1975. Fossil Proboscidea from Taiwan. Science Reports of the Yokohama National University. Section II, Biological and Geological Sciences, 22: 13-62.

Steeman, M. E. 2007. Cladistic analysis and a revised classification of fossil and recent mysticetes. Zoological Journal of the Linnean Society 150: 875-894.

Sumich, J. L., T. Goff, and W. L. Perryman. 2001. Growth of two captive gray whale calves. Aquatic Mammals 27: 231-233.

Swofford, D. L. 2002. PAUP. Phylogenetic Analysis Using Parsimony. Sinauer Associates, Sunderland, Massachusetts.

Tan, K. 1937. Notes on the remains of fossil Delphinidae from two different localities in Taiwan. Taiwan Tigaku Kizi 8: 92-95.

Thompson, D. W. 1890. On the systematic position of zeuglodon. Studies from the Museum of Zoology 9: 1-8.

Tseng Z. J. and C. H. Chang. 2007. A study of new material of *Crocuta crocuta ultima* (Carnivore: Hyaenidae) from the Quaternary of Taiwan. Collection and Research 20: 9-19.

Uhen, M. D. 2004. Form, function and anatomy of *Dorudon atrox* (Mammalia: Cetacea): An archaeocete from the middle to late Eocene of Egypt. University of Michigan Papers on Paleontology 34: 1-222.

Uhen, M. D. 2010. The origin of whales. The Annual Review of Earth and Planetary Science 38: 189-219.

Uhen, M. D. 2011. Cetacea: Online Systematics Archive 9. http://www.paleodb.org/cgi-bin/bridge.pl?user= Guest&action=displayPage&page=OSA_9_Cetacea

Wada S, Oishi M, Yamada TK (2003) A newly discovered species of living baleen whale. Nature 426:278–281

Whitmore, F. C. and J. A. Kaltenbach. 2008. Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. Virginia Museum of Natural History Special Publication 14: 181-269.

Winge, H. 1921. A review of the interrelationships of Cetacea. Smithsonian Miscellaneous Collections 72: 1-97.

Weems, R. E. and L. E. Edwards. 2007. The age and provenance of '*Eschrichtius*' *cephalus* Cope (Mammalia: Cetacea). Journal of Vertebrate Paleontology 27: 752-756.

Xiong, Y., M. C. Brandley, S. Xu, K. Zhou, and G. Yang. 2009. Seven new dolphin mitochondrial genomes and a time-calibrated phylogeny of whales. BMC Evolutionary Biology 9: 20.

Yablokov, A. 1964. Convergence or parallelism in the evolution of cetaceans. International Geology Review 7: 1461-1468.

LIST OF FIGURES

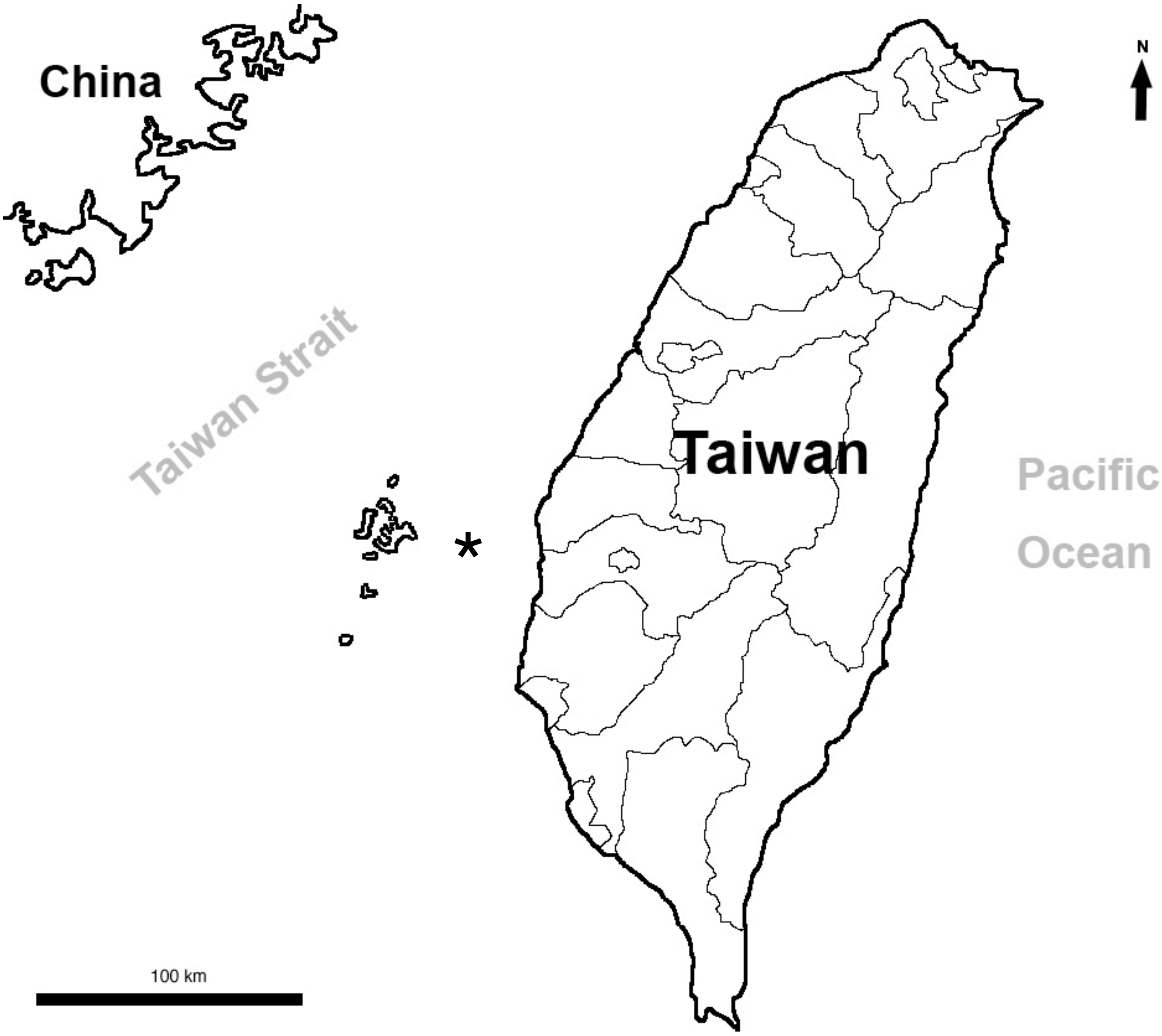


Figure 1. Sign * indicates the locality of two newly-discovered eschrichtiid specimens.

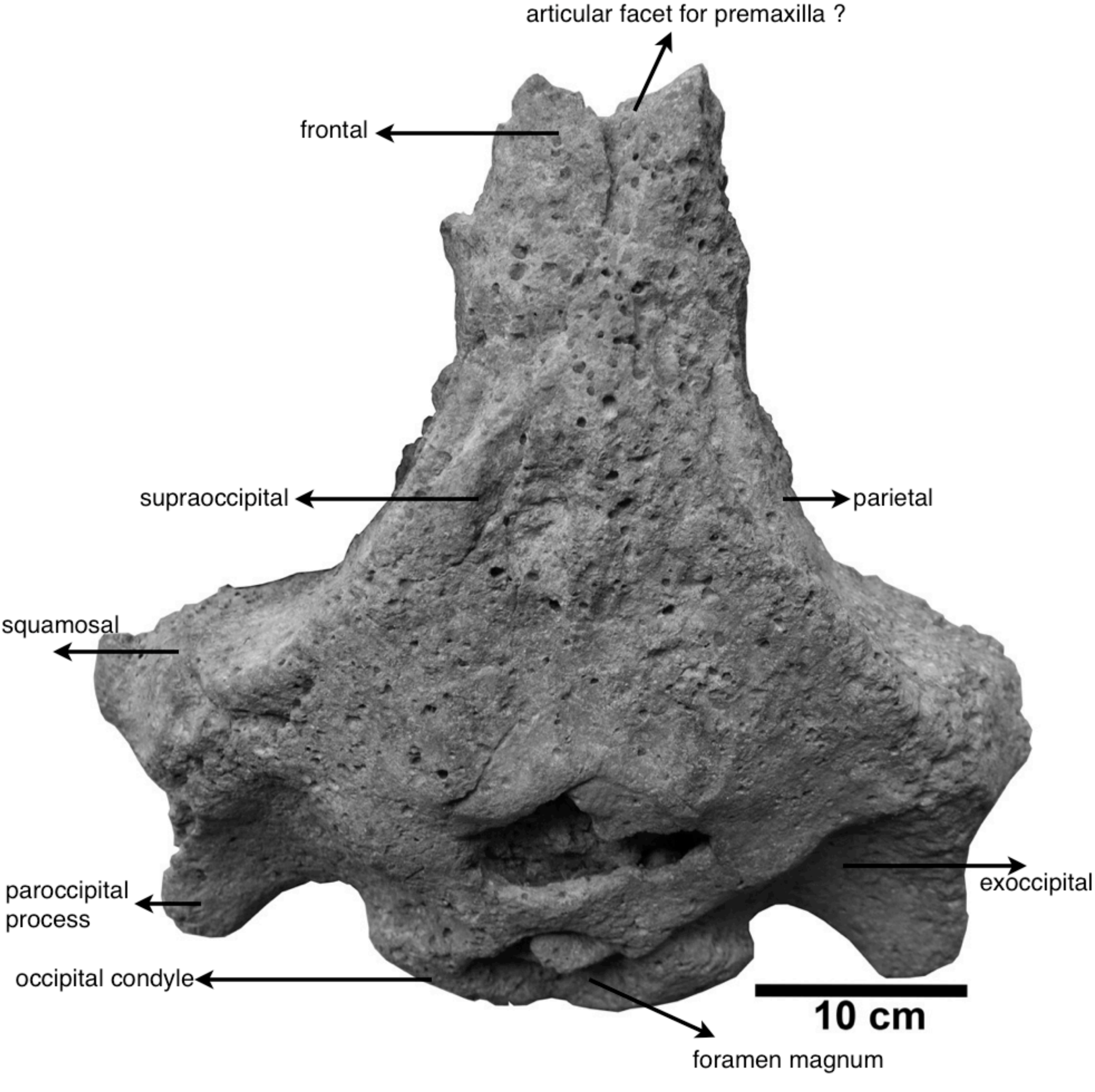


Figure 2. Dorsal view of NMNS-F051728

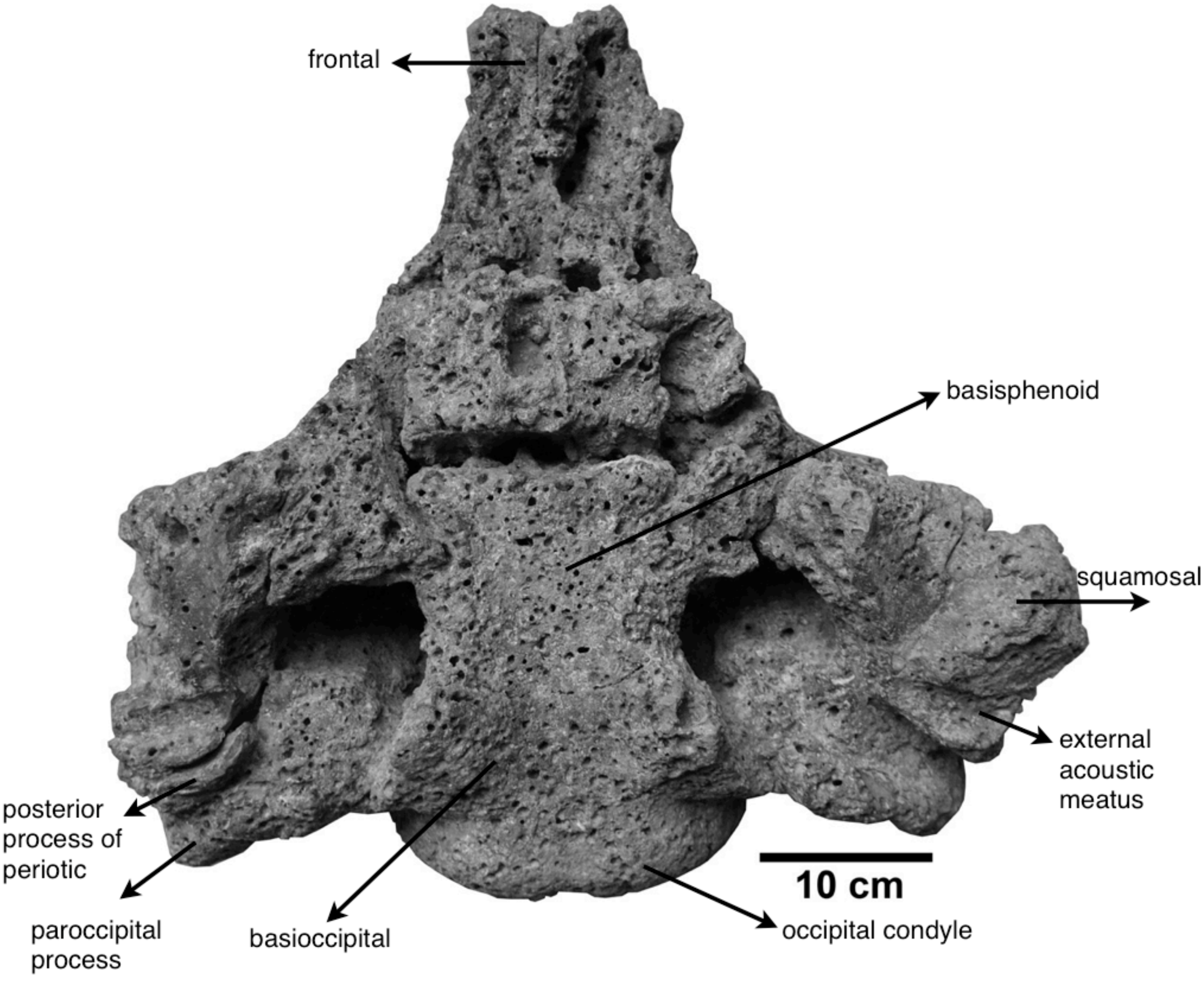


Figure 3. Ventral view of NMNS-F051728

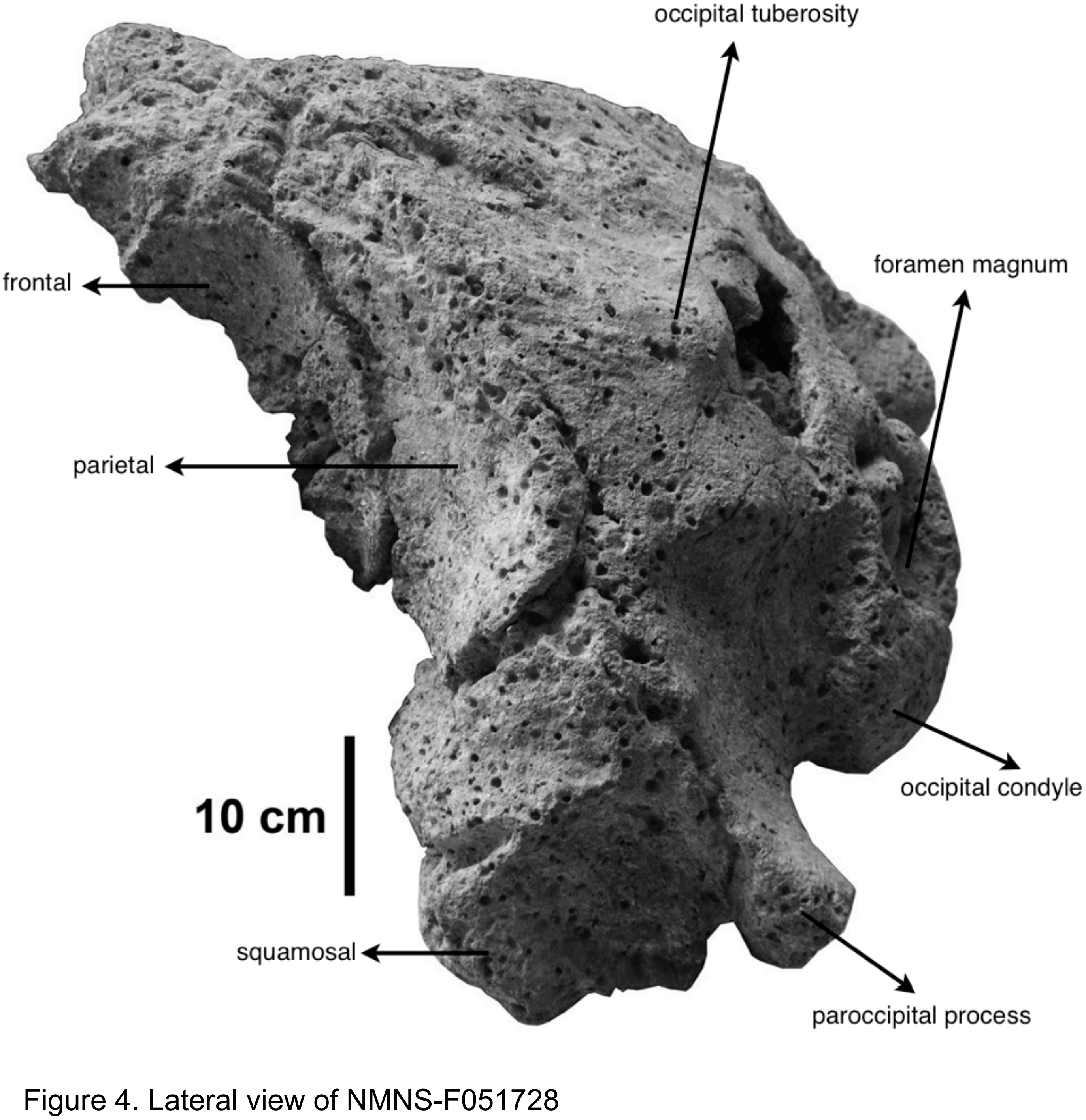


Figure 4. Lateral view of NMNS-F051728

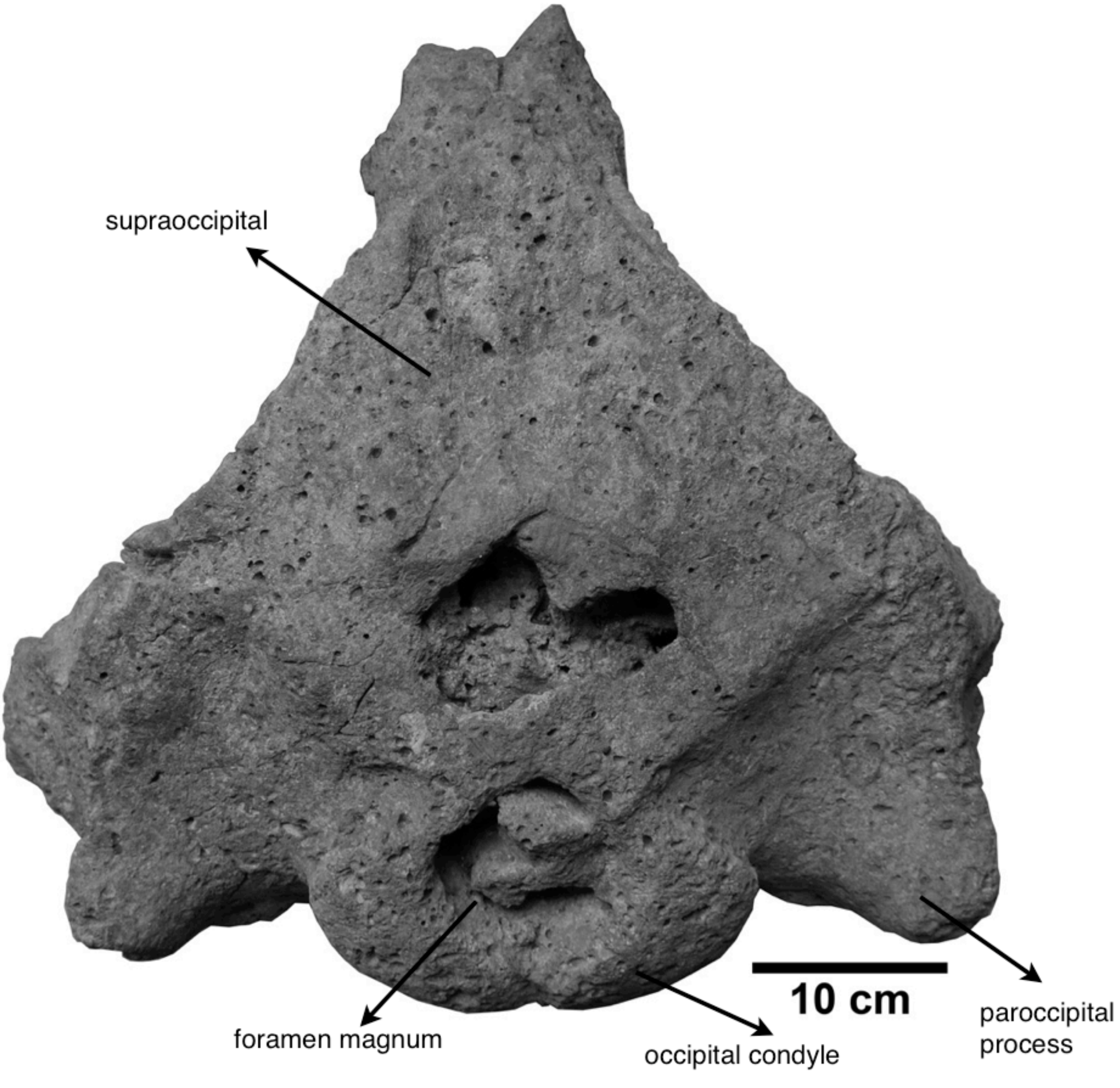


Figure 5. Posterior view of NMNS-F051728

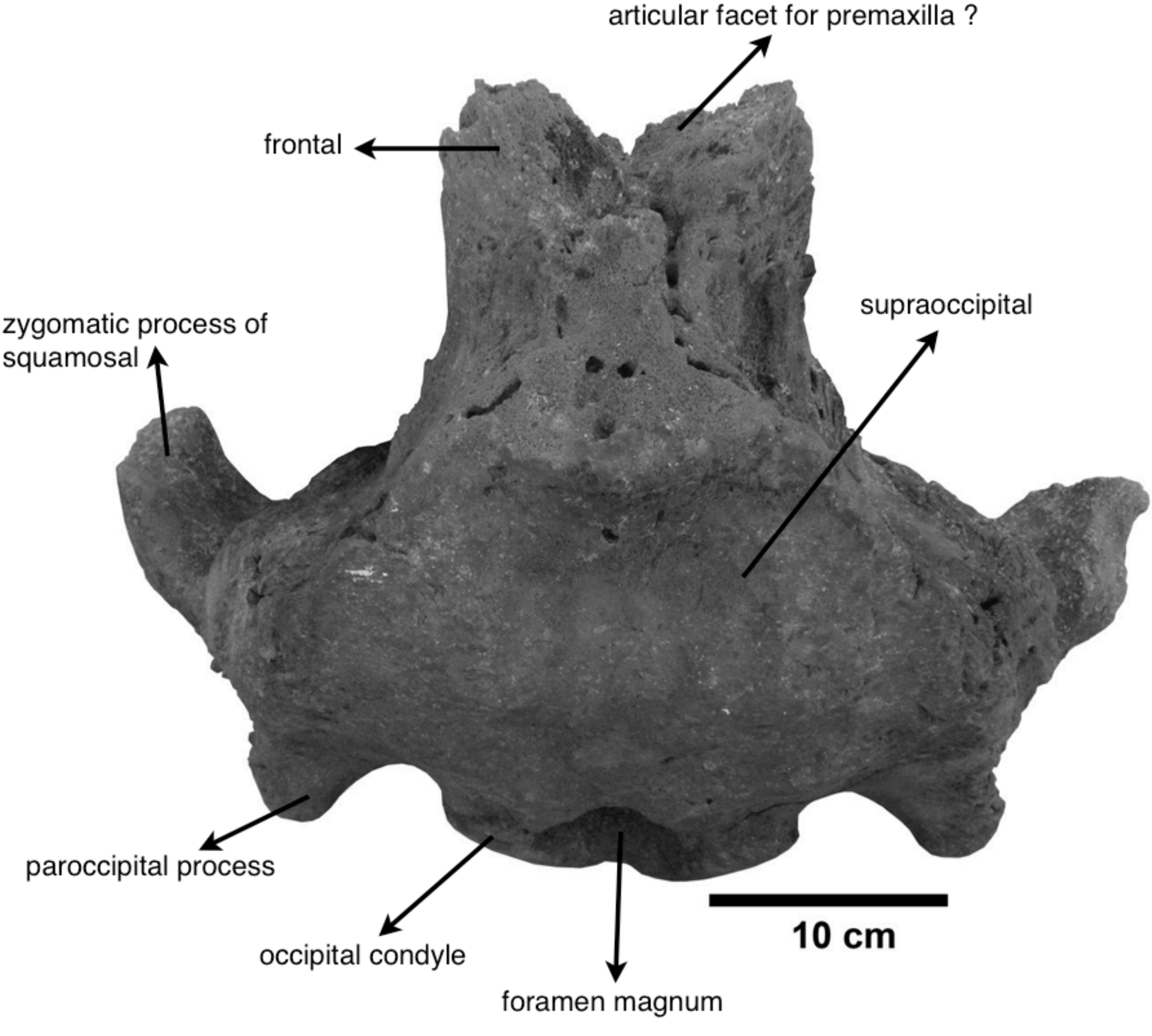


Figure 6. Dorsal view of LFMM-W-001

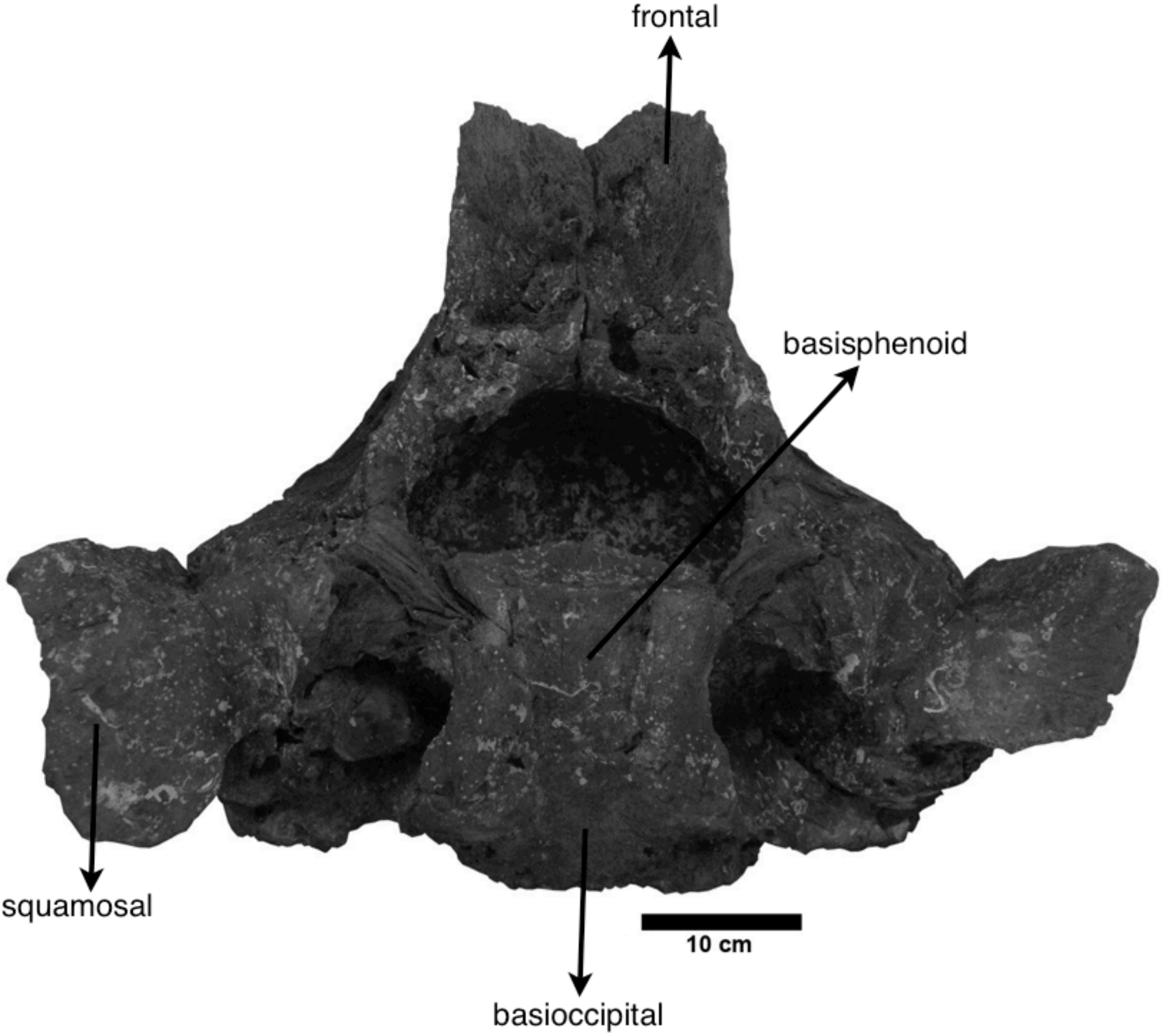


Figure 7. Ventral view of LFMM-W-001

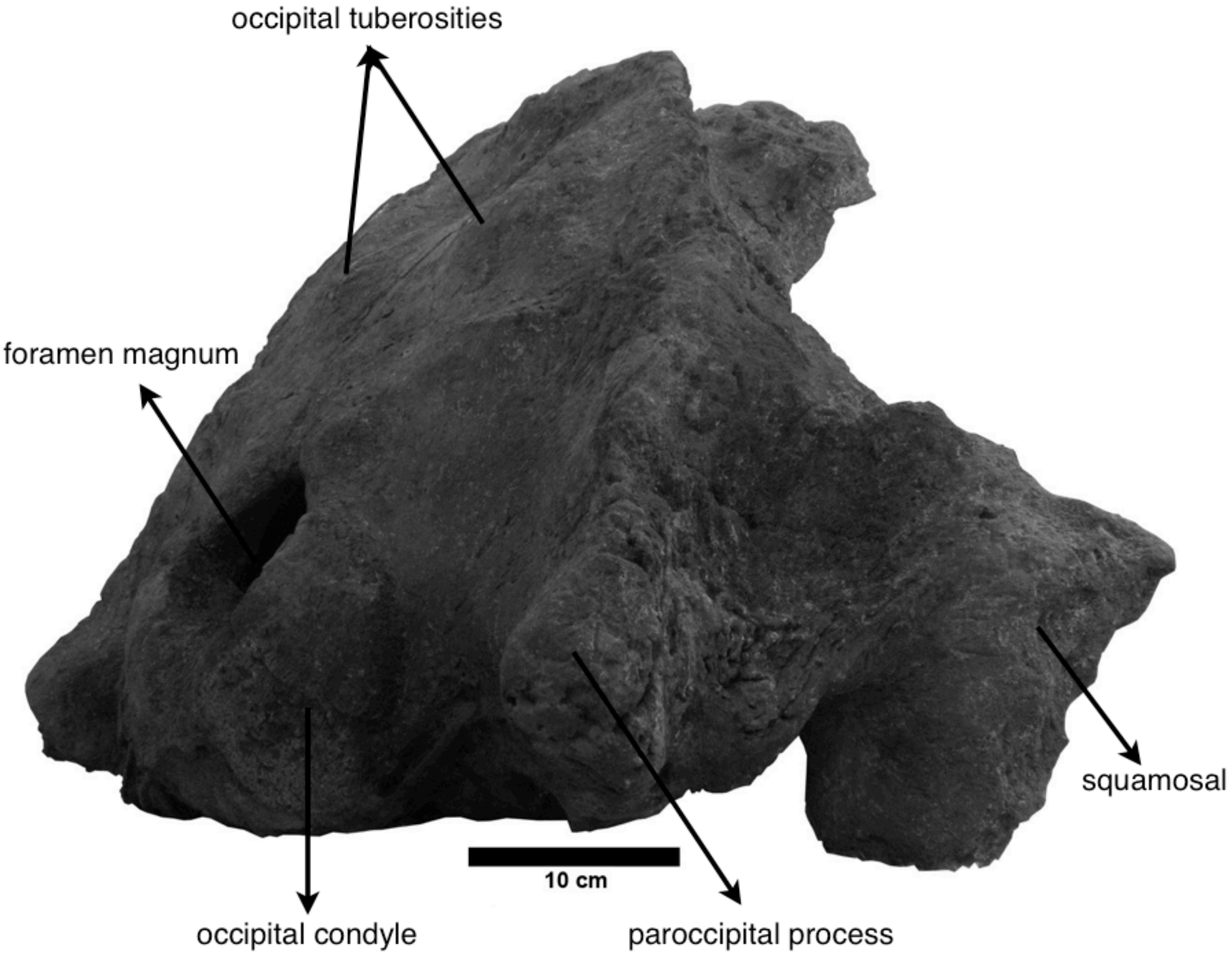


Figure 8. Lateral view of LFMM-W-001

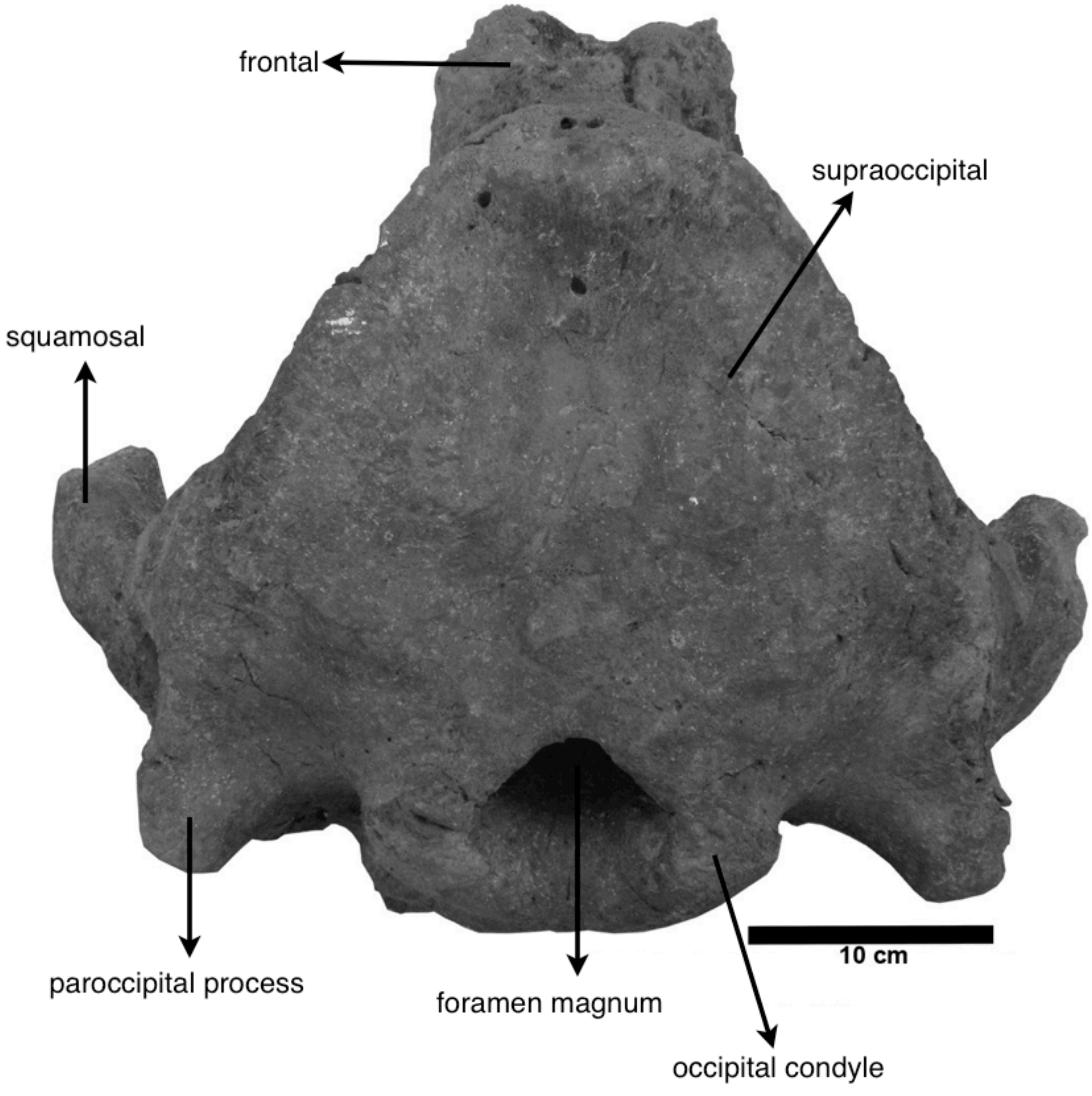


Figure 9. Posterior view of LFMM-W-001

Figure 10. Fifty percent majority rule consensus tree of the parsimony analysis by PAUP. Left numbers indicate the frequency of occurrence of the respective node; right numbers are bootstrap values.

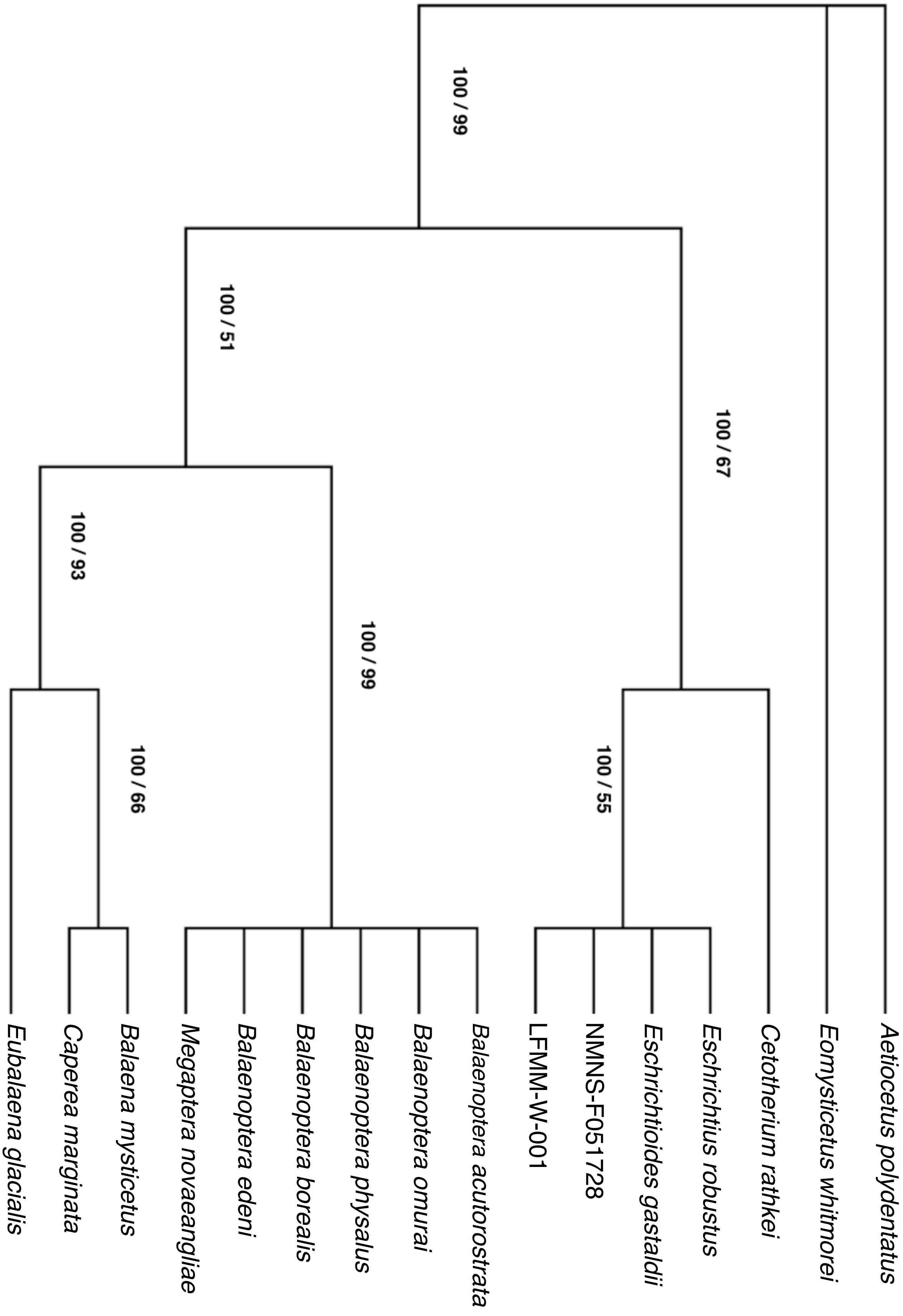

Aetiocetus polydentatus
Eomysticetus whitmorei
Cetotherium rathkei
Eschrichtius robustus
Eschrichtioides gastaldii
NMNS-F051728
LFMM-W-001
Balaenoptera acutorostrata
Balaenoptera omurai
Balaenoptera physalus
Balaenoptera borealis
Balaenoptera edeni
Megaptera novaeangliae
Balaena mysticetus
Caperea marginata
Eubalaena glacialis
100 / 99
100 / 51
100 / 67
100 / 93
100 / 99
100 / 66
100 / 55

Figure 11. Bayesian tree with posterior probability value.

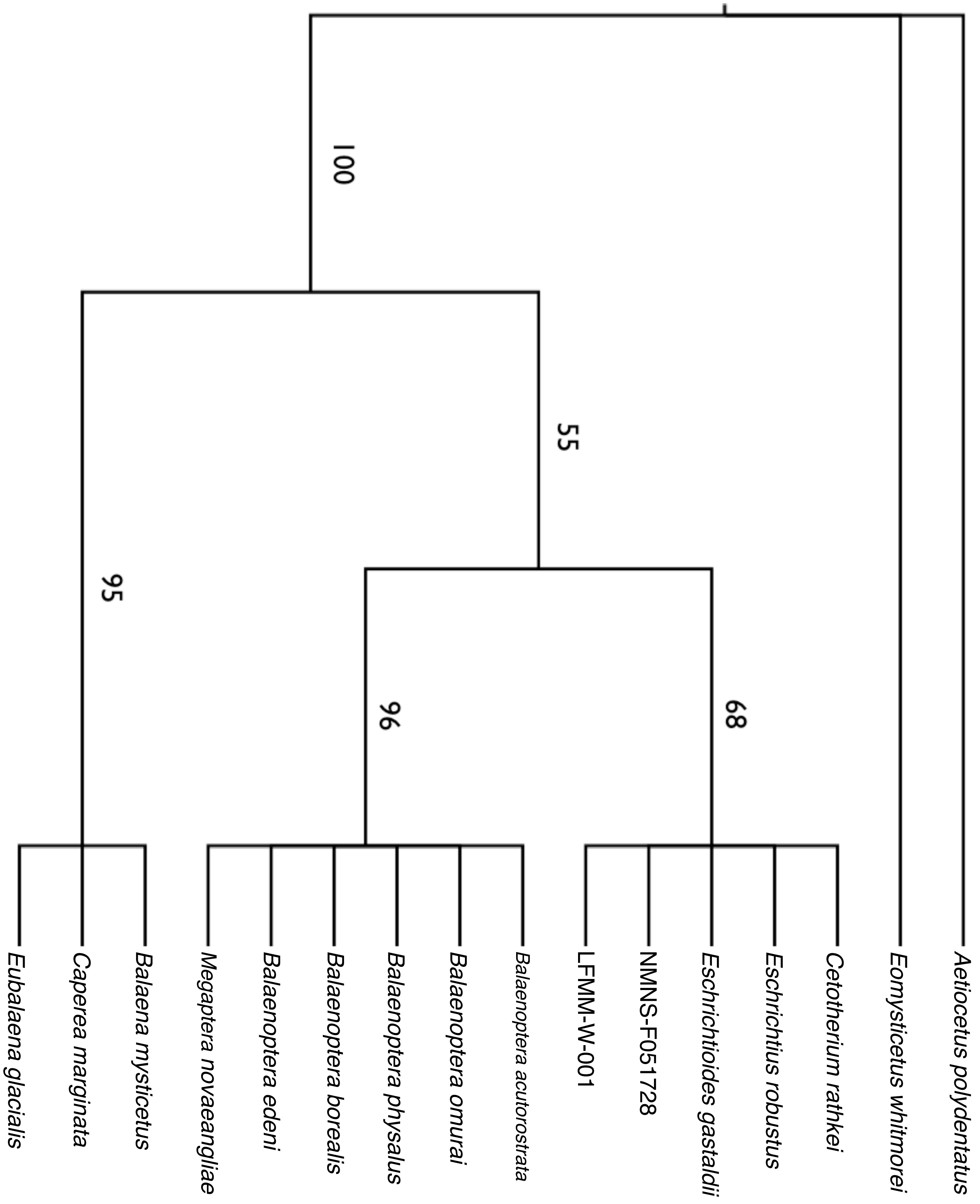
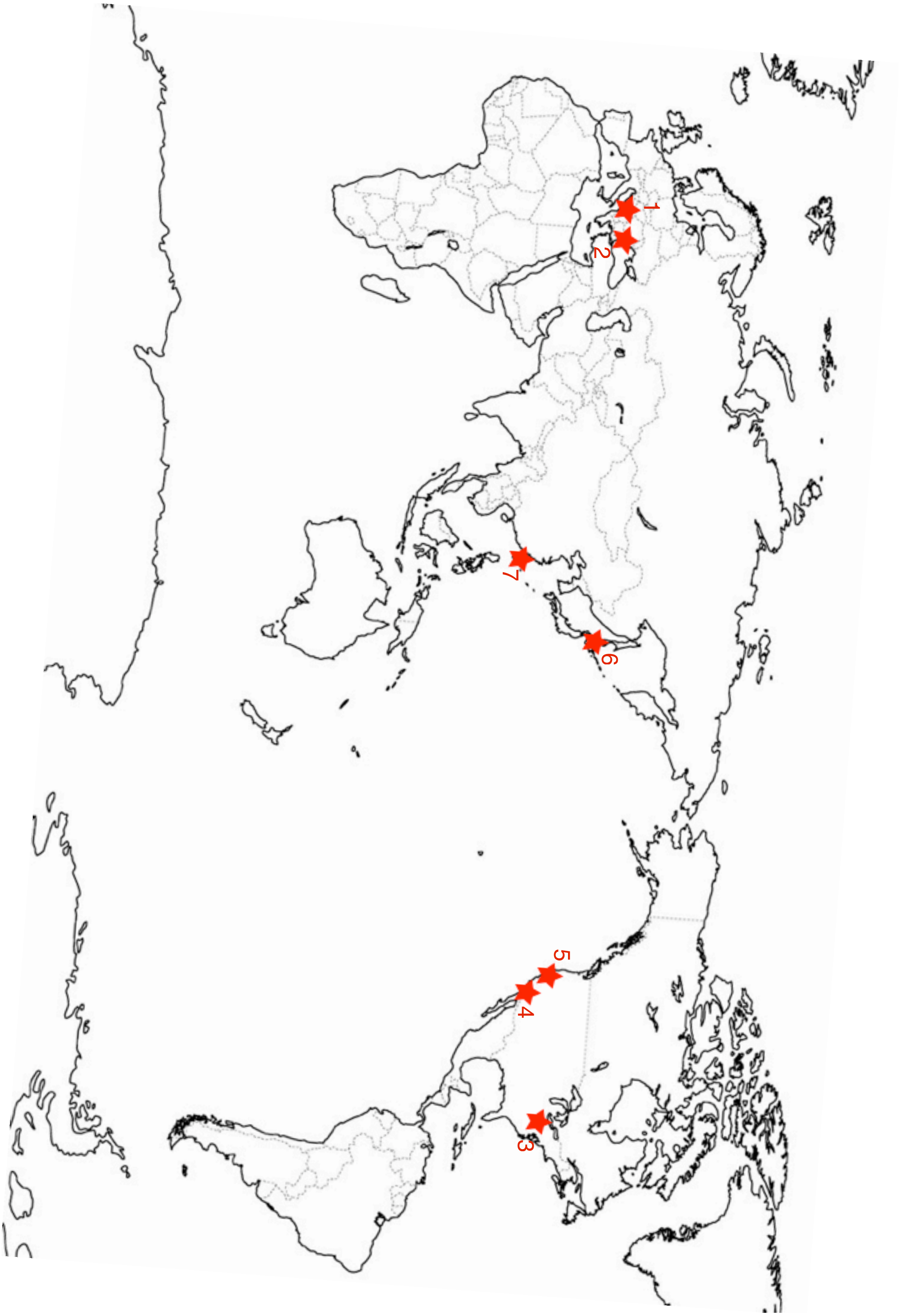

Aetiocetus polydentatus
Eomysticetus whitmorei
Cetotherium rathkei
Eschrichtius robustus
Eschrichtioides gastaldii
NMNS-F051728
LFMM-W-001
Balaenoptera acutorostrata
Balaenoptera omurai
Balaenoptera physalus
Balaenoptera borealis
Balaenoptera edeni
Megaptera novaeangliae
Balaena mysticetus
Caperea marginata
Eubalaena glacialis
100
55
68
96
95

Figure 12. Distribution of fossil Eschrichtiidae. Star sign indicates the locality of fossil eschrichtiids. Star 1 is *Archaeschrichtius ruggieroi* Bisconti and Varola, 2006; star 2 *Eschrichtioides gastaldii* Bisconti, 2008; star 3 *Gricetoides aurorae* Whitmore and Kaltenbach, 2008; star 4 unnamed species; star 5 and 6 *Eschrichtius;* and star 7 Taiwan specimens. The next figure outlines the possible living period of these specimens.



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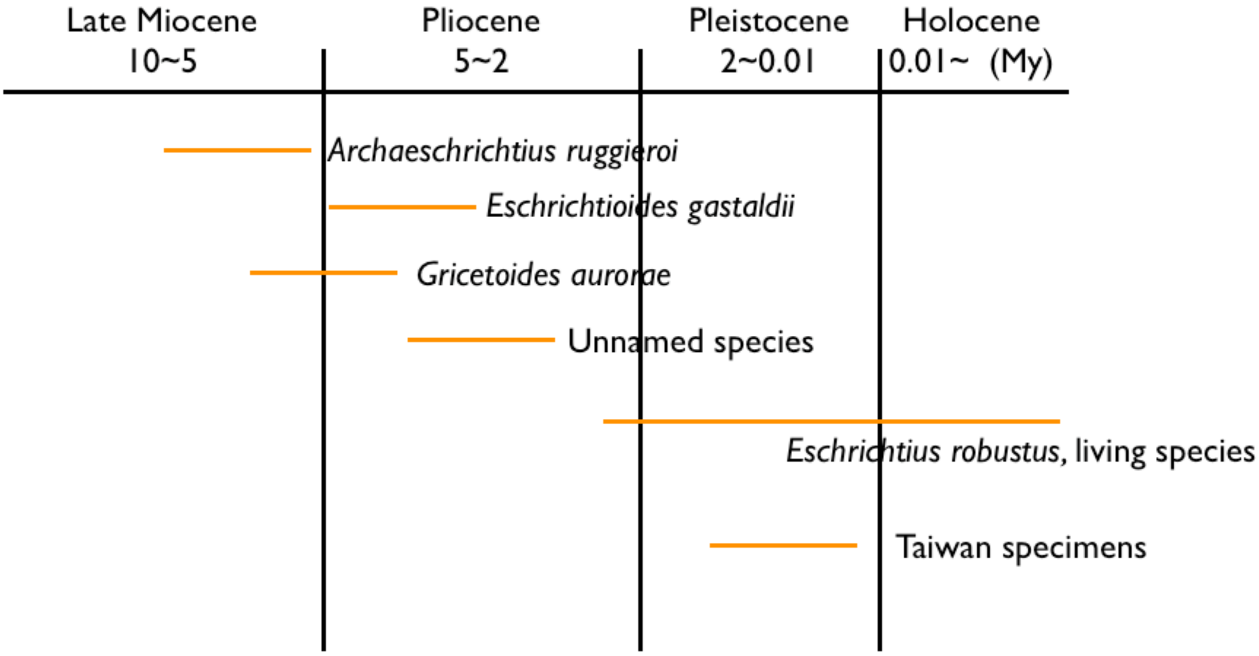

Figure 13. The possible living period of eschrichtiids.

TABLE

Table 1. Measurements of NMNS-F051728 and LFMM-W-001

Skull	**NMNS-F051728**	**LFMM-W-001**	**HMT-F-1**
Total length of skull preserved	556	437	528
Width across zygomatic processes of squamosals (at base)	557 (broken)	594.5	646
Minimum width, intertemporal constriction	122	149.2	104
Vertical external height of braincase, from midline of basisphenoid to summit of supraoccipital	372	208.5	334
Distance from dorsal margin of foramen magnum to anterior apex of supraoccipital	333	277.5	370
Width across paroccipital processes	481	439.5	540
Transverse distance between outer margins of occipital condyle	217	208.1	240

Table 1. Measurements of NMNS-F051728 and LFMM-W-001 and the specimen discovered from Teshio Township, Hokkaido, Japan for comparison.

APPENDIX

Appendix 1. Taxon and Character Coding

Appendix 2. Character List

Appendix 1. Taxon and Character Coding

Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Aetiocetus polydentatus	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0
Eomysticetus whitmorei	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	1	0
Cetotherium rathkei	0	1	0	1	0	0	1	0	0	0	1	1	1	1	0	0	1	1	1	2
Balaenoptera acutorostrata	4	2	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	2	1	2
Balaenoptera omurai	4	2	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	2	1	2
Balaenoptera physalus	4	2	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	2	1	2
Balaenoptera borealis	4	2	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	2	1	2
Balaenoptera edeni	4	2	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	2	1	2
Megaptera novaeangliae	2	2	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	2	1	2
Balaena mysticetus	0	3	0	0	0	1	1	2	0	0	0	0	0	1	2	1	0	2	2	1
Eubalaena glacialis	3	3	1	0	0	0	1	2	0	0	0	0	0	0	2	1	0	2	2	1
Caperea marginata	2	3	0	0	0	1	1	2	0	0	0	0	0	1	1	0	0	2	2	1
Eschrichtius robustus	0	0	0	3	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	2
Eschrichtioides gastaldii	2	1	0	2	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	0
NMNS-F051728	1	1	0	3	0	0	1	1	1	0	0	1	1	1	?	0	1	1	1	2
LFMM-W-001	4	0	0	3	0	0	1	1	1	0	0	1	1	1	?	0	1	1	1	2

Taxa	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**
Aetiocetus polydentatus	0	0	0	0	0	0	0	1	0	0	0	0	?	0	?	0
Eomysticetus whitmorei	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	0
Cetotherium rathkei	1	0	2	0	1	1	2	0	1	0	0	0	?	?	?	0
Balaenoptera acutorostrata	1	1	1	2	1	1	2	0	1	1	0	0	0	?	0	1
Balaenoptera omurai	1	1	1	2	1	1	2	1	1	1	0	0	0	?	0	1
Balaenoptera physalus	1	1	1	2	1	1	2	0	1	1	0	0	0	?	0	1
Balaenoptera borealis	1	1	1	2	1	1	2	0	1	1	0	0	0	?	0	1
Balaenoptera edeni	1	1	1	2	1	1	2	0	1	1	0	0	0	?	0	1
Megaptera novaeangliae	1	1	1	2	1	1	2	0	1	1	0	0	0	0	0	1
Balaena mysticetus	1	0	0	1	1	1	1	?	1	1	0	1	0	1	?	0
Eubalaena glacialis	1	0	0	1	1	1	1	2	1	1	0	1	0	0	0	0
Caperea marginata	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0	0
Eschrichtius robustus	1	0	2	1	1	1	2	0	1	0	0	0	0	0	0	0
Eschrichtioides gastaldii	1	0	2	1	1	1	2	?	1	0	0	0	0	?	0	0
NMNS-F051728	1	0	?	1	?	1	2	?	?	0	?	0	1	0	0	0
LFMM-W-001	1	0	?	1	?	1	?	?	?	0	0	0	1	0	0	0

Appendix 2. Character List

1. Anterior tip of supraoccipital:

    0, narrow and squared;

    1, pointed;

    2, narrow and round;

    3, wide and round;

    4, wide and squared. Modified from Bisconti, 2008

2. Anteriormost point of the supraoccipital, in dorsal view:

    0, in transverse line with space between posterior edge of skull and anterior edge of the floor of squamosal fossa;

    1, in line with space between anterior edge of the floor of squamosal fossa and the anterior tip of zygomatic process of squamosal;

    2, in line with supraorbital process of frontal;

    3, in line with or anterior to anterior edge of supraorbital process of frontal. Modified from Geisler and Sanders, 2003

3. Dome on the supraoccipital:

    0, absent;

    1, present. Bisconti, 2008

4. Lateral borders of supraoccipital:

0, continuously convex;

1, sigmoid convexity;

2, continuously concave;

3, straight. Bisconti, 2008

5. Height of the supraoccipital relatively to the frontals and/or nasals:

0, at same level as frontals and/or nasals;

1, higher than frontals and/or nasals. Modified from Geisler and Sanders, 2003

6. Supraoccipital breadth:

0, supraoccipital not compressed (the crest projects posteriorly and medially);

1, supraoccipital compressed at the level of the posterior apex of the nuchal crest (the crest projects only posteriorly). Modified from Bisconti, 2008

7. Supraoccipital length in dorsal view:

0, supraoccipital very long and narrow when compared with the maximum breadth;

1, supraoccipital long but not narrow. Modified from Bisconti, 2008

8. Dorsal surface of supraoccipital:

0, strongly concave;

1, anteriorly convex and posteriorly concave;

2, mainly convex. Modified from Bisconti, 2008

9. Paired tuberosities on the supraoccipital:

0, absent;

1, present. (this study)

10. Nuchal crest of supraoccipital:

0, directed dorsolaterally, not or only slightly overhanging temporal fossa;

1, horizontal and directed laterally, overhanging temporal fossa. Kimura and Hasegawa, 2010

11. Medial nuchal crest:

0, absent or ridge only;

1, present and elevated. Kimura and Hasegawa, 2010

12. Basioccipital process (strong and massive tubercle on the basioccipital crest for the origin of the longus colli):

0, absent;

1, present. Bouetel and de Muizon, 2006

13. Shape of the basioccipital processes:

0, wing-like;

1, massive, square, or triangular. Steeman, 2007

14. Posterior outline of the exoccipital in lateral view:

    0, squared;

    1, round. Bisconti, 2008

15. Height of the ventral surface of the exoccipital:

    0, lower than the orbit;

    1, at the same level of the orbit;

    2, higher than the orbit. Bisconti, 2008

16. Paroccipital process, skull in ventral view:

    0, angled posterolaterally, extends posterior to posteriormost edge of condyle;

    1, posterior edge in transverse line with posterior edge of condyle;

    2, posterior edge is well anterior to posterior edge of condyle. Geisler and Sanders, 2003

17. Paroccipital process:

    0, smooth;

    1, thick and extending noticeably posterior to the extent of the nuchal crest. Steeman, 2007

18. Position of posterolateral corner of exoccipital relative to postglenoid process of squamosal:

    0, far and medial;

1, far and posterior;

2, close and medial. Bisconti, 2008

19. Occipital condyle:

0, situated on a swelling;

1, not on a swelling;

2, almost leveled with the skull. Steeman, 2007

20. Parietal exposure on the dorsal wall of the skull:

0, present;

1, absent, located under the supraoccipital;

2, absent, divided into two halves by the interposition of the supraoccipital. Bisconti, 2008

21. Parietal moved onto the posterior portion of the interorbital region of the frontal:

0, no;

1, yes. Bisconti, 2008

22. Frontal exposure on the dorsal wall of the skull:

0, short;

1, totally covered by rostral bone. Modified from Bouetel and de Muizon, 2006

23. Exposure of interparietal on the dorsal wall of the skull:

0, absent;

1, small;

2, large. Bisconti, 2008

24. Exposure of parietal and frontal at interorbital region:

    0, parietal > frontal;

    1, frontal > parietal;

    2, both reduced. Modified from Kimura and Hasegawa, 2010

25. Intertemporal constriction:

    0, wide and long;

    1, wide and short. Modified from Bisconti, 2008

26. Intertemporal region distinctly depressed anteriorly to the anterior border of the supraoccipital:

    0, yes;

    1, no. Bisconti, 2008

27. Interorbital region of frontal:

    0, wide;

    1, narrowed anteroposteriorly;

    2, reduced to a subtle sheet posterior to the caudal tip of the ascending process of the maxilla. Bisconti, 2008

28. Position of foramen pseudovale:

0, squamosal and pterygoid;

1, squamosal only;

2, pterygoid only. Kimura and Hasegawa, 2010

29. Shape of the temporal fenestra:

0, longer (anteroposteriorly) than wide (lateromedially);

1, wider than long. Steeman, 2007

30. Posteromedial wall of temporal fossa:

0, visible in dorsal view;

1, hidden in dorsal view by lateral edges of supraoccipital (cannot be scored for taxa where the anteriormost point of supraoccipital is posterior to the level of the anterior edge of the floor for the squamosal fossa). Geisler and Sanders, 2003

31. Position of glenoid fossa of the squamosal:

0, posterior to orbit;

1, under the orbit. Bisconti, 2008

32. Position of coronal suture:

0, anterior to the anterior border of the supraoccipital;

1, posterior to the anterior border of the supraoccipital. Bisconti, 2008

33. Dorsal condyloid fossa:

0, absent;

1, present. Kimura and Hasegawa, 2010

34. Jugular notch, gap between paroccipital process and basioccipital crest:

    0, open notch, opening and depth of the notch are roughly equal;

    1, narrow and almost slit-like, depth is much greater than width of opening. Geisler and Sanders, 2003

35. Rectus capitus anticus muscle fossa:

    0, absent or poorly developed;

    1, present with a well-defined anterior edge (the anterior edge forms a curved ridge that joins the basioccipital crest laterally and curves posteromedially to join its counterpart at the sagittal plane). Geisler and Sanders, 2003

36. External auditory meatus:

    0, broad and short;

    1,long and narrow. Steeman, 2007