

**Paleocene mammalian fauna from the Nanxiong Basin,
Guangdong Province**

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Synopsis of contents

This volume is divided into three sections: (1) General discussion of the Paleocene stratigraphy of the Nanxiong Basin, the mammalian fossil localities, their stratigraphic position, and a discussion of the faunal nature and geochronology. (2) Description of specimens with their phylogenetic relationships and a documentation of *Bemalambda nanhsiungensis*, the thirteenth species in the genus (among ten other genera, seven families, and four orders). (3) A comparative cranial and post cranial study of *Bemalambda* (within the order Pantodonta and family Bemalambdidae).

Lower Tertiary sediments in the Nanxiong Basin include the (?) Eocene Danxia Fm.* and Paleocene Lufozhai Fm. (formerly Lofochai) which is further subdivided into the lower Shanghu Mem. and upper Nongshan Mem. Specimens described in this paper were derived from the Shanghu Mem. and thus comprise the Shanghu Fauna, representing the oldest Tertiary mammalian fauna in Asia.

* The authors erroneously romanize nomenclature as Danya Fm. and Nonshan Mem. in their extensive English summary. (wd)

Preface

Upper Cretaceous, Lower Tertiary, and younger sediments in the Nanxiong Basin were first recognized in 1962, and as stated by the authors of this text, have only been described recently in several short reports. It is only now possible to publish upon the most significant data contained within these sediments which are represented by the Paleocene mammals.

This text consists of detailed research conducted by Minchen Chow and his colleagues on the Paleocene mammal fauna from Nanxiong, Guangdong Province. The following aspects of their work are worthy of great appreciation:

(1) As stated by the authors, formerly, the only Paleocene mammal fauna recognized in China was from the Turpan Basin in Xinjiang Autonomous Region. The Nanxiong Fauna is not only taxonomically more diverse and predates those localities in Xinjiang, but moreover, the specimens are more complete, as witnessed by the pantodont genus *Bemalambda*, which is represented by numerous species, several of which are represented by complete skeletons. Additional taxa are also relatively complete, including the anagalid *Linnania lofoensis*, which is extremely important in understanding the Anagalida. Although some taxa are rather fragmentary, they still constitute significant faunal members and lend credence to the legitimacy of the Nanxiong Paleocene Mammalian Fauna which supplements the globally rare Paleocene mammalian assemblage.

(2) The authors herein conduct detailed descriptions and in depth discussion while summarizing previous knowledge and proposing solutions for current research problems. Aspirations for the future include more discoveries of specimens in addition to the comprehension of the Paleocene of China with its related faunas.

(3) Geological literature regarding the Nanxiong Basin is noted as early as 1927 (Young, 1934, pp. 497-498), although at that time several aspects of the basin's geochronology had yet to be understood due to the absence of paleontological data. In this text Chow and his colleagues describe four orders of mammals containing seven families, ten genera and thirteen species which, to date, comprise the most abundant Paleocene fauna in China and provides a legitimate and reliable basis for stratigraphic subdivision.

Since the establishment of the People's Republic of China, and particularly since the unprecedented great proletarian Cultural Revolution, research in vertebrate paleontology and paleoanthropology have genuinely surged forward. It is not sufficient that we remain content with results accumulated to date, but believe it necessary to focus on the future and the numerous problems contained therein. Aspirations are rather formidable, and thus it is necessary to utilize a continuous effort to promote our scientific endeavors along Mao Zedong's revolutionary line, which unceasingly urges to "go on discovering, inventing, creating, and advancing."

C.C. Young
October 5, 1973
Beijing

Part I General Discussion

Foreword

The initiation of the Tertiary, the Paleocene, is an extremely significant phase in the evolution of the Mammalia, although specimens representing the various stages within this epoch are rather rare, and represented globally predominantly in western North America with secondary occurrences in France, Germany, Argentina, Brazil, and Mongolia.

The first discovery of Paleocene mammals in China occurred in 1959 in the Turpan Basin of Xinjiang Autonomous region with a fauna that correlates precisely with the Mongolian Gashato Fauna. The assemblage documented in this volume is derived from Nanxiong Co., Guangdong Province, and to date, with the exception of the North American faunas, constitutes one of the oldest Tertiary mammalian faunas in the world.

After the discovery of this paleontological data at Nanxiong, several short stratigraphic papers were published assigning nomenclature to some of the specimens. However, due to a variety of reasons, completion of research upon all the Nanxiong specimens has been delayed until now, while a portion of the taxonomic nomenclature has been cited in several publications. For this reason, a previous paper (Chow et al., 1973) was published summarizing the Nanxiong taxa with their associated characters. These taxa are described in more detail in this volume.

A vast majority of the mammal specimens from Nanxiong are fragmentary; available pertinent literature and comparative specimens are scarce; and there is a lack of experience conducting research upon such archaic mammals, rendering the conclusions regarding the taxonomy and phylogenetic relationships of several taxa in this collection preliminary despite a detailed comparison to related taxa. Better preserved specimens found in the future will confirm or amend the research conducted here and will lead to the revision of several conclusions.

The best preserved specimens in the collection belong to the pantodont genus *Bemalambda*. These specimens represent a new family and genus with three species represented by complete skeletons and many complete skulls. To date, Paleocene mammal skeletons are relatively rare globally and consequently, emphasis is placed upon detailed description and discussion. Specimens that are too fragmentary are not named but merely described.

Because some specimens are poorly represented or fragmentary and the current availability of illustration equipment is lacking, several illustrations and photographic plates are less than ideal and must await later supplementary endeavors.

This volume is a preliminary analysis and discussion of the faunal characteristics and phylogeny of the fossil mammals from Nanxiong. Specimens were collected primarily during two field seasons by the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP). Additional specimens were collected by colleagues from the Hubei Provincial Institute of Geology (formerly the South Central Institute of Geology) and were transferred to IVPP for study. The authors hereby express their gratitude.

Synopsis of the biostratigraphy of the Nanxiong region in northern Guangdong Province.

The Cretaceous and Tertiary "Red Bed System" is relatively widespread within South China. However, a long-standing controversy exists regarding the age and stratigraphic subdivision of several of these rock units, as a majority of workers have generally assigned the

lower Red Beds to the Cretaceous and upper beds to the Tertiary with an ambiguous Cretaceous-Tertiary boundary.

Reconnaissance of sediments within the Nanxiong Basin of Guangdong was initiated as early as the end of the previous century, but it was not until later that more detailed and systematic work was conducted by the Chinese geologists such as Jinglan Feng, (?)Zhisheng Zhu, and Guoda Chen. After the establishment of the People's Republic, and between 1959 and 1962, more detailed surveys were conducted by geologists Xu Ren, Zuoming Li, Jiaguang Rao and others, in addition to the Nanxiong Co. Geological Corps of the Guangdong Bureau of Geology, and the Guangdong Provincial Geological Survey. The conclusion of this work resulted in abundant data regarding the subdivision and correlation of sediments in northern Guangdong, although precise recognition of the age of the "Nanxiong Group" was still vague due to the absence of diagnostic macrofossils, particularly fossil vertebrates.

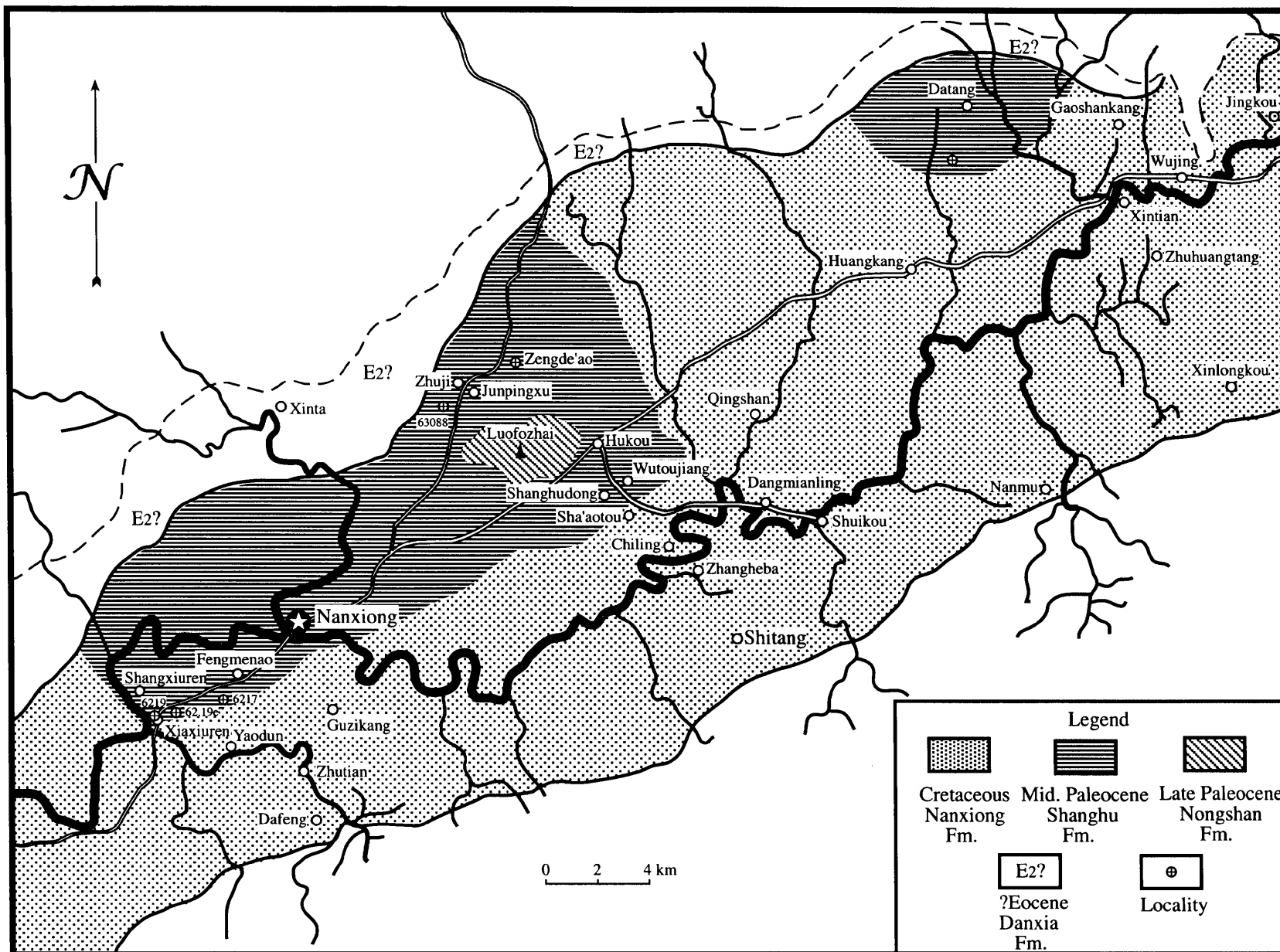
After 1960 great advances were made regarding the age, subdivision, and correlation of the Guangdong Red Beds, not only were preliminary subdivisions of Cretaceous and Lower Tertiary recognized, but Late Cretaceous dinosaurs and Paleocene mammals were discovered in the extensive region of southeast China. In 1961 colleagues from the Guangdong Provincial Bureau of Geology conducted field work at Shixing and Nanxiong counties, where they made the first discovery of fossil vertebrates including a damaged turtle and several fragmentary dinosaur limb bones. After being studied by C.C. Young and Minchen Chow (Young and Chow, 1962), the higher sediments, producing the turtle *Anosterira lingnanica* Young and Chow, were recognized as Early Tertiary, and based upon the characteristics of the specimen, perhaps Paleocene. The dinosaur phalanges were diagnosed as belonging to a coelurosaur (?) and thus the age of Late Cretaceous to earliest Tertiary was assigned to the lower sediments containing them.

Continuing along this line, in the winter of 1962 a contingent from IVPP including Yuping Zhang, Yongsheng Tong, and Cunyi Wang, conducted field work in the Shixing region where they discovered a large quantity of dinosaur eggs, turtles, and mammals. Based upon their preliminary taxonomic diagnoses and stratigraphic relationships, Zhang et al. subdivided the upper sediments of what was then regarded the Dengtayan System (Nanxiong Group) and named the Luofozhai Fm. with an age of Paleocene, while retaining the lower sediments of the Nanxiong Group as Cretaceous (Zhang and Tong, 1963). The following year, Jiajian Zheng et al. from IVPP made additional collections and measured stratigraphic sections which were published much later (Zheng et al, 1973). Reptile specimens resulting from the 1962 and 1963 field seasons were published in Young (1963, 1965) and Ye (1966), respectfully. Recently, geological investigations have continued, including work conducted by the Third Division of the 706th Geological Corps of Datang Commune, Nanxiong, which discovered theropod dinosaur teeth, turtles, and fossil mammals in the vicinity of Datang.

Synopsis of the stratigraphy in the Nanxiong Basin

The Nanxiong Basin borders the southern flanks of the Nanling mountain range as a narrow northeast-southwest trending extensional basin. The basin is approximately 80 km long and exceeds 18 km in breadth with the Zhenshui River traversing westward along its midline. Basin topography consists of red sedimentary hills exceeding 50 meters in height. At the northern margin of the basin these sediments represent the Early Tertiary "Danxia Fm." where they form the characteristic "Danxia topography."

The Mesozoic and Cenozoic red beds in the Nanxiong Basin directly overly older granites and may be subdivided into four stratigraphic units according to lithologic character and paleontological complexes:



3. Danxia Fm.	
2. Luofozhai Fm.:	Nongshan Mem.
Tertiary	Shanghu Mem
Cretaceous	
1. Nanxiong Fm.	

Late Cretaceous Nanxiong Fm.:

Unconformably overlying Mesozoic granites, Nanxiong Fm. sediments span approximately 1,300 to 2,900 meters of terrestrial clastics extending throughout the entire basin. Sediments are best exposed in the regions of Zhutian, Mabu, Huangkeng, and Wujing. Thickness increases from southwest to northeast and has a general dip to the northwest. At the basin margins the angle of dip increases greatly but toward the center of the basin gradually decreases to between 14°-22°.

From the Upper Cretaceous Nanxiong Fm.* bones, and teeth, of dinosaurs (Carnosauria, Nodosauria, Hadrosauria, etc.) and lacertilian reptiles in addition to eggshells have been discovered. Lithologically the Nanxiong Fm. consists mainly of dark brown sandy marls, marls, and marly shales with intercalating thin beds of green sandstone and sandy conglomerates. The highest Cretaceous bone-bearing bed is only about one meter below the lowest mammal-bearing Paleocene and no discernible structural or lithological lines of demarcations are observed between it and the overlying Paleocene.

Luofozhai Fm.:

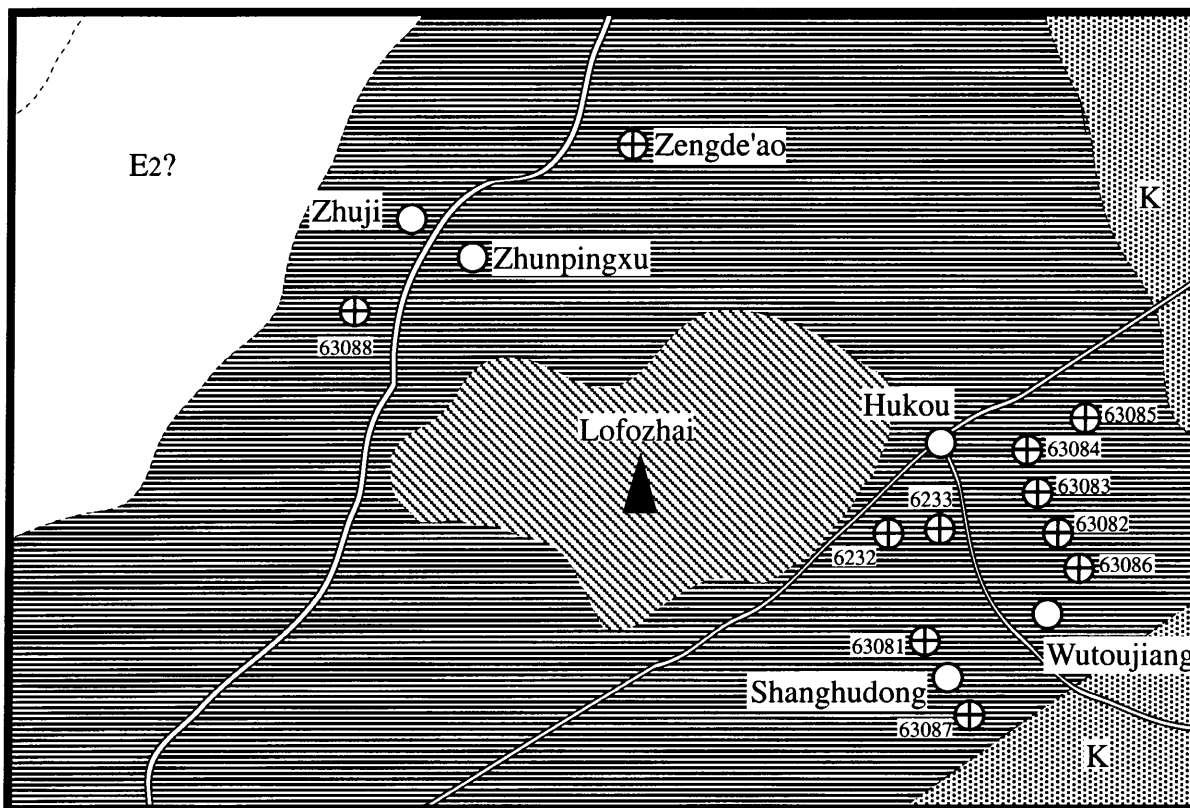
When Zhang and Tong (1963) first made their discoveries of fossil mammals in the Nanxiong Basin, they recognized the sediments in the upper Nanxiong Group (Dengtayan System) which underly the Danxia Fm. as an independent formation and erected the nomenclature Luofozhai Fm. representing Paleocene sedimentation. This unit may attain 800 m in thickness and is further subdivided into two members, the upper of which produces fossil turtles and the lower being the source of mammals. Because of the indistinct contact relationships between these two members, they were not provided with formation status. This subdivision was recognized as the most parsimonious and applicable from the perspective of the paleontological data. At that time, Early Tertiary paleontological data in South China was neither abundant or adequate for the foundation of stratigraphic subdivision.

Later, Zheng et al. (1973) recognized two members in the Luofozhai Fm. based upon field work conducted in 1964, and as mammals were still unknown from the upper member, did not assign a stratigraphic age for it, although they hypothesized that the sediments were Late Paleocene or even younger. They recognized the lower member as either middle Paleocene or late middle Paleocene.

Currently, Early Tertiary subdivision at Nanxiong is relatively detailed and stable,. However, the fossil evidence from the upper member is distinctly deficient while the lower member clearly documents middle Paleocene mammals. Furthermore, type localities in the vicinity of the village of Luofozhai do not represent the lower member of the formation but only the upper member, which creates certain difficulties for current and future endeavors, as the nomenclature is

* This paragraph adapted from the English summary. (wd)

already used extensively in the literature, and is recognized as the regional standard for middle Paleocene sediments and faunas.



Therefore, in order to resolve this problem adequately, this text regards the Lower Tertiary Luofozhai Fm. in the Nanxiong Basin and the faunal nature contained therein with the following criteria below (reference is also applied from data recovered recently from several other South China provinces including Hunan, Jiangxi, and Anwei).

(1) The designation, Luofozhai Fm. should be retained as the stratigraphic unit representing the basal Tertiary sediments of the Nanxiong Basin that underlie the Danxia Fm.

(2) The Luofozhai Fm. is subdivided into upper and lower members. The lower member is here named Shanghu Member and the upper member is recognized as the Nongshan Member. The best exposures producing Shanghu Mem. localities lie in the vicinity of Hukou Commune in Nanxiong Co. However, the nomenclature Hukou is preoccupied as the Permian Hukou Coal System, and thus the nomenclature Shanghu, derived from the village of Shanghudong, is hereby applied. The age of the Shanghu Mem. is recognized as middle Paleocene. Furthermore, the Shanghu Fauna is hereby recognized as the middle Paleocene local fauna in northern Guangdong Province.

(3) The upper Nongshan Mem. is named for a small hilltop by the name of Nongshanding that lies west of Hukou Commune and north of the village of Luofozhai. There is still no diagnostic data to determine the age of this member but inference from the geologic conditions in several South China provinces suggests that it is probably not younger than Late Paleocene.

Synopsis of lithologic characters is as follows:

(1) The basal Shanghu Mem. is predominantly exposed in the regions of Canren, Hukou, and Shanghudong where it overlies the Nanxiong Formation disconformably or paraconformably. Exposures are also present in the vicinity of Datang. Thickness exceeds 600 m of tabular beds that dip northwest at 7°-12°, but in the vicinity of Zhuji Commune the dip becomes southeast, reflecting part of a broad and gentle syncline. Lithologic character consists predominantly of brown-red and purple-red mudstones, argillaceous sandstones, and sandy mudstones interbedded with thinly laminated sandy conglomerates with a base consisting of an approximately two to five meter thick gray-white, and gray-red sandy conglomerate. Abundant fresh-water gastropods and fossil vertebrates are present including mammals, turtles, crocodiles, and other reptiles.

(2) The Upper Paleocene (?) Nongshan Mem. lies conformably on the Shanghu Mem. and is predominantly exposed in the center of the basin in the vicinity of Lufozhai Village and Nongshanding with an approximate thickness of 200 meters. Beds are tabular with a broad and gentle synclinal dip of 5°-8° and are composed of a set of thinly laminated gray-green and light purple-red mudstones, siltstones, sandstones, and fine conglomerates. Paleontological data includes a large quantity of turtle, crocodiles, and coprolites.

(3) The Eocene (?) Danxia Fm. overlies the Lufozhai Fm. with an unconformable contact and consists of massive sandy conglomerates with a brown weathered surface, but fresh exposures are gray-yellow or purple-brown. Conglomerates are poorly sorted, poorly rounded, and poorly bedded with a complex composition consisting predominantly of quartz clasts but also containing granite, slate, phyllites, and sandstones. Clast size varies from several millimeters to greater than ten centimeters. Exposures are between 100-550 m thick and increase in thickness from northeast to southwest. Beds are extremely contorted and faulted and after weathering compose a characteristic landform designated "Danxia topography" by geomorphologists.

Localities and stratigraphic characteristics

Exposures of the Shanghu Mem. of the Lufozhai Fm. occur in the central portion of the basin. Mammalian fossil localities are predominantly distributed around Hukou Commune, northwest of Nanxiong Co. seat and in the Xiuren vicinity south west of Nanxiong (Fig. 1) as are enumerated below:

(1) Xiuren: 6217, 6219.

(2) Shanghudong, Hukou: 6232, 6233, 63081, 63087.

(3) Wutoujiang, Hukou: 63086, 63082, 63083, 63083, 63085

(4) Zhuji: 63088

(5) Zengde'ao vicinity: Collected by the Hubei Institute of Geology

(6) Tatangyoushan vicinity: Collected by the Third Division of the 706th Geological Corps of the Guangdong Bureau of Geology.

(7) ?Phenacodontidae indet., locality unknown.

The Nanxiong localities are relatively widespread. In order to clarify stratigraphic positions and relationships, units in the Shanghu Mem. are recognized as follows:

(1) Basal section: Fossil localities at the base of the Shanghu Mem. are located predominantly in purple-red mudstones but the basal stratigraphic unit is a white sandy conglomerate not easily distinguished from the underlying Cretaceous sandstones, although at several localities there appears to be a vague angular unconformity between the two units. The greatest thickness of these exposures is found in the vicinity southeast of Xiuren. At the village of Shanghudong the unit attains 281 m, and is equivalent to units 1-IV in cross-section 4, as measured by Zheng et al. (1973). This region documents localities 6217, 6219, and 63087 which produce *Bemalambda pachyoesteus*, *Yuodon protoselenoides*, *Palasiodon siurensis*, *Dissacusium shanghoensis*, and a small quantity of *B. nanhsiungensis*.

Table 1. Correlation of principle fossil mammals, localities, and stratigraphic sections in the Nanxiong Basin.

Xiuren		Shanghu dong Luofozahi section		Hukou Wutoujaing section		Zhuji
				Nongshan Mem.		
		Nongshan Mem.	Upper beds	<i>B. nanhsiungensis</i> (63085)	Capping beds	<i>B. crassa</i> (63088) <i>Lofochaius brachyodon</i>
		<i>B. nanhsiungensis</i> <i>Dissacus feiganensis</i> (6233) <i>Linnania lofoensis</i> (63081) <i>B. pachyoesteus</i> (6232)	Middle beds	<i>B. nanhsiungensis</i> ? <i>Ectoconus</i> sp. (63084) <i>B. nanhsiungensis</i> (63083) <i>Hukoutherium ambigum</i> (63082) <i>B. pachyoesteus</i> (63086)		Loess covered
<i>Bemalambda pachyoesteus</i> <i>Palasiodon siurensis</i> (6217, 6219)	Lower beds	<i>B. nanhsiungensis</i> <i>B. pachyoesteus</i> <i>Yuodon protoselenoides</i> <i>Dissacusium shanghoensis</i> (63087)		Nanxiong Fm.		
Nanxiong Fm.		Nanxiong Fm.				

(2) Medial section: This is the most fossiliferous unit consisting predominantly of intertonguing brown-red and purple-red mudstones bearing calcareous concretions and small green marl lenses. The sandy conglomeratic base of this section is conformable with the underlying strata. The greatest thickness is 320 m and these strata appear to correlate with units V-VIII of Zheng et al. (1973) section 4 and units I-VII of their section 5. Exposures lie north of Shanghudong and Wutoujiang where the following localities are documented: 63086, 63082, 63083, 63084, 63081, and 6233. These localities produce abundant specimens of *Bemalambda*

nanhsiungensis, and a small number of *B. pachyoesteus*, *Dissacus feiganensis*, *Hukoutherium ambigum*, and *Linnania lofoensis* specimens.

(3) Upper section: The poorly fossiliferous sediments consist of 234 m of purple-red mudstones containing gray-green patches. The base is gray-white sandy mudstone interbedded with sandy conglomerates that are conformable with the medial section. This section appears equivalent to units VIII-X in section 5 of Zheng et al. (1973). Exposures lie east of Hukou with only locality 63085 producing *Bemalambda nanhsiungensis*.

(4) Capping section: The uppermost fossiliferous sediments of the Shanghu Mem. are variegated light purple-red mudstones but lighter than the underlying sediments of the Shanghu Mem. Contact relationship with the upper section and total thickness are unobservable as the basal portion is obscured by loess. Exposures are principally located in the vicinity of Zhuji Commune and Zengde'ao where locality 63088 and localities of the Hubei Institute of Geology produce *Bemalambda crassa* and *Linnania lofoensis*.

Characteristics and chronology of the mammalian faunas from the Shanghu Member of the Luofozhai Fm.

Fossil mammals from the lower Shanghu Mem. of the Luofozhai Fm. in the Nanxiong Basin are derived from four stratigraphic units: the lower, middle upper, and capping units, with the two lowest units being the most fossiliferous and containing the same taxa. Although the superpositional relationship between the two lower units is distinct, the assemblages represented in them are consistent. The stratigraphically higher upper sedimentary unit has a thickness exceeding 200 m and produces only the single species *Bemalambda nanhsiungensis*, which is also recorded from the two underlying assemblages. Consequently, data recovered from the upper section to date suggests it should also be regarded as the same fauna as the lower and middle units.

The capping sediments of the Shanghu Mem. produce only two taxa, *Bemalambda crassa* and the tillodont *Lofochaius brachyodon*, both of which are absent from the underlying units. The bemalambdid species is distinctly more derived than the underlying taxa and consequently, the capping unit is recognized as representing a distinctly younger faunal zone. Currently, though, data is insufficient and taxa from the capping unit are still regarded in general as members of the Shanghu Fauna. But in the discussion of the age and correlation of the fauna, only the taxa from the lower three units are utilized. Those from the capping unit are regarded only in a referred status.

Nanxiong specimens are rather abundant with the vast majority representing the genus *Bemalambda* in low species diversity. However, those taxa present represent new species and genera which are relatively derived such that contemporaneous or nearly contemporaneous faunas from North America and other regions display extremely few directly comparable taxa. In recent years, numerous generally contemporaneous or slightly younger specimens have been recovered in other regions of South China including Qianshan and Xuancheng Counties, Anwei Province; Dayu Co., Jiangxi Province; and Chaling Co., Hunan Province, but these specimens are predominantly undescribed. Recorded below are taxa from the various units of the Shanghu Mem. and unpublished referred taxa from other regions. Recorded here are 13 species within 10 genera:

Anagalida

Anagalidae

Linnania lofoensis Chow, et al., 1973

Tillodontia

Esthonychidae

Lofochaius brachyodus Chow et al., 1973

Condylarthra

Mesonychidae

- Dissacus feiganensis* Chow et al., 1973
- Dissacusium shanghoensis* (Chow et al.), 1973
- Hukoutherium ambigum* Chow et. al., 1973

Hyopsodontidae

- Yuodon protoselenoides* Chow et al., 1973
- Palasiodon siurensis* Chow et al., 1973

Periptychidae

- ?*Ectoconus* sp.

?Phenacodontidae, gen. et sp. indet.

Pantodonta

Bemalambdidae Chow et al., 1973

- Bemalambda nanhsiungensis* Chow et al., 1973
- B. pachyoesteus* Chow et al., 1973
- B. crassa* Chow et al., 1973
- B.* sp.

The 13 species listed above belong to seven families within four orders. The order Anagalida is characteristic of Asia, while the other three orders are represented in the Paleocene or Eocene of North America and Europe.

The family Anagalidae has for many years been recorded only from the Oligocene of China. Most recently, Szalay and McKenna (1971) described fragmentary specimens representing two species of this family from the Late Paleocene Gashato Fauna of Mongolia, but their relationship to the Shanghu genus *Linnania* is unclear. The dentition of *Linnania* is complete and represents a brachydont plesiomorphic form with a conspicuous tribosphenic talonid basin. This primitive form displays an archaic morphology for the family and hence represents an earlier age.

The family Mesonychidae is represented by three species. Specimens of *Hukoutherium* are extremely fragmentary and although its phylogenetic relationship is not completely clear, it displays very few apomorphies and may be basically recognized as a relatively primitive mesonychid. It is worth noting that *Dissacus*, a primitive and archaic mesonychid, represents the longest recorded genus in the family as it extends from the Middle Paleocene to Late Eocene in North America. Upper molars of the Nanxiong species are not only particularly transversely broadened but are also morphologically distinct from the American genus. Although available data is limited, comparison to other taxa from the northern hemisphere suggest that there is insufficient justification to exclude the Nanxiong specimens from the currently known genera. Thus, *D. feiganensis* recorded as being relatively close to *D. navajovius* in size and morphology and is consequently retained in the same genus.

The Hyopsodontidae is represented by the two new genera *Yuodon* and *Palasiodon* which are similar to but clearly distinct from their North American middle Paleocene counterparts *Protoselene* and *Promioclænus* (*P. aquilonius*).

The Esthonychidae is represented by *Lofochaius brachyodus*, the most primitive tillodont known to date. This taxon is much more primitive in morphology and lower in stratigraphic position than *Esthonyx* from the Early Eocene (perhaps including terminal Paleocene) from North America and Europe. This is also further evidence supporting the discovery of this family in Chaling Co., Hunan. Furthermore, tillodonts that are extremely similar to this genus have been recovered from sediments bearing *Bemalambda nanhsiungensis* in Qianshan Co., Anwei, and appear slightly more primitive than the specimens from the Shanghu capping sediments, indicating a younger age for *Lofochaius*.

Table 2. Distribution of middle Paleocene mammal sites in the Shanghu Member of the Luofozhai Fm.*

	Xiuren		Shanghudong, Hukou				Wujtoujiang, Hukou					Zhuji		Loc. indet.
	6217	6219	63087	63081	6232	6233	63086	63082	63083	63084	63085	63088	Zeng-de'ao	
<i>Linania lofoensis</i>				X										
<i>Lofochaius brachyodus</i>													X	
<i>Dissacus feiganensis</i>						X								
<i>Dissacussium shanghoensis</i>			X											
<i>Hukoutherium ambigum</i>								X						
?Phenacodontidae indet.														X
<i>Yuodon protoselenoides</i>			X											
<i>Palasiodon siurenensis</i>	X													
? <i>Ectoconus</i> sp.										X				
<i>Bemalambda nanhsiungensis</i>			X			X			X	X	X			
<i>B. pachyoesteus</i>	X	X	X		X		X							
<i>B. crassus</i>												X		

*Localities are arranged stratigraphically from bottom to top.

The new family Bemalambdidae represents the most abundant order in the Luofozhai Fm. Unexpectedly absent from the Nanxiong Paleocene deposits are the prolific Late Paleocene Asian families Archaelambdidae, the common Early Eocene Coryphodontidae, and the North American nearly stratigraphically equivalent Pantolambdidae as well as other North American families such as the Barylambdidae and Titanoideidae. The bemalambids are extremely derived, with characters distinct from all other known pantodonts. From the perspective of a general evolutionary grade, the pantodonts show a conspicuous trend from small to large size with the premolar morphology becoming more complex. In this respect *Bemalambda* is generally consistent with the developmental phase of *Pantolambda bathmodon* from the middle Paleocene of North America, only the P2 root shows vestiges of bifurcation indicating that it is slightly more primitive than the latter. Compared to *P. cavirictus*, *Bemalambda* is much smaller and has a more simplified premolar morphology. Consequently, it is believed that *Bemalambda* and *P. bathmodon* are nearly equivalent in evolutionary grade and age and that both represent index fossils for the middle Paleocene of their respective regions.

A fragmentary mandible containing a small number of damaged teeth is questionably assigned to the Phenacodontidae based upon mandibular morphology and size.

Preliminary conclusions regarding the relationships of the Nanxiong Fauna to other regions, and age of the Shanghu Fauna are provided below:

(1) Several genera are shared with, similar to, or are at the same level of systematic development as taxa in Europe, North America, and Mongolia. These include *Dissacus*, *?Ectoconus*, *Yuodon* (“*Protoselene*”), and *Palasiodon* (“*Promioclænus*”) and indicate that the age of the fossil complexes are constrained by the upper and lower ranges of the middle Paleocene.

(2) With the exception of *Dissacus*, there are no Late Paleocene taxa at Nanxiong that are shared with the Asian Late Paleocene Gashato Fauna. However, the Shanghu Fauna vaguely approaches the Gashato fauna but with major discrepancies as the Gashato Fauna is distinctly older. Although the Gashato equates to the European Thanetian and North American Tiffanian stages, the upper boundary of the Shanghu Mem. cannot exceed the North American Torrejonian Stage.

(3) With reference to the ages of several recently discovered local faunas in South China and particularly assemblages from several stratigraphic units in Anwei, the age of the Shanghu Fauna (or at least the three lowest units) may slightly predate the North American Torrejonian or more closely approach the Dragonian. The capping unit of the Shanghu Mem. producing *Bemalambda crassa* and *Lofochaius brachyodon* is probably closer to the Torrejonian Stage. Thus the Nanxiong Fauna is provisionally erected as an independent middle Paleocene cronofauna.

Other characteristics of the fauna such as paleobiogeographic relationships and paleoecological inferences may only be addressed in a preliminary fashion as current data is insufficient for more substantial conclusions.

(1) The general complexion of the Nanxiong fauna is distinctly endemic, as it contains taxa unknown from other equivalent age localities, including members of the Anagalidae, Esthonychidae, and Bemalambdidae.

(2) Several families are represented in equivalent age faunas in North American, such as the mesonychids and hyopsodontids, although phenacodontid and periptychid data is extremely rare, with specimens only provisionally assigned to these families.

It is questionable whether the shared taxa and plesiomorphic nature permit significant comparison with North American and European faunas. North American and European Late Paleocene and Early Eocene faunas are comparable by their distinct primitive faunal complexion and appear to share the main fundamental taxa with Nanxiong as well as with the entire East Asian Paleocene Fauna. This should be related to Asian paleogeographic conditions around the middle Paleocene, although more precise elaboration cannot be addressed here due to the broad scope of this discussion.

(3) To date the Lufozhai Fm. has not produced North Asian Late Paleocene taxa such as the Multituberculata, Dinocerata, Notoungulata, Archaelambdidae, or other anagalid families such as the Pseudictopidae and Eurymylidae. This is predominantly due to the limited collection that currently represents the fauna although other reasons are undoubtedly due to ecological or paleobiogeographical considerations.

(4) Habitat characteristics expressed through the faunal elements suggest the majority of the Shanghu fauna appears to be adapted to riparian, paludal, or other habitats proximal to aquatic systems. The assemblage in general appears to lack typical plain or forest dwelling inhabitants such as primates, insectivores, multituberculates, or carnivores, although obviously *Linnania* may be regarded as a forest taxon.

Faunal characteristics, taphonomy, and depositional characters suggest the Lofozhai sediments are predominantly central basin quiet water lacustrine or riparian sediments which differ distinctly from the faunal and fluvial characters expressed in the Late Paleocene sediments of Xinjiang and Mongolia.

(5) Analysis of *Bemalambda* dentition, cranial, and postcranial elements suggest that this family represents a primitive pantodont that shares numerous cranial and dental characters with *Deltatheridium*, and possibly expresses a closer relationship between the two genera. It is possible that the Pantodonta had its genesis in Asia at the terminal Cretaceous or basal Paleocene.

Conclusions

The mammalian fossil complex from the Nanxiong Basin of northern Guangdong Province represents a new middle Paleocene assemblage named the Shanghu Fauna, or the Shanghu Local Fauna, which represents the oldest Cenozoic mammal fauna known in the Old World to date.

The Lower Tertiary of Nanxiong includes the upper Danxia Fm. and the lower Lofozhai Fm. Precise dating of the Danxia Fm. is unclear but it is generally recognized as Eocene. The Lufozhai Fm. is subdivided into the upper Nongshan Mem. and the lower Shanghu Mem. with the Paleocene fauna produced completely from the Shanghu Mem. Fossil data from the Shanghu Mem. are derived from four stratigraphic units: the lower, middle, upper, and capping units, with the majority of data derived from the lower and middle units and few specimens recovered from the upper unit. These three sedimentary packages are recognized as a single middle Paleocene chronounit while the capping sediments represent an independent later stratigraphic unit. The age of the entire Nanxiong fauna distinctly predates faunas from the Turpan Basin, Xinjiang, and the Gashato Fauna in Mongolia. The age of the Nanxiong Fauna lower boundary is constrained possibly to the early middle Paleocene. The age of the stratigraphically higher Nongshan Mem. may represent Late Paleocene or perhaps Early Eocene.

Four orders, seven families, ten genera, and thirteen species are represented in the Shanghu Fauna. Its most distinctive characters lie in its endemic autapomorphies such as the presence of the Anagalidae, Esthonychidae, and Bemalambdidae, which are unknown from other Paleocene sediments. From another perspective, there are several genera that are extremely close to those

from the middle Paleocene of North America, to the extent that they may be congeneric, suggesting an affinity between the two continents during this period.

A majority of the Nanxiong faunal elements are adapted to riparian or paludal to lacustrine habitats with a near absence of typical plain or forest elements.

The family Bemalambdidae represents the most primitive member of the Pantodonta that had its genesis in the terminal Cretaceous or Early Paleocene from a primitive Asian therian resembling *Deltatheridium*.

Part II Specimen descriptions and phylogenetics

Anagalida

Anagalidae

Linnania Chow, Chang, Wang and Ting, 1973

Linnania lofoensis Chow, Chang, Wang, and Ting, 1973

(Plate I, Figs. 1,2; Plate II, Fig. 1; Text figs. 1-5)

Linnania lofoensis Chow et al., 1973; Vertebrata PalAsiatica **11**(1), 31.

Type: A relatively complete skull and mandible (IVPP #V4234).

Stratigraphic position: Middle Paleocene middle portion of Shanghu Mem., Lofozhai Fm.

Genus and species diagnosis: Cranial and dentition morphology basically resembles the anagalid *Anagale gobiensis*, being relatively primitive and slightly small. Skull is relatively short, narrow, low and flat. Temporo-orbital fossa is small, ramus is slender and weak, upper dental formula is $? \cdot 3 \cdot 1 \cdot 4 \cdot 3$, and lower dental formula is $? \cdot 3 \cdot 1 \cdot 4 \cdot 3$. Canine is small, weak, and simple in morphology and the first and second premolars have bifurcated roots. Protocone on P3 to M3 is nearly crescentic, P4 paracone is well developed, metacone is small, metaconule is undeveloped or incipient, dentition is unilaterally hypsodont, enamel extends into the dental trough. Upper molar paracone and metacone are isolated and conical. Pre- and postprotocristae extend to the external sides of the paracone and metacone to contact the anterior and posterior cingula respectively. On the mandible, the protoconids of the third and fourth premolars are bifid. Degree of p4 molarization is higher than the P4. Lower molar paraconid is just slightly lower than the metaconid, and trigonid is extremely high on p4-m3, being twice the height of the talonid. Trigonid cusps are in a v-shaped alignment with a deep trigonid basin. The p3-m3 protoconid is rather elongated and hypoconid gradually reduces in size posteriorly along the sequence.

Description: At the time of its recovery, the specimen's mandible was in tight occlusion with the skull. The skull is relatively completely preserved in outline but due to compressional distortion it is fractured, such that individual cranial elements are missing and its precise morphology is unclear. The skull is relatively short, narrow and low. Anterior to the P3 the skull is even more narrow due to compressional distortion and the rostral end has been shattered such that it does not preserve the incisors. Laterally, the skull has suffered some displacement with the left side shifted 1.7 mm anteriorly. The dorsal surface of the skull is extremely flat with the nasals lying nearly on the same plane as the parietals. The frontals are very slightly inflated and lack sagittal crests. The temporo-orbital fossa is confluent with the temporal fossa, and lacks a medial

boundary line to compose a relatively small temporo-orbital fossa with its anterior end situated dorsal to the M1. The zygomatic arch is completely broken with no vestiges remaining.

The palate is relatively flat with the dental sequences rather widely spaced. The P4-M3 sequences are parallel but from P3-C the dentitions gradually attenuate with palatal breadth at P4 being 18 mm but at the P2 it is 11 mm. The sphenoid is relatively broad and the basioccipital region is rather deeply concave. The dorsal surface of the skull is rectangular, relatively thin, flat, and precipitous. The occipital crest is flat, straight and slightly dorsally projected.

Dentition on the right side is complete with the exception of the P1. Each tooth in the sequence is in tight association with its preceding and posterior counterparts (less than a millimeter separates the P2 from P3). On the left side, the P3-M2 are preserved, the P3 is incomplete, and the M3 only preserves its paracone.

Table 3. Cranial measurements of *Linnania lofoensis* (mm).

Facial length (anterior temporo-orbital fossa - anterior canine)	19.4
Cranium length (anterior temporo-orbital fossa - occiput)	28.6
Lateral diameter of temporo-orbital fossa	11.4
Dorsal diameter of temporo-orbital fossa	15.3
Length of skull (occiput - anterior canine)	47.4
Height of skull (at M2)	15.7

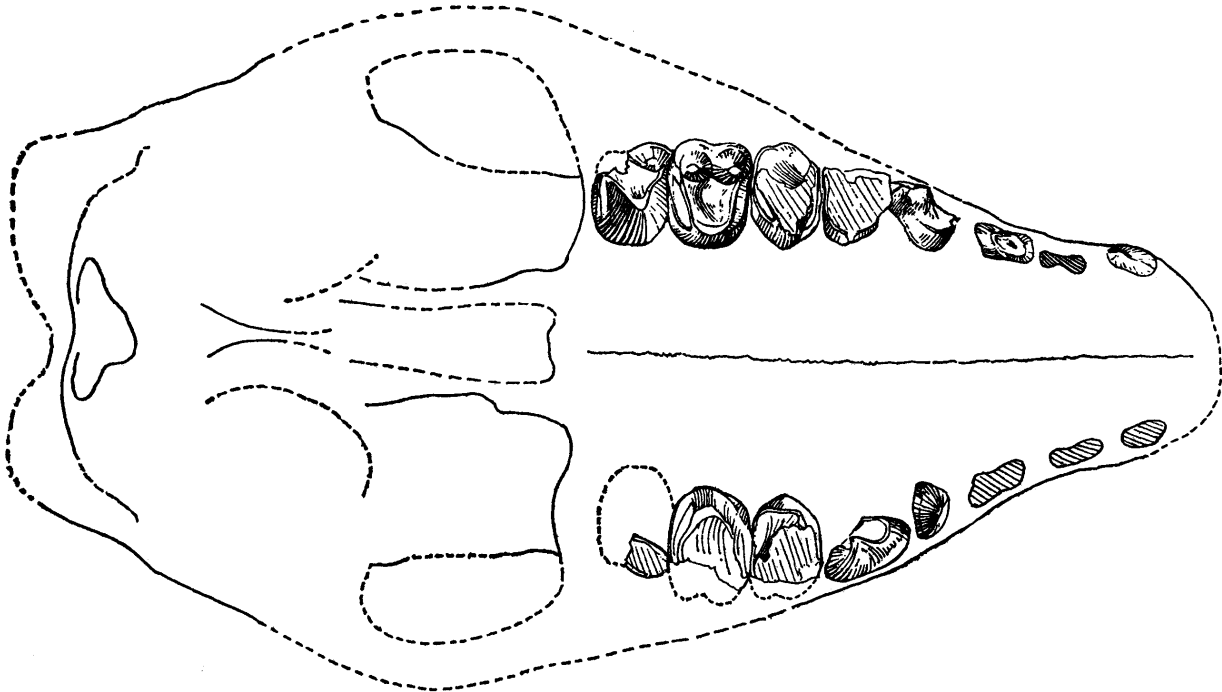


Figure 2. Ventral view of V4234, *Linnania lofoensis* Chow et al., 1973 (X3).

The canine is small, weak, as long as the P2, and has damaged lingual enamel.

Four upper premolars are present. The P1 preserves two roots, the posterior of which is slightly larger. The P2 also maintains two roots, the posterior root being large with a thin and flat labial side, convex lingual side, and slightly inflated posterior portion. Less than a millimeter separates this tooth from the P3. Both the left P1 and P2 are missing.

On the right side the P3 is newly erupted with three roots present, the protocone is low, thinly crescentic, and supported by the lingual root. The paracone is extremely high with a relatively precipitous anterior face. Compressional distortion has shifted the cusp posterior to the paracone (ectometacone) onto the posterior tooth distorting the triangular morphology of the P4. This distortion is also probably the cause of its anteriorly obtuse triangular morphology.

The P4 on the right side is deciduous, damaged, and only recognizable as subsquare in outline with a remnant morphology very similar to the M1. On the left side the P4 has been displaced due to compressional distortion with the lophes anteriorly oblique and its outline subsquare. The protocone is well developed and thinly crescentic, the paracone is extremely high, twice the height of the protocone, in direct opposition to the protocone, and is slightly damaged anterolabially. The metacone is extremely low, the cingulum is weak, and the preprotocrista extends directly to the anterior paracone where it becomes confluent with the cingulum.

On the right side all molars are present but the M3 metacone is missing while on the left side the M1 and M2 are present but the M3 preserves only its paracone.

Crowns of the M1 are shattered such that only the outline and lingual morphology are recognizable. The crown is circular with a well developed protocone, paracone, and metacone of equivalent size; cingulum is extremely well developed; and parastyle and metastyle are absent.

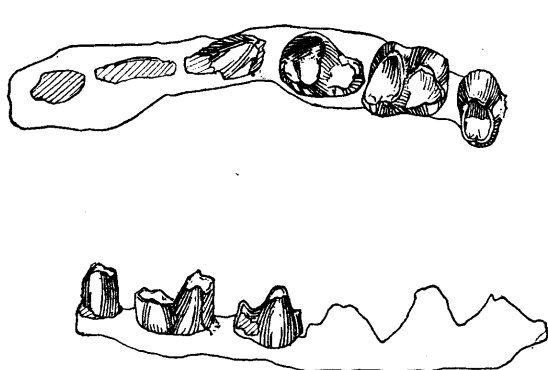


Figure 3. Right mandible with p1-m2 (V4234) of *Linnania lofoensis* Chow et al., 1973. Upper. Occlusal view; Lower. Lateral view (X3)

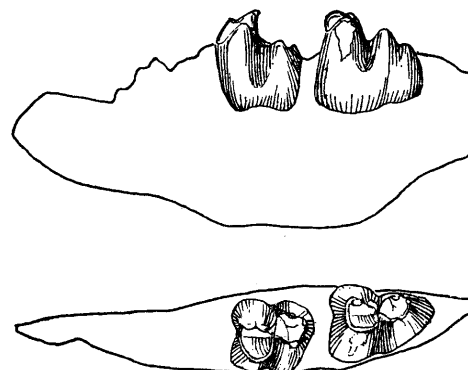


Figure 4. Left mandible with m2-m3 (V4234) of *Linnania lofoensis* Chow et al., 1973. Upper. Lateral view; Lower. Occlusal view (X3)

The M2 is square, larger than the M1, paracone and metacone are isolated with the paracone slightly larger; cingula are well developed labially, anteriorly, and posteriorly with the posterior cingulum extending around to the anterolingual side of the protocone. Pre- and post protocristae both extend to the exterior sides of the paracone and metacone to contact the cingula. Parastyle and metastyle are weak.

Table 4. Comparison of anagalid dental measurements (mm).

	<i>Linnania lofoensis</i>	<i>Anagale gobiensis</i>	<i>Anagalopsis kansuensis</i>	<i>Khashanagale zofiae</i>
P1 L	3.12	2.70		
P1 W		1.60		
P2 L	3.20	2.90	3.40	
P2 W	2.92			
P3 L	3.25			
P3 W	3.30			
P4 L	3.26			
P4 W	3.32			
M1 L	3.30			
M1 W	3.50			
M2 L	3.42			
M2 W	3.60			
M3 L	3.18			
M3 W	3.55			
P1-M3 L	22.7	22.3-22.7	~27.5	
P2-M3 L	19.8	18.9	23.9	
p1 L	3.12			
p1 W	2.78			
p2 L	3.18			
P2W	2.88			
p3 L	3.20			
p3 W	2.95			
p4 L	3.33	3.30	3.70	
Trig. W	3.15	2.4-2.4	3.80	
Tal. W	2.95	~2.2	3.30	
m1 L	3.45	3.70	4.20	2.45
Trig. W	3.18	3.5-3.6	4.30	1.90
Tal. W	3.20	3.2-3.3		1.80
m2 L	3.40	3.60	4.70	2.30
Trig. W	3.28-3.30	?2.9-3.5	4.50	1.90
Tal. W	3.20	3.30		1.60
m3 L	3.63	4.3-4.4	6.20	2.10
Trig. W	3.36	3.0-3.3	4.40	1.60
Tal. W	3.18	2.5-2.6		1.30
m1-m3 L	~12.4	11.3-11.4	14.9	~7.2
p1-m3 L	~26.8	23.9	31.3	
p4-m1 L	7.6	7.4		
p2-m3 L	~23.8	21.1	~26-27	

Addendum: ?*Kashanagale* sp. nov. (Szalay and McKenna, 1971) m3 Trig. W: 1.15, Tal. W:0.9

The M3 is newly erupted, situated lower and is slightly smaller than the M2, and morphologically resembles the M1 and M2. The anterior margin is very slightly posteriorly oblique and as such the tooth is not square in outline. Pre- and postcingula are reduced and do not extend to the lingual side. Pre- and postprotocristae resemble those on the M2, and a parastyle is more conspicuous than on the M2. A character shared between the P4-M3 is that the lingual side is higher than the labial side.

Right lower dentition preserved includes the trigonid of the m2 to the p1 and half the root of the canine. On the left side only a piece of dentary bearing an m2, m3 and roots of the m1 are present. The lower canine appears to have been small on the basis of half a root present. Lower molars are not tightly associated as small diastemae lie between the teeth.

The p1-p3 are all incomplete, p1 outline is vague, p2 is broken lingually and is thin and flat labially. The p3 has been shattered anteriorly and posteriorly, but the protoconid is completely preserved with a labial side that is rather thin and flat, the lingual side is convex, and there is a small inflation both anteriorly and posteriorly representing an incipient paraconid and metaconid, developing the tendency toward a well developed trigonid. Posterior to the protoconid is a small, extremely narrow, semicircular talonid.

The lower fourth deciduous premolar is extremely worn (Pl. II, Figs. 1a,1c,1d) and morphologically resembles the m1. A complete p4 is erupting posterior to it (Pl. II, Fig. 1b).

The right side preserves only the m1 and m2 trigonids, while the left side preserves a relatively complete m2 and m3. The dentition is not tightly associated as there are small diastemae between the teeth. Lower molar trigonids are nearly twice the height of talonids. The protoconid is high and long, the metaconid is slightly lower than the protoconid, and the paraconid lies anterior to and lower than the metaconid, with an extremely deep v-shaped groove lying between the three principle cusps. The talonid is small, nearly half the length of the trigonid, with a high entoconid and hypoconid and hypoconulid of equivalent height. All three cusps encompass a narrow basin. The cristid obliqua extends slightly labially to the midpoint of the trigonid. From a lingual perspective the entire tooth resembles a trident.

The m1 is rectangular with a short trigonid, metaconid higher than protoconid, and paraconid much higher than on the p4, being nearly the height of the metaconid. Both paraconid and the metaconid are aligned nearly opposite to the protoconid. Between the paraconid and metaconid there is still a relatively deep, flat, and expanded nearly u-shaped groove that provides an elongation to the trigonid. The talonid is slightly broader than the trigonid, with the hypoconid the largest cusp, hypoconulid the smallest cusp, and the entoconid as the tallest among the three cusps which encompass a broad and spacious basin. The reduced height of the protoconid and hypoconid is due to occlusal wear. The cristid obliqua extends slightly labially to the midpoint of the trigonid

Table 5. Cranial measurement comparison of three anagalid species (mm).

	<i>Linnania lofoensis</i>	<i>Anagale gobiensis</i>	<i>Anagalopsis kansuensis</i>
Supratemporo-orbital fossaal width	15.3	20	22
Palatal width at p4	12.9	12	13
Foramen magnum-canine length	47.4	48	63

The m2 resembles the m1 in morphology although trigonid and talonid lengths are equivalent and the trigonid is more narrowly rectangular. The m3 resembles both anterior lower molars but with an extremely high hypoconid that is situated slightly lower than the protoconid and a talonid that is rather elongated.

A shared character between the p4-m3 is the labial enamel extending further than lingual enamel such that labial crown height exceeds the lingual crown height.

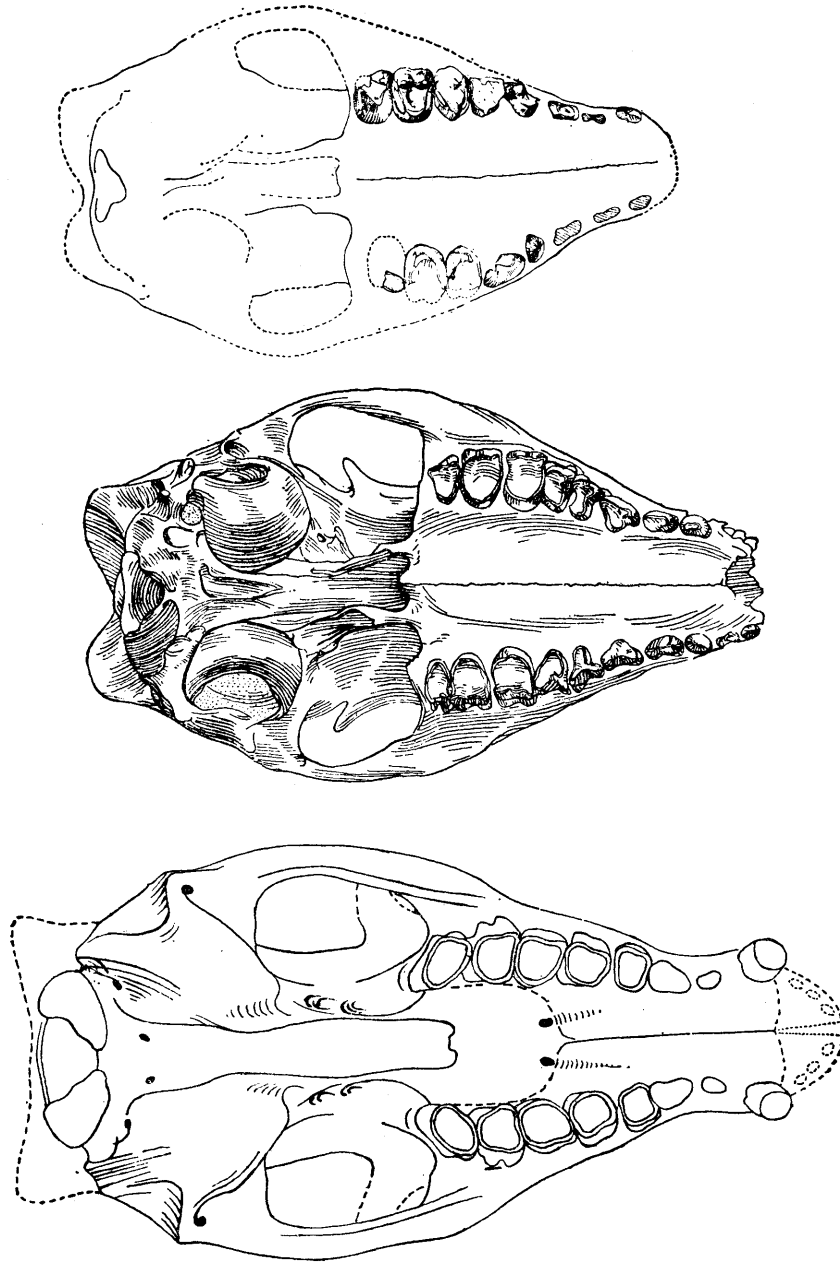


Figure 5. Cranial comparison between *Linnania lofoensis*, *Anagale gobiensis*, and *Anagalopsis kansuensis*.
Upper. *Linnania*; Middle. *Anagale*; Lower. *Anagalopsis*.

Comparison and discussion: The Nanxiong specimen is comparable to the anagalid taxa *Anagale gobiensis*, *Anagalopsis kansuensis* and *Kashanagale zofiae*. Its skull length approaches but is slightly shorter and much narrower than *Anagale*, and compared to *A. kansuensis* it is even shorter, as displayed in Table 5.

In addition to the narrow and short cranial outline, the size of the temporo-orbital fossa is conspicuously short at 11.4 mm whereas on *A. gobiensis* it is 14.6 and on *A. kansuensis* it is 33 mm. Dorsal cranial morphology is also distinct as the Nanxiong specimen is relatively flat but *A.*

gobiensis has a gradual increase in height from the nasals to the parietal and *A. kansuensis* is particularly high and inflated in the frontoparietal region.

Dentally, *Linnania* shares fundamental characters with *Anagale*, *Anagalopsis*, and *Kashanagale*, including nearly square upper molars, compact dentition, equivalent degree of hypsodonty, rectangular lower molars, and nearly equivalently lengthened trigonid and talonid. However, compared to *Kashanagale zofiae*, the latter's lower molar trigonids are not rectangular but are nearly triangular in occlusal outline; the protoconid is more anteroposteriorly compressed or columnar in form; the metaconid is more anteroposteriorly elongated or nearly equivalent to the protoconid; and the paraconid is low, widely separated from the metaconid, and not as tightly associated as on *Linnania*. Consequently, both cusps lie distantly from the protoconid and provide the trigonid with its triangular morphology. ?*K.* sp. nov. is represented only by a portion of a mandible with a deep ramus, and m3 talonid that is approximately half the size of *Linnania*.

Anagale gobiensis has a relatively large dentition, the P2 has three roots, and the P4 is more molariform in maintaining four cusps with the appearance of a hypocone and metaconule. The *Linnania* P2 maintains only two roots and its P4 lacks a hypocone and metaconule. Furthermore, the *A. gobiensis* M3 is distinctly smaller than the M2.

Anagalopsis kansuensis is quite different in its large morphologically distinct dentition. Its P1 is single rooted, the P4 is square and highly molariform, the M3 is reduced and distinctly smaller than the M2, p4 is more molariform than P4, and its trigonid is short and broad, whereas the *Linnania* P1 is double rooted, the P4 is subsquare, the M3 is not extremely reduced, being only slightly smaller than the M2, and the p4 is submolariform with a long trigonid.

The preceding descriptions indicate clearly that *Linnania* is distinct from the other three anagalid genera. The type species of *Anagale*, which is representative for the family, is from the Oligocene Ulan Gochu Fm. of the northern Sharamurun region of Ulanqab Meng, Inner Mongolia. The initial description by Zengsheng Xin (1931) erected a new insectivore family that approached the Tupaiidae, a phylogenetic interpretation that was accepted and utilized for a long time. But following placement of the tupaiidae within the Primates, the family Anagalidae became an excluded extinct member of the order. In 1951 Bohlin described the Oligocene *Anagalopsis* from the Huihuibu (Huihuipu) region of Gansu. He considered *Anagalopsis* extremely close to *Anagale* and believed that the family lay in an uncertain phylogenetic position, unassociated with either the tupaiids or primates. Later, McKenna (1963) reevaluated the type and supplementary specimens for *Anagale*, after which he advanced and supported the conclusions of Bohlin (1951).

Recently, Szalay and McKenna (1971) reviewed the Gashato Fauna from Mongolia, described the new genus *Khashanagale*, and elevated the family to the order status of Anagalida, recognizing within the order the four families Anagalidae, Zalambdalestidae, Pseudictopidae, and Eurymylidae. This order is considered as endemic to the Cretaceous to Early Tertiary of Asia. Although these families share conspicuous synapomorphies (Szalay and McKenna, 1971, p. 301), their phylogenetic relationship is still suspect pending the acquisition of more data, particularly with regard to the Eurymylidae. This recent phylogeny however is generally more parsimonious than those of the past.

Linnania is distinctly phylogenetically close to the genus *Anagale* and undoubtedly represents the most primitive genus in the order known to date. In cranial morphology it is relatively short, small, narrow, low, and flat with a small temporo-orbital fossa. The stratigraphically younger *Anagale* has a broader skull and an enlarged temporo-orbital fossa. The precise chronology of *Anagalopsis* is unclear but it is also distinctly younger with an elongated and broadened skull and a more enlarged temporo-orbital fossa.

The relatively primitive dental sequence of *Linnania* is reflected in its sub-square P4 lacking a hypocone while the *Anagale* P4 is highly molariform by being square, possessing four cusps, one of which is the hypocone, and having a rather projected metaconule. Another significant distinction of *Linnania* is the third upper molar which is not distinctly reduced but which is reduced on *Anagale*. *Anagalopsis* is more dentally derived than both *Linnania* and *Anagale* with both upper and lower fourth premolars highly molariform and an M3 that is distinctly reduced.

Worth noting is the double rooted condition of the P1 and P2 on *Linnania*, whereas in *Anagale* both upper and lower first premolars are double rooted, but the P2 has three roots, and in *Anagalopsis* the P1 is single rooted and P2 is double rooted, which probably represents the plesiomorphic condition. In general dental morphology *Anagale* and *Anagalopsis* are more derived than *Linnania*.

The age of *Khashanagle* approaches that of *Linnania* but because the specimen is too fragmentary, adequate comparisons are difficult. The lower molars display the m3 as distinctly more reduced than the m2, which resembles *Anagale* and *Anagalopsis* but differs from *Linnania*.

Another distinction also worth noting is the relatively well developed paraconid on *Linnania* which is nearly equivalent in size to the metaconid. The plates illustrating *Kashanagle* indicate an undeveloped paraconid lower than the metaconid, but this may be the result of occlusal wear. However from the perspective of the developmental trends within the genera it appears the paraconid tends to become reduced.

The anagalids are evidently very abundant and represented by diverse closely related forms in East Asia during the middle and Late Paleocene, as documented by the rich data collected in Anhui Province which is now under investigation.

Tillodontia

Esthonychidae

Lofochaius brachyodus Chow, Chang, Wang, and Ting 1973

(Plate II, Figs. 3-5; Plate III, Figs. 1-3)

Lofochaius brachyodus Chow et al., 1973; Vertebrata PalAsiatica **11**(1), 31-32.

Type: A poorly preserved skull that is relatively complete in outline bearing left P4-M3 with damaged crowns and right P2, M2 and M3 (V4239).

Locality and stratigraphic position: Middle Paleocene capping sediments of the Shanghu Mem., Lofozhai Fm. Yadoao (perhaps mistaken for Zengde'ao), Nanxiong Co., Guangdong Province.

Genus and species diagnosis: A relatively small species with dental morphology precisely that of the Tillodontia but with a size nearly half that of *Esthonyx bisulcatus*. Skull is narrow and long with a primitive rostrum that is short and small. Upper dental formula is 3?·1·4·3, P1 and P2 are double rooted, and brachydont molars are relatively broad. Apices of paracone and metacone approach the midline of the molar, labial wall is particularly gently sloping, and parastyle and metastyle are well developed with the parastyle particularly large, being nearly the size of the paracone. Protocone is larger than the principle labial cusps and rises precipitously; anterior and posterior cingula are well developed with the posterior cingulum particularly conspicuous, although it does not extend to the lingual portion of the protocone but comprises a

hypocone shelf posterior to the protocone. Metastyle on the third molar has become lost causing the diminishment of the posterior half of the tooth. Conules are well developed.



Figure 6. Ventral view of *Lofochaius brachyodus* Chow et al., 1973 (V4239) X2.

Description: Weathering and compressional distortion have damaged the skull. The right side is slightly askew and sutures are indistinct, prohibiting the determination of individual cranial elements. In outline the skull is narrow and long with a rostrum that rapidly constricts anterior to the P3 where it becomes primitively short and narrow. The nasals and maxillae are fragmented but coalesced by matrix and lack any distinguishable sutures. Frontals are narrow and slightly inflated; a supraorbital process is slightly projected on the right side but is not preserved on the left side; the parietal is also slightly projected; and sagittal crest is relatively well developed to compose a narrow ridge. Orbit and temporal fossae are confluent with an anterior margin located anterodorsal to the M1. On the right side only an extremely small piece of the zygomatic arch is preserved but on the left side only the middle portion of the arch is missing, with the remaining arch as being relatively robust, flat, and straight. The suborbital foramen is located dorsal to the P3. The palate is relatively flat with relatively close dental batteries. From the M3 to the P3 the dentition gradually converges but anterior to the P3 the tooth rows become parallel. Palatal width at the M3 is 12.2 mm and at the P3 is 7.9 mm. The occipital plane is relatively high with several depressions upon it, the occipital crest is semicircular and projects posteriorly; and occipital condyles are relatively small.

Table 6. Cranial measurements of *Lofochaius brachyodus* (mm).

Estimated cranial length	72.0
Facial length (anterior orbit to anterior P1)	20.5
Cranium length (anterior orbit to occiput)	47.8
Orbit length	23.7
Dorsal orbital breadth	19.2
Cranial height (at M2)	24.2

On the left side the M2 and M3 are completely preserved but other cheek teeth only preserve roots or crown outline, and canine and incisors are absent. Remnant dentition and alveolae indicate the presence of four premolars and three molars in compact association. Molars are brachydont and slightly higher lingually.

Among the four upper premolars, only the P4 is distinguishable in outline. The P1 is represented by two equivalently sized linearly aligned roots. The P2 is also only represented by two roots, the anterior of which is relatively small and situated close to the labial plane while the posterior root is twice the size of the anterior root and is located more lingually. On the right side a portion of the lingual wall of the P2 principle cusp is retained suggesting the cusp is semicircular in occlusal view. The P3 has three roots, on the left side there is a well developed lingual cusp which is crescentic lingually, relatively precipitous labially. A posterior cingulum is present.

The P4 outline, remnant portion of protocone, and metaloph indicate its high degree of molarization. It is equivalent in size to the M1 with a well developed robust and bluntly conical protocone that is crescentic lingually. The metaloph is preserved and a posterior cingulum is well developed which ascends from the metaloph lingually to compose a low hypocone shelf or balustrade, although it does not extend as far as the lingual protocone.

Three upper molars with very distinct cusps are preserved on the left side with the exception of the M1 which is damaged and represented as a transverse rectangle in outline. On the right side only the M2 and M3 outlines are represented.

The M2 is also a transverse rectangle, slightly larger than the M1, and the broadest tooth in the sequence. The protocone is well developed, relatively long and broad, and relatively precipitous lingually and labially. From occlusal perspective there is a small groove at its apical midpoint causing it to be antero-posteriorly bifid, however, this groove is extremely shallow and may be the result of fracturing as the anterior half of the lingual protocone is damaged. Paracone and metacone are blunt, their lingual side is roundly convex, labial side is thin and flat, or crescentic, their apices approach the tooth's midline, and the labial wall is particularly gently sloping. Preparacrista and postmetacrista are well developed to contact the parastyle and metastyle. The parastyle is particularly well developed with a size approaching the paracone. Anterior and posterior cingula are also well developed with the posterior cingulum being more conspicuous but its terminus does not reach the lingual side of the protocone but does ascend to compose a low hypocone shelf. The trigon basin separates the protocone from the paracone and metacone. The enamel is damaged on the protoloph and metaloph but the protoconule and metaconule are still visible vestigially.

Table 7. Dental measurements of *Lofochaius brachyodus* (mm).

		M3	M2	M1	P4
Length	Labial	4.25	4.41	4.00	3.50
	Medial	3.74	4.00		3.00
	Lingual	3.20	3.50		
Width		7.60	7.74	7.71	6.70
P1-M3 length		29.5			

The M3 is morphologically similar to but slightly smaller than the M2 and has been fractured at its mid-section due to compressional distortion, resulting in the lingual side being anteriorly askew. The protocone is relatively blunt and not as elongated as on the M2. A metaconule is extremely well developed but the protoconule is damaged and thus indistinct. The metastyle has become lost causing the posterior half of the tooth to be contracted. Anterior and posterior cingula are well developed and a hypocone shelf is extremely conspicuous.

Comparison and discussion: The cranial and dental characters described above indicate *Lofochaius* to be an extremely primitive ungulate that shares a number of plesiomorphies with the Esthonychidae, such as the slender and long skull which rapidly narrows anterior to the P3 and a relatively well developed sagittal crest. These characters are also distinct on stratigraphically younger genera such as *Tillodon*, which is larger and more derived.

Lofochaius possesses several principle characters that are shared with *Esthonyx*, the most primitive genus in the family, including brachydonty, upper molars higher lingually, relatively high degree of P4 molarization, well developed protocone, pronounced parastyle and metastyle, well developed anterior and posterior cingula on molars extending to the lingual protocone, and the loss of the M3 metastyle. Particularly shared with *E. auctidens* is the extremely well developed posterior cingulum on P4-M3 which ascends to compose a hypocone shelf, and the gently sloping labial wall of the paracone and metacone which are present as crescentic cusps. Particularly shared with *E. bisulcatus* is the double rooted P2 and moderately acute tooth cusps. However the most conspicuous character is the much smaller size of *Lofochaius* compared to the other species in the family, being approximately half the size of *E. bisulcatus* which is currently the smallest species known.

Lofochaius is dentally distinct from *Esthonyx* in numerous characters, the most notable of which is the presence of four premolars, whereas the dental formula for the family is three. Moreover, *Lofochaius* has an extremely compact dentition that lacks small or large diastemae; but other members of the family possess a diastema anterior to the third premolar, particularly on younger taxa where this feature becomes elongated. Additionally, *Lofochaius* lacks a hypocone. Only a hypocone shelf is present that is composed of the posterior cingulum. This also differs from other members in the family.

Current data is extremely inadequate, with the absence of a mandible, lower cheek teeth, and particularly upper incisors and canines. However, from perspective of the data at hand, the Nanxiong specimen is a primitive ungulate that appears to represent the most primitive species of the Tillodontia.

The Nanxiong specimen shares several characters with adapid primates such as the relatively narrow and long skull, well developed sagittal crests, the presence of four premolars and three molars in compact association, and particularly the characters of transversely broadened upper molars and a well developed parastyle. However, observation in detail notes conspicuous distinctions in the adapids, as the primates have a broader skull with a laterally projected zygomatic arch, relatively elevated frontals and parietals, upper molars are not higher lingually, and anterior and posterior cingula completely encompass the protocone. Consequently, *Lofochaius* is recognized as a primitive ungulate that only shares plesiomorphies with several taxa of primates.

Formerly, a number of workers placed the tillodonts within the Carnivora (Cope 1876; Schlosser, 1923; Abel, 1914; Winge, 1923). But the *Lofochaius* specimen, although limited, indicates extreme distinctions from this order. Prior to the discovery of the Nanxiong specimen the most primitive tillodont was recognized as *Esthonyx*, about which there were numerous controversies regarding its origin, with some workers believing it arose from the family Oxyclaenidae (now included in the Arctocyonidae) (Gregory, 1910; Gasin, 1953), while other workers regarded the genesis of the tillodonts as unclear or from the Insectivora (Simpson, 1945). Van Valen (1963) proposed that the tillodonts arose from the Paleocene arctocyonid "*Claenodon*" *procyonoides* and therefore should be regarded as a suborder of the Condylarthra. He moreover conducted a detailed comparison of the dentition and postcranial characters of *Esthonyx spatularius* from the Late Paleocene Clark Fork Basin (AMNH 56620 and 16065) and a "*C.*" *procyonoides* collected from the Paleocene of the San Juan Basin (AMNH 16554). The *Esthonyx* specimens preserve only a single M2 that Van Valen believed resembled "*C.*" *procyonoides* in morphology, moderate cusp height, labially placed paracone and metacone, and a posterior cingulum that does

not extend to the lingual side. However, there are also conspicuous distinctions such as the high degree of “*C.*” *procyonoides* P4 molarization and well developed hypocone. On another “*C.*” *procyonoides* specimen the posterior cingulum reaches the lingual side. Despite these distinctions, Van Valen believed that from an evolutionary perspective, later species of *Esthonyx* also gradually embody these characters and thus its descendance from “*C.*” *procyonoides* is evident.

The Nanxiong specimen had yet to be studied at the time of Van Valen’s publication and at that time *Esthonyx* was regarded as the most primitive tillodont genus, a status which is currently replaced by the *Lofochaius*, and which should be contemporaneous with “*C.*” *procyonoides*. Based upon the dental characters of the three molars, *Esthonyx* and *Lofochaius* are hereby considered to have a closer affinity than to the arctocyonid mentioned above and it would therefore be inappropriate to consider the Tillodontia a suborder of the Condylarthra. The retention of the Tillodontia as an independent order is also supported by Rose (1972).

Sloan and Van Valen (1965) described the new arctocyonid *Protungulatum donnae* from the Cretaceous of Montana which, from its description and illustrations, shares several features with *Lofochaius* such as its transversely expanded M2 which constitutes the largest molar in the sequence, a well developed parastyle and metastyle, loss of the M3 metastyle and well developed anterior and posterior cingula. However, the Montana specimen is generally smaller with an M2 length of 4 mm and width of 6 mm and hence the shared characters are regarded symplesiomorphic for the most primitive ungulates. The description above suggests the Nanxiong specimen approaches the Condylarthra and may be descended from a primitive arctocyonid, but this cannot be confirmed with the limited data at hand.

Some specimens that are definitely related to *Lofochaius* have been found at Chaling, Hunan. They possess nearly all the essential features necessary to fill the gaps between *Lofochaius* and *Esthonyx*. These specimens are more advanced but approach the older taxon. They are from a higher stratigraphic horizon (probably Late Paleocene) and bear chisel-like incisors typical of tillodonts. Therefore the tillodont affinity of *Lofochaius* appears to be well founded.

The *Lofochaius* skull was collected in 1964 by the Hubei Academy of Geology (formerly the Southcentral Academy of Geology) and was mailed to IVPP for diagnosis. Also contained within the package were three small limb bones including a proximal humerus (V4239.3), distal femur (V4239.1), and a proximal tibia (V4239.2). A description of these elements is not conducted due to their fragmentary nature, although it appears, from a perspective of their preservation, that they probably represent post crania of *Lofochaius brachyodus*.

Condylarthra

Mesonychidae

Dissacus feiganensis Chow Chang, Wang, and Ting, 1973

(Plate IV, Fig. 1,2,4)

?*Dissacus feiganensis* Chow et al., 1973. *Vertebrata Palasiatica* **11**(1), p. 32.

Type: A damaged anterior portion of skull with left P3-M2 and right P4-M3 (V4229).

Paratype: An extremely fragmentary anterior portion of skull (V4230).

Locality and stratigraphic position: Middle Paleocene, middle portion of Hukou Mem., Lofozhai Fm., Hukou Commune, Nanxiong Co. Guangdong Province.

Diagnosis: Dental formula of $3? \cdot 1 \cdot 4 \cdot 3$ that approaches in size but is slightly smaller than *Dissacus navajovius*. Upper molars vary in breadth with M3 slightly smaller than M2 and protocone is well developed as an isolated lingual cusp that has a relatively precipitous lingual wall. A conspicuous longitudinal groove lies between the protocone and the two principle labial cusps, paracone and metacone are distinctly smaller and in tight association, with low vertical crests extending from the anterior paracone and the posterior metacone. The lingual cusp on the P4 and P3 is relatively well developed. A constriction is present on the posterior nasals at the P1.

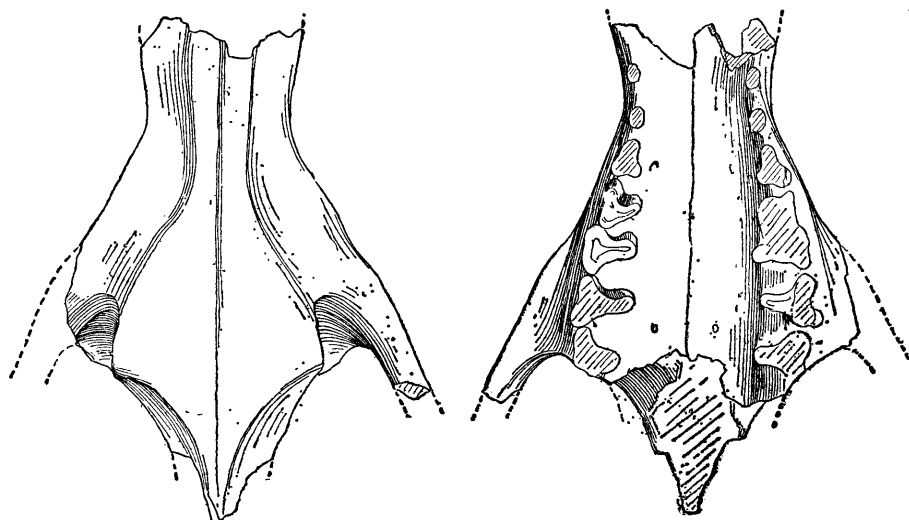


Figure 7. Type (V4229) of *Dissacus feiganensis* Chow et al., 1973.
Left. dorsal view; Right. Ventral view

Description and comparison: Two pieces of skull are preserved, among which V4229 is relatively well preserved with frontals, a large portion of nasals, maxillae, premaxillae, a portion of zygomatic arch, and anterior sagittal crests. The frontals have suffered slight compressional distortion, are relatively short, have a well developed frontal ridge, and the frontal parietal suture composes a relatively well developed sagittal crest. Additionally, a supraorbital process is extremely conspicuous. Nasals are slender and long with an extremely conspicuous longitudinal groove which broadens slightly anteriorly as it runs along the suture line. Nasals are constricted at their midpoint and become inflated posteriorly where they insert directly into the midpoint of the frontals. The contact of the premaxilla with the nasal process forms a relatively long slender line that extends distantly between the maxilla and nasal. The maxilla is relatively high, zygomatic arch is relatively straight and robust, the lacrimal extends into the facial region, anterior orbit runs anterior to the M2, and the suborbital foramen is positioned low and dorsal to the P3. On the palate, the maxillary fossae are relatively large and anterior foramina lie posteriorly, or at the posterior M2. Palatal breadth at the M2 is 39.2 mm and at the P4 is 32.3 mm.

Specimen V4230 has been shattered and heavily compressionaly distorted, preserving only the anterior half of the skull. No dorsal characters may be distinguished but an incomplete left and right M2 indicate that it is conspecific with the former specimen.

D. navajovius is a third larger than the Chinese specimens and is also incomplete but as in *D. feiganensis* has an anterior orbit that runs anterodorsal to the M2 and displays a similar placement of the suborbital foramen which is dorsal to the P3. The zygomatic arch on this genus is extremely straight and long indicating a particularly elongated cranium, and although the Nanxiang specimen only preserves a portion of the arch, it too appears by be relatively linear. The jugal of

D. feiganensis also resembles other members of the family by lacking an anteroventral branch and only possessing the dorsal branch which composes a relatively low ventral orbital margin.

The Nanxiong dentition is extremely restricted and very poorly preserved limiting the comprehension of its morphology. On the type the dentition has been completely worn or is only represented by tooth roots, although its dental formula may be recognized as $3? \cdot 1 \cdot 4 \cdot 3$. Incisors are not preserved; the canine appears to have been relatively robust based upon its alveolus; the P1 is extremely close to the posterior canine with a single root and conical cusp; and the P2 is also single rooted with a 2.7 mm diastema between it and the P1. The outline of the P3 is unclear although it is similar in size to *D. navajovius* and alveolae indicate that the relatively well developed lingual principle cusp is supported by an independent root,. The P4 is preserved on both the left and right sides and although the crown is worn, its outline indicates a length greater than breadth, the presence of a well developed lingual cusp nearly the same size as the labial cusps, and a well developed anterior cingulum.

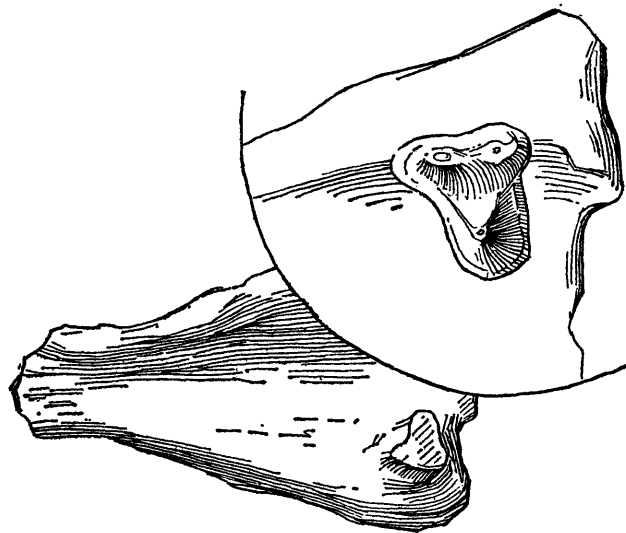


Figure 8. *Dissacus feiganensis* Chow et al., 1973 (V4230) X1, magnification X2.

Although the upper molars are all preserved, they have all suffered heavy occlusal wear. Their most significant characters lie in the excessive transverse breadth of the dentition, the base of the protocone is anteroposteriorly compressed, anterior and posterior margins of the teeth are nearly parallel, and the M3 is smaller than the M2.

On specimen V4230 the M2 is relatively well preserved with three well developed principle cusps. The protocone is a small isolated conical cusp with a precipitous lingual wall, the metacone is relatively small, or slightly smaller than the paracone, and a low anterior crest projects off the paracone. The M1 resembles the M2 but is slightly smaller. The M3 is extremely poorly preserved but from occlusal outline is it determined that it is distinctly shorter and narrower than the M2 with an unprojected posterolabial angle.

The reduced M3 is a character that is difficult to compare to other Asian mesonychid genera as currently there are no upper third molars available and other comparative specimens are younger taxa that are twice as large or larger. Furthermore, on the younger taxa the molars are quite distinct from *D. feiganensis*, being either longer than broad, or equivalent in dimension to compose an equilateral triangle, contrary to the Nanxiong specimens in which molar breadth greatly exceeds its length.

Table 8. Comparison of femoral measurements between *Dissacus feiganensis* and *Mesonyx obtusidens* (cm).

	<i>Dissacus feiganensis</i>	<i>Mesonyx obtusidens</i>
Length	11.33	22.48
Distal breadth	1.76	4.2
Proximal breadth	2.55	4.72

There are currently seven species of *Dissacus* recognized in North America, although the majority of these are known only from lower dentitions. *D. navajovius* and *D. saurognathus* preserve complete upper dentitions with a dental formula resembling *D. feiganensis*, and their M3 is reduced, although their morphology is distinct in that their length and breadth are nearly equivalent (particularly the M2) to compose an equilateral triangle, while the outline of *D. feiganensis* is an isosceles triangle. Moreover, the North American species have relatively well developed cingula which are absent (or only restricted to the labial side) on the Chinese species. Table 9 illustrates the dental measurement discrepancies between the North American and Chinese species.

Table 9. Comparison of dental measurements between three species of *Dissacus* (mm)

	<i>D. feiganensis</i>	<i>D. navajovius</i>	<i>D. saurognathus</i>
Left P1-M2 length	54.0	80.4	90.0
Left P1-P4 length	30.2	49.2	51.3
Left M1-M2 length	17.5	25.9	32.3
Right P4-M2 length	25.9	38.2	45.4
P1 LxW	4.8x3.6		8.8x 5.7
P2 LxW	5.5x4.6		11.2x7.5
P3 LxW	7.2x5.7	10.8x6.9	12.2x9.8
P4 LxW	7.3-8.7x6.5	12.0x9.5	13.6x12.3
M1 LxW	8.0x8.9-10.0	12.5x11.0	15.4x16.3
M2 LxW	9.0x10.4-12.0	13.1x12.4	17.1x16.9
M3 LxW	7.4x7.5	7.9x8.5	10.0x12.7
P1 L/W ratio	1.33		1.54
P2 L/W ratio	1.19		1.49
P3 L/W ratio	1.26	1.55	1.25
P4 L/W ratio	1.23	1.26	1.15
M1 L/W ratio	0.90-0.80	1.13	0.95
M2 L/W ratio	0.83-0.58	1.06	1.01
M3 L/W ratio	0.96	0.89	0.79

Comparisons conducted above indicate that *D. feiganensis* is particularly distinct from its North American counterparts and that it very possibly may represent a new genus. However the paucity of current data from Nanxiong and particularly the absence of a lower dentition prohibits the erection of a higher rank. Recently, several complete lower dentitions have been recovered from equivalent age strata in Qianshan Co., Anwei Province, which may provide supplemental or revised descriptions for this species.

A left femur (V4231) is also represented in the Nanxiong collection that is identified as representing the Mesonychidae. It is completely preserved with a relatively narrow, high, and convex anterior surface; posterior surface is relatively flat and straight; and a lesser trochanter is

well developed, situated relatively high, or at a point approximately one-fifth from the proximal end. The third trochanter is also well developed and located approximately one-third down the shaft from the proximal end. Proximally, the femur is relatively broad with an anteriorly projected elliptical head, the greater trochanter sits just slightly higher than the head, and the trochanteric fossa is extremely deep. The distal end is relatively narrow and rather anteroposteriorly excavated; the lateral condyle is slightly large, intercondylar fossa is relatively shallow, troclea is narrow, and the medial condyle is distinctly more inflated than the lateral condyle.

Table 8 indicates that although there is a wide discrepancy between *D. feiganensis* and *Mesonyx*, as the latter is nearly twice the length of the former, their morphology is extremely similar in the rather broad proximal end, the greater trochanter lying on nearly the same plane as the femoral head, the high placement of the lesser trochanter being only one-fifth from the proximal end, and the third trochanter being one-third down the shaft. However, there are several distinctions distally as *Mesonyx* is proportionally twice the breadth with a broader troclea.

The presence of the genus in the Gashato Fm. of Mongolia has recently been reported by Szalay and McKenna (1971), but no corresponding parts are available for comparison.

***Dissacusium* gen. nov.**

***Dissacusium shanghoensis* (Chow, Chang, Wang, and Ting)**

(Plate IV. Fig. 3)

?*Dissacus shanghoensis* Chow et al., 1973, *Vertebrata Palasiatica* **11**(1), p. 32.

Type: A completely preserved right M2 (or M1) (V4232)

Locality and stratigraphic position: Middle Paleocene lower Shanghu Mem. of the Lofozhai Fm. from Shanghudong, Hukou Commune, Nanxiong Co., Guangdong.

Genus and species diagnosis: A mesonychid species approximately twice the size of *Dissacus feiganensis*, tribosphenic with breadth greatly exceeding width, relatively robust protocone, relatively low metacone, and well developed labial cingulum.

Description and comparison: Only an upper molar referable to an M1 or M2 represents this species. The enamel has been damaged around the protocone, although its remnant morphology indicates it is robust, conical, and much larger than the paracone and metacone with a rather precipitous lingual wall. Cingula at the external angles are well developed and extend from the paracone and metacone to encircle the labial wall. Both paracone and metacone are conical and in close association. Consequently, there is formed a single oblique wear facet composed of paracone and metacone. Extending from both the anterior paracone and posterior metacone from their apices to their base is a low relatively linear crest. Tooth length is 10.5 mm and width is 16.6 mm.



Figure 9. Upper molar (M1?) of *Dissacusium shanghoensis* Chow et al., 1973 (V4232).

Measurements and morphology of the Shanghudong specimen distinguish it from *Dissacus feiganensis*. Although both share the characters of being tribosphenic with a breadth that exceeds length, the Shanghudong specimen has a more well developed cingulum, is larger, and has a smaller breadth to length ratio of 0.63 which is less than the M1 ratio or average of the M2 ratios of *D. feiganensis*. Compared to other species of *Dissacus* the Shanghudong specimen is also extremely distinct in its length breadth ratio, being nearly half that of *D. navajovius*.

***Hukoutherium ambigum* Chow, Chang, Wang, and Ting, 1973**

(Plate V, Figures 1 and 2)

Hukoutherium ambigum Chow et al., 1973. *Vertebrata Palasiatica* **11**(1), pp. 32-33.

Type: A damaged mandible (V4233).

Locality and stratigraphic position: Middle Paleocene, middle Shanghu Mem. of the Lofozhai Fm., Nanxiong Co., Guangdong.

Genus and species diagnosis: A moderate sized mesonychid (?) with a mandibular dental formula of 3·1·4·3. Canine is robust, trenchant, and posteriorly curved. Mandibular condyle is situated low or nearly on the same plane as the dentition, lower premolars are single circularly blunted cusps, lower molar talonids are extremely well developed and rectangular in occlusal view, and paraconid is small. A well developed lingual cingulum is present and a diastema is absent.

Description: The specimen has suffered compressional distortion and as such is fragmentary, although the left mandible is slightly better preserved with three incisors, the basal portion of a canine, three premolars, and the majority of an m3.

The coronoid process is relatively broad, being 65.3 mm at its base, but its apex has been broken. Mandibular condyle is situated low, or at the same level as the dentition, and is relatively small, being 25.4 mm in transverse diameter and 17.9 in vertical diameter. The angular process is missing. The anterior end of the coronoid process initiates at the m1 as a relatively oblique lateral ridge at a 135° angle to the ramus. At the m2-m3 it increases in thickness causing an expansion of the ramus. The masseteric fossa is relatively shallow although a relatively deep sulcus is present posteroventrally on the anterior margin which may be due to taphonomic conditions rather than reflecting its true morphology. Only a vestigial remnant of the mental foramen is present anteroventral to the p2.

The right mandible is fragmentary, preserving only two incisors, a nearly complete canine, portions of two premolars, and portions of two molars. Coronoid process, angular process, and condyle are missing.

Incisors are well preserved with three in tight association on the left side while the right side preserves the two posterior incisors the third of which is represented only by its root. The i1 is the smallest in the series with a rounded anterior wall and constricted posteriorly. The left i2 is relatively large and is nearly square in cross-section with a longitudinal groove lying medially and which is rather conspicuous posteriorly. The right i2 is relatively narrow and is morphologically vague, including its longitudinal groove, due to compressional distortion. The i3 is slightly larger than its preceding tooth with a root that is triangular in cross-section.

The right canine is relatively complete, trenchant, elliptical, posteriorly curved, but has a broken apex. Laminations or corrugations are indistinct due to damaged enamel.

The p1 is preserved only on the left side as a single cusp and root and is much smaller than the posterior premolars. Its labial side is slightly rounded, lingual side is relatively flat, and there is a conspicuous 5.2 mm diastema between it and the canine. The p2 is indistinct in outline due to the loss of its posterior portion. The tooth is relatively thin and flat, labial side is slightly rounded, and its principle cusp is posteriorly oblique. The p3 is distinctly divided into a principle and secondary cusp which may be due to compressional distortion. Nevertheless, the crown is conspicuously posteriorly oblique, the principle cusp is relatively high, the secondary cusp is low, distinct, and positioned labially.

Table 10. Mandibular measurements of *Hukoutherium ambigum* Chow et al., 1973 (V4233) (mm).

Mandible length	260.2
Ramus height	31.5
Ramus thickness at m3	25.4
Canine-m3 length	136.0
Length of p1-p4	53.0
Length of m1-m3	54.9
Left i1 LxW	3.6x4.9
Left i2 LxW	5.0x6.9
Left i3 LxW	7.4x7.8
Right i2 LxW	5.0x6.8
Right i3 LxW	5.9x—
Remnant canine height	32.9
Basal canine anteroposterior length	21.2
Basal canine breadth	12.5
p1 LxW	6.4x4.2
p2 LxW	8.9x4.5
p3 LxW	10.4x5.3
p4 LxW	18.0x8.6
m1 LxW	16.2x9.0
m2 LxW	20.4x11.6
m3 LxW	18.85x10.1

The p4 on the right ramus is represented by the paraconid and anterior half of the protoconid as the posterior portion of the tooth is damaged. It is slightly molariform, broader than the p3 with a higher crown, the labial side is very slightly rounded, but lingual side is damaged. The paraconid is a small, well developed cusp and the entire tooth crown is posteriorly oblique. The left ramus only preserves the p4 root.

Three molars are present but are all incomplete. All the trigonids appear to be rounded and blunt with no indication of carnassial blades, unlike the condition of hyaenodontids. The m1 is only represented by tooth roots in the left ramus. The m2 is also only represented by tooth roots on the left side but on the right side preserves a trigonid. The tooth's lingual side has been shattered, labial side is relatively rounded, its apex displays a very slight wear facet, and anteriorly there lies a very low and undeveloped cusp that may represent the paraconid. A labial cingulum is absent.

The left m3 is relatively complete with only the anterolabial side of the trigonid damaged, while on the right side only the labial side of the trigonid is preserved. Thus, a composite m3 may be described as nearly rectangular in occlusal view, the lingual trigonid is slightly flat, there is no distinct cingulum, the talonid is square, hypoconid is well developed, and the labial side of the

tooth is rounded resembling the m2 but not as pronounced as the latter. A paraconid is indistinct but the protoconid is extremely well developed.

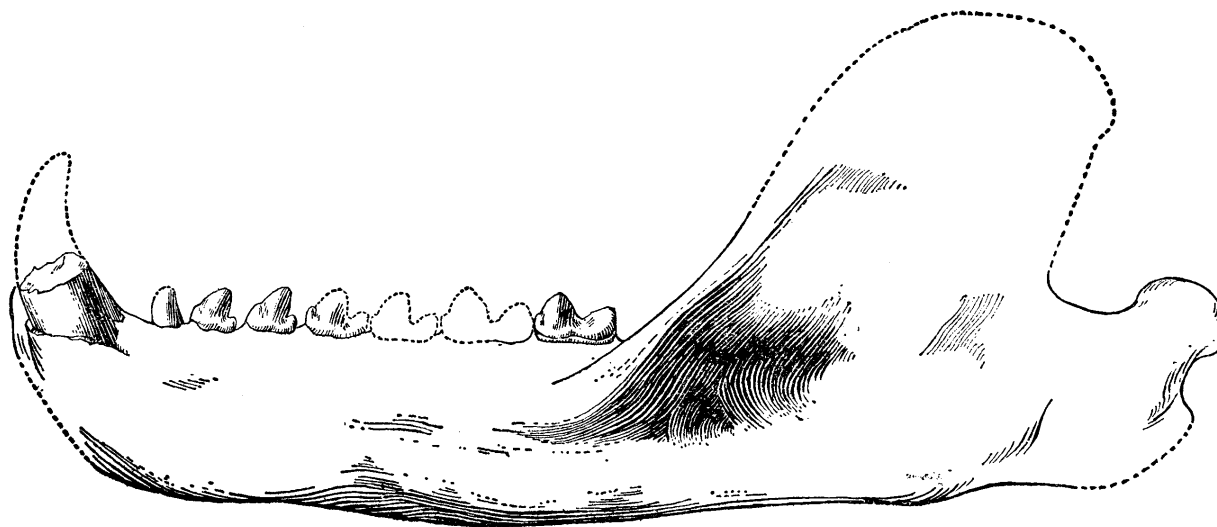


Figure 10. Lateral view of *Hukoutherium ambigum* Chow et al., 1973
left mandible (V4233) x2/3.

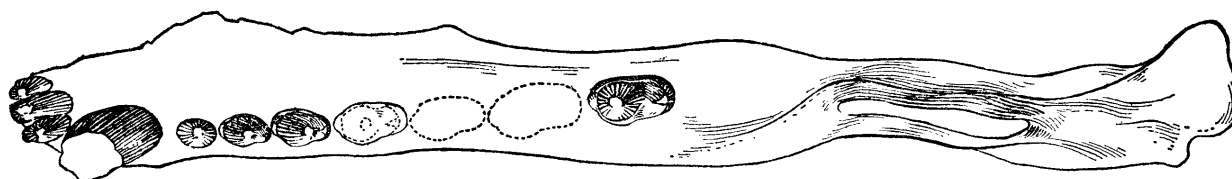


Figure 11. Occlusal view of *Hukoutherium ambigum* Chow et al., 1973
left mandible (V4233) x2/3

Comparison: The Hukou mandible very closely approaches the hyaenodontid genus *Apternodon* with characters including the dentition lying parallel to the base of the ramus and the low position of the mandibular condyle. However, distinctions lie in the morphology of the dentition, as the premolar principle cusp is posteriorly oblique, an incipient but distinct talonid occurs on the p3, a paraconid is present on the p4, and lower molar paraconids are small and don't compose a carnassial notch. On hyaenodontid premolars, principle cusps are not posteriorly oblique, p3 lacks a talonid, and paraconid is absent on p4 but rather conspicuous on the molars.

The Hukou specimen's p4 is not conspicuously high whereas on the Hyaenodontidae the p4 is the highest of the premolars to the point of exceeding the height of the m1. The hyaenodontid canine is nearly circular in cross-section, whereas on the Hukou specimen it is elliptical. These dental characters much more closely resemble the Mesonychidae. The Hukou specimen also displays an m3 that is more reduced than the m2 and lacks a carnassial notch, whereas on the Hyaenodontidae the m3 is the largest molar in the sequence with a distinct carnassial notch.

The Hukou specimen shares characters with *Dissacus saurognathus* including the relatively compressed and elongated molar morphology and the distinctly reduced m3. But *D. saurognathus* has a relatively straight and precipitous canine that doesn't curve posteriorly until its apex, while on the Hukou specimen this curvature initiates at the midpoint of the tooth with a larger degree of curvature. *D. saurognathus* has an extremely large diastema between the p1 and p2 while the p4 and m1 are nearly equivalent in size. On the Hukou specimen there is no diastema between the p1

and p2 which are instead in tight association and the p4, from the perspective of its roots, appears to have been slightly larger than the m1. These characters clearly distinguish the Hukou specimen from the genus *Dissacus* in addition to other genera of the mesonychines. In general, lower third molars of Asian mesonychines are not present, only two incisors are represented, and the taxa are much larger. The Hukou specimen is also distinguished from *Pachyaena* which has larger 25 mm long molars, in addition to a larger paraconid

This species is the largest mammal known in the fauna at present.

Hyopsodontidae

Hyopsodontinae

Yuodon protoselenoides Chow, Chang, Wang and Ting, 1973

(Plate VI, Figure 1)

Yuodon protoselenoides Chow et al., 1973; *Vertebrata Palasiatica* **11**(1), p. 33.

Type: A right mandible with p2-m3 (V4236)

Locality and stratigraphic position: Middle Paleocene lower portion of the Shanghu Mem. Lofozhai Fm. from Shanghudong, Hukou Commune, Nanxiong Co., Guangdong.

Genus and species diagnosis: Mandible and cheek teeth narrow, gracile, and long. Lower premolars (p2-p4) all display lophate talonids which gradually increase in size posteriorly. The p4 is not highly molarized, possess an incipient trigonid and displays a small projection at the position of the entoconid. Lower molar paraconids are relatively well developed, situated near the midpoint of the tooth, and are not in alignment with the metaconid. Talonids are basin-shaped with a relatively well developed hypoconid. The m3 talonid is elongated.

Description: The specimen is represented only by a ramus with p2-m3, p1 root, and canine root. The ramus is laterally compressed with a relatively shallow masseteric fossa, mental foramina lie anterior to the p2, and posteroventral to the p3.

The canine root is elliptical in cross-section and larger than the p1 root, with merely a 1 mm diastema between the two. Four premolars are represented with p2-p4 morphology generally equivalent, alignment is relatively compact, lingually the teeth are relatively flat, and labially they are rather rounded.



Figure 12. Occlusal view of *Yuodon protoselenoides* Chow et al., 1973 (V4236) with p2-m3 (x2)

The P1 is single rooted and subcircular. The p2 is damaged anteriorly, double rooted, labially rounded, principle cusp is high, and posteriorly there is a small crest representing the talonid.

The p3 is larger than the p2 with a rather conspicuous anterior cusp and a lingual crest that extends posteriorly from the principle cusp to the posterior cusp. Consequently, the anterior

portion of the tooth basically composes a relatively long and narrow “trigonid” posterior to which is a talonid that is composed of a high crest that is larger than on the p2.

The p4 is larger than the p3, morphologically similar, but with a more conspicuous and larger trigonid. The metaconid is basically discernable but distant from the paraconid. A small projection is present posterolingually suggesting the presence of an entoconid. Damaged enamel prevents a more detailed description of the morphology.

Table 11. Dental measurements of *Yuodon protoselenoides* (mm).

	p1 root	p2	p3	p4	m1	m2	m3
Length	1.95	3.4	3.75	4.0	4.2	5.0	7.0
Trigonid width		1.65	1.95	2.5	3.35	3.64	3.6
Talonid width		1.25	1.70	2.1	3.0	3.22	2.7

All three molars are present although there is some damage to the enamel and dentine. The lingual sides are relatively flat while the labial sides are rounded. The m1 is rectangular with a broad triangular trigonid, metaconid is relatively well developed or equivalent in size to the protoconid, and the paraconid is also rather conspicuous, not in alignment with the metaconid, and positioned mediolingually. The talonid basin is nearly the length of the trigonid, has a well developed hypoconid and entoconid, but a hypoconulid is unobservable due to damaged enamel. Cristid obliqua and metalophid are well developed. The m2 resembles the m1 in morphology with the three trigonid cusps encircling a shallow trigon basin. The talonid is damaged lingually, a hypoconid is conspicuous, and a well developed cristid obliqua extends to the midpoint of the trigonid. The m3 trigonid resembles that on the m2 with a high metaconid. The talonid is elongated to approximately one-third longer than the trigonid. The hypoconid is relatively well developed, cristid obliqua and metalophid are also well developed, but the condition of the entoconid is unobservable due to damaged lingual enamel.

Comparison and discussion: Dental characters of *Yuodon* are fundamentally consistent with genera in the subfamily Hyopsodontinae and may be compared more closely to the Middle Paleocene North American *Protoselene*. Nine genera are contained within this subfamily with characters including a P4 that is moderate in size, uninflated, and slightly molarized; a p4 that is generally broadened with a weak metaconid and a talonid basin; lower molar paraconid medially situated and not in contact with the metaconid, conspicuous entoconid, a completely enclosed talonid basin, and m3 that is very slightly or basically not reduced. These characters are also consistent with *Yuodon*.

Yuodon approaches *Protoselene opisthacus* in size, molar morphology, and with a thin, long, and gracile mandible. Additional shared characters include long double rooted p2-p4, well developed p4 talonid, trigonid cusps similar in morphology, well developed hypoconid and entoconid, and absence of molar cingula. However, distinctions between the Nanxiong specimen and North American forms are extremely notable as *Yuodon* does not maintain an inflated p3 or p4 but possess relatively well developed talonids, and paraconid and metaconid basically compose trigonids, whereas *Protoselene opisthacus* displays several inflations on the p3 and p4, p3 is not fully developed, p4 has only a well developed protoconid (anterior principle cusp) and a single posterior heel. On *Yuodon* lower molars the paraconid is lower than the metaconid and is posteromediolingually situated, while the hypoconulid is indistinct on the m1 and m2. But on the North American form the paraconid is situated precisely medially and a hypoconulid is distinct on the m1 and m2. Consequently, *Yuodon* has a higher molariform p4 and a more lingually placed paraconid on the molars indicating that it is a more derived genus than *Protoselene*.

P. novissimus (Gazin, 1956) is a Late Paleocene North American form that is not completely diagnostic. Its molars are relatively elongated and paraconid is medially and very slightly lingually situated which approach *Yuodon*. As other characters are indistinct, further comparisons cannot be conducted.

Mioclaeninae

Palasiodon siurenensis (Chow, Chang, Wang, and Ting)

(Plate VI, Figure 2)

Promiocleanus siurenensis Chow et al., 1973. *Vertebrata Palasiatica* **11**(1), p. 33.

Type: A damaged right mandible with p4-m3 (V4235).

Locality and stratigraphic position: Middle Paleocene Lower Shanghu Mem., Lofozhai Fm. from Xiuren, Nanxiong Co., Guangdong.

Etymology: *Siurenensis*, derived from the village of Xiuren near the locality.

Genus and species diagnosis: Size and basic morphology of cheek teeth particularly resembles the mioclaenid *Promioclaenus aquilonius* with a relatively short and small p4 that lacks a distinct metaconid and entoconid, m2 as the largest tooth in the sequence with breadth slightly larger than length, m3 slightly reduced, trigonid higher than talonid, protoconid and metaconid equivalent in size, and paraconid slightly reduced, positioned lingually, and in alignment with the metaconid. A distinct open valley on the talonid basin isolates the metaconid from the well developed entoconid, hypoconid is high, hypoconulid is medially situated and not in contact with the entoconid.

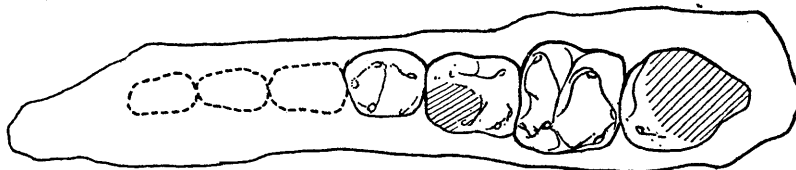


Figure 13. Right mandible with p4-m3 (V4235) of *Palasiodon siurenensis* (Chow et al., 1973) x3.

Description: Only a poorly preserved mandible represents this taxon. Canine and first three premolars are represented only by roots, p4-m2 are relatively well preserved, particularly the m2, while the m3 only preserves a portion of its trigonid. The p4-m2 length is 11.9 mm. Dental formula is $3\cdot 1\cdot 4\cdot 3$ with an extremely compact dentition that lacks any diastemae. The canine root is extremely small and columnar. The p1 is represented by an extremely small single root closely situated to the canine root. The p2 is double rooted, and the p3 appears to have a relatively large posterior portion based upon the remnant outline of the root.

The relatively short and broad outline of the p4 is quite distinct. The trigonid is particularly demarcated from the talonid with a remnant outline indicating it is extremely long, and with a lingually situated protoconid. There appears to be a projection at the anterior terminus of the paralophid, or the anterior slope of the protoconid, which may represent the paraconid, but the presence of this cusp is vague due to breakage of the enamel. Posterolingual to the paralophid is a relatively distinct metaconid. Together these three features compose an oblique trigonid. The talonid is much narrower than the trigonid and lingually there is still remnants of enamel. A distinct entoconid provides the tooth it with a high degree of molarization.

The outline of the m1 is extremely distinct with a trigonid and talonid nearly of equivalent length and breadth. The talonid basin is well preserved with a relatively worn hypoconid and entoconid but the hypoconulid is higher due to the lack of wear. The entoconid is quite distinctly isolated from the hypoconulid. The well preserved m2 is larger than the m1 with its breadth exceeding its length. The trigonid is very slightly compressed, enamel on the crown has been slightly damaged, the labial side is rounded, lingual side is flattened, trigonid is both higher and broader than talonid, protoconid and metaconid are nearly equivalent in size, and paraconid is slightly reduced and lingually situated. The talonid basin has a relatively well developed hypoconid that is situated near the hypoconulid. Cristid obliqua is short, extends obliquely to the midpoint of the trigonid, postmetaconid sulcus is relatively deep, and there is a conspicuous open valley separating the entoconid from the metaconid. Only a remnant of the m3 trigonid is present preserving the metaconid and paraconid. The m3 trigonid is narrower than that on the m2 and is closer in size to the m1.

Table 12. Dental measurements of *Palasiodon siurenensis* (mm).

	p4	m1	m2	m3
Length	3.74	3.85	4.24	4.75
Trigonid width	3.30	3.70	4.51	4.10
Talonid width	3.30	3.50	3.94	3.35

Comparison and discussion: Although the specimen representing this taxon is relatively restricted, it is diagnosed as a hyopsodontid particularly on the basis of its elongated and slightly inflated p4, slightly reduced m3, and medially situated paraconid in contact with the metaconid. These characters particularly resemble *Promioclænus aquilonius*.

On a number of species of *Promioclænus* the paraconid has either been reduced or become lost, but on *P. aquilonius* the paraconid is still quite distinct, positioned medially, and is in alignment with but lies slightly lower than the metaconid. This condition is identical in *Palasiodon*. Furthermore, the talonid basin of *Palasiodon* has an extremely well developed crescentic hypoconid, and the entoconid is quite conspicuous, being separated from the metaconid by a narrow open valley, which are characters also shared with *P. aquilonius*. But the most notable shared characters lie in the morphology of the p4 with *P. aquilonius* displaying a more derived p4 morphology for the genus as other species display only a single p4 principle cusp anteriorly and a small undeveloped talonid posteriorly. *P. aquilonius* also maintains a relatively complete trigonid with a distinct and low metaconid posterolingual to the protoconid, the occasional presence of a paraconid, and a relatively distinct entoconid. These characters are all consistent with the p4 of *Palasiodon*. Characters distinguishing *P. aquilonius* from *Palasiodon* include the near equivalent height of trigonid and talonid and m1 talonid is broader than the trigonid. *Palasiodon* differs in its entoconid being distinctly isolated from the hypoconid whereas on *P. aquilonius* the two cusps are extremely close.

Palasiodon's relatively high degree of p4 molarization approaches the mioclaenid *Litalesetes* although *Palasiodon* differs in its well developed entoconid not contacting the hypoconulid. Furthermore, *Litalesetes* does not have a reduced m3 which on *Palasiodon* is slightly reduced.

Palasiodon dental outline resembles *Ellipsodon* by being nearly rectangular in shape, but the latter's molars are longer than broad while the m2 of *Palasiodon* is broader than long. Additionally, the entoconid on *Ellipsodon* is not well developed.

Compared to two other hyopsodont subfamilies, the Hyopsodontinae and Ampheliscinae, *Palasiodon* differs completely from taxa in the latter subfamily which has only two equivalent

sized, rounded cusps in juxtaposition on the trigonid and the p4 maintains only a single principle cusp with the talonid represented by a single loph. *Palasiodon* shares several characters with some taxa of hyopsodontines such as a presence of a metaconid on the p4 and a distinct and extremely high entoconid, but principle characters of *Palasiodon* more closely approach the Mioclaeninea.

Periptychidae

?*Ectoconus* sp.

(Plate II, Figure 2)

Specimen: A relatively complete sacrum (V4226).

Locality and stratigraphic position: Middle Paleocene middle Shanghu Mem. of Lofozhai Fm. from north of Wutoujiang, Hukou Commune, Nanxiong Co., Guangdong.

Description: Sacral outline is a posteriorly attenuating trapezoid composed of four vertebra. Damage has been sustained to the left anterior end, anterior prezygopophyses, and dorsal spines. Diapophyseal fusion composes a thin and flat plate although neural spines are unfused. The dorsal sacral foramina are large, ventral spines are inconspicuous, centra are particularly laterally compressed, very slightly concave, and ventral sacral foramina are slightly small. The posterior sacral surface is slightly longer than the anterior surface.

The Nanxiong sacral count and morphology resembles *Ectoconus majusculus* although as the data is restricted it cannot be compared in more detail.

? Phenacodontidae gen. et sp. nov.

(Plate VI, Figure 3)

Specimen: A fragmentary right mandible (V4237) with a complete p2 and roots of ?i3, canine and p1-m2.

Locality and stratigraphic position: Middle Paleocene Shanghu Mem. of Lofozhai Fm. from Hukou Commune, Nanxiong Co., Guangdong.

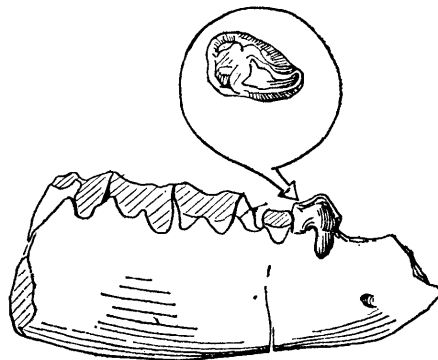


Figure 14. Left mandible with p2 of ?Phenacodontidae gen. et sp. nov. (V4237) x1, p2 x2.

Description: The mandible is relatively long and robust with a symphysis that extends obliquely to the anterior p2. A mental foramen is present ventral to the p1. The dentition is rather transversely compressed and extremely compact (with the exception of a 2 mm diastema between

the canine and the p1). Dental formula is $? \cdot 1 \cdot 4 \cdot ?3$. The i3(?) root is elliptical, the root of the canine indicates it was relatively small, and the p1 is small and single rooted. The p2 is the only completely preserved tooth in the sequence, is larger than the p1, double rooted, maintains thick enamel, small folds, and tuberosities on the lateral walls. Furthermore, it is not substantially molarized as a trigonid is not completely formed, the protoconid is relatively large, and the metaconid is small and only barely visible lingual to the protoconid. A paraconid is not evident. The talonid is barely recognizable or incipient, is extremely low, anteroposteriorly short, and transversely broadened. There is a small cusp at the approximate location for a hypoconid. Cingula are extremely well developed on the lingual and labial side of the talonid in addition to the lingual paraconid, but from the lingual talonid directly to the metaconid and at the labial protoconid, the cingulum is rather weak. The dentition gradually increases in size from the p1-m1, at the m2 it increases abruptly and greatly in size with relatively robust roots. An extremely thin enamel layer is present labially between the roots of the m1 and m2 and anteriorly and posteriorly on the roots into the alveolae. The depth of mandible at p3-4 is 18.95 mm and at m1 is 20.25 mm.

Table 13. Dental measurements of ?Phenacodontidae gen. et sp. nov.

c-m2 roots	p1 roots		p2		p3 roots		p4 roots		m1 roots		m2 roots	
	L	W	L	W	L	W	L	W	L	W	L	W
51.25	3.35	2.50	6.75	4.65	6.0	3.9	8.05	4.75	8.00	~4.9	10.25	~7.15

Comparison and discussion: This specimen is unlike any taxon in the Nanxiong Fauna and clearly represents a new genus and species. Mandible morphology and dentition alignment, particularly the anterior compaction of dentition and canine size, most closely resembles hypsodontid and phenacodontid condylarths although it is larger than other contemporaneous hypsodontids and approaches several phenacodontids in both size and morphology of p2. Preservation however prohibits more detailed description and consequently it is assigned only to the familial level until more complete specimens are recovered in the future.

Part III Systematics and skeletal morphology of the Bamalambdidae.

Specimens and systematics

Pantodonta

Bemalambdidae Chow et al.

Family diagnosis: As for Genus

***Bemalambda* Chow et al.**

Genus diagnosis: Skull is robust, being broad and short. Cranium is primitively small, oral region is relatively small, and facial region is extremely low, or much lower than other families in the order. Sagittal crest is extremely well developed and bifurcates with a distinct angle posterior to the facial region. Nasals are posteriorly transversely expanded and anteriorly in contact the premaxillae. A supraorbital process is conspicuous and the frontal is separated from the temporal by the parietal and sphenoid. Postglenoid process is rather compressed dorsoventrally. Posttympanic process and mastoid process are shorter than the postglenoid process, paramastoid process is extremely small, occipital condyles are relatively small, and the occipital surface is posteriorly oblique. Palatal foramina are located at P4 or M1, while basitubercle and postglenoid processes lie upon the same plane. Both a postglenoid foramen and pterygoid canal are present.

Osseous bulla is not observable. Mandible is short, robust, rather precipitous anteriorly, constricts distinctly posterior to the m3, and ventral margin of the ramus is sinuous. The anterolabial margin is convex while the coronoid process is straight and anteroposteriorly expanded. The mandibular condyle constitutes a transverse axle that is situated relatively low, or at the level of the dentition. The angular process is large, principally ventrally directed, and slightly posteriorly extended, but does not exceed the posterior margin of the condyle.

Dental formula is 3·1·4·3/3·1·4·3. Dentition is brachydont with incisors as small semicircular cones. The first incisor is smallest and the second incisor is largest in the series. Upper canine is trenchant with anterior and posterior carinae. Transverse axes of the cheek teeth are slightly posteriorly oblique to the axis of the dentition. P1 is single rooted and in a derived location, being slightly posterolingual to the canine. Molars are tribosphenic, particularly broad and short with a relatively deeply concave lingual margin. M1 and M2 metacone and paracone are weak and extremely closely set with an extremely small labially convex loph between them that composes a weak W-shaped ectoloph. The paracone and metacone are lingually positioned, being lingual to the midline of the tooth, and sit lower than the protocone, parastyle, and metastyle. The parastyle is larger than the metastyle and more labially projected. Hypocone and conules are absent. The M3 metastyle is reduced and the metacone has migrated labially to compose an asymmetrical V-shaped loph with the paracone.

The lower canine is a large triangular cone. The p1 is single rooted, p3 and p4 talonids consist of longitudinal crests, p3-m3 paraconids are extremely reduced; the metaconid is extremely well developed and on the p4 is equivalent in size to the protoconid, while on the molars it is more robust than the protoconid. The trigonid is much higher and slightly broader than the talonid with a rather narrow internal angle. The posterior sulcus is more gently open and broadened than the anterior sulcus, metastylid is absent, and entoconid is present. As opposed to the m1 and m2, the m3 talonid is longer than the trigonid with a relatively large hypoconulid that is not posteriorly projected to compose a hypolophid.

Seven cervical vertebrae are present with relatively well developed neural spines. There are approximately 17 thoracic vertebrae, eight lumbar vertebrae with well developed dorsal spines and diapophyses; three fused sacrals with diapophyses fused into a single plate, and the caudal series is long with the anterior nine vertebrae displaying zygapophyses for functional mobility. Scapula is fan-shaped with an open and spacious scapular notch and a robust spine. Clavicle is large and robust with a sinuous curvature. Humeral shaft is flat and straight, deltoid tubercle is located approximately two-fifths from the proximal end, a proximomedial condylar foramen is present, and the dorsal crest on the lateral condyle is extremely well developed and very high, expanding laterally at the proximal end. Radius and ulna are not fused, radial shaft is straight, and relatively flattened. Occasional longitudinal grooves are present at the apex of the olecranon process of the ulna. Forelimb is semi-plantigrade and relatively gracile, carpals are flat, and centrale and radiale are fused but completely unreduced. Metacarpals are relatively long, thin, and uncurved. The third phalanx is saddle-shaped. Iliac crest is relatively narrow. Femoral shaft is flat and straight, capitular fossa is relatively shallow, third trochanter is located one third down the shaft, and greater trochanter lies on either the same plane as the femoral head or is slightly higher. Tibia and fibula are not fused, distal tibia does not articulate with the astragalus, and the fibula is flat and straight with greatly inflated termini. Manus and pes are hoofed, hind limb is semi-plantigrade and rather dexterous in construction, metatarsals are flattened, and calcaneum possesses a distinct head, neck, and calcaneal foramen. The external cuneiform does not articulate with the calcaneum or the fourth metatarsal, metatarsals are flat and straight, and the third metatarsal articulates with the cuboid.

Species: *Bemalambda nanhsiungensis*

***Bemalambda nanhsiungensis* Chow, Chang, Wang, and Ting, 1973**

(Plates IX and XII; Plate IXXX, Figures 1-3; Plates XVI-XIX; Plate XX, Figure 1; Plate XXVII)

Bemalambda nanhsiungensis Chow et al., 1973, *Vertebrata Palasiatica* **11**(1), p. 34.

Type: A relatively complete skull lacking incisors, P1, and P2 (V4116).

Hypodigm: Six relatively complete skulls (V4114, V4117, V4118, V4119, V4120, V4121), two preorbital portions of skulls (V4124, V4125), right maxilla with P3-M3 (V4219), left maxilla with P3-M2 (V4126), left maxilla with M2 and M3 (V4127), left maxilla with M1 and M2 (V4144.14), right P4 and M1 (V4223.1), upper molar (V4223.2), right P2 (V4149), two left upper canines (V4151, V4152), two right upper canines (V4153, V4155), two relatively complete mandibles (V4130, V4131), eight right mandibles (V4132, V4134, V4136, V4138, V4140, V4141, V4147, V4156), four left mandibles (V4133, V4135, V4137, V4158), 18 fragmentary mandibles (V4139, V4142, V4143, V4144.8, V4144.1, V4144.9, V4144.10, V4144.11, V4144.12, V4144.13, V4145, V4146, V4217, V4220, V4221, V4222, V4225, V4227), left I2 (V4148), left P1 (V4150), Left M3 (V4154), and right P2 (V4223.3).

A partial skeleton includes posterior dorsal, lumbar, and sacral vertebrae, left ilium, femur, and ribs (V4157), atlas (V4159), axis (V4160), fifth cervical vertebra (V4161), five thoracic vertebrae (V4162.1, V4162.2, V4162.3, V4163.1, V4163.2), last dorsal to the eighth lumbar vertebra (V4164.20), rib (V4164.17) four lumbar vertebrae (V4164.1, V4164.2, V4164.3, V4165), three caudal vertebrae (V4144.8, V4164.4, V4228), one complete right scapula (V4169), six fragmentary scapulae (V4144.2, V4164.5, V4172.1, V4172.2, V4173.1, V4173.2), seven right humeri (V4164.6, V4174, V4175, V4177, V4178, V4179, V4180), three left humeri (V4181, V4182, V4185), two right radii (V4164.7, V4187), two left radii (V4188, V4189), a fragmentary radius (V4164.8), two left ulnae (V4164.9, V4166), four right ulnae (V4164.10, V4171, V4176, V4190), two fragmentary ulnae (V4191, V4192), three right ilia (V4170, V4193, V4194), two left ilia (V4195, V4196), a fragmentary ilium (V4144.3), a right femur (V4164.11), three left femora (V4164.12, V4199, V4200), five fragmentary femora (V4144.6, V4144.7, V4201, V4202, V4203), three patellae (V4164.13, V4164.14, V4204), two right tibiae (V4206, V4207), two left tibiae (V4164.15, V4205), eight fragmentary tibiae (V4144.15, V4144.16, V4144.17, V4164.16, V4164.18, V4209, V4210, V4211), proximal end of tibia and fibula (V4208), several left hindlimb phalanges (V4215), right astragalus (V4212) right calcaneum (V4214), left astragalus, V4213), and right astragalus and calcaneum (V4164.19).

The aforementioned specimens have been subjected to compressional distortion, and lie in varying degrees of breakage and deformity, which is particularly noticeable in the skull, humerus, femur, tibia, and astragalus. Deformation occurs in two distinct modes: compressed and broadened or thinly elongated, although morphological characters remain consistent.

Species diagnosis: Size approaches *Pantolambda bathmodon*. Body is relatively slender, skull is relatively short with the facial region approximately two-thirds the length of skull. Dorsal nasals are relatively flat and straight, lie slightly lower than the nasal-maxillary suture, anterior end is transversely broadened, medial portion is constricted, the nasal-maxillary suture composes a medially concave arc, and nasal process of the premaxilla extends approximately to the midpoint of the nasals. Sagittal crest is relatively long, high, and bluntly convex; zygomatic arch is relatively thin and from lateral perspective lies horizontally; mandibular corpus is relatively short with a posterior margin that lies approximately at the p1; mandibular fusion occurs extremely late; and anterolateral convex margin of the ramus is relatively well developed.

Table 14. Localities and stratigraphic positions of *Bemalambda* specimens.

Locality	Stratigraphic position	Specimen numbers
63083: Approximately 1 km north of Wutoujiang	Middle Shanghu Mem.	4144,4118,4126,4136,4137, 4138,4139,4140,4141,4142, 4143,4145,4147,4151,4153, 4155,4156,4158,4166,4169, 4171,4175,4176,4177,4180, 4181,4182,4188,4193,4195, 4200,4201,4205,4206,4209, 4212,4214,4217,4228,4159
63084: Approximately 200 m north of locality 63083, north of Wutoujiang	Middle Shanghu Mem.	4116,4117,4119,4120,4121, 4124,4127,4130,4131,4132, 4133,4134,4135,4146,4148, 4149,4150,4154,4157,4160, 4161,4162.1-3, 4163.1, 4163.2,4165,4170, 4172.1,4172.2,4174,4178, 4179,4185,4187,4189,4190, 4191,4194,4196,4199,4210, 4211.4213
63085: Approximately 1.5 km northeast of Wutoujiang	Upper Shanghu Mem.	4215
63087: One-half km southeast of Shanghudong	Lower Shanghu Mem.	4144.1-.3,4144.6-.18, 4223.1-.3
6233: 2 km south of Hukou	Middle Shanghu Mem.	4152, 4164.1-.20
Locality indet.		4173.1,4173.2,4192.4202, 4203,4204,4207,4208,4215, 4219,4222,4227,4225,4220, 4221

P2 is single rooted with a v-shaped ectoloph, a distinctly concave lateral wall, and maintains a small single principle cusp. M1 and M2 are relatively broad and short, paracone is larger than metacone, the v-shaped loph of the protocone is relatively acute, and lingual cingulum is relatively weak. Lateral carinae are present anteriorly and posteriorly on the p1, the p2 is single rooted with an indistinct trigonid, p3 is relatively narrow and long with a rather openly spacious v-shaped trigonid and a talonid present as a longitudinal crest. The p4 talonid is weak and crescentic.

Postcrania are comparatively longer, slender, and lightly built. The atlas is anteroposteriorly compressed, axis neural spine is shaped as an anterior facing right triangle, and lumbar diapophyses extend anteriorly and are dorsoventrally flattened. Glenoid fossa on the scapula is relatively long and narrow, humerus is relatively short, deltoid tubercle projects laterally, and humeral head is relatively flat. Ulna shaft is rather gracile and transversely compressed, olecranon process is rather transversely compressed with a sinuous notch, and there is a rather conspicuous groove at the apex of the olecranon. Radius shaft is anteroposteriorly compressed. Iliac notch is an obtuse triangle, iliac tubercle is rather weak, and the iliac crest is relatively thin. Proximal and distal ends of the femur are rather flattened and the third trochanter lies approximately one-third from the proximal end. Calcaneal neck is long with a convexly rounded head, there is an acute ridge between the tibia and fibula articular facets, and the sustentacular tali facet is concave. The astragalus is relatively slender with a relatively low sustentaculum tali that has a laterally extended and flattened facet for articulation with the cuboid, the medial astragalus is concave, while

laterally it maintains a distinct ridge that extends from the calcaneal articular surface to the distal end.

***Bemalambda pachyoesteus* Chow, Chang, Wang, and Ting, 1973**

(Plate VII and VIII; Plate XIII, Figure 4; Plate XIV and XV; Plate XX, Figures 2-7, and Plates XXI-XXVI)

Bemalambda pachyoesteus Chow et al., 1973; *Vertebrata Palasiatica* **11**(1) p. 34.

Type: Obliquely compressed skull and mandible. Left zygomatic arch is broken (V4122).

Hypodigm: A relatively complete skull and mandible (V4167); three crushed skulls and mandibles (V4123.1, V4128, V4129); a skeleton with skull, mandible, cervical, dorsal, sacral, and caudal vertebrae, scapula, clavicle, ilium, forelimb, hindlimb, and ribs (V4115); four damaged mandibles (V4123.17, V4128.1, V4218.2, V4218.25); a canine (V4123.14); atlas (V4123.5); axis (V4123.7); two lumbar vertebrae (V4123.11, V4218.3); two sacral vertebrae (V4123.4, V4123.16), a caudal vertebra (V4123.13, V4218.4); two incomplete left scapulae (V4168, V4218.5); two left humeri (V4184.1, V4183); a right humerus (V4186); five damaged humeri (V4123.18, V4123.19, V4218.7, V4218.8, V4218.9); left radius with carpals (V4216); two damaged ulnae (V4123.15, V4218.6); a left ilium (V4123.6); a right ilium (V4198); seven damaged ilia (V4218.10-V4218.16); two femora (V4123.2, V4123.3); nine damaged femora (V4144.4, V4144.5, V4184.2, V4218.17-V4218.22); two patellae (V4123.8, V4218.23); right calcaneum (V4123.10); left calcaneum (V4218.24); a damaged astragalus (V4123.9); and distal elements that may belong to this species including 10 metacarpals, metatarsals, and phalanges (V4224).

Table 15 *Bemalambda* localities and their stratigraphic positions.

Locality	Stratigraphic position	Specimen number
62.19e: 1 km east of Xiuren	Lower Shanghu Mem.	4122,4167,4123.2-4123.11,4123.13k-4123.19
6232: 1.5 km southwest of Hukou	Middle Shanghu Mem.	4115,4184.1,4184.2,4216
62.17a: 4 km southwest of Xiuren	Lower Shanghu Mem.	4218.1-4218.25
63086: Approximately 800 m northeast of Wutoujiang	Middle Shanghu Mem.	4128,4168,4183
63087: .5 km southeast of Shanghudong	Lower Shanghu Mem.	4144.4,4144.5
Locality indet.		4129,4186,4198,4224

Species diagnosis: Body size is similar to but more robust than *B. nanhsiungensis* with a longer facial region that is approximately four-fifths the length of the skull. Dorsal nasals are transversely convexly rounded, constricted at their midpoint, and unexpanded anteriorly. Nasal-maxillary suture is straight, nasal process of the premaxilla only penetrates the anterior third of the nasals, sagittal crest is short and low, and zygomatic arch is robust and sinuously curved such that in lateral perspective it is anteriorly low and ascends posteriorly. Mandibular corpus is relatively long with a posterior margin that attains the p2, symphyseal fusion is early, ramus is robust, the anterolateral convex margin is relatively weak, and masseteric fossa is deep.

Upper incisors are semicircular cones with lateral carinae, P1 is conical, P2 is subcircularly conical with a rounded labial wall, displays anterior and posterior carinae, and is double rooted.

M1 and M2 are relatively long and narrower, paracone and metacone are nearly equivalent in size, protocone crest is rather gently rounded, and lingual cingulum is relatively well developed. Lower incisors are rather bluntly convex and lack conspicuous lingual or labial carinae, p1 is a compressed cone with a single root, p2 is double rooted with a relatively distinct trigonid, and p3 is broad and short with paraconid and metaconid in tight association causing the trigonid to be a U-shaped crest.

Postcrania are much more robust than the preceding species. The atlas is anteroposteriorly elongated and lumbar diapophyses are greatly thickened dorsoventrally. The scapular glenoid fossa is relatively broad and short, humerus is relatively long, deltoid tubercle does not noticeably project laterally, and humeral head is relatively bluntly convex. Ulnar shaft is nearly circular, olecranon process with its sinuous notch are extremely transversely expanded, and olecranon apex is shallowly grooved. Radial shaft is nearly circular, ilium is triangular in cross-section, iliac tubercle is robust, and iliac crest is relatively thick. Calcaneal neck is relatively short, ridge between the tibia and fibula articular surfaces is rather gently rounded, and articular surface for the sustentaculum tali is convex. The sustentaculum tali is positioned rather high on the astragalus with an articular surface that does not project laterally. The distal articular surface for the cuboid is concave and the lateral side of the astragalus does not possess a distinct ridge.

***Bemalambda crassa* Chow, Chang, Wang, and Ting, 1973**

(Plate XIII, Figure 5)

Bemalambda crassa Chow et al., 1973; *Vertebrata Palasiatica* **11**(1), p. 34.

Type: Right maxilla with M1-M3.

Locality and stratigraphic position: Middle Paleocene top of the Shanghu Mem., Lofozhai Fm. from northeast of Nanlaoxucun hamlet, Juji Village, Nanxiong Co., Guangdong Province.

Species diagnosis: A relatively large and robust taxon with molars a little broader and shorter, or approximately 1.5 times the breadth of *B. nanhsiungensis*. Paracone and metacone are relatively well developed, being rather large and high, paracone is larger than metacone, both cusps are distinctly separated, and parastyle is particularly well developed, being relatively thick, large, and conspicuously laterally projected. Metastyle is relatively weak and very slightly laterally projected. M2 labial margin does not compose a V-shaped embayment but is an S-shaped curvature. M3 metastyle is completely reduced, parastyle is extremely well developed and constitutes nearly the entire labial margin causing the tooth to be oval in outline. Cingula are relatively well developed. M1-M3 length is 35 mm.

Table 16. *Bemalambda crassa* dental measurements (mm).

M1			M2			M3		
L	W	L/WX100	L	W	L/WX100	L	W	L/WX100
10.5	20.0	190.0	12.5	22.5	180.0	9.3	23.4	251.6

***Bemalambda* sp.**

Material: Posterior halves of a right (V4144.8) and left (V4144.9) mandible.

Locality and stratigraphic position: Middle Paleocene middle portion of the Shanghu Mem., Luofozhai Fm., one-half km from Shanghudong, Nanxiong Co., Guangdong.

Description and comparison: Ramus distinctly constricts posterior to the m3, anterior margin of coronoid rotates laterally to compose a 120° angle between it and the dentition. Masseteric fossa is extremely deep with a conspicuous anterior oblique ridge; mandibular condyle is positioned low, or on the same plane as the dentition, and extends mediolaterally as a transverse axle slightly oblique to the longitudinal axis of the mandible. Angular process is well developed, distinctly ventrally directed and slightly posteriorly extended. Pterygoid fossa is distinctly bifurcated by a ridge.



Figures 15 and 16. Dorsal and right lateral lateral view of *Bemalambda nanhsiungensis* Chow et al., 1973 (V4116) X1/2.

These characters correspond to the genus *Bemalambda* only the specimens are smaller, particularly V4144.8. Ramus is comparatively lower, medial longitudinal ridge of the ascending ramus is weaker, does not contact the condyle, and disappears ventral to the mandibular foramen. The alveolae of the m3 suggests it is much smaller than any known on *Bemalambda*, and hence may represent a new species.

Discussion

Four species are contained within the genus *Bemalambda*: *B. nanhsiungensis*, *B. pachyoesteus*, *B. crassa*, and *B. sp. indet.* but it is currently difficult to conduct a discussion on their phylogenetic relationships due to absence of pertinent data, although the following observations may be recorded: *B. nanhsiungensis* and *B. pachyoesteus* are similar in size but the P2 of *B. pachyoesteus* is more primitive, as it lacks a V-shaped ectoloph and is instead represented by a single subcircular cone with a rounded labial wall. The upper and lower second premolars of *B. pachyoesteus* are also double rooted and p2 and p3 have more distinctly defined

trigonids than on *B. nanhsiungensis*. It is possible that these two species represent distinct early lineages although chronology and stratigraphic relationships between the two are still slightly vague. It is possible that *B. pachyoesteus* is contemporaneous with, or slightly older than, *B. nanhsiungensis*. *B. crassa* is more derived by being distinctly larger and more robust than the other two species although morphologically it approaches *B. nanhsiungensis* in having its molar proportions and paracone being larger than metacone. It is also possible that it is derived from stratigraphically higher sediments.

Bemalambdidae skeletal morphology

Skull: (Plates IX-XI, XIV, and XV, Figures 1 and 2; Text figures 15 and 16) The skull of *Bemalambda* is short, broad, low, has an extremely small cranium, and in outline is nearly rhomboid. The facial region is short and broad with an elongated cranium. The facial region of *B. nanhsiungensis* is two-thirds the length of the skull, but on *B. pachyoesteus* this proportion increases to four-fifths. The nasals are relatively long and on *B. nanhsiungensis* have a relatively flat dorsal surface that lies slightly lower than the nasomaxillary suture. Anteriorly, and posteriorly the nasals are transversely broadened while medially they are constricted approximately one-third or one-quarter the breadth of the face. The nasomaxillary suture is medially crescentic. On *B. pachyoesteus* the dorsal nasals are transversely convex, do not broaden anteriorly, and contact the maxilla with a relatively straight suture line. The *B. nanhsiungensis* frontal is relatively short, anteriorly rather flat, and posteriorly gradually ascends to compose an anteriorly oblique plane. A supraorbital process is conspicuous. On the majority of *B. nanhsiungensis* specimens there are relatively short frontal ridges that abruptly contact the sagittal crest. The sagittal crest is relatively narrow, long, and only most posteriorly broadens to form an acute anteriorly directed triangle. A distinct longitudinal groove lies upon the crest. On a juvenile specimen of *B. pachyoesteus* (V4115) the frontal ridges are relatively short, but on V4122 they are rather long and make a gradual contact with the sagittal crest. The zygomatic arch is rather narrow, extends crescentically laterally, is slightly narrower anteriorly than posteriorly, and attains its greatest breadth as its posterior base.

The facial and rostral regions are extremely low while the cranium is long and high. Anterior to the supraorbital process the dorsal facial region is rather low, flat, and lies upon the same plane as the supraorbital process. On *B. nanhsiungensis* the sagittal crest is well developed to compose a high convexly rounded ridge that diverges with a distinct angle in the facial region, but on *B. crassa*, the sagittal crest is relatively low and diverges to form a rather large and spacious angle in the facial region. The occipital surface is posteriorly oblique to the occipital crest and extends posterior to the occipital condyles.

External nares are situated anteriorly, the anterior premaxilla extends beyond the anterior nasals, and the nasal process of the premaxilla is long and in contact with the nasals. On *B. nanhsiungensis* the nasal process of the premaxilla extends into the mid-portion of the nasals, but on *B. pachyoesteus* it merely extends to approximately the anterior third of the nasals. The maxilla is long with a relatively short, low, and sinuous nasomaxillary suture that is the result of the premaxilla penetrating the maxilla and nasals.

The infraorbital foramen is large and lies beneath the ventral margin of the orbit, approximately dorsal to the P4. The orbit is small, composed of the frontal, lacrimal, and jugal, with the maxilla nearly completely excluded. The anterior margin of the orbit lies dorsal to the M1 or M2 with a notch and lacrimal tubercle. The lacrimal extends into the facial region where, within the orbit, it is perforated by foramina of varying sizes and quantity. Although in the majority of specimens there are two foramina, on V4120 there is a single foramen on each side, and on V4119 and V4114 the left side possesses a single foramen but the right side possesses two foramina. A ridge lies ventral to the lacrimal foramina isolating them from the maxillary recess. Within the recess lie two foramina, the dorsal of which is relatively large and represents the maxillary

foramen, and the posteroventral which is small and represents the sphenopalatine foramen. Ventral to the orbit in the region of the maxilla is a triangularly shaped plate with its maximum breadth posteriorly. Upon it posteromedially lies a posterior palatal foramen.

The temporal fossa is extremely large, with its posterior two-thirds being bounded by the parietal. Numerous grooves, ridges, and nutrient foramina lie upon the parietal within the temporal fossa. Anteroventral to the parietal are the combined frontal, sphenoid, and temporal, but the frontal does not contact the temporal as it is separated by the parietal and sphenoid.

The anterior zygomatic arch initiates dorsal to the P4 as a rounded inflation that separates the infraorbital foramen from the orbit. The arch itself is composed of the jugal process of the maxilla, jugal process of the temporal, and the jugal, among which the jugal process of the maxilla is relatively large with its posterior end lying approximately at the posterior margin of the M3. Anteriorly, the jugal is bifurcated into two branches, the ventral branch is short while the dorsal branch is relatively long and extends to contact the dorsal maxilla and lacrimal notch. Posteriorly, the jugal remains thin. The jugal process of the temporal becomes relatively thick and enlarged, particularly dorsoventrally, and reaches its maximum thickness anterior to the glenoid fossa anterior to which it gradually thins. The zygomatic arch on *B. nanhsiungensis* is rather thin, particularly at the horizontally extended jugal. On *B. pachyoesteus* the arch is relatively short and robust, composing an anteriorly low and posteriorly high sinuous curvature.

The postglenoid process is relatively large, anteroposteriorly elongated, and rather compressed dorsoventrally. The glenoid fossa is longer than the postglenoid process and composes a dorsally curved surface that includes the anterior side of the postglenoid process. There is a relatively large vacuity between the postglenoid process and the posttympanic process. The posttympanic process and the mastoid process are fused to compose a ventrally extended element that is more robust than the postglenoid process. A relatively small mastoid foramen is located posterolaterally on the mastoid process. The paramastoid process is small and is penetrated by the occipitotemporal suture line. Occipital condyles are extended principally posteriorly but also very slightly ventrally, and lie more ventral than the mastoid processes, being on the same plane as the postglenoid processes.

The pterygoid is laterally concave with an anterodorsally oblique pterygoid canal located at its posterior base. There is an extremely large elliptical anterior foramen of the pterygoid canal anterior to which is a smaller orbital foramen, and still further anterior there is yet a smaller optical foramen. These three foramina are aligned nearly linearly along an oblique anterodorsal direction.

From a ventral perspective the anterior premaxilla is rounded with a small anterior incisive notch. The palatal fissure is divided into two vacuities by the premaxillary and palatine process and are located upon a line drawn between the third incisors. The palate is relatively broad and slightly concave with a medial longitudinal groove that gradually disappears posteriorly. The palatine sulcus runs parallel to this longitudinal groove and posteriorly becomes confluent with the large anterior palatine foramen, which is located medial to the p4 or m1. The palatine is long and linguoid shaped with an anterior margin that constitutes the boundary for the anterior palatine foramen. Upon it lies accessory palatal foramina and grooves. The ventral boundary of the posterior internal nares (nasopharyngeal meatus) is a relatively thick and rugose transverse ridge. A conspicuous notch lies between this ridge and the posterior maxillary tubercle. The two pterygoids terminate by extending nearly parallel posteriorly and then open and expand laterally.

The basitubercle lies nearly in line with the postglenoid process. The foramen ovale is large, elliptical, and is situated posterior to the foramen of the posterior pterygoid canal, to which it is connected by a groove. The basioccipital is anteriorly narrow and posteriorly broad with a distinct vertical ridge anteromedially that is concave on each side and becomes rather flattened at its posterior end.

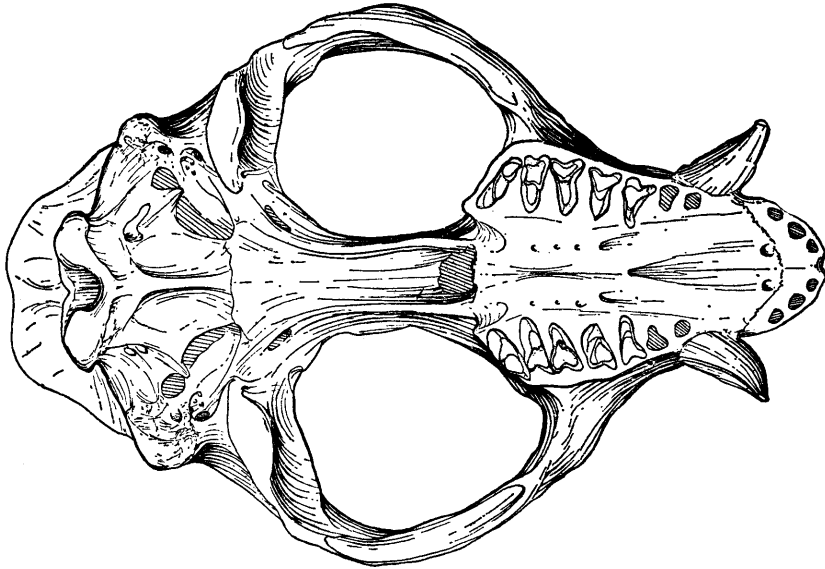


Figure 17. Ventral view of *Bemalambda nanhsiungensis* Chow et al., 1973 (V4116) X1/2.

Occipital condyles are relatively small and nearly unified ventrally, with only a shallow groove separating them. The intercondylar notch is relatively openly spacious. The hypoglossal foramen lies approximately 5-10 mm anterior to the occipital condyle, and is inconsistent in size and quantity. On the majority of specimens there is only one but on V4120 three small foramina are present on the right side while the left side displays only one; and on V4116 and V4119 the left sides maintain two foramina. The glenoid fossae is oblique to the longitudinal axis of the skull but the postglenoid process is nearly perpendicular to this axis. A postglenoid foramen is distinct and confluent with the medial side of the postglenoid process by a canal. No vestige of an osseous bulla is present, a distinct stylomastoid foramen is located posterior to the postglenoid foramen, and the tympanic and mastoid processes are fused medially. An extremely small anteriorly directed foramen is present which is convergent with the facial foramen by a groove. The petrosal is relatively well preserved with a slightly blunt convex promontorium that possesses a posterolateral groove for the stapedial artery. The fenestra ovalis is extremely small, nearly circular, and located on the lateral promontorium medial to the groove for the facial nerve. The fenestra rotunda is a small and oval foramen located extremely close and posteromedial to the fenestra ovale. The foramen for the anterior lacerum is relatively small, the foramen for the medial lacerum is large and elongated, and the foramen for the posterior lacerum is large, circular, and isolated from its medial counterpart by a thin osseous baton. These three foramina are collectively located anterolateral to the hypoglossal foramen.

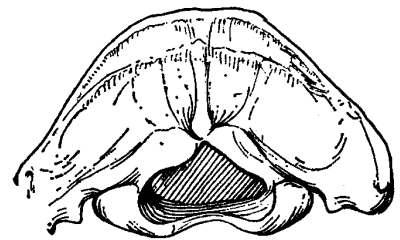


Figure 18. Occipital view of *Bemalambda nanhsiungensis* Chow et al., 1973 (V4116) X1/2.

In posterior perspective, the skull of *B. nanhsiungensis* is nearly semicircular and dorsoventrally concave. The occipital crest is nearly crescentic, relatively coarse and thick at its mid-region, and rather thin at its extremities, which extend anteroventrolaterally to contact the temporal ridge at the dorsal mastoid process. Ventral to the occipital crest are two large and coarsened surfaces to facilitate ventral musculature and ventral to these are conspicuous crescentic lineations (*linea semicircularis*). Laterally, the occipital crests are distinct, concave, and ornamented with numerous longitudinal grooves and ridges. The foramen magnum is large,

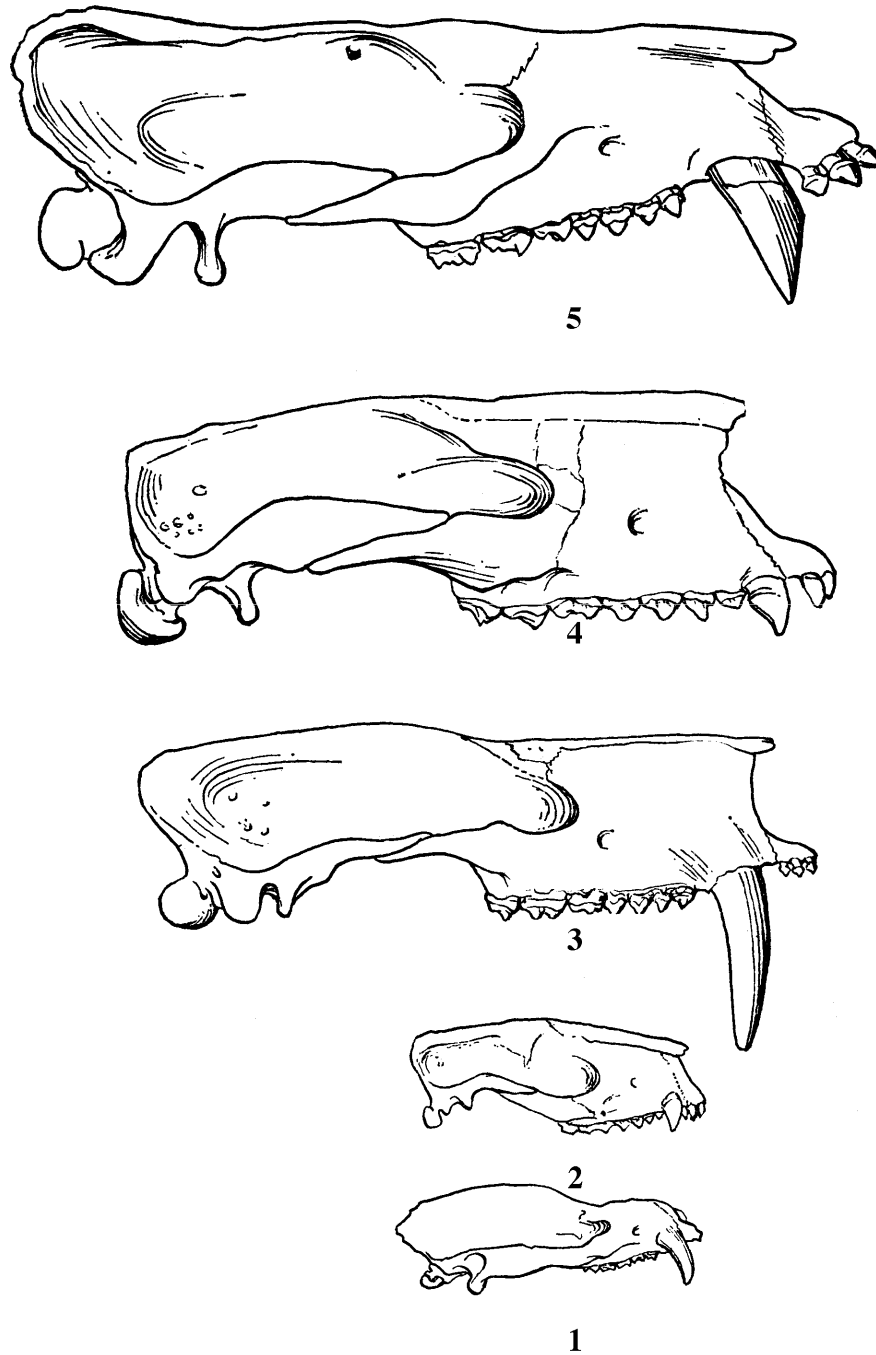


Figure 19. Cranial comparison of five pantodont genera X1/5.

1. *Bemalambda nanhsiungensis* Chow et al., 1973
2. *Pantolambda bathmodon* Cope from Matthew, 1937, p. 173, Fig. 38.
3. *Titanoides primaevus* Gidley, from Patterson 1939, p. 355, Fig. 100.
4. *Barylambda fameri* (Patterson), from Patterson, 1935, p. 147, Fig. 1.
5. *Coryphodon* Owen, from Simons, 1960, p. 9, Fig. 1A.

elliptical, rather spaciouly broadened dorsal to the occipital condyles, and there are a pair of large inflations on the medial occipit dorsal to the foramen magnum.

Comparisons: The skull of *Bemalambda* resembles the Pantolambdidae in size and with characters including the relatively short and broad rostrum; skull becoming constricted, narrow, and long posterior to the orbit; well developed sagittal and occipital crests; semicircular occiput; occipital condyles small compared to the size of the cranium; nasals long and posteriorly transversely broadened; nasal process of the premaxilla in contact with the nasals; lacrimal rather abruptly extended into the facial region; lacrimal foramen within the orbit; and zygomatic arch as large, broad, and relatively thick. However, *Bemalambda*'s rostrum is situated much lower than the Pantolambdidae, sagittal crest is more pronounced, premaxilla is lower and longer, and it possesses a supraorbital process and pterygoid canal.

Bemalambda resembles the Barylambdidae with a relatively short and broad rostrum, semicircular occiput, and supraorbital process. However, there are conspicuous distinctions as the oral region of *Bemalambda* is much lower than the Barylambdidae and nasal process of the premaxilla is rather well developed and in contact with the nasals, whereas on the Barylambdidae the premaxilla does not contact the nasals. The *Bemalambda* maxilla is relatively low with a relatively short nasomaxillary suture, parietal is relatively narrow, and sagittal crest is strong, but on the Barylambdidae the parietal is relatively broad and flat. The occipital condyles on *Bemalambda* are rather small in proportion to its skull and are primarily posteriorly projected, whereas on the Barylambdidae the condyles are primarily ventrally projected. The occipital surface of *Bemalambda* is posteroventrally oblique with an occipital crest that extends posterior to the occipital condyles, but on the Barylambdidae the occiput is nearly vertical with occipital condyles that extend further posterior than the occipital crest. A single anterior palatal foramen on *Bemalambda* is located in the vicinity of the P4 or M1 but on the latter family is dispersed in the vicinity of the M2. On *Bemalambda* the posttympanic and mastoid processes are fused and a mastoid foramen is present, but on the Barylambdidae a posttympanic process and mastoid foramen are absent.

Bemalambda is quite distinct from the Titanoideidae with a much lower facial and rostral region, a somewhat stronger sagittal crest, and a longer nasal process of the premaxilla in contact with the nasals, whereas on the Titanoideidae the nasal process of the premaxilla is slender and does not extend to the nasals. The zygomatic arch of *Bemalambda* is robust, a supraorbital process is present, and the anterior palatal foramen lies at the P4 or M1, while on the titanoideidae this foramen lies approximately at the M2. Furthermore, the hypoglossal foramen on *Bemalambda* is further anterior.

Bemalambda is extremely distinct from the Coryphodontidae in its much smaller size. The premaxilla of *Coryphodon* is robust but its nasal process is small and on a majority of specimens does not contact the nasals. Its dorsal cranium is relatively broad and flat with a sagittal crest that is narrow anteriorly and becomes extremely broad posteriorly. *Bemalambda* has a supraorbital process and expanded posterior nasals, while on *Coryphodon* the nasals are slender and unexpanded posteriorly. The posttympanic and postglenoid processes on *Bemalambda* are extended much more ventrally than on *Coryphodon*. The maxilla of *Coryphodon* constricts conspicuously posterior to the canine in contrast to *Bemalambda* and a paramastoid process is absent.

Compared to the Archaeolambdidae, both maintain anterior palatal and infraorbital foramina generally in the same locations although *Bemalambda*'s palate is broader with the distance between dentition approximately twice the breadth of the teeth whereas on the Archaeolambdidae this distance is approximately equivalent to the breadth of the teeth. The posterior palatal margin on *Bemalambda* lies at the M3 while on the latter it is at the M2.

Mandible: (Plate XII, Figures 2,3,5, and 6; Plate XIII, Figure 2; Plate XV, Figure 3; and Text figure 20). The mandible of *Bemalambda* is robust. On *B. nanhsiungensis*, the corpus is robust and short with a nearly perpendicular anterior wall and its posterior margin lies approximately at the p1, but on *B. pachyoesteus* the posterior margin extends to the p2. On V4130 the anteroventral corpus is very slightly anteriorly projected. Mandibles either lack mental foramina completely or possesses two to three foramina. A vast majority of *B. nanhsiungensis* specimens have an unfused symphysis suggesting that its fusion occurred extremely late during its ontogeny, or at very least postdating the complete eruption of permanent dentition and occurring only after relatively deep occlusal wear. On *B. pachyoesteus* complete mandibles indicate a symphyseal fusion relatively earlier.

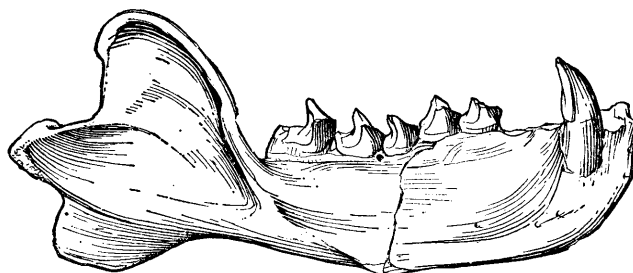


Figure 20. Lateral view of *Bemalambda nanhsiungensis* Chow et al., 1973 right mandible (V4132), x 1/2.

Left and right mandibles are nearly parallel but the rami are not strictly perpendicular as laterally surfaces are slightly anteriorly oblique, and anteroventral ends are particularly thickened to form laterally projected margins. On *B. nanhsiungensis* this anterolateral margin is well developed such that from dorsal perspective they appear as a processes but on *B. pachyoesteus* this feature is weaker. The quantity and locations of the mental foramina are inconsistent, with the majority of specimens maintaining two foramina: one located approximately ventral to the lower canine and one located approximately ventral to the p3. There are also specimens with three or four foramina although the most posterior foramen never surpasses the p4. The ramus is deepest at the m1 or anterior to the m2, posterior to which it gradually reduces, and posteroventral to the m3 distinctly constricts. Therefore, from lateral perspective, the ventral margin of the ramus appears as an anteriorly convex and posteriorly concave sinuous line.

The coronoid process is relatively straight, high, and anteroposteriorly expanded with a thickened anterior margin that is laterally rotated to compose an approximate 115°-120° angle with the dental trough. The mandibular condyle constitutes a low transverse axle located nearly along the same plane as the dentition. This transverse axle is perpendicular, or very slightly posterolaterally oblique, to the axis of the ramus. The articular surface of the condyle is transversely linear and anteroposteriorly rounded to compose a semicircular articular surface. The mandibular column or neck is short and shallow. The masseteric fossa is large and ascends to the dorsal coronoid process with its anterior boundary as the anterior margin of the coronoid process. The masseteric fossa of *B. pachyoesteus* is deeper than on *B. nanhsiungensis*. On the medial surface of the ascending ramus there is a ridge that extends from the medial side of the condyle directly ventral to the m3, ventral to which is a distinct groove. A large mandibular foramen is located ventral to this medial ridge, approximately at the posteroventral margin of the coronoid process or slightly anterior. The angular process is relatively large, nearly rectangular, and directed slightly posteroventrally, but does not exceed the posterior margin of the mandibular condyle. Its posteroventral margin is relatively straight, thick, coarsened, and rotates medially. The pterygoid fossa is large and bordered with a distinct anterior ridge. Within the fossa is another ridge that bifurcates it into two fossae, the ventral of which is relatively large, smooth, and glossy,

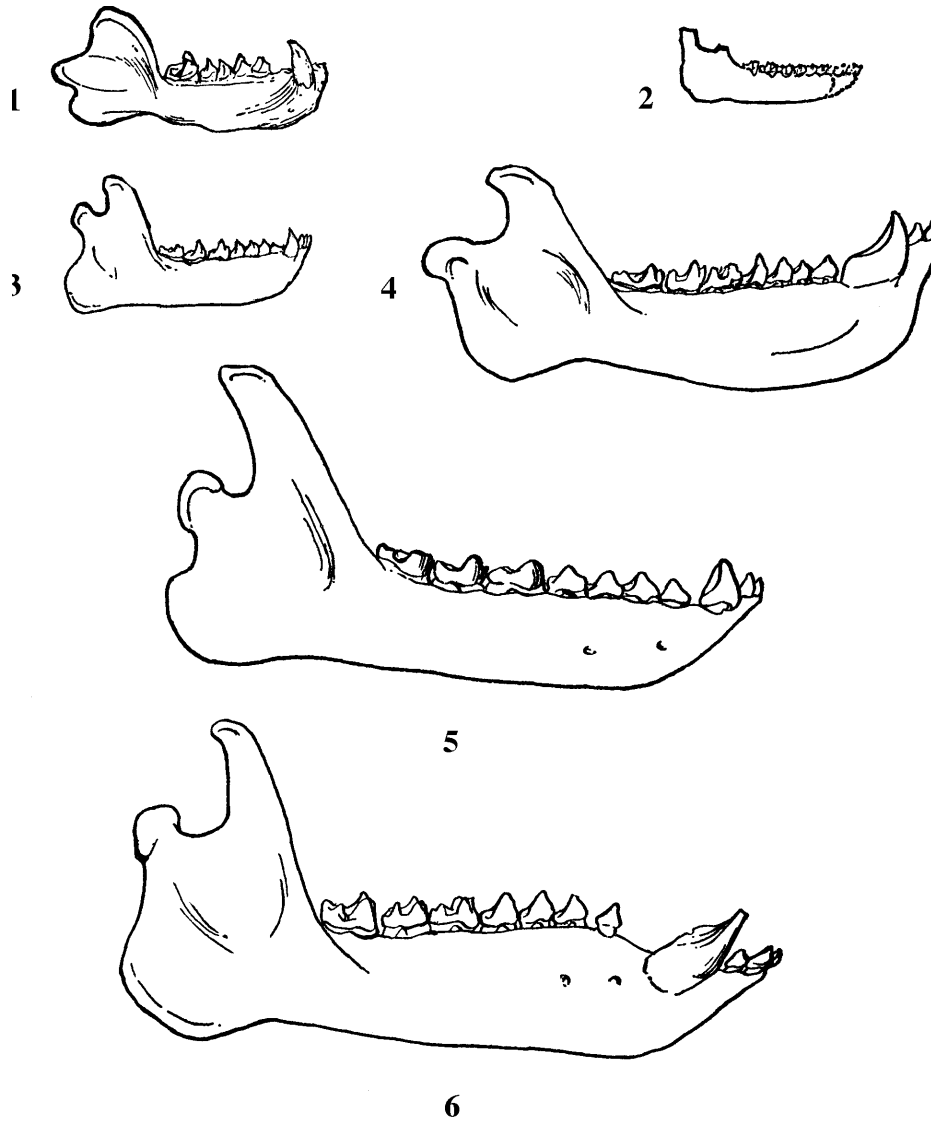


Figure 21. Comparison of pantodont mandibles (X1/5).

1. *Bemalambda nanhsiungensis* Chow et al., 1973.
2. *Archaeolambda planicanina* Flerow (from Flerow, 1952; p. 51, Plate I, Fig. 5).
3. *Pantolambda bathmodon* Cope (from Matthew 1937; p. 173, Fig. 38.).
4. *Titanoides primaevus* Gidley (from Patterson 1939; p. 355, Fig. 100).
5. *Barylamba faberi* (Patterson) (from Patterson 1935; p. 147, Fig. 1).
6. *Coryphodon* Owen (from Simons 1960; p. 9, Fig. 1A).

while the dorsal fossa lying between the ridge and the mandibular neck is relatively small and deep with a coarsened surficial texture.

Comparisons: (Fig. 21) *Bemalambda* mandible characters that differ from all other pantodont families include the rather expanded coronoid process and the ventrally situated mandibular condyle. The rectangular angular process that is primarily ventrally extended and does not exceed the posterior margin of the condyle is a character shared with *Coryphodon* but distinct from other members of the Order. The mandible compares to the Pantolambdidae in size, with a rather robust ramus and the presence of a convex anterolateral margin. It is distinct from the

Barylambdidae in a number of characters as it is rather robust and short with a nearly perpendicular anterior corpus, whereas the Barylambdidae mandible is rather gracile, long and obliquely inclined with the posterior symphysis extending to the p3, an anterolateral convex margin is absent, and the ventral margin of the ramus is rather linear, as opposed to the sinuous ventral curvature on *Bemalambda*. Several characters are shared with the Titanoideidae as both have a robust and perpendicular corpus, a relatively deep anterior ramus, and a conspicuous constriction posterior to the m3. There are extremely conspicuous distinctions between *Bemalambda* and the Coryphodontidae, for with the exception of the morphology of the angular process, *Bemalambda* is distinct in its robust corpus with a nearly precipitous anterior wall, the presence of a convex anterolateral margin, and the distinct constriction of the mandible posterior to the m3 creating a sinuous ventral curvature. *Bemalambda* differs from the Archaeolambdidae in its rather robust corpus, presence of a convex anterolateral margin, and sinuous ventral margin. On the Archaeolambdidae the ramus increases in depth anteroposteriorly and there is only an extremely small constriction posterior to the m3.

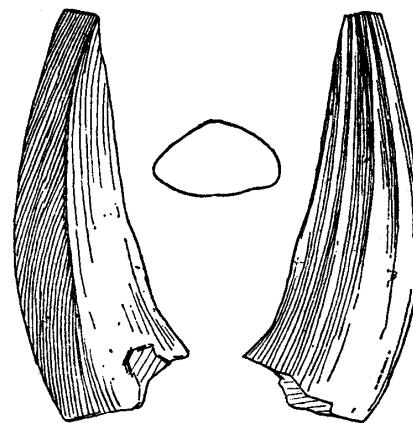


Figure 22. Left upper canine (V4125) of *Bemalambda nanhsiungensis* Chow et al., 1973 (X1).
Left. Lateral view; Center. Cross-sectional view; Right. Medial view.

Dentition: (Plate IX, Plate X, Fig. 1; Plates XII, XIII, and Plate XV, Fig. 3) Among the *B. nanhsiungensis* specimens only V4118 preserves the incisors (I1 and I2 on the right side and I2 and I3 on the left side) although a majority of these teeth have been subjected to occlusal wear prohibiting a precise description of their characters. Dentition is thinly enameled and has a formula of 3·1·4·3/3·1·4·3. Upper incisors are in crescentic alignment and are directed very slightly anteriorly. The I1 is the smallest and I2 the largest in the series. Diastemae are present between the left and right I1 and between the I3 and canine. On *B. pachyoesteus* the incisors are subconical with lateral carinae.



Figure 23. Right P2 of *Bemalambda nanhsiungensis* Chow et al., 1973 (V4124) X2.
1. Posterior view; 2. Apical view; 3. Labial view.

The upper canine is extremely prominent, long, trenchant, extends slightly anteriorly and is laterally compressed. Carinae are present anteriorly and posteriorly which extend from the apex to the base of the crown, the posterior of which is relatively acute. Anterior carina disappears after occlusal wear such that the surface becomes relatively flat, smooth, and lingually oblique. At this stage of wear the canine is triangular in cross-section (Text Fig. 22). Labially, it is convexly rounded with abundant corrugations, while the lingual surface is relatively flat or very slightly convex with corrugations toward its apex. On *B. nanhsiungensis* specimen V4117 the corrugations are relatively weak with the lingual side rather flat and glossy.

The upper dentition occurs as nearly parallel compact dental batteries that are in closer proximity anteriorly. Transverse axis of the molars are either perpendicular or very slightly posteromedially oblique to the longitudinal axis of the dentition. Protocones are all situated on the transverse axes of the teeth. Upper premolars are not molarized. The P1 is situated slightly posteromedial to the canine and on *B. nanhsiungensis* is located more anteriorly allowing the P2 to be in direct contact with the canine. On *B. pachyoesteus* the P1 is more posteriorly located and the P2 is not in contact with the canine. On *B. nanhsiungensis* the P1 is not preserved but the alveolus indicates it to be single rooted. On *B. pachyoesteus* the P1 is also single rooted with a sub-conical crown.

The P2 on *B. nanhsiungensis* (Fig. 23) is nearly a trilaminar cone that is distinctly labially concave and relatively flat and straight anteriorly and posteriorly with its breadth slightly exceeding its length. The para-metacone (generally regarded as the ectocone) is connected to the parastyle and metastyle to compose a gently expanded V-shaped ectoloph with its breadth just slightly smaller than the breadth of the tooth. The anterior wing of this loph (paraloph) is slightly longer than the posterior wing (metaloph). The parastyle is more lingually projected and sits lower than the metastyle. A protocone is extremely undeveloped and is present only as a small protrusion in the vicinity of the lingual root. Labially, the tooth is distinctly concave with a weak longitudinal ridge. A labial cingulum is distinct but anterior and posterior cingula are weak. The tooth is single rooted with longitudinal grooves on all three faces and expresses an incipient division into a three rooted morphology. The P2 of *B. pachyoesteus* (Fig. 24) has a length greater than breadth, and a crown as a subconical single cusp with a convexly rounded labial wall and anterior and posterior carinae. Two roots are present.

The P3 is particularly broad, short, and configured as an isosceles triangle. The anterior wall is equivalent to, or very slightly broader than, the posterior wall, both of which are rather planar. Labially, the tooth wall is extremely excavated with a V-shaped wall. The ectocone constitutes a V-shaped loph which penetrates the tooth over one-half its breadth, the anterior wing of the ectoloph is equivalent to or slightly longer than the posterior wing, its labial wall is distinctly concave and relatively straight, and its lingual wall is precipitous and convexly rounded. The parastyle is equivalent to or very slightly longer than the metastyle but sits slightly lower than the latter. The protocone is slightly lower than the ectoloph as a V-shaped loph with two asymmetrical wings, the anterior of which is high, short, and extends anterolabially to the base of the anterior wall of the ectoloph, while the posterior wing is relatively low and long, extending directly to the posterior region of the metastyle. The labial wall of the protocone is slightly concave and posteriorly oblique while the lingual wall is precipitous. A labial cingulum is rather pronounced, a lingual cingulum is weak or absent, and an anterior cingulum is strong, extending from the labial end of the preprotocrista directly anterior to the parastyle.



Figure 24.
Occlusal view
Bemalambda
pachyoesteus
left P2 (V4128)
X2.

The P4 basically resembles the morphology of the P3 but is larger. With the exception of *B. nanhsiungensis* specimen V4120 which lacks any cingula, the vast majority of specimens display an extremely strong lingual cingulum that that runs continuously anteroposteriorly.

Molars are anteroposteriorly compressed, extremely transversely broadened, and compose a broad and short triangle with a low labial wall. The M1 is a transversely broadened isosceles triangle with a very slightly convex anterior wall, a slightly concave posterior wall, and a labial wall that is deeply excavated to compose a V-shaped configuration. A weak W-shaped ectoloph is composed of a relatively low paracone and metacone that are barely separated by an extremely short loph, the labial wall is extremely small or is not labially convex, and lingual wall is slightly labially embayed. The parastyle is higher, longer, and projects more labially than the metastyle. The ectoloph is excavated beyond the midline of the tooth with a concave labial wall that is more

gently curved than on the premolars. The protocone is much higher than the labial cusps and displays a narrower preprotocrista-postprotocrista angle than on the premolars, with both cristae of equivalent lengths and extending respectively to the bases of the paracone and metacone. A labial cingulum is relatively well developed, extending continuously to the base of the lingual protocone. Hypocone, protoconule, and metaconule are absent.

The M2 resembles the M1 in morphology but is larger with a more conspicuous W-shaped ectoloph. The paracone and metacone are distinctly separated but linked by a slightly labially convex loph. Parastyle is more labially projected than metastyle and the two wings of the ectoloph are distinctly asymmetrical with the anterior wing longer. In outline, the crown is an obtuse triangle. The M1 and M2 of *B. nanhsiungensis* are rather broad and short with a paracone slightly larger than the metacone, have relatively acute pre- and postprotocristae, rather weak lingual and anterior cingula, and posterior cingulum is inconspicuous (Fig. 25). The M1 and M2 of *B. pachyoesteus* are relatively narrow and long, paracone and metacone are equivalent in size, pre- and postparacrestae are rather gently rounded, and the lingual cingulum is relatively well developed.



Figure 25. Occlusal view of *Bemalambda nanhsiungensis* right canine to M3 (V4124) X2.

The M1 and M2 of *B. crassa* are large, proportionally broader, and shorter than *B. nanhsiungensis* with a breadth 1.5 times that of the older species. Paracone and metacone are rather well developed and distinctly separated with the paracone larger than the metacone. Lingual cingulum is extremely strong, anterior cingulum is strong, and posterior cingulum is distinct, extending from the labial end of the postparacrista to the metastyle. On the M2, the parastyle is particularly well developed and distinctly labially projected, while the metastyle is small, low, and barely projects labially, such that the labial margin is an anteriorly convex and posteriorly concave sinuous line (Fig. 26).

In outline, the M3 on *B. nanhsiungensis* and *B. pachyoesteus* is an obtuse triangle, more transversely broadened than the M2, paracone and parastyle are enlarged, metastyle is reduced, and the metacone is reduced and migrated labially. The ectoloph is an asymmetrical V that surpasses the midline of the tooth with its anterior wing longer than its posterior wing. The protocone is more well developed than on the M1 or M2 with more gently rounded and asymmetrical pre- and postparacristae. The preparacrista is rather high and short, extending to the base of the paracone, while the postparacrista is rather low and long, extending directly to the posterolabial angle. Paraconule and metaconule are absent, concave labial margin is inconspicuous, labial cingulum is

well developed, and lingual cingulum is extremely strong, continuously surrounding all three sides of the protocone.

On *B. nanhsiungensis*, the lingual cingulum of the M3 posterior to the protocone has a large range of variation. On V4121 it is relatively weak, while on specimens V4119, V4117, and V4120 it is particularly broadened to nearly form a small cusp with a posterior groove isolating it from the rest of the tooth's margin. On the right M3 of V4114, there appears to be a vague secondary cingulum underlying the principle cingulum, while on the left M3 the medial portion of the posterior cingulum possesses an additional cingular loph that extends labially to contact the labial end of the postparacrista.

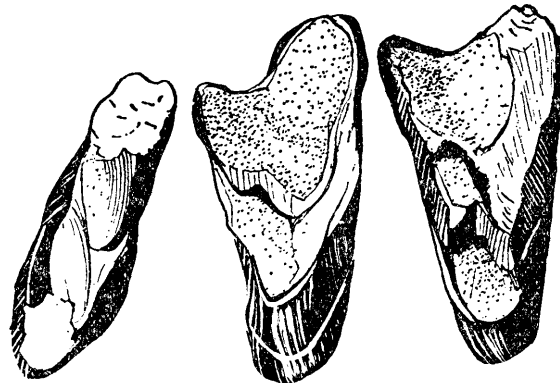


Figure 26. Occlusal view *Bemalambda crassa* right M1-M3 (V4197) X2.

On *B. pachyoesteus* the posterior M3 is poorly preserved prohibiting a detailed description. The M3 of *B. crassa* is extremely transversely expanded to provide it with an oval outline. The parastyle is high, robust, and constitutes nearly the entire labial margin, the metastyle is completely reduced, and the protocone is a V-shaped loph with a relatively high and short preprotocrista that extends to the base of the paracone. The postprotocrista is rather low, long, and extends to the base of the metacone. The lingual cingulum is extremely well developed and anterior cingulum is relatively conspicuous.

Lower incisors are upright and in tight crescentic alignment with the i1 being the smallest and i2 the largest in the series. Among *B. nanhsiungensis* specimens, only V4140 preserves the i2 and i3, but an additional isolated specimen of a left i2 is also represented. The i1 is poorly preserved. The i2 and i3 are semiconical with distinct lateral carinae that maintain a small cusp at each of their bases and are in alignment with the principle cusp of the tooth causing it to be trifoliate. The incisors are labially convex. On the lingual side there is a sharp medial longitudinal ridge bifurcating the surface into a concave medial and lateral side with the medial side slightly broader than its counterpart. *B. pachyoesteus* does not display conspicuous lateral carinae or a medial longitudinal ridge and its lingual surface is rather convexly rounded.

The lower canine is smaller than its upper counterpart and is principally upright with a slight posterolabial inclination. *B. nanhsiungensis* specimen V4130 is distinctly posterolabially inclined. Upon occlusion the lower canine shears against the anterior upper canine. The crown is triangularly conical with convexly rounded lingual and labial surfaces, the labial of which is more pronounced. Lingual and labial faces maintain numerous corrugations, but the posterior surface is smooth, glossy, and concave, and on unworn specimens displays a medial longitudinal ridge which disappears after occlusal wear. Three distinct carinae delineate the surfaces with the anterior carina becoming ventrally bifurcated. A diastema between the i3 and canine is absent and between the p1 is either extremely small or absent.

Premolars are not molariform and are in tight alignment. The p1 is single rooted and on *B. nanhsiungensis* is laterally compressed with distinct anterior and posterior carinae. The principle cusp is laterally compressed with an anterior and posterior crest that are connected by an anterior and posterolabial ridge. No conules are present, the tooth is labially convex, lingually concave, and medially there is a slightly convexly rounded longitudinal ridge. The p1 of *B. pachyoesteus* is an anteroposteriorly elongated and compressed cone.

The p2 of *B. nanhsiungensis* resembles the p1, being single rooted and laterally compressed, but the principle cusp is more well developed, being high and acute with oblique anterior and posterior carinae that possess a small cusp at their termini. These three cusps are in direct alignment with the anterior cusp higher than the posterior cusp. At the basal region of a lingual longitudinal ridge, which divides the lingual side into two facets, there is a small indistinct conule which may represent an incipient metaconule (Fig. 27). The p2 of *B. pachyoesteus* is double rooted with a relatively well defined trigonid, metaconid is higher and larger than paraconid, and talonid is a simplified longitudinal crest (Fig. 28. Left).



Figure 27. Occlusal view of *Bemalambda nanhsiungensis* juvenile mandibular dentition (c1,p1,p2,dp3,dp4,m1,m2) (V4147) X2.

The p3 is double rooted with a distinct high and broad trigonid. The talonid consists of a simplified longitudinal crest extending from the posterior wall of the protoconid. On *B. nanhsiungensis*, the p3 is relatively narrow and long with a rather weak paraconid but extremely well developed protoconid and metaconid. The paralophid and protolophid connect to form an asymmetrical V-shaped crest. The paralophid is rather low and obliquely long, the protolophid is rather high and short, and between them lies a sulcus that sits just slightly lower than the protoconid and metaconid. The anterior valley is spacious and rather precipitous (Fig. 29). On *B. pachyoesteus* the p3 is relatively broad and short with a closely associated paraconid and metaconid; the protolophid and paralophid are connected to form a more gently rounded crest; the anterior valley is not openly spacious as on *B. nanhsiungensis*; and the metaconid is not particularly enlarged (Fig. 28 Right).

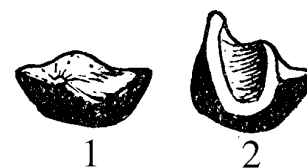


Figure 28. Occlusal view of *Bemalambda pachyoesteus* premolars.
1. Right p2 (V4167);
2. Left p3 (V4122) X2.

The p4 of *B. nanhsiungensis* resembles the p3 but the trigonid is more well developed. The paraconid is extremely reduced, while the protoconid and metaconid are more pronounced, nearly equivalent in height, and distinctly lingually extended. There is an extreme distinction between the heights of the trigonid and talonid with the talonid composed as a weak crescentic loph. Posterior to the longitudinal crest is a transverse crest that is lingually extended. A p4 of *B. pachyoesteus* is poorly preserved, prohibiting a comparison.

The m1 of *Bemalambda* has an extremely well developed trigonid that is represented by a V-shaped loph, a reduced paraconid, and an extremely well developed protoconid and metaconid, the latter of which is larger and more robust. The paralophid is short, low, and extends obliquely ventrolabially. The protolophid is very high, slightly depressed at its midpoint and there is a notch that divides the loph into two segments. The angle between the paralophid and protolophid is narrower than on the p3 or p4. The anterior valley is relatively narrow and precipitous, metastylid

is absent, and the talonid is shorter, narrower, and sits much lower than the trigonid with a V-shaped crest composing a much larger angle than the trigonid. The cristid obliqua extends to the posterior base of the protolophid one-third from the lingual side. A hypolophid is crescentic, the hypoconid is larger than the hypoconulid, and the entoconid consists of a transverse loph that extends lingually with a slightly anteriorly curved terminus that leaves the gently spacious posterior valley open. Lingual and labial cingula are extremely weak or absent.

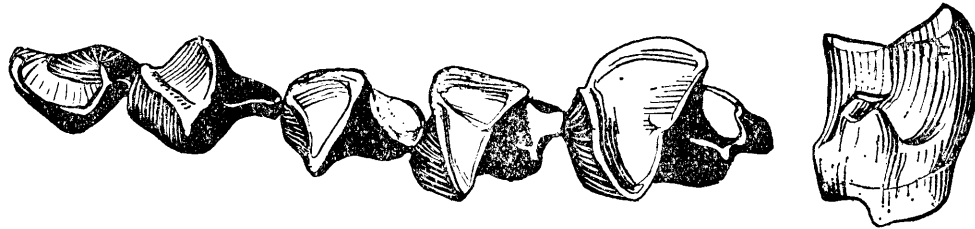


Figure 29. *Bemalambda nanhsiungensis* adult mandibular dentition. Left. Occlusal view of left p3-m3 (V4158); Right. Posterior view of m3 (V4158) X2.

The m2 resembles the m1 but is larger. The trigonid is extremely well developed, paraconid is more reduced than on the m1, and paralophid is lower, more oblique, and positioned closer to the protolophid to compose an even more distinct asymmetrical angle. The metaconid is larger than the protoconid, entoconid and hypoconulid are rather well developed, there is a shallow groove between the hypoconid and hypoconulid on the lateral wall of the hypolophid, and the posterior valley is rather spacious open.

The m3 is larger than the m2 with an even more accentuated trigonid, the metaconid is much larger than the protoconid, and the difference in height between trigonid and talonid is even more pronounced. The hypolophid between the hypoconid and hypoconulid has become narrow and a groove on the labial wall is rather distinct. The hypoconulid has become enlarged and the talonid is elongated but is neither particularly posteriorly projected nor trifoliate in form. An entoconid is extremely distinct.

B. nanhsiungensis specimen V4147 preserves the third and fourth deciduous premolars that are smaller than their associated permanent dentition (Fig. 27). The dp3 is simple in morphology, more complex than the p2, but more simplified than the p3. The paralophid and protolophid are weak with a relatively broad angle between them. The protoconid is extremely high, paraconid and metaconid are extremely low, and the anterior valley is shallow but precipitously bounded. The talonid consists of a weak oblique crest.

The dp4 is molariform with three distinct cusps, the metaconid is the most well developed cusp, and paraconid is the smallest cusp. Paralophid and protolophid are asymmetrical with the protolophid being higher. The anterior valley is lingually rather deeply excavated and there is a transverse groove that separates the base of the protoconid from the metaconid. The talonid resembles those on the molars, being composed of a V-shaped crest; the cristid obliqua extends from the hypoconid to the posterior wall of the protolophid; and the hypolophid is crescentic. The posterior valley is spacious open. A weak lingual cingulum is present and a weak labial cingulum is present between the base of the metaconid and protoconid.

Comparisons

The dentition of *Bemalambda* is relatively derived and readily distinguished from all other known pantodont families. Principle characters include the first incisor as smallest in the series while second incisor is largest; upper canine is trenchant, predominantly straight, extremely long and large, or larger and more robust than the lower canine, which is triangularly conical and upright; P1 is posterolingual to the upper canine; upper molars are extremely broad and short with M1 and M2 as broad and short triangles with a weak W-shaped ectoloph; M3 ectoloph is an asymmetrical V; molars lack a protoconule or metaconule; m1 and m2 trigonids are much higher than the talonids; paraconid is reduced; and metaconid is thicker and larger than protoconid. However, the P2 crown of *B. nanhsiungensis* resembles *Pantolambda bathmodon* which is distinct from all other pantodont genera, but the former is distinguished by being single rooted. The *B. pachyoesteus* P2 is relatively derived by having two roots and a subconical crown with a rounded labial wall.

Bemalambda and the Pantolambdidae, both share relatively similar premolar morphology and their first upper and lower premolars are single rooted. *Bemalambda*, however, is distinct with its conically semicircular lower incisors with lateral carinae, close proximity of paracone and metacone, ectoloph extends beyond the midline of the crown, M1 and M2 labial margin is rather deeply excavated, p3 talonid is a longitudinal crest, p4-m3 paralophid and protolophid are spaciouly open, a metastylid is absent, m3 talonid is not particularly elongated, and its posterior end does not project acutely.

In addition to the aforementioned distinctions, *Bemalambda* differs from the Barylambdidae in the transverse axes of the cheek teeth being posteriorly oblique to the longitudinal axis of the dentition, whereas on the Barylambdidae the P2-P4 are anteriorly oblique. On *Bemalambda*, the paracone and metacone are positioned lingually and in close proximity, there is a relatively deeply excavated labial margin, the parastyle is distinctly larger than metastyle, and is more laterally projected. On the Barylambdidae, the parastyle and metastyle are nearly equivalent in size. On *Bemalambda* a diastema is absent posterior to the p1 and the p3 talonid is a longitudinal loph, but on the Barylambdidae the p3 talonid is a crescentic loph. On *Bemalambda* the trigonids are wider than the talonids with trigonid angles smaller than talonid angles and a metastylid is absent. On the Barylambdidae, the m1 and m2 trigonid is narrower than the talonid, the angles of the lophes are nearly equivalent, and a metastylid is present. Characters shared between the two dentitions include the spaciouly open paralophid-protolophid angle, presence of an entoconid, first upper and lower premolars single rooted, p2-p4 lack basal cingula, are not rectangular, and enlarge posteriorly; m1 and m2 trigonid is longer than talonid, and m3 talonid is rather gently rounded and not particularly acutely projected posteriorly.

Bemalambda and the Titanoideidae both share relatively similar mandibular dentition including the presence of lateral carinae on lower incisors, p3 talonid as a longitudinal loph, m1 and m2 trigonid longer and broader than talonid, the presence of an entoconid, and absence of a metastylid. But their upper dentitions are extremely distinct as the *Bemalambda* P1 is single rooted as opposed to all the genera in the Titanoideidae which have a double rooted P1, *Bemalambda* P3 and P4 protocones lie on the transverse axis of the tooth as a V-shaped loph, but on the Titanoideidae the protocones lie anterior to the transverse axis as a single anterior wing, with a posterior wing absent but a particularly well developed and enlarged posterior cingulum present. The ectoloph of the P3-M3 on *Bemalambda* extends distinctly lingually beyond the midline of the tooth, the M1 and M2 labial margin is rather deeply excavated, paracone and metacone are in close proximity, and parastyle is more well developed than metastyle, being projected further labially. On the Titanoideidae the parastyle and metastyle are nearly equivalent in size and project to the same degree labially. Additionally, *Bemalambda* p3 and p4 are nearly triangular while on the

Titanoideidea they are subrectangular. *Bemalambda* trigonid angles are smaller than their talonid angles but on the Titanoideidae are nearly equivalent.

Bemalambda dental characters are extremely distinct from the Coryphodontidae as the former has a triangular P3 and P4 while on the latter these teeth are nearly oval with parastyle and metastyle in close proximity. Upper molars are quite distinct as *Bemalambda* lacks a hypocone, but the coryphodonts have an M2 and M3 that occasionally display a hypocone. *Bemalambda* p3 and p4 have a low paraconid with a distinctly well developed protoconid and metaconid. The Coryphodontidae have a relatively low paraconid and metaconid, protoconid is the highest cusp, and protolophid and paralophid descend abruptly from the protocone to the lingual base of the crown. The *Bemalambda* paraconid is quite distinct from that on a coryphodont as the latter has a paraconid, paralophid, and cristid obliqua that is greatly reduced to the point of being absent; the m1 and m2 trigonids are rarely higher than the talonids, their lengths are nearly equivalent, and the talonid is occasionally broader than the trigonid.

Bemalambda shares many characters with the Archaeolambdidae including a progressive posterior enlargement of the cheek teeth, labial margin deeply excavated, ectoloph invading past the midline of the tooth, P1 as single rooted, lower dentition in tight alignment and lacking diastemae, and m1 and m2 trigonid being wider, longer, and higher than the talonid. *Bemalambda* is distinct with a P3 and P4 protocone as a V-shaped loph and a metaconule is absent. Archaeolambdid P2-P4 protocones are not V-shaped, lack a posterior wing, and a metaconule is present. The lingual apex of *Bemalambda* cheek teeth is posterior to the transverse axis of the teeth, while the parastyle is larger than the metastyle and protects more labially. Archaeolambid cheek teeth are anteriorly oblique, metastyle is larger than the parastyle, paracone and metacone are higher than the protocone, and positioned more lingually than on *Bemalambda*. *Bemalambda* possesses an entoconid, and the posterior embayment of the m3 talonid is not lingually enclosed as on the Archaeolambdidae. The hypoconulid is relatively large, projects slightly posteriorly, and is separated from the hypoconid by a groove, whereas on the archaeolambdids the m3 talonid is relatively small and crescentically configured.

Cervical vertebrae: (Plate XX, Figure 3) The atlas is oval in outline, anteroposteriorly compressed, and transversely expanded. The articular surface for the cranium is elliptical, deeply concave, and the dorsal articular fossa is a broad transversely expanded trough with right angle sides. Postzygopophyses are very slightly concave and slightly semicircular. The dorsal neural arch is slightly convex with a small medial dorsal tubercle, and ventrally it is concave. An intervertebral foramen lies anterolaterally on the arch posterior of which is a groove that extends to the zygapophyseal foramen. The dorsal surface of the ventral arch is concave, but the ventral surface is convex, and a distinct ventral tubercle is absent. An odontoid fossae is indistinct, the atlas wings (alae atlantis) possess anterior and posterior grooves, are short, narrow, not greatly thickened, and dorsolaterally warped, while at their base is a relatively large diapophyseal foramen which penetrates the wing. A foramen of the wing (foramen alare) is absent. On *B. nanhsiungensis* the dorsal and ventral atlas arches are more anteroposteriorly compressed than on *B. pachyoesteus*.

The axis (Plate XVI, Figure 3) has a relatively large odontoid process with a nearly circular and slightly convex facet for articulation with the atlas. Ventrally the centrum has a distinct spine with two oblique crests that extend from the posterior odontoid process to the bases of the diapophyses. Postzygopophyses are nearly triangular with convex articular surfaces. Diapophyses are triangular and extend posterolaterally. The neural spine is extremely robust and is a right triangle in outline with a perpendicular posterior margin.

Third through seventh cervical vertebrae Cv3-Cv7 (Plate XVI, Figure 3) are preserved only on *B. pachyoesteus* specimen V4115, and have been damaged, prohibiting a complete description. On *B. nanhsiungensis* only an incomplete fifth cervical is preserved (V4161) that has a short

approximately nine mm long centrum, a well developed ventral spine, and relatively large prezygopophyses with slightly concave circular articular facets. Diapophyses are thinly plate-shaped and distinctly divided into two branches, the lower of which is relatively small with a large diapophyseal foramen. On Cv6, diapophyses are also divided into two branches with the ventral being broad and a neural spine is well developed. The seventh cervical lacks a diapophyseal foramen but maintains a well developed neural spine.

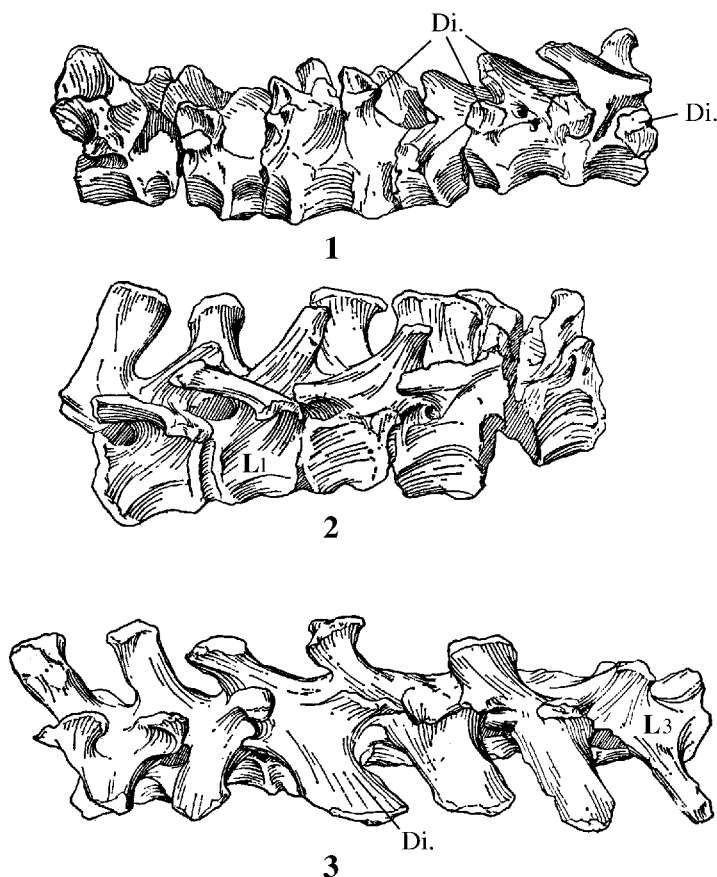


Figure 30.

Left. Lateral view of *Bemalambda pachyoesteus* thoracic vertebrae (V4115, X1/2).

Center. Lateral view of *Bemalambda nanhsiungensis* thoracic and lumbar vertebrae (V4115, X1/2).

Right. Lateral view of *Bemalambda nanhsiungensis* lumbar vertebrae (V4157, X1/2). (Par.-parapophysis; Di.-diapophysis; L3-Third lumbar)

Comparison: *Bemalambda* cervicals compare to the Pantolambdidae in length (*P. bathmodon* Cv6-10 mm, *Bemalambda* Cv5-9 mm), and morphology with Cv6 resembling that on *Caenolambda*, being distinctly divided into two branches, the lower of which is broad. Cv7 resembles *P. bathmodon* in its lack of a diapophyseal foramen. *Bemalambda* cervicals are distinct in the morphology of their axis spine which is a right triangle with a straight posterior margin, whereas on the Pantolambdidae the posterior margin is posteriorly oblique. Compared to the Barylambdidae, both maintain relatively short cervical centra, but *Bemalambda* differs with its anteriorly extended atlas diapophyses, which, on the Barylambdidae, are posteriorly directed. The axis resembles *Haplolambda* in morphology but is distinct from *Barylamba fabri*. The *Bemalambda* cervicals are shorter than those on the Titanoideidae. Compared to the

Coryphodontidae, *Barylambda* has more compressed centra, neural spines are not as well developed, and the axis neural spine is not posteriorly directed.

Simons (1960, p. 47) recognized two cervical morphologies among the Middle Paleocene Torrejonian and Tiffanian pantodonts: The barylambdid morph with relatively short centra and the titanoideid morph with relatively long centra and rather high spines. *Bemalambda* displays relatively short centra and rather well developed spines placing it between the two morphs of Simons.

Thoracic vertebrae: The first through twelfth thoracic vertebrae are preserved on *B. pachyoesteus* V4115. On *B. nanhsiungensis* specimen V4157 the three most posterior thoracic vertebrae are preserved in articulation with lumbar vertebrae, and on two additional specimens the thoracic count is incomplete. However on specimen V4115 the twelfth thoracic vertebrae resembles the third thoracic vertebrae from the end on specimen V4157 in its morphology of the mastoid process and degree of diapophyseal development such that between the two sequences there are probably only one or two missing vertebrae. Through this calculation *Bemalambda* is expected to possess 16 to 17 thoracic vertebrae.

The first and second thoracic centra are approximately 15 mm in length, are very slightly laterally concave, lack a ventral spine, and have short diapophyses. Dorsal portions of the neural spines are not preserved but the remnant bases suggest they were pronounced. Articular facets for the ribs are indistinct. Centra on T3 and T4 are approximately 18 mm in length with relatively complete and very slightly concave elliptical rib facets on the dorsal left side. Ventral spines are indistinct, prezygopophyses are elliptical, postzygopophyses are relatively small, diapophyses are convexly rounded tubercles, and neural spines are more robust than on T1 and T2, being posteriorly oblique with a thinly acute anterior margin and rather broad posterior margin. Diagnostic characters of T5 through T8 resemble those of T4 only the spine is not as posteriorly robust and a ventral spine is becoming more well developed. Centra of T9 and T10 are approximately 20 mm in length with slightly weaker but straight neural spines. A posterodorsally directed triangular and thin mastoid process is distinctly isolated from the relatively small diapophyses, and the articular facets for the ribs are slightly smaller than those on the anterior series. Characters for T11 and T12 resemble those for T9 and T10 only the ventral spine is more well developed, articular surfaces for ribs are smaller, the mastoid process is larger and thicker, and the diapophyses are more reduced. On V4157, the third thoracic from the end resembles the T12 of V4115, with its centrum approximately 20 mm long, ventral spine and mastoid process are more well developed than those on the anterior series, and the diapophyses are posteriorly extended. The second thoracic from the end has a centrum length of approximately 24 mm, the mastoid process is more anteriorly located, parapophyses are well developed, extend posteriorly from the dorsomedial diapophyses as long lineations, and the neural spine has become perpendicular and distinctly shortened with a slightly inflated terminus. The terminal thoracic has extremely well developed parapophyses that are positioned more posteriorly and a well developed mastoid process that has migrated anteriorly. Diapophyses are weak, prezygopophyses are located at the medial base of the mastoid process, faint facets for rib articulation are still present anterodorsally but posteriorly have become lost. Terminus on the dorsal spine is slightly inflated, the anterior margin is thin and acute and the posterior margin is rather broad.

Comparison: *Bemalambda* thoracic vertebrae resemble the Pantolambdidae in centrum length and height, postzygopophyses being slightly larger than prezygopophyses, mastoid processes and parapophyses increase in size posteriorly along the series, the morphology of the neural spines are similar, both display relatively long and robust anterior thoracic vertebrae, and from T9 posteriorly the neural spines shorten. *Bemalambda* differs from *Caenolambda* in its rib facets not being anteroposteriorly expanded or obliquely inclined. On *Caenolambda* the mastoid process is a spherical tubercle but on *Bemalambda* it is thinly plate-shaped. The termini of bemalambdid parapophyses are broadened but on *Caenolambda* are thin and acute. Diapophyses

are also distinct, for on the T2 and T3 of *Caenolambda* they gradually increase in size posteriorly. The Barylambdidae have a thoracic count of 15, whereas *Bemalambda* appears to have possessed many more but with spines and centra that are not as robust. Coryphodontidae have a thoracic count of 17, or very possibly matching *Bemalambda* although coryphodont neural spines are more robust and the posterior increase in size is more pronounced.

Lumbar vertebrae: Eight relatively well preserved lumbar vertebrae are present on *B. nanhsiungensis* specimen V4157, while *B. pachyoesteus* preserves only five isolated and incomplete specimens. Centra length of first and second lumbar is approximately 27 mm, ventral spine is well developed, lateral fossae are conspicuous, diapophyses are extremely small, parapophyses are particularly well developed with approximate lengths of 18-20 mm and with an inflated termini that articulate with the lateral sides of the succeeding mastoid process. The mastoid process has a thin dorsal end and broadened base that fuses with the prezygopophyses. Neural spine is short, transverse notch is nearly triangular, and the terminus is inflated. The dorsal spine of the first lumbar (L1) has an acute and thin anterior margin and rather broadened posterior margin, but the dorsal spine on the second lumbar has anterior and posterior margins of nearly equivalent breadth. L3 through L6 diapophyses are broad and flattened plates that are slightly constricted at their bases, have very slightly indented anterior margins, and very slightly convex posterior margins. Initiating with L3, the diapophyses gradually increase in size posteriorly, with those on L6 being the largest. Parapophyses are short, small, and extend posteriorly from the base of the diapophyses. Mastoid processes are smaller than on L1 and L2 and are fused to the prezygopophyses. Prezygopophyses gradually curl and enclose posteriorly. Neural spines are robust with conspicuously enlarged termini, are triangular in cross section, anterior margins are thin and concave, and posterior margins are broad, flat, and straight. L7 and L8 resemble the preceding in morphology but L8 lacks a ventral spine, and diapophyses are slightly narrower and shorter. Parapophyses are not present, a mastoid process is still relatively well developed, and posterior margin of the neural spine is broad and slightly concave. On *B. pachyoesteus* the diapophyses are more dorsoventrally thickened than on *B. nanhsiungensis*.

Comparison: Bemalambdid lumbar resemble the Pantolambdidae in their length increasing slightly posteriorly, diapophyseal morphology being long, thin, and flattened plates with termini directed slightly anteriorly, and neural spines being distinctly inflated and triangular in cross-section. *Bemalambda* differs in having a higher lumbar count, diapophyseal termini are not thin and acute, and posterior lumbar parapophyses are more conspicuous than on *Caenolambda*. Bemalambdid diapophyses are as well developed as on the Barylambdidae but the former has a higher lumbar count and the neural spines are not as prominent. Compared to the Coryphodontidae, both display diapophyses with constricted bases but *Bemalambda* does not have as well developed mastoid processes.

Sacral vertebrae: (Plate XXIV, Figure 2) Three fused sacral vertebrae are present with centra that are broader than long, the first sacral being the broadest and posteriorly the sequence gradually narrows. Sacrals are not fused to the ilium. The dorsal surface and neural spines are damaged but the bases are preserved as unfused, except on specimen V4123.4 on which the posterior two spines are fused. Dorsal sacral fenestrae are large, pelvic surface is anteriorly broad and posteriorly narrow with two distinct centrum delineations, and the ventral sacral fenestrae gradually diminish in size anteroposteriorly. The sacral wing is robust, anteriorly is slightly concave, and does not contact the sacral vertebrae. The auricular surface is nearly perpendicular with a relatively convex surface. The terminus of the sacrum is narrow.

Comparison: *Bemalambda* sacral characters generally resemble the Pantolambdidae with a vertebral count of three but the former's first and second sacrals are in complete contact with the ilium whereas on the latter only the first and anterior half of the second vertebrae are in contact. The Barylambdidae also share the same vertebral count but the neural spines on *Bemalambda* are not as high, and diapophyses are not completely fused to the ilia as on the former. The

Titanoideidae share the same vertebral count and both have sacra that are not in complete contact with the ilia. On the Coryphodontidae the sacra are completely fused to the ilia as opposed to the bemalambdid condition and the coryphodonts possess distinct pseudosacral anterior caudals.

Caudal vertebrae: The caudals are relatively flat, lack haemal arches, but possess ventral spines in varying degrees of development. On *B. pachyoesteus* specimen V4115 ventral spines are inconspicuous, but on *B. nanhsiungensis* they are relatively distinct. Anterior nine zygapophyses are all capable of functional mobility with prezygapophyses slightly larger than postzygapophyses. On the eighth caudal (Cd8) postzygapophyseal functional mobility has been reduced. Diapophyses on Cd1 are relatively short, thin, flat, and plate shaped. On Cd2-Cd4 they are large, rather thickened dorsally, and are thinly elongated plates with distant posteriorly directed termini. Diapophyses on Cd8 and Cd9 are shortened and narrowed. The first caudal neural spine is relatively large but the rest are relatively weakly developed. The centrum foramen on Cd9 has nearly become lost.

Comparison: There are two morphs among pantodont caudals: an elongated series represented in the Pantolambdidae and Barylambdidae, and a relatively reduced series as represented in the Titanoideidae and Coryphodontidae (Simons, 1960, p. 49). *Bemalambda* approaches the former morph and resembles the Pantolambdidae in its gently platycoelus centra, neural arches on the anterior caudals are complete, diapophyses lack foramina, and haemal arches are absent. *Bemalambda* is distinct from the Barylambdidae by being more gracile, the latter maintains strong haemal arches, and diapophyses on Cd8-Cd10 possess foramina which are absent on the bemalambdids. Barylambdid neural spines are extremely well developed but gradually diminish to become weak on the first ten caudals. Barylambdid anterior eleven caudals have complete neural arches but on *Bemalambda* only the anterior eight caudals have complete neural arches. The Titanoideidae and Coryphodontidae maintain a short caudal series with small and flattened caudals which differs from *Bemalambda*'s robust anterior caudals.

Ribs: The rib shaft is rather flattened with a low degree of curvature and is elliptical in cross-section. The rib angle is positioned relatively high, the capitulum has been subjected to compressional distortion such that its articular surface is not preserved. The neck is relatively long, the tuberculum is relatively small, and its articular surface is also vague. The first rib is the shortest and medial ribs are relatively long.

Ribs are incompletely represented within the order Pantodonta. The distal end of the *Bemalambda* rib being inflated and the shaft being elliptical in cross section resembles *Caenolambda jepseni*. Barylambdid ribs are more robust than on *Bemalambda*.

Sternum: *B. pachyoesteus* preserves two halves of a sternum (V4115). The manubrium is short and robust with a relatively broad anterior margin and narrow posterior margin. The sternal body is shorter than the manubrium, both ends are enlarged, but the medial portion is constricted. Articulation with the ribs is unclear. Sternum specimens are extremely rare within the Order but these specimens resemble *Pantolambda bathmodon*.

Scapula: The scapula is fan-shaped in outline with a short neck and a high spine that is slightly anteriorly oblique and extends directly to the vertebral margin. The suprascapular fossa is nearly triangular in shape, opens as it approaches the vertebral margin, and constricts at the neck. The spinous tubercle is slightly posteriorly oblique. The costal surface and subscapular fossae are very slightly concave, the anterior margin is convexly rounded and relatively short, the posterior margin is relatively long, flat, and straight, and at its midpoint is slightly medially concave. The vertebral margin is relatively broad, at its midpoint is slightly convex, the margin is coarsely textured, and is slightly shorter than the scapular spine. The anterior and posterior angles are extremely well developed. The glenoid fossa is a slightly concave transversely expanded ellipse. From dorsal and ventral perspectives, the acromion process is robust and nearly triangular. Its

posterior process (metacromion) is relatively large but does not distinctly diverge from the acromion. The scapular tubercle is relatively robust, a coracoid process is present, and scapular notch is rather shallow and spaciouly open. On *B. pachyoesteus* the glenoid fossa is circular, broader, and shorter than on *B. nanhsiungensis*, and the scapular notch is even more shallow.

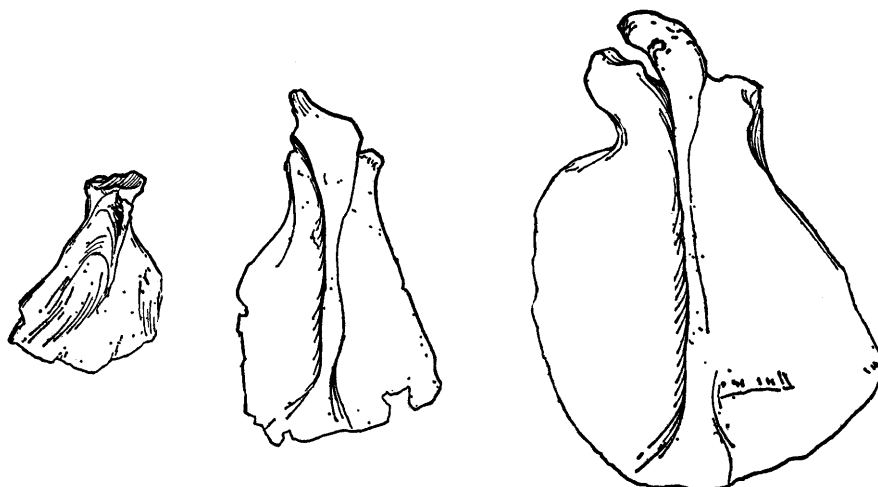


Figure 31. Comparison of pantodont scapulae (X1/6).

1. Lateral view of *Bemalambda pachyoesteus* Chow et al., 1973.
2. Lateral view of *Caenolambda jepseni* Simons (from Simons, 1960, p. 52. Fig. 6A).
3. Lateral view of *Leptolambda schmidti* Patterson and Simons (from Simons, 1960, p. 52. Fig. 6b)

Comparison: *Bemalambda* resembles the Pantolambdidae in its fan-shaped outline, high scapular spine, long acromion process, and well developed posterior extension of the acromion process. However the former differs in the posterior extension of the acromion process not being as projected as on *Caenolambda*, spinous tubercle is not as well developed as on *Pantolambda*, and spinous notch is slightly deeper than *Caenolambda*. *Bemalambda* is rather distinct from the Barylambdidae in its scapula being relatively narrow and long, whereas on the Barylambdidae it is relatively circular. Also, the former's suprascapular notch is not as deep and coracoid and scapular tubercle are not as well developed. *Bemalambda* differs in outline from the Titanoideidae in the posterior and ventral margins not being as projected, and the coracoid process not being as well developed. *Bemalambda* differs greatly from the Coryphodontidae which has a scapula that is triangular in outline, the former has an anterior and ventral margin that is not as projected, and the acromion process is longer.

Clavicle: This element is only preserved on *B. pachyoesteus* specimen V4115 as a robust element with a relatively flattened body, enlarged termini, constricted midsection, sinuous curvature, anterior margin is slightly convex, and posterior margin is relatively thin and slightly concave. The scapular end is not greatly inflated but is thin and flat, while the sternal end is relatively robust.

Comparison: *Bemalambda* compares to the Pantolambdidae in being a large and thick element, although the former maintains a sinuous curvature while the latter is relatively straight. Compared to the Barylambdidae it is not as robust and its sinuous curvature is more pronounced. Compared to the Titanoideidae, *Bemalambda* is dorsoventrally compressed but on the latter is rather dorsoventrally thickened. Compared to the Coryphodontidae, both maintain a relatively robust sternal end.

Specimen V4115 preserves a right forelimb but missing digits I, II, and V.

Humerus: (Plate XVI, Figure 2; Plate XVII, Figure 1; Plate XXII, Figure 1, Plate XXIV, Figure 1) The shaft is rather anteroposteriorly compressed with a relatively smooth and flat lateral face and a shallow brachial groove (sulcus for the *m. brachialis*). The medial face is longitudinally slightly concave to create a thinly acute ridge with a well developed and circular tuberosity two-fifths the distance from the proximal end. The anterior face is nearly triangular with its lateral side bounded by the humeral crest, while its medial side displays a distinct longitudinal ridge that extends from the anterolateral tuberosity to the distal end and intersects the humeral crest one-third the distance from the head. The deltopectoral tuberosity is located two-fifths down the shaft. The posterior face is convexly rounded, smooth, and glossy. The humeral head is large and convexly rounded, transversely broadened, and on specimens V4174 and V4185 is longitudinally elongated due to compressional distortion. The humeral neck is relatively distinct at the posterolateral side of the head; the lateral tuberosity is relatively large and high, being at the same level or surpassing the height of the head; the small and convexly rounded medial tuberosity is located anteromedial to the head; and the intertubercle sulcus is relatively deep. The distal end is slightly broader and flatter than the proximal end with the troclear axis perpendicular to the shaft. The medial condyle is relatively small with a medial margin as a coarsened convex ridge, while the lateral condyle is large and convexly rounded. Medial and lateral epicondyles are well developed, and the lateral supracondylar ridge (crista condyloidea) extends two-thirds from the distal end to form the lateral boundary of the brachial groove. The medial epicondyle is more robust than the lateral epicondyle with a well developed medial epicondylar ridge. A relatively large medial epicondylar foramen is present and the coronoid and olecranon fossae are shallow.

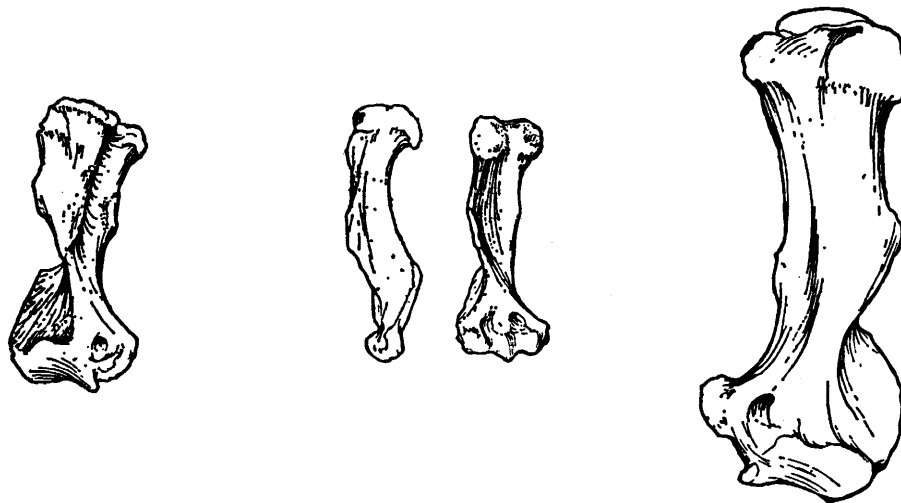


Figure 32. Comparison of pantodont humeri.

1. Dorsal view of V4175 *Bemalambda nanhsiungensis* Chow et al., 1973 (X1/4).
2. Dorsal and lateral views of *Pantolambda bathmodon* Cope (from Osborn, 1898, p. 185, Fig. 11; and Matthew, 1937, p. 462, Pl. XVI, Fig. 6) (X1/4).
3. Dorsal view of *Barylamba faberi* Patterson (from Patterson, 1934, p. 84, Fig. 6) (X1/8).

Comparison: *Bemalambda* shares characters with the Pantolambdidae including the high location of the lateral condylar ridge and deltoid tuberosity, medial tuberosity sits relatively close to the humeral head, and medial epicondylar foramen is relatively large. *Bemalambda* is distinct in its deltoid tuberosity being placed slightly higher, its shaft being relatively straight as opposed to being strongly posteriorly curved as on *P. bathmodon*, a more distinctly coarse laminar ridge is

present on the anterior shaft, there is a more well developed teres tuberosity, dorsal end of the medial epicondylar ridge is slightly higher, and the intertubercular groove is deep.

The *Bemalambda* humerus is extremely distinct from the Barylambdidae in its deltoid tuberosity being slightly higher, not as conspicuous a groove separating the humeral head from the medial tuberosity, the presence of a more distinct and coarsened laminar ridge on the anterior shaft, teres tuberosity placed much higher, medial epicondyle not as robust, medial epicondylar ridge placed slightly lower, lateral condylar ridge slightly higher with a dorsal margin that is not as smoothly rounded, and the lateral trochlea being larger. Compared to the Titanoideidae, *Bemalambda* has a more dorsally placed deltoid tubercle. Compared to the Coryphodontidae, *Bemalambda* is extremely distinct in its more dorsal position of the deltoid tuberosity, the medial tuberosity is located anterior to the humeral head, medial epicondylar foramen is large, its intertubercular groove is deeper and narrower, and teres tubercle is well developed. On the coryphodonts a teres tuberosity is indistinct and the medial tuberosity is located lateral to the femoral head.

Radius: (Plate XVII, Figure 3; Plate XXII, Figure 2; Plate XXIII, Fig. 2) The radial shaft is very slightly curved and relatively flattened dorsally. The dorsal face is convexly rounded with a coarsened surficial texture very slightly ventrally. The posterior surface is longitudinally slightly concave which creates a space between the radius and ulna. The medial margin is concave with a flat and smooth proximal end, the lateral margin is slightly convex with a surficially coarsened ventral region, the proximal end is anteroposteriorly compressed, there is a distinct neck at the ventral region of the radial head, the articular surface for the humerus is convexly rounded, and radial, medial, and lateral tuberosities are all inconspicuous. The distal end is broader and deeper than the proximal end with a relatively flat and straight dorsal surface. The articular surface for the intermedium is a relatively large elliptically concave facet, while that for the radiale is a small and slightly convex facet. The styloid process is relatively large.

Comparison: The bemalambdid radius is straighter than in the Pantolambdidae and does not display a pronounced anterior longitudinal ridge. However, both have distinct medial curvature of the shaft, elliptical radial heads, and slightly inflated proximal and distal ends. *Bemalambda* differs distinctly from the Barylambdidae as its radius is straight with a distinct neck, the distal end is not as inflated, and it lacks a distinct groove anteroventrally. The Titanoideidae has a more pronounced styloid process than *Bemalambda*, and the Coryphodontidae have a weaker anterior crest on the shaft.

Ulna: (Plate XVII, Figure 2; Plate XXII, Figure 2; Plate XXIII, Figure 3) The ulnar shaft is relatively straight, extremely transversely flattened, and has a thin and acute proximal surface that becomes distinctly surficially coarsened ventrally. The distal margin is flat, smooth, dorsally convex, and ventrally concave. The medial surface is very slightly concave and the medial side of the shaft has a distinct interosseous ridge. The lateral face is slightly convex with a surficially coarsened ventral region. The olecranon process is relatively short, robust, and from a dorsal perspective, triangular in shape. The anconeus process is relatively broad and extends laterally. The semilunar notch is short and broad and together with the lateral side of the radial articular facet composes an elliptically concave surface that lacks a distinct anterolateral process. The coronoid process is conspicuously medially extended and the distal end is slightly inflated with a distinct styloid process.

Comparison: *Bemalambda* shares characters with the Pantolambdidae in its posterior margin of the shaft being slightly convex and equivalent length ratio of olecranon process to shaft. *Bemalambda* differs in its apex of the olecranon process occasionally possessing a longitudinal groove, a slightly longer semilunar notch, and a more distinct styloid process. *Bemalambda* is extremely distinct from the Barylambdidae with a shaft that is not as robust or straight, olecranon process is longer in proportion to the shaft, and distal end is not as inflated. Compared to the

Titanoideidae, *Bemalambda* has a more conspicuous styloid process and the occasional presence of a longitudinal groove at the apex of the olecranon process. It also differs from the Coryphodontidae in its occasional presence of a longitudinal groove on the apex of the olecranon process and the absence of a large sinuous groove at the distal end of the ulna.

Manus: (Plate XXVI, Figure 2, Text figure 33, 1) Eight carpals are present, but due to compressional distortion articular facets are all vague. Among the proximal series, the centrale is fused distolaterally to the unreduced scaphoid is square, and anterolaterally expanded. The scaphoid is an irregular rectangle, transversely expanded, rather compressed anteroposteriorly, higher and wider than deep, proximal articular facet for the radius is convexly rounded, lateral articular facet for the semilunar is slightly concave, and facet for the magnum is relatively flat but becomes slightly concave posteriorly. Medially, the articular facets for the trapezium and trapezoid are concave, dorsomedially its surface is slightly convexly rounded, and the ventromedial and ventrolateral sides are concave. The semilunar is an irregular cube with approximately equivalent measurements in all three dimensions, proximal articular facet for the radius is convexly rounded, medial facet for the scaphoid is concave, distomedial facet for the magnum is anteriorly rather flat and slightly convex and posteriorly distinctly concave. Distolaterally, the facet for the unciform is relatively deeply concave and there is a distinct ridge bifurcating the facet for the magnum. The lateral facet for articulation with the ulna is unclear. The ventral side is convexly rounded and the ventromedial side is relatively posteriorly elongated.

The cuneiform is an irregular rectangle, anteroposteriorly elongated, transversely narrow, and is larger dorsally than ventrally. Articular facet for the ulna is relatively flat, medial facet for the semilunar is concave, distal facet for the unciform is relatively flat but slightly convex at its midpoint, distoventrally it contacts the fifth distal carpal, and ventrally the articular facet for the pisiform is slightly convex. The pisiform is irregular in morphology with a ventrally thickened, enlarged, and circular articular facet. Its dorsal surface is planar, medial facet for the cuneiform is very slightly concave, lateral facet for the styloid process of the ulna is concave, and there is a thick ridge that bifurcates both these latter articular surfaces.

Among the distal series, the trapezium is nearly triangular and extremely flattened dorsoventrally, anteroposteriorly elongated, facet for the scaphoid is deformed, facet for the trapezium is concave, medially it is relatively flat, laterally the facet for the trapezoid is concave, and ventrally it is larger and broader than dorsally. The trapezoid dorsal and ventral sides are damaged, it is slightly larger than the trapezium, nearly triangular, relatively transversely compressed, anteroposteriorly elongated, proximolaterally and ventrally it articulates with the scaphoid, the distal facet for the second metacarpal is very slightly concave, medial facet for the scaphoid is slightly convex, and lateral facet for the magnum is relatively flat. The magnum is irregular in shape, anteroposteriorly elongated, rather transversely compressed, proximolateral facet for the semilunar is anteriorly convex and posteriorly concave, proximomedial facet for the scaphoid is medially oblique, medially it articulates with the trapezoid, ventromedially it articulates with the second metacarpal, laterally it articulates with the cuneiform, distal articular facet for the third metacarpal is rectangular and slightly concave, and dorsally and ventrally it is flat. The unciform is the largest carpal in the distal series, irregularly rectangular in outline, transversely broadened, anteroposteriorly shortened, proximomedial facet for the semilunar is convexly rounded, proximal facet for the cuneiform is medially convex, laterally concave and obliquely inclined, distomedially it barely contacts the third metacarpal, facet for the fourth metacarpal is concave, lateral facet for the fifth metacarpal is concave with a distinct ridge bifurcating it, medial facet for the magnum is slightly concave, but becomes thinned laterally. Dorsally it is a transversely elongated rectangle and ventrally there is a small and inconspicuous tubercle.

Metacarpal shafts are broad and flat, distal articular surfaces are not distinctly constricted, and as such the medial shafts are thin and become thick at the termini. Dorsally, the metacarpals are smooth and very slightly convex, ventrally, they are concave, distal articular surfaces for the

phalanges are convex and lack ridges, proximal surfaces maintain a distinct ridge, are saddle-shaped, and articulate with sesamoids. Metacarpal I is rather thin and 28.6 mm in length with a slightly transversely projected proximal articular surface for contact with the trapezium, and a relatively convexly rounded proximomedial facet for contact with the second metacarpal. The second metacarpal is 38.6 mm in length with a saddle-shaped proximal facet for the trapezoid and magnum that is anteroposteriorly slightly convex and transversely concave. The medial side is relatively narrow, is in contact with the first metacarpal, and dorsomedially contacts the trapezium. Laterally, it is relatively long, and anterolaterally and posteriorly it articulates with the third metacarpal. The third metacarpal is 44.6 mm long with an irregular quadrangular convexly rounded proximal articular facet for the magnum. Medially, it articulates with the second metacarpal, a dorsolateral facet is convexly rounded for articulation with the unciform, distally and ventrally there are facets for articulation with the fourth metacarpal, ventral surface is relatively limited and slightly anteriorly oblique, and dorsal surface is relatively expansive and slightly ventrally oblique. The fourth metacarpal has a narrower proximal end than the third metacarpal with a convexly rounded facet for the unciform, medially there are two articular surfaces for contact with the third metacarpal that are slightly convexly rounded, anteriorly large, posteriorly small, and laterally there is a concave facet for articulation with the fifth metacarpal. The fifth metacarpal has a convexly rounded and nearly trapezoid proximal facet for contact with the unciform, a medial facet is convexly rounded and nearly rectangular for contact with the fourth metacarpal, dorsolaterally there is a distinct and coarsened lateral process that is posteriorly slightly concave, and ventrally there is a coarsened inflation.

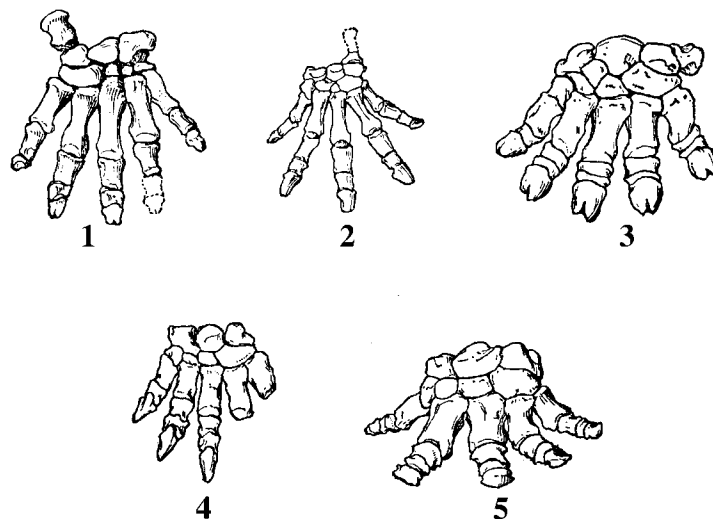


Figure 33. Anterodorsal views of pantodont mani.

1. *Bemalambda pachyoesteus* (V4115) Chow et al., 1973 (X1/4).
2. *Pantolambda bathmodon* Cope (from Osborn, 1898, p. 187, Fig. 12) (X1/4).
3. *Leptolambda schmidtii* Patterson and Simons (from Simons, 1960, p. 52, Fig. 6D) (X1/9).
4. *Titanoides primaevus* Gidley (from Simons, 1960, p. 52, Fig. 6C) (X1/9).
5. *Coryphodon testis* Cope (from Piveteau, 1958, p. 152, Fig. 13) (X1/9).

Among the five digits, the first is completely preserved, the second preserves three phalanges, and the third preserves two and a half phalanges. The first digit is the longest, or approximately twice the length of the succeeding digit. Shafts are flattened with proximal ends broader than distal ends, articular surfaces for contact with the metacarpals are slightly concave while distal articular surfaces for contact with the second phalanx are posteriorly extended, slightly medially concave, and distal surface is not shortened or constricted. The second phalanx is broader than long, ventrally concave, and dorsally flat. The unguis phalanx is hoofed and

approximately equivalent in length and breadth. The hoof on digit three has a conspicuous medial fissure, but this fissure on the first digit is not as noticeable.

Comparison: *Bemalambda* and the Pantolambdidae share manus characters of being equivalently robust, carpals are relatively short, metacarpals and phalanges are relatively long, phalangeal morphology is similar with the ungual phalanx hoofed, and semilunar, pisiform, cuneiform, and unciform share similar dorsal morphology. *Bemalambda* is distinct in its fusion of the centrale and scaphoid, and trapezium is smaller than the trapezoid with an irregularly shaped anterior surface, whereas on the Pantolambdidae the trapezium is larger than the trapezoid and the anterior surface is trapezoid-shaped. The former's trapezoid and magnum are nearly equivalent in size but the latter has a trapezoid larger than the magnum. The latter has a trapezoid that articulates with the centrale but on the former it articulates with the scaphoid. On *Bemalambda* the magnum, semilunar, and scaphoid are in articulation but on the Pantolambdidae these elements also articulate with the centrale. *Bemalambda* has relatively straight metacarpals as opposed to the curved form of the pantolambdids.

Bemalambda is quite distinct from the Barylambdidae as its manus is not as robust and carpals are relatively short, while on the latter the carpals, metacarpals and phalanges are all relatively long. The distal semilunar on *Bemalambda* has two articular facets while on the latter there are three, the centrale of the former is fused to the scaphoid and the trapezium is smaller than the trapezoid, which is the opposite condition on the barylambdids. On *Bemalambda* the trapezoid is an irregular rectangle, but on the latter is nearly square. The bemalambdids have a magnum that contact the trapezoid, scaphoid, and semilunar, but on the latter the magnum only articulates with the semilunar and does not articulate with the trapezoid. Bemalambdid phalanges are relatively long but on the barylambdids are particularly short, and the bemalambdid hooves are not as cloven.

The Titanoideidae shares characters including the fusion of the scaphoid with an unreduced centrale, and the morphology of the scaphoid and other carpals are similar. It differs in its unguals being clawed whereas on *Bemalambda* they are hoofed, the trapezium is an irregular quadrangle but on the latter is rather compressed, and the pisiform is ridged. *Bemalambda* has more gracile and long metacarpals.

The Coryphodontidae are extremely distinct as *Bemalambda* has a rather dexterous manus as opposed to the more graviportal mode of the former. The bemelambdid carpals are relatively short while the coryphodonts are rather elongated and their centrale is reduced. Bemalambdid metacarpals are not constricted anteriorly as on the coryphodonts. *Bemalambda* phalanges are relatively long and cloven while on the coryphodonts they are short and broadened. The only major character shared between these two groups is the fusion of the centrale to the scaphoid.

Pelvis: (Text figure 34) The ilium is an obtuse triangle with a relatively long wing and slightly expanded anterior margin. The gluteal surface is slightly concave, smooth, and glossy. The pelvic face is slightly convex and medial side displays an auricular shaped facet for the sacral vertebrae, and from which there extends an arched ridge. On V4194, relatively conspicuous lumbar tubercles are present, the iliac crest is coarsely thickened, the medial margin has a relatively short greater sciatic notch, and the lateral margin is relatively thin and medially depressed. Both a sacral and coxae tubercle are present. The pelvic face of the ischium is slightly concave as is the ventral face which is also smooth and glossy. Anterior and posterior margins are thin and acute, lateral margin is rounded and relatively thick, and the lesser sciatic notch is rather straight. The anterolateral angle (acetabular ramus) is triangular in cross-section and the posterolateral angle (ischial tuberosity) is relatively large but not particularly laterally extended. Only a portion of the pubis is preserved on V4194 with a slightly concave pelvic face, relatively flat ventral face, and inconspicuous iliopubic eminence.

Comparison: Characters shared with the Pantolambdidae include the arched ventral iliac line, the slightly convex iliac crest, lateral iliac angle is slightly posteriorly directed, the ratio of the post acetabular region is similar with that on *Bemalambda* as 44% and that on the pantolambdidae as 47%, and both maintain narrow ischia. *Bemalambda* differs in the midpoint of its ischiac crest not being depressed as it is on *P. cavirictus*. The barylambdid pelvis is extremely distinct as its pelvic wings are triangular, more laterally extended, the anterolateral wings are very slightly anteriorly extended, an arched line on the ilium is absent, and the ischial spine is constricted, whereas on *Bemalambda* the ischiac wings are narrow, crescentic, do not extend laterally, are slightly posteriorly extended, and ischiac spine is not as constricted. Titanoideidae share characters including the slightly posteriorly directed anterolateral angle of the ischium and slightly convex ischiac crest, but *Bemalambda* differs in its ischiac wing being not as broad and its postacetabular ratio as 44% vs. the 41% proportion on *Titanoides*. The Coryphodontidae are extremely distinct in having semicircular ischiac wings, a robust arch-shaped iliac crest, an extremely strong posteriorly directed anterolateral angle of the ischiac wing, a 38-40% postacetabular ratio, and a constricted medial ischial spine.

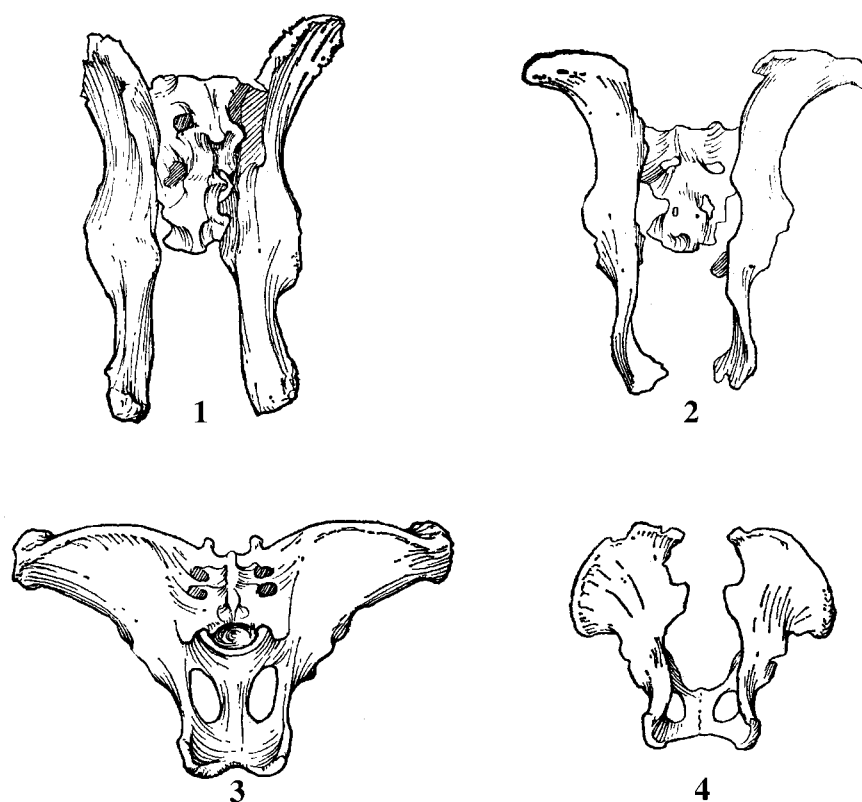


Figure 34. Dorsal comparison of pantodont pelvises.

1. *Bemalambda pachyoesteus* Chow et al., 1973 (V4115 X1/4).
2. *Pantolambda bathmodon* Cope (from Matthew, 1937, p. 466, Plate LXVII, X1/4).
3. *Barylambda faberi* Patterson (from Patterson, 1935; p. 153, Fig. 4a, X1/16).
4. *Coryphodon lobatus* Cope (from Osborn, 1898, p. 206, Fig. 24, X1/20).

Femur: (Plate XVII, Figure 6; Plate XVIII, Figures 1 and 2) The anterior face of the shaft is convex and posterior face is rather flat and straight. The lesser trochanter is well developed and located on the medial shaft one-third from the femoral head. A medial supracondylar crest is well developed, the third trochanter is also located one-third from the head but on specimens V4164-11 and 12 it is located at the midpoint of the shaft. A conspicuous ridge runs dorsally from the base of the third trochanter to the greater trochanter and ventrally this ridge extends to intersect the well

developed lateral supracondylar crest. A supracondylar fossa is absent. The proximal end of the femur is relatively broad, the femoral head is nearly elliptical, and is directed dorsomedially. On specimen V4164-11 the head is transversely broadened due to compressional distortion. A small indistinct fossa on the femoral head (capitular fovea) is present medially and slightly posteriorly; the femoral neck is distinct; and the greater trochanter is well developed, situated nearly equivalent to or slightly lower than the head. The trochanteric fossa is deep and trochanteric crest is a thickened ridge. The distal end is rather excavated anteroposteriorly, medial and lateral condyles are well developed with the medial being larger, anteroposteriorly expanded, and rather broadened. An intercondylar fossa is relatively deep, medial epicondyle is stronger than the lateral epicondyle, the trochlea is spaciouly open, and an extensor and popliteal fossa are present.



Figure 35. Comparison of pantodont femora.

Left. Dorsal view of *Bemalambda nanhsiungensis* Chow et al., 1973 (V4164.11, X1/4).

Center. Dorsal view of *Pantolambda bathmodon* Cope
(from Osborn, 1898, p. 185, Fig. 11, X3/8).

Right. Dorsal view of *Barylamba faberi* Patterson (from Patterson, 1935, p. 156, Fig. 5).

Comparison: Compared to the Pantolambdidae both share the same degree of robusticity. *Bemalambda* differs in its capitular fovea being shallower, lesser trochanter is less well developed, greater trochanter is situated slightly lower, third trochanter is also situated slightly lower and is not laterally extended, and medial and lateral condyles are not equivalent in size but on the Pantolambdidae are nearly equivalent. Compared to the Barylambdidae, both are relatively straight. Principle distinction of the Bemalambdidae is its relatively distinct capitular fovea which is lacking on the barylambdids, greater trochanter is higher, the lesser and third trochanters are much weaker, lesser trochanter is located slightly lower, third trochanter is slightly higher, and trochanteric fossa is deeper. The Titanoideidae has distal condyles of equivalent size but *Bemalambda* has a medial condyle larger than the lateral condyle and its third trochanter is positioned more ventrally. Compared to the Coryphodontidae, *Bemalambda* has a stronger third trochanter.

Patella: (Plate XXV, Figure 5) This element is oval in outline, dorsoventrally elongated, transversely narrow, anteriorly slightly convex, articular surface is transversely convexly rounded, longitudinally very slightly concave with a medial longitudinal ridge that divides the articular facet into medial and lateral surfaces, the base is relatively wide, apex is acute, and medial and lateral margins are convexly rounded. It resembles the Pantolambdidae but has a slightly wider apex.

Tibia: The shaft is relatively flat and straight, triangular in cross-section, anteroposteriorly expanded, transversely compressed at its midpoint, and both ends of the shaft are broadened. The medial face is relatively flat, lateral face is concave, and posterior face is relatively narrow, smooth, glossy, and convexly rounded. Lineations for musculature are inconspicuous, a robust and well developed cnemial crest is present that is slightly curved with a thin acute medial margin. The proximolateral margin is concave to create an interosseus vacuity with the fibula. Proximally, medial and lateral condyles are well developed and the medial condyle is relatively long with a saddle-shaped articular facet upon it. An intercondylar eminence is absent, intercondylar fossa is shallow, a scar for popliteal musculature is relatively deep, and contact for the fibula is posteroventral. The anterodorsal tibial tuberosity is robust, ligament sulcus is inconspicuous, and a groove for musculature is present. Distally, the facet for the calcaneum is quadrilateral and concave, medial and lateral condyles are robust and extend distally, and a distinct boundary between the two condyles is absent.

Comparison: Compared to the Pantolambidae, both shafts have triangular proximal ends, distal ends are slightly inflated, cnemial crest is high, robust, extends rather distantly, and tibial tuberosity is undeveloped. *Bemalambda* differs in its straightened shaft whereas on the pantolambids it is distinctly posteriorly curved and the medial condyle of *Bemalambda* is more well developed. Compared to the Barylambdidae, both have straight shafts, undeveloped tibial tuberosities, and well developed medial condyles. *Bemalambda* differs in its termini not being inflated and its proximal end being triangular while in barylambdids this end is quadrilateral. Compared to the Titanoideidae, *Bemalambda* has a cnemial crest that extends more distally. Compared to the Coryphodontidae, *Bemalambda* has a stronger cnemial crest.

Fibula Plate XXV, Figure 4) The shaft is relatively straight, proximal cross-section is nearly triangular, but distal end is elliptical. Lateral surface is smooth, glossy, and convexly rounded. Medial side maintains a distinct ridge and both ends are rather thickened. The fibular head contacts the posterolateral side of the tibia's lateral condyle. On the lateral side of the head are two tuberosities. The distal end is greatly inflated with a roundly inflated lateral condyle, a distinct groove is present posteriorly, medially the facet for contact with the tibia is slightly convex, and distally the facet for the astragalus is oval, relatively flat, and medially oblique. The Pantolambidae also has a relatively gracile shaft but it is more curved. Barylambdid fibular shafts have more swollen termini.

Pes: (Plate XIX, Figures 2,3; Plate XX, Figure 1; Plate XXVI, Figures 1,3,4) Two hind feet are preserved on *B. pachyoesteus* V4115 and on *B. nanhsiungensis* V4215 an incomplete pes is represented.

Seven tarsals are present. The astragalus is proximodistally elongated, proximally there is a relatively large foramen, dorsally the facet for the tibia is broad but not deep, fibular facet is large and slightly convex, distally there is a concave facet for articulation with the lateral side of the cochlear process, and the facet for the sustentaculum tali is convex. A groove runs dorsomedially-ventrolaterally between the aforementioned facet and the lateral side within which lies the astragalar foramen. The neck is relatively long and astragalar head is large, convex, and rather broad where it articulates with the cuboid. Facet for the navicular is also convex.

The calcaneum has a robust proximal tuberosity that is rather elongated dorsoventrally and transversely rather compressed. Distally there is a large facet for the cuboid which is slightly concave and triangular. The sustentacular tali lies ventromedially with a relatively spacious tarsal groove posterior to it and a tubercle lies lateral to this groove. Laterally on the calcaneum is the cochlear process which contacts the ventromedial astragalus with a convexly oval facet.

The navicular is elliptical and flat, relatively thick dorsoventrally, dorsal surface is narrow, and metatarsal facet is broad. Distally, the facet for the cuneiform is convex. Posterolaterally it

does not contact the cuboid, the lateral facet for the astragalus is in contact with the facet for the external cuneiform, and a posterolateral process is well developed and separated from the main body of the element. Posteromedially, there is a posteriorly extended process that is separated from the posterolateral process by a sulcus.

Among the distal series, the internal cuneiform is transversely compressed, greatly elongated dorsoventrally, rather high, rectangular, superficially coarsened, anterior margin is relatively thin, distal end contacts the first metatarsal with a slightly concave articular facet, and dorsolateral side contacts the middle cuneiform. The middle cuneiform is the smallest among the series, is baton-shaped, rather elongated dorsoventrally, distal end is not greatly expanded, medial side contacts the internal cuneiform, dorsal surface articulates with the navicular, laterally there is a narrow and slightly convex facet for the external cuneiform, and the distal end has an elongated concave facet for the second metatarsal. The external cuneiform is baton shaped, dorsal surface is an irregular quadrangle and is dorsoventrally enlarged; distal end becomes narrow, short, and possesses a tubercle; proximal end contacts the navicular with a relatively narrow, concave, and medially oblique articular surface; medial side contacts the middle cuneiform with an extremely shallow articular facet, lateral side articulates with the cuboid, distal end articulates with the third metatarsal, and there is a small secondary ventromedial facet for articulation with the middle cuneiform. The cuboid is the largest element in the distal series, rather elongated dorsoventrally, proximolateral side has a convex triangular and slightly oblique articular facet for articulation with the calcaneum, medial side has a concave and slightly laterally oblique facet for the astragalus, anterolateral side articulates with the external cuneiform, posteriorly it contacts the navicular, the lateral side is coarsely textured and convex, posterior margin possesses a distinct groove that runs obliquely dorsoventrally, distal end articulates with the fourth and fifth metatarsals with a concave facet, and the medioventral angle has a narrow facet for articulation with the third metatarsal.

Five metatarsals are present with lateral metatarsals being unreduced, shafts are rather compressed, and termini are slightly inflated. The first metatarsal is the shortest in the series with its dorsal surface slightly shorter than its ventral surface, proximal end is dorsoventrally enlarged with a convexly rounded facet for the internal cuneiform, the ventral side is narrower than the broad ventral portion of the dorsal margin, termini possess distinct ventrally extended tubercles which are deeply concave at their midpoints, the proximomedial side is convexly rounded, and the lateral facet for the middle cuneiform is relatively flat. The second metatarsal is longer than the first, the proximal end is dorsoventrally enlarged, facet for the middle cuneiform is nearly a convex elongated triangle with its apex directed posteriorly, medial side contacts the first metatarsal and dorsally contacts the internal cuneiform, dorsolateral side is relatively flat and contacts the external cuneiform, ventrally there is a concave facet for articulation with the third metatarsal, the shaft is triangular in cross-section, dorsal surface is flat, and ventral surface is concave. The third metatarsal has a triangular proximal facet for the external cuneiform, the dorsal surface is relatively flat, ventral surface has become constricted, medial side contacts the middle cuneiform, laterally the contact for the fourth metatarsal is concave, and dorsally it articulates with the cuboid. The fourth metatarsal is longer than the third, dorsal surface is flat, ventral surface is concave, proximal end is equivalent in length and breadth, facet for contact with the cuboid is an anteriorly expanded obtuse triangle, medial facet for the third metatarsal is slightly convex, and lateral facet for contact with the fifth metatarsal is concave. The fifth metatarsal is relatively gracile, distinctly laterally curved, proximal end is thick and large, medial facet for the cuboid is anteroposteriorly convexly rounded, posterolateral angle has a distinct tubercle, and medial facet for the fourth metatarsal is slightly convex.

Only two phalanges of the first right digit are preserved. They are rather thin, dorsally slightly convex, ventrally slightly concave, and ungual is a semicircular cone.

B. pachyoestus differs in having an astragalar neck that is slightly shorter than *B. nanhsiungensis*, it lacks a distinct ridge between the tibial and fibular facet, and facet for the

sustentaculum tali is convex, whereas on *B. nanhsiungensis* this facet is concave. The *B. pachyoesteus* calcaneum displays a sustentaculum tali that is slightly higher its articular facet is not as laterally extended, and distal facet for the cuboid is concave, while on the older taxon the cuboid facet is laterally flattened and medially concave. The *B. nanhsiungensis* calcaneum has a distinct lateral ridge that extends from the calcaneal tuberosity directly to its distal end, which is absent on the latter species.

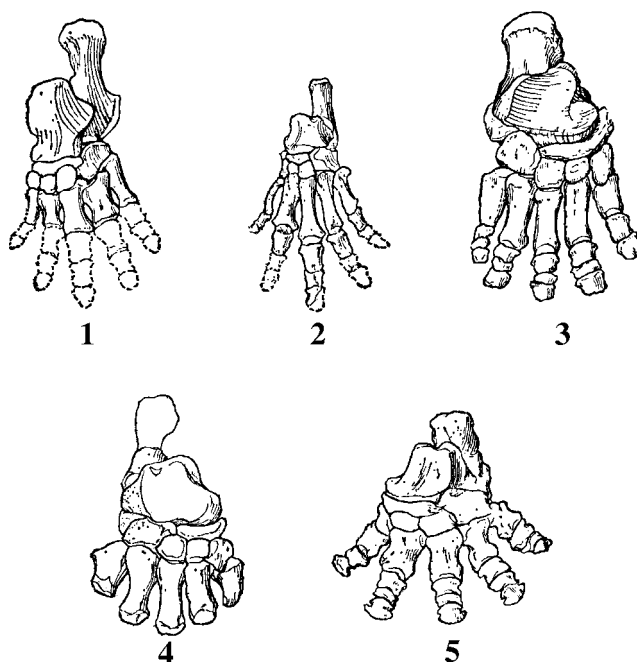


Figure 36. Comparison of pantodont pes from dorsal perspective.

1. *Bemalambda pachyoesteus* Chow et al., 1973 (V4115 X1/4)
2. *Pantolambda bathmodon* Cope (from Osborn, 1898, p. 181, Fig. 12, X1/4).
3. *Barylambda faberi* Patterson (from Patterson, 1935, p. 159, Fig. 6, X1/9).
4. *Titanoides primaevus* Gidley (from Patterson, 1939, p. 360, Fig. 103, X1/6).
5. *Coryphodon testis* Cope (from Piveteau, 1958, p. 152, Fig. 13, X1/9).

Comparison: *Bemalambda* shares pes characters with the Pantolambidae including the agile construction of the foot, tarsals are relatively short, metatarsals and phalanges are relatively long, calcaneum, cuneiforms, and cuboid are morphologically similar, and metatarsal morphology is similar. *Bemalambda* is distinct in having a more robust calcaneal tuberosity, navicular is represented as a single element while on the latter is two elements, the external cuneiform is slightly more acute than on *P. bathmodon*, the astragalus has a distinct head and neck which is vague on the latter, the pantolambdids have a fourth metatarsal that articulates with the external cuneiform, and the third metatarsal does not contact the cuboid, whereas on the bemalambdids the third metatarsal articulates with the cuboid.

The bemalambdid pes is very distinct from the Barylambdidae as it is not as robust, and contrasts completely with tarsals being shorter, and metatarsals and phalanges being longer, whereas on the latter the tarsals are long and metatarsals and phalanges are short. On the latter, the navicular has an extremely well developed posterolateral process which is absent on the former. The bamalambdid cuboid-calcaneum articular surface is convex but on the barylambdids is concave. The Bemalamdid astragalus has a distinct head, neck, and astragalular foramen, but on the barylambdids the head and neck is ambiguous and the foramen is absent. Bemalambdid tibial articular facet is shorter, metatarsals are longer and more gracile, and the third metatarsal articulates

with the cuboid. But on the barylambdids the external cuneiform articulates with the fourth metatarsal. Characters shared between the two include the morphology of the navicular, cuboid, and cuneiforms.

Characters shared with the Titanoideidae include tarsal articulation formula, external cuneiform does not contact the astragalus, and navicular and cuneiform morphology are similar. *Bemalambda* differs in being more gracile, tarsals are shorter, and dorsomedial angle of the cuboid is relatively flat, whereas on the latter the dorsomedial angle it is medially convex. The bemalambdid astragalus has a distinct transversely constricted neck but on the titanoideidids the neck is indistinct. The former's astragalar head is convex but on the latter is relatively flat, the former's tibial facet on the astragalus is narrow and deep but on the latter is shallow and spacious. The third metatarsal on *Bemalambda* articulates with the cuboid, but these two elements are not in contact on the Titanoideidae.

The Coryphodontidae are extremely distinct as *Bemalambda* has an agile pes, shorter tarsals, external cuneiform does not contact the astragalus, the astragalar neck is distinct, and head is convexly rounded. The coryphodonts lack a distinct astragalar neck and its head is relatively flat. Tibia articular facet on *Bemalambda* is narrow and deep but on the latter is shallow and spacious. On the former the navicular is narrower. Coryphodonts have shorter and thicker metatarsals than bemalambdids.

Phylogenetic position of the Bemalambdidae

Preliminary diagnosis of this new family was based upon unprepared specimens. Consequently they were initially regarded as a member of the Pantolambdidae based upon the anterior skull morphology and W-shaped crests of the dentition which resembled the genus *Pantolambda* (Young and Chow, 1962; Zhang and Tong, 1963). Subsequently, after a more detailed study, it was realized that not only were there fundamental conspicuous distinctions between these specimens and *Pantolambda*, but that it was difficult to make direct comparisons with any other pantodont known as cranial, mandibular, and dental morphology resembles the Carnivora and Insectivora and not that of other pantodonts. Consequently, the genus was recognized as a new family within the order (Chow and Qiu, 1964) even though a comprehensive analysis and comparison were yet to be undertaken.

General morphological characters of *Bemalambda* are extremely similar to the Pantodonta. These include the small cranium, robust skull and mandible, robust limbs with radius-ulna and tibia-fibula separated, and the presence of five digits. Dental morphology of *Bemalambda* is particularly close to the pantodonts in the dental formula being complete, brachydont, and lophate, premolars are unmolarized, P3 and P4 are a double V-shaped, molars have a W-shaped ectoloph, protocone is V-shaped, a hypocone is absent, M3 metastyle is reduced, lower molars are W-shaped, and m3 talonid is elongated but not trifoliate. Of particular interest is the molarization of the dp4 and the transverse groove between the bases of the metaconid and paraconid within the anterior valley which are synapomorphies for the Pantodonta. Obviously, the upper molar morphology of *Bemalambda* is distinct from the other known families within the order but these distinctions are not as pronounced as between *Bemalambda* and other orders in the Class.

The post crania of *Bemalambda* and particularly the presence of a distinct astragalar head and neck resembles that on *Ecoconus* and particularly *Periptychus*. However, cranial morphology distinguishes it strongly from these two genera and particularly in the dentition where the cheek teeth are transversely broadened lophate triangles, and the canine is large. *Bemalambda* resembles *Deltatherium* in upper molar and cranial morphology but the former has a complete dental formula and its lophate morphology differs distinctly from the bunodont morphology of the latter. Other

Bemalambda dental characters resemble the palaeoryctid insectivores* such as *Didelphodus* and *Puercolestes*. These include transversely broadened and triangular upper molars with paracone and metacone in close proximity, and trigonid much higher than the talonid. But *Bemalambda* is a much larger genus with a lophate dentition and robust limbs that are hoofed, which clearly distinguishes it. Consequently, *Bemalambda* is distinguished from the Condylarthra and Insectivora and more appropriately assigned to the Pantodonta.

In addition to sharing abundant pantodont synapomorphies *Bemalambda* displays numerous autapomorphies distinguishing it from other members of the order. On the skull these characters include the short rostrum, depressed facial region, relatively well developed sagittal crest with a distinct divergent angle posterior to the face, frontal is in contact with the temporal but the two are separated by the sphenoid and parietal; and the postglenoid process lies upon the same plane as the basitubercle. On the mandible, the ramus is relatively short; the coronoid process is rather anteroposteriorly expanded; the condyle lies relatively low and on the same plane as the dentition, and has a transverse axis that is nearly perpendicular or slightly posteriorly oblique to the dentition; and the angular process is well developed and predominantly ventrally and slightly posteriorly projected but does not surpass the posterior margin of the condyle. Dentally, the first incisor is the smallest, while the second is the largest, the P1 is located medial to the canine, upper cheek teeth are transversely broadened triangles with a distinctly concave labial margin, W-shaped ectoloph is extremely weak, paracone and metacone are in close proximity and are located lingual to the midline of the tooth, lower molar talonids are particularly low, m2 and m3 trigonids are longer and broader than the talonids, p3-m3 paraconid is distinctly reduced, and metaconid is extremely well developed to the point of being larger than the protoconid. Postcranially, there are eight thoracic vertebrae and the astragalus maintains a distinct neck and head.

Moreover, *Bemalambda* possesses some characters shared with some families but that differ from others in the order, such as the convex anterolateral mandibular margin, premolar morphology, and postcranial characters which resembles the Pantolambdidae and particularly *P. bathmodon* but differ from other families in the order. Synapomorphies shared with the Titanoideidae include the large upper canine, presence of a lower molar entoconid, absence of a metastylid, and fusion of the centrale and scaphoid. Characters shared with the Barylambdidae to the exclusion of the other families include the presence of a supraorbital process and the openly diverged wings on the trigonid. And finally there are characters shared with the Archaeolambdidae including the depressed labial margin of the upper molars, the close proximity of the paracone and metacone which are positioned lingually, and extreme distinction in height between the trigonid and talonid. These combined features all express the extreme autapomorphic nature of *Bemalambda*, suggest that it is inappropriate to assign it to any known family of pantodont, and that it represents a new previously unknown family.

The origin of the Pantodonta

The genesis of the order Pantodonta is indeed obscure. As early as 1898, Osborn hypothesized that the Amblypoda was directly descended from the Creodonta based upon the presence of an astragalus with a neck. Later, Gregory (1910, p. 358) stated that an elementary analysis of characters is adequate to demonstrate the ancestral-descendant phylogeny of the Pantolambdidae, Coryphodontidae, and Uintatheriidae. Linked at the base of this lineage is the Periptychidae while from another branch there emerges the condylarth families Phenacodontidae and Meniscotheriidae. Subsequently, Matthew (1937, p. 313) recognized a relationship between the Periptychidae and the Pantolambdidae and concurred with their assignment to the single order Taligrada but believed the actual ancestor of *Pantolambda* was yet unknown.

* MacIntyre (1966), Szalay (1968), and McKenna (1969) place the *Palaeroryctidae* in the insectivora.

Concurrently, Simpson (1937, p. 266) demonstrated that among the periptychids, there were relatively derived members possessing distinctly large feet resembling *Pantolambda*, and that the Periptychidae could not possibly be ancestral due to being contemporaneous, but also because of their extreme morphological distinctions which partially includes the structure of the feet. Thereupon, he believed a more parsimonious hypothesis lay in the unification of the pantolambdid and coryphodont lineages, and that it would be inappropriate to unify the coryphodonts and uinatheres as they represent a convergent lineages. He thereupon placed the Periptychidae within the Condylarthra and the Pantolambdidae within the Pantodonta, and abolished the Amblypoda. This phylogeny received the support of the vast majority of workers, after which only a very few such as Flerow (1956, p. 255), recognized a periptychid-pantolambdid relationship.

Flerow (1952, p.49) conducted a study of the Archaeolambdidae in which he proposed that the basic dental characters of *Archaeolambda* and *Pantolambda* resembled the Insectivora and more specifically, several taxa of Chiroptera. He attributed these characters to not only their phylogenetic relationship but additionally to a dietary habit, and further believed that although *Archaeolambda* postdated *Pantolambda* the former possessed numerous characters more primitive than any known member of the order, and that the genesis for the order lay in Asia.

Simons (1960, pp. 70-71) conducted a comparison of the Pantodonta with other Early Tertiary orders and suggested that the genesis of the vast majority of these forms originated from a common therian ancestor, but then evolved convergently. The Pantodonta possessed a wide array of characters such that genuine characters expressing the most primitive lineage were indeterminate and, hence he proposed that pantodont dentitions were in a developmental phase toward a state of complexity, and further hypothesized that taxa representing a phase predating *Pantolambda* possessed only a P4 with morphology resembling the pantodonts. Consequently, he believed that several arctocyonids, and even tillodonts, displayed morphology similar to this but that there were no species in these two orders that were archaic enough to be ancestral to the pantodonts.

Subsequently, McKenna (1969) proposed that the pantodonts arose from an arctocyonid condylarth such as *Deltatherium* in the Paleocene of North America or Asia. Olson, (1971, p. 405) hypothesized that the four suborders within the Amblypoda (Pantodonta, Dinocerata, Xenungulata, and Pyrotheria) had their genesis from two orders of condylarths or another placental common ancestor at the same level of the condylarths, and that they evolved in the Western Hemisphere and finally in the Eocene radiated to Asia. Concurrently, Szalay and McKenna (1971, p. 441) recognized the Asian Paleocene *Archaeolambda* as a barylambdid pantodont that emigrated to Asia prior to the Eocene with the Mesonychidae and the vast majority or all of the condylarths, and that *Bemalambda* may represent a small species of *Barylambda*.

Although higher rank phylogeny of the Pantodonta is still unclear, familial classification is distinct and secure. Following is an interpretation of evolutionary trends and a comparison of primitive pantodont taxa to attempt to elucidate the general tendency of pantodont evolution. The species *Pantolambda bathmodon* is recognized as a primitive form.

(1) Body size increases from small to large and graviportal with individual post cranial elements altering from rather small and gracile to large and robust.

(2) The nasal process of the premaxilla alters from having a relatively elongate contact with the nasals such as on *Pantolambda* to become gradually shortened as on the Titanoideidae, Barylambdidae, and *Coryphodon*.

(3) Premaxillary teeth alter from being simplified to complex: first premolar alters from being single rooted (*Pantolambda*) to double rooted (*Titanoides*) and protocone gradually increases in size (*P. bathmodon* P2 protocone is small and P1 lacks a protocone but on the Barylambdidae,

Titanoideidae, and *Coryphodon* the P2 protocone is lophate and P1 protocone is a small cusp or resembles the P2 on *P. bathmodon*).

(4) Molar length ratio gradually increases such that morphology alters from a broad and short triangle (*Pantolambda*) to rectangular (*Titanoides*, *Barylambda*) or to nearly square (*Coryphodon*).

(5) Upper molar morphology increases in complexity and gradually becomes more lophate. *P. bathmodon* mesostyle is relatively weak, paracone and metacone are in close proximity, W-shaped ectoloph is rather weak, and protoloph is relatively large. On the *Barylambdidae*, *Titanoideidae*, and *Archaeolambdidae* the mesostyle is relatively well developed to compose a conspicuous W, and finally on the youngest member, *Coryphodon*, the paracone is reduced and migrated labially, while metacone, metaloph, and postparacrista are reduced to become bilophid.

(6) Protoconule and metaconule alter from being weak or inconspicuous. On *P. bathmodon* the protoconule is small, M1 metaconule is small while M2 and M3 lack a metaconule. *Barylambdidae*, *Titanoideidae*, and *Archaeolambdidae* all maintain a distinct protoconule and metaconule.

(7) Degree of molarization of lower molars increases. Paralophid and anterior wing of hypolophid gradually reduces from the double V-shape on *Pantolambda* to the double loph form of *Coryphodon*. Trigonid/talonid heights gradually reduce in contrast and the entoconid transforms from absent to present.

(8) Postcranial elements become more robust, forelimbs broaden, deltoid tuberosity alters from high to low, as does third trochanter, centrale alters from being isolated as on *P. bathmodon* to become gradually fused with the scaphoid such as on *Titanoides*, and finally to become reduced as on *Coryphodon*. Astragalar neck and foramen gradually become lost and astragalar head alters from being convexly rounded to relatively flat.

The aforementioned tendencies illustrate several apomorphic characters of *Bemalambda* and numerous symplesiomorphs shared with *P. bathmodon* but to the extent that the former is more primitive. *B. nanhsiungensis* shares premolar morphology and body size with *P. bathmodon* but the former displays more primitive characters such as a much lower paracone and metacone in extreme close proximity, W-shaped ectoloph is weaker, protoconule and metaconule are absent, deltoid tuberosity is higher, astragalar neck and foramen are relatively pronounced and astragalar head is convexly rounded. These characters indicate a more detailed discussion of pantodont origins is warranted.

Matthew (1937) and Simons (1960) have documented numerous characters shared between *Deltatherium* and *Pantolambda*, and which are also noted to be basically shared with *Bemalambda* although they do not necessarily imply a direct relationship. There are rather conspicuous distinctions between *Bemalambda* and *Deltatherium*, including the incomplete dental formula of *Deltatherium* (lacking its first premolar), premolars simplified as single conical cusps, molars as conically lophate, and the presence of numerous postcranial characters not shared with the Pantodonta. Simpson (1937) suggested that taxa such as *Peryptichus* were not contemporaneous with *Pantolambda* and thus could not be its direct ancestor. Simons (1960) concurred but emphasized that there was indeed a relationship between the two. *Deltatherium* and the archaic pantodont *P. bathmodon* are basically contemporaneous, both being derived from the Middle Paleocene Torrejonian Stage, but the latter perhaps being slightly younger. This stage had already witnessed a distinct radiation of the Pantodonta and there are notable distinctions between the taxa and faunas of North America and Asia, indicating that prior to the Middle Paleocene, the Pantodonta had already experienced a long developmental phase, and suggesting that a genesis from a *Deltatherium*-like arctocyonid is not as appropriate as previously suggested. Obviously, the

numerous characters shared between the Pantodonta and *Deltatherium* are worthy of notation, however as noted by Mathew (1937) and Simons (1960), these characters are recognized as plesiomorphic homoplasies.

A comparison of pantodonts, and particularly *Bemalambda*, to earlier even more primitive placental mammals indicates that *Deltatheridium*, produced from the upper Cretaceous of Mongolia, shares numerous characters. McKenna et al. (1971) proposed an alternative hypothesis for the dental formula of this therian, emphasizing that it was impossible that it represented an ancestral lineage to mammals with three molars. However, the characters shared between this taxon and *Bemalambda* are worthy of notation and suggest a certain degree of phylogenetic relationship.

Distinctions between *Bemalambda* and North American pantodont families have already been noted and the presence of its plesiomorphic and autapomorphic characters indicate clearly that it could not have immigrated from North America. In the same manner, the Archaeolambdidae is also an extremely autapomorphic family that is distinct from other North American taxa and, regardless of generic or familial rank, is not appropriately aligned with any North American form. This paper concurs with the conclusions of Flerow (1952) and Keilan-Jaworowska (1968, p. 135) who stated that the Archaeolambdidae should represent an independent family. With regard to its relationship to *Bemalambda*, as noted above, it shares numerous characters that distinguish it from the North American forms indicating that throughout its phylogenetic development there may have been a relatively close relationship to *Bemalambda*.

In conclusion, it is extremely possible that the Pantodonta originated in the Late Cretaceous of Asia from a primitive therian resembling *Deltatheridium* and that a lineage from this stock migrated to North America to become prolific while a second lineage radiated rapidly in Asia to lead to the Bemalambdidae and Archaeolambdidae. Between these two families the former is a bit more primitive. The genus *Archaeolambda* is a Late Paleocene taxon that is extensive and prolific in Asia (Xinjiang Autonomous Region, Jiangxi, and Anwei provinces, Inner Mongolia, and Mongolia) while *Bemalambda* attains its apex of development in the Middle Paleocene. The genesis of *Bemalambda* should at least lie in the Early Paleocene or even Late Cretaceous where the genus and the entire Order evolved from a deltatheridian ancestor.

The ecological conditions associated with the Bemalambdidae

Analysis of ecological conditions and their relationship to functional development and the extinction of archaic mammalian faunas is a topic that is complex and difficult to address. However, it is possible, more or less, to comprehend the general body morphology of *Bemalambda* based upon the abundant fossil data. Subsequently, it is possible to conduct a preliminary and superficial interpretation of its habitat based upon the principle characters of the skeleton. But, the degree of development of cranial and other sensory systems, dietary mode, dental formula, and ambulatory mode varies between species. *Bemalambda* displays an extremely small and primitive cranium that constitutes a negligible proportion of the skull. Skull morphology is rather derived as the sagittal crest is extremely high (20-25 mm), being approximately one-half the height of the skull, and constitutes nearly half the length of the skull in lateral perspective. Furthermore, sensory systems are not extremely derived as the orbits are extremely small, being one-sixth or one-seventh the size of the temporal fossa, nasals are short, and an osseous tympanic bulla is not documented on any of the specimens.

There is extensive conjecture regarding the dietary nature of pantodonts, including foraging of budding trees, arthropods, invertebrates, or a mixed diet. The dentition of *Bemalambda* is brachydont and enamel is thin with simple corrugations, indicating a dentition inappropriate for the mastication of siliceous grassy stalks but more appropriately adapted to soft foliage. However, it also shares characters with several insectivores: Upper dentition lacks a broad occlusal surface

which is inappropriate for grinding mastication as on ungulates, lower molars display a great disparity in trigonid talonid height, and cusp apices are acute. From one aspect these characters indicate a closer relationship to the Insectivora, but from another aspect may merely indicate a convergence of dietary preference for insects and other small animals.

The *Bemalambda* dentition differs from a typical carnivore, but it is peculiar that its skull shares several characters with the Carnivora such as the extremely well developed sagittal crest, large temporal fossa, deep masseteric fossa, large coronoid process, and pronounced canine. These characters are inferred to be related strictly to food capture and mastication. Because mastication is solely dependent upon mandibular movement, its morphology is a distinct reflection of musculature development associated with to the cranial morphology which also delineates the musculature. For instance, mastication is controlled by three muscle groups: the temporalis, facilitated by the sagittal crest and coronoid process; the masseter, facilitated by the zygomatic arch and the masseteric fossa; and the pterygoid, facilitated by the palatine, sphenoid, and the coronoid process of the mandible. Morphology of all these osteological features vary extremely with masticatory mode which is reflected by morphological variation within phylogenetic lineages. Compressional shearing is the predominant method of carnivores in addition to the necessity for the hunting of prey, and thus this behaviour requires extreme mandibular force which is reflected in the temporalis and extremely well developed and deep masseter as facilitated by the broad and large coronoid process and masseteric fossa. The well developed sagittal crest and large temporal fossa indicates a massive temporalis and deep masseter musculature.

In ungulates the principle mastication mode is grinding and as such the superficial masseter is well developed, while the temporal and deep masseter are relatively weak. Therefore, ungulate mandibles have a relatively small coronoid process, shallow masseteric fossa, weak sagittal crest and small temporal fossa. Thus the dietary nature of *Bemalambda* more closely resembles that of a carnivore in its condition of the condyle which restricts mandibular movement to the vertical plane along the long-axis of the jaw. Also, the extreme disparity in trigonid and talonid height and occlusal wear indicates that its predominant masticatory direction is vertical and hence the shared cranial characters with Carnivora. Furthermore, the well developed canines on *Bemalambda* from one aspect indicates a defensive mechanism but from another aspect indicates a tool for excavation of insects, tubers, or the grooving and pulling of shrub branches and vines. This mode of feeding also requires a large and strong temporalis and masseter.

The postcranial skeleton of *Bemalambda* is extremely ungulate-like, however, its rather graviportal torso and limb morphology suggest a rather slow and cumbersome gait. Cursorial mammals possess rather gracile limbs with relatively short femora and humeri, elongated ventral shafts, and specialized articular surfaces for strict control of mobility along a direct line. The limbs of *Bemalambda* are in distinct contrast to this with relatively robust femora and humeri that are rather long, ulnae and fibulae are unreduced, and lateral phalanges are well developed. This limb design reflects graviportal locomotion and not cursoriality.

In conclusion it appears as if *Bemalambda* was an ungulate that inhabited marshlands or riparian lacustrine habitats and subsisted on insects, fruiting structures, or foliage.

Paleopathology

Fused dentition: On *B. nanhsiungensis* V4127 there is an additional tooth posterolateral to the M3 that is extremely small and transversely oval with an approximate 8 mm breadth and 4.5 mm length. This tooth has two cusps of equivalent height with very slightly anteriorly curved apices. The lingual cusp is conical and labial cusp is triangularly conical with a distinct crest that extends labially from the apex of the cusp. The tooth is single rooted with a longitudinal groove posterolabially. The anterior margin of the crown is fused to the posterolateral margin of the M3 although the root is separate. The M3 itself is slightly deformed as the metacone is smaller and

more labially situated than on other specimens, placing it in alignment with the paracone. The labial wall of the M3 is rather elongated and nearly perpendicular to the longitudinal axis of the tooth.

Early loss of deciduous dentition (Plate XXVIII, Figure 3): Normally, during the process of permanent dentition eruption, the base of the deciduous dentition is resorbed when the crown becomes lost. On *B. nanhsiungensis* V4147 it is noted that the p1, p2, m1, and m2 have erupted, and the dp3 and dp4 are present. However, there are three additional juvenile mandibles (V4141, V4142, and V4217) that have a ramus height nearly two-thirds that of an adult and that of V4147, which have a newly erupted m1, the p1 is newly erupted on V4141 but not erupted on V4122, the p2 is not yet erupted on all three, the p3 and p4 are incipient, and the dental trough at this location has begun to become sealed and narrow indicating that the dp3 and dp4 had already been shed. But X-ray studies of these specimens indicate the rami are not pathologically deformed such that this phenomenon was possibly due to either nutritional deficiency or a septic condition of the entire body.

Early loss of permanent dentition: In the absence of pathologic conditions, the standard condition of mammals entails a retention of the permanent dentition throughout life. Postmortem dental loss should retain distinct alveolae within the maxillae and mandibles. But on specimen V4118, the dentition and alveolae indicate the apparent presence of I2-M2 only on the left and right sides with no vestigial trace of the M3. Initially, it was believed that the dental formula was incomplete, however, after more detailed observation it was noted that the region posterior to the M2 on V4118 differed from the same position on other individuals in which the palatine posterior to the M3 is not extended and contains the smoothly surfaced posterior root of the M3. But on V4118, the palatine posterior to the M2 composes a relatively thin plate that is posteriorly extended with a coarsened surficial texture and vestiges of alveolae at the posterior margin, indicating that initially V4118 possessed its M3 but that it became lost during life, the palatine resorbed the bone to become thin and cause the alveoli to migrate posteriorly. The cause of the early loss of the M3 on this specimen is probably due to its advanced age in which the onset of atrophy occurs and nutritional deficiency or pathologic complexities caused the resorption of alveolae and loss of the terminal molar.

Osteoporosis: *B. nanhsiungensis* specimen V4115 has distinctly asymmetrical limbs although their lengths are equivalent. The left side is more robust than the right side, the osteological surface is coarsely textured, which is particularly noticeable on the humerus, with secondary occurrences on the radius and ulna. X-ray images were taken of the left and right humeri (Pl. XXVIII, Figs. 1 & 2) to reveal a thickening and osteoporosis of the periosteum on the left humerus. This phenomenon is generally rare and it is difficult to determine its cause.

Appendix: *Bemalambda* measurements.

Table 17. *Bemalambda* cranial and mandibular measurements (mm).

	<i>Bemalambda nanhsiungensis</i>			<i>Bemalambda pachyoesteus</i>		
	Count	Range	Mean	Count	Range	Mean
Dorsal Skull length	6	179.0-231.1	208.4	3	167.7-208.0	190.2
Ventral Skull length	6	167.0-219.0	193.3	3	174.5-245.0	200.5
Facial length (from postorbital process)	7	71.3-96.0	81.9	3	74.6-116.8	92.9
Cranium length (from postorbital process)	7	114.0-135.4	127.3	2	93.0-109.5	101.2
Skull breadth (between zygoma)	7	117.2-153.1	142.6	2	124.0-125.0	124.5
Mandible length	8	146.3-166.4	156.9	3	142.3-174.4	156.6
Symphyseal depth	11	24.0-32.0	27.7	3	31.4-34.0	32.3
Depth at p1	14	22.0-37.0	31.2	3	23.7-29.3	27.3
Depth at m3	11	20.7-35.0	29.9	3	27.3-36.7	31.0

Table 18. *Bemalambda* upper dentition measurements (mm).

	<i>Bemalambda nanhsiungensis</i>			<i>Bemalambda pachyoestus</i>		
	Count	Range	Mean	Count	Range	Median
P1-M3	7	45.4-62.2	57.7	3	55.7-56.7	58.4
M1-M3	8	18.3-31.8	26.6	2	30.1-30.5	30.3
I1 Length	4	4.6-6.2	5.3	1	3.5	3.5
I1 Width	4	3.0-5.9	4.2	1	4.7	4.7
I2 Length	4	5.3-7.8	6.6	1	3.7	3.7
I2 Width	3	5.3-5.9	5.6	1	5	5
I3 Length	4	4.6-6.1	5.1			
I3 Width	4	4.7-6.3	5.4			
C Length	8	12.2-15.2	13.9	3	12.5-16.7	14.0
C Width	8	9.0-14.0	21.1	3	11.3-12.5	12.0
P1 Length				2	3.2-3.2	3.2
P1 Width				2	2.5-3.4	3.0
P2 Length	1	5.7	5.7	3	5.0-6.6	5.7
P2 Width	2	6.8-7.4	7.1	2	4.5-4.7	4.6
P3 Length	9	7.2-9.1	8.2	3	7.3-8.0	7.6
P3 Width	9	10.6-13.6	11.9	3	9.5-10.5	10.2
P4 Length	8	7.0-9.6	8.3	3	7.8-9.3	8.6
P4 Width	8	11.7-15.5	13.4	3	11.8-13.0	12.5
M1 Length	9	7.8-9.5	8.6	3	8.5-11.0	9.4
M1 Width	9	13.9-16.0	14.3	3	12.7-14.3	13.5
M2 Length	9	9.0-12.6	9.7	3	11.0-12.0	11.3
M2 Width	9	13.5-16.2	14.7	2	14.8-16.6	15.5
M3 Length	8	7.5-9.7	8.6	3	8.6-10.2	9.4
M3 Width	7	16.4-20.0	17.8	3	17.0-19.4	17.9

Table 19. *Bemalambda* lower dentition measurements (mm).

	<i>Bemalambda nanhsiungensis</i>			<i>Bemalambda pachyoestus</i>		
	Count	Range	Mean	Count	Range	Mean
p1-m3	10	64.5-73.4	68.1	1	65.3	65.3
m1-m3	7	34.0-38.5	35.7	1	35.7	35.7
I1 length	1	4.2	4.2	1	3.3	3.3
I1 width	1	2.5	2.5	1	4.0	4.0
I2 length	2	5.4-5.9	5.7	2	4.4-5.0	4.7
I2 width	2	6.4-7.2	6.8	2	3.7-5.5	4.6
I3 length	3	4.7-5.0	4.9			
I3 width	3	3.8-4.0	3.9			
C length	9	9.6-11.9	10.8	1	11.5	11.5
Cwidth	9	7.9-10.0	9.0	1	10.8	10.8
p1 length	1	6.3-7.0	6.7	1	4.7	4.7
p1 width	2	2.7	2.7	1	2.8	2.8
p2 length	1	7.5	7.5	1	7.0	7.0
p2 width	1	3.2	3.2			
p3 length	5	8.3-10.6	9.6	1	7.5	7.5
p3 width	5	4.2-6.4	5.3	1	8.0	8.0
p4 length	6	7.0-11.2	9.6	1	8.4	8.4
p4 width	5	5.8-8.7	7.1	1	7.0	7.0
m1 length	8	8.8-11.0	9.7	1	9.6	9.6
m1 trigonid length	4	5.9-6.7	6.3			
m1 trigonid width	8	5.0-8.0	6.5	1	9.3	9.3
m2 length	10	10.0-12.3	11.3	1	11.2	11.2
m2 trigonid length	9	6.0-7.0	6.5			
m2 trigonid width	9	7.7-10.6	9.4	1	12.0	12.0
m3 length	7	12.8-16.3	14.5	1	15.2	15.2
m3 trigonid length	6	6.3-7.9	7.5			
m3 trigonid width	7	8.2-11.7	10.0	1	10.5	10.5

Table 20. *Bemalambda* limb measurements (mm).

	<i>Bemalambda nanhsiungensis</i>			<i>Bemalambda pachyoesteus</i>		
	Count	Range	Mean	Count	Range	Mean
Scapula length	1	194.5	194.5	1	152.8	152.8
Scapula width	1	110.5	110.5	1	116.0	116.0
Glenoid length	3	34.0-41.0	38.1	2	31.0-43.0	37.1
Glenoid width	3	20.0-24.0	22.0	2	28.0-29.3	28.6
Humerus length	4	154.6-168.3	160.8	3	160.2-195.6	177.5
Humerus proximal breadth	7	35.7-58.8	51.4	5	42.0-55.0	49.6
Humerus ant.-post. thickness	5	33.7-48.8	39.8	5	40.0-57.8	49.5
Humerus distal breadth	7	50.0-69.0	62.8	3	50.5-73.4	63.9
Humerus distal ant.-post thickness	8	18.6-26.5	21.4	3	24.4-34.5	29.7
Ulna length	3	157.0-170.0	162.8	1	149.5	149.5
Olecronon breadth	6	14.8-19.4	16.5	3	22.1-35.0	29.5
Olecronon ant.-post. thickness	6	26.5-31.0	29.4	3	22.1-34.4	29.2
Radius length	2	102.0-114.0	108.0	1	113.3	113.3
Radius proximal ant.-post. thickness	2	16.2-16.2	16.2	1	15.8	15.8
Radius distal breadth	2	29.0-32.3	30.6	1	34.0	34.0
Radius distal ant.-post. thickness	2	13.5-15.6	14.5	1	24.8	24.8
Pelvic breadth	4	32.0-38.0	35.1	3	27.0-37.0	33.6
Pelvic thickness	4	13.0-24.0	17.2	3	23.0-27.1	25.0
Femur length	4	190.5-204.0	195.6	1	189.0	189.0
Femur proximal breadth	3	47.0-62.4	55.8	5	55.7-84.9	71.8
Femur proximal thickness	4	24.5-37.4	29.2	5	35.2-40.5	37.1
Femur distal breadth	7	41.9-58.0	49.9	3	49.0-72.0	59.3
Femur distal thickness	22.0-51.8	34.1	3	3	32.0-64.3	46.4
Tibia length	3	132.3-135.6	133.9	1	149.5	149.5
Tibia proximal breadth.	5	34.0-47.4	39.4	1	42.4	42.4
Tibia proximal thickness	5	32.0-49.6	40.1	1	57.8	57.8
Tibia distal breadth	3	27.3-39.8			29.0	29.0
Tibia distal thickness	3	19.2-25.0	21.9	1	32.3	32.3

Table 21. *Bemalambda* cranial dental ratios (mm).

	<i>Bemalambda nanhsiungensis</i>			<i>Bemalambda pachyoestus</i>		
	Count	Range	Mean	Count	Range	Mean
Facial length/cranial lengthX100	6	60.6-73.0	64.6	2	79.5-80.4	79.9
Cranial breadth/cranial lengthX100	4	66.2-87.8	70.5	2	64.0-73.8	68.9
Cranial breadth/basicranial lengthX100	5	66.2-87.8	78.3	68.6-71.2	69.9	
M1-M3/P1-M3X100	5	43.7-53.7	48.3	2	53.1-58.4	55.8
Canine breadth/lengthX100	7	62.5-134.3	92.4	2	62.8-88.3	75.6
P1 breadth/lengthX100				1	78.1	78.1
P2 breadth/lengthX100	2	102.0-160.0	131.0	2	71.2-81.8	76.5
P3 breadth/lengthX100	8	135.0-164.0	148.7	3	126.7-143.8	133.9
P4 breadth/lengthX100	7	130.0-200.0	161.4	3	137.6-151.3	146.0
M1 breadth/lengthX100	8	121.0-187.0	167.9	3	130.0-156.3	145.2
M2 breadth/lengthX100	8	111.0-168.5	151.8	3	134.5-138.3	136.4
M3 breadth/lengthX100	6	181.5-247.0	204.6	3	182.80207	193.3
m1-m3/p1-m3X100	6	44.3-54.5	53	1	54.7	54.7
C breadth/lengthX100	9	70.0-95.0	82.1	1	43.9	43.9
p3 breadth/lengthX100	4	49.2-75.3	56.8	1	106.7	106.7
p4 breadth/lengthX100	7	51.4-82.8	71.3	1	83.3	83.3
m1 breadth/lengthX100	8	51.8-88.5	69.8	1	96.9	96.9
m2 breadth/lengthX100	9	46.7-96.0	79.6	1	107.1	107.1
m3 breadth/lengthX100	7	70.0-95.0	82.1	1	43.9	43.9

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* Several references in the Chinese text were omitted from the Bibliography, therefore this translation lists the omissions with an asterisk followed by a brief description of the subject matter in parentheses in order to inform the reader that the literature exists but a complete citation is unknown at this time.-wd

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