Zhejiangopterus linhaiensis (Pterosauria) from the Upper Cretaceous of Linhai, Zhejiang, China

Zhengquan Cai and Feng Wei
Zhejiang Museum of Natural History, Hangzhou, Zhejiang, 310012

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Translated by Will Downs
Bilby Research Center
Northern Arizona University
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Abstract

The text describes a new genus and species of pterosaur from Late Cretaceous sediments around the municipality of Linhai, Zhejiang Province: *Zhejiangopterus linhaiensis* gen. et sp. nov.* which morphologically approaches *Nyctosaurus* from the Upper Cretaceous Santonian Stage of Kansas, in the U.S. The new taxon is thereby assigned to the family Nyctosauridae.

Introduction

In April of 1986, Chengfa Xu, a young local from the village of Aolicun, Shangpanzhen, in the municipality of Linhai, Zhejiang Province, was splitting Late Cretaceous calcareous tuff in a quarry behind the village when he noticed a skeleton of a nearly complete fossil vertebrate. After informing the Zhejiang Museum of Natural History by written correspondence, the institution's Director, Hua Ming, verified the discovery and made a preliminary identification to the Pterosauria. Subsequently, the museum repeatedly dispatched research personnel, Feng Wei, Zhenquan Cai, and Weitang Wu, to the site to continue investigations and confirm that the specimen was indeed derived from the Cretaceous sediments. The municipal government acknowledged the discovery, directed the Natural History Museum to issue declarations to the local populace about the significance of regional vertebrate paleontology, and further initiated protective measures to insure the security of the rock quarry. The discoverer of the specimen, Chengfa Xu,** was a middle school graduate who became ardently devoted to amateur paleontology. After commendations by professional paleontologists, he became an expert at recognizing fossil bone and paid even more strict attention when conducting his quarrying operations to subsequently recover three additional specimens in various degrees of preservation in addition to several isolated skeletal elements. Subsequently, another local recovered a complete skull of this taxon. In 1990 financial support was provided by the National Foundation for Natural Sciences to facilitate research.

Taxonomy

Pterosauria Kaup, 1834

Dsungariapteroidea Young, 1964

Nyctosauridae Williston, 1903

Zhejiangopterus gen. nov.

Diagnosis: As for species.

Zhejiangopterus linhaiensis sp. nov.

(Plates I and II)

Etymology: Derived from the name of the province in which the specimens were produced.

Type: A relatively complete skull impression (Zhejiang Museum of Natural History #M1330).

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* Financed by the National Foudation for Natural Science.

** Mr. Xu met an unfortunate demise in Febuary of 1988.

Hypodigm: Type; most of a skull with complete cervical region (M1324); a relatively complete specimen lacking the skull (M1325); a relatively complete skeleton (M1328); and an incomplete skeleton (M1329).

Diagnosis: A large pterosaur with wingspan exceeding five meters. Skull is long, low, perfectly arched from the posterodorsal premaxilla to the posterior end of the parietal, and lacks a median keel or any other crests. Nasal and antorbital fenestra are confluent to compose a single oval fenestra that occupies nearly one half the length of the skull. Rostrum is long, gracile, acute and edentulous. The cervical region is long and composed of seven long and gracile vertebrae, the notarium is composed of six fused vertebrae, the sacrum is fused, and the caudal region is extremely short. Sternum is thin with a carinal apex. Six sets of inverted V-shaped gastralia are present. Sacral girdle is typical for edentulous pterosaurs. Forelimbs are robust with a short and stocky humerus that possesses a well developed deltopectoral crest. Wing finger metacarpal is longer than radius-ulna. Femur is long, gracile, and nearly one and a half times the length of the humerus.

Locality and stratigraphic position: Lower Upper Cretaceous Tangshang Fm. at Aolicun Village, Shangpanzhen, Linhai Municipality, Zhejiang Province.

Description

Skull and mandible.

Specimen M1330 represents the complete left side of a skull (Fig. 1) with extremely distinct morphology. M1324 represents the right side of a skull lacking the anterior nasal-antorbital fenestra and features further anterior. Both specimens are consistent in morphology but differ in size.

Skull is long and low, flattened dorsally, rounded posteriorly, and lacks a medial keel, projections, or other crests. Rostrum is long, gracile, acute, and edentulous. The cranial length of M1330 is 287 mm with a maximum height of 45 mm at the posterior premaxilla. Nasal and antorbital fenestra are completely confluent to compose an oval fenestra that is 118 mm in length, or nearly one half the length of the skull. Greatest height of the fenestra is equivalent to the height of the cranium at 38 mm. Length from anterior rostrum to anterior margin of naso-antorbital fenestra is 125 mm where the skull is 29 mm high. The anterior premaxilla lacks keels, crests, or any other projections and is extremely acute with a dorsal surface that extends directly to the posterior naso-antorbital fenestra. The edentulous maxilla composes the ventral border of the of the naso-antorbital fenestra and extends approximately 50 mm anterior to the border of the fenestra where it fuses tightly with the premaxilla in a straight suture. The frontal-premaxilla contact originates one-third of the distance posterior along the naso-antorbital fenestra. A suture between parietal and frontal is inconspicuous, and as such the two elements compose a completely rounded posterior parietal region that also lacks either crests or projections. The cranial region posterior to the fenestra is less than one-sixth the length of the skull. Morphology of this region is somewhat obscured due to compressional distortion, however the cranial sutures are vaguely discernible. The orbit is situated relatively low and preserves its original nearly circular morphology with a 13 mm length, 11 mm height, and a dorsal margin that lies approximately at the midline of the posterior naso-antorbital fenestra. A well preserved sclerotic ring is composed of 12-13 overlapping plates. An extremely gracile and curved osteological element lies at the anterodorsal portion of the orbit that may represent the nasal. The lacrimal is situated ventral to the nasal between the naso-antorbital fenestra and the orbit. Ventral to the orbit lies the jugal, which possesses an anterior projection that overlaps the lateral side of the maxilla. A small piece of gracile bone lies within the naso-antorbital fenestra that probably represents the anterior portion of the right jugal which has been broken and shifted in position. The postorbital is situated dorsal to the temporal fenestra. The quadratojugal is rather gracile, situated ventral to the temporal fenestra,

and is in tight association with the posterior quadrate. The squamosal abuts with the postorbital and is situated posterodorsal to the quadratojugal and quadrate. Posterior to the squamosal lies the opisthotic.

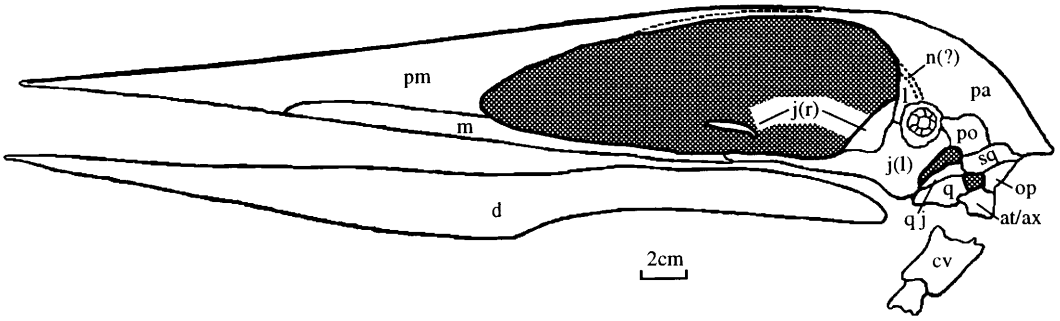

Figure 1. Left lateral view of skull and mandible of *Zhejiangopterus linhaiensis.* at/ax-atlas/axis; cv-cervical vertebra; d-dentary; f-frontal; j(l)-left jugal; j(r)-right jugal; l-lachrymal; m-maxilla; n-nasal; op-opisthotic; pa-parietal; pm-premaxilla; po-post orbital; q-quadrate; qj-quadratojugal; scl-sclerotic right; sq-squamosal.

The mandible is basically consistent with that of *Pteranodon,* with an edentulous absolutely straight dorsal margin in direct opposition to the ventral margin of the maxilla and which attenuates to a sharp point. The mandible of specimen M1330 is 250 mm long.

Vertebrae.

Partial vertebral columns are exposed on specimens M1323, M1324, and M1325, while a relatively complete vertebral column is present on specimen M1328 which is composed of seven cervicals, a notarium composed of six anterior fused dorsals, six posterior dorsals, five to six sacrals, and three to four caudals.

Specimens M1323, M1324 and M1328 all possess seven articulated cervicals ventral to the occipital condyle. The atlas-axis is completely fused and extremely short but morphological details are indistinct due to being obscured by the cranium. Cervicals 3-7 are all long and gracile, lack ribs, have slightly expanded anterior and posterior ends, and are slightly constricted at their mid-points. Only length measurements of these vertebrae are available due to their embedding in matrix (see Table 7). Length gradually increases from CV3-5, attaining a maximum at CV5, and then shortening from CV6 to CV7. The morphology of the zygopophyses and their articular facets are not discernible due to their articulation. CV3 on specimens M1324 and M1328 display two small anteriorly directed articular processes on the anterior end, while specimen M1323 shows two posteriorly directed small articular processes at the posterior ends of CV5 and 6. Specimens M1324 and M1328 are exposed on their right sides and preserved in life position with a slight ventral curvature at the center of the cervical column.

Presumably, a total of twelve dorsal vertebrae is present, the six anterior of which are fused. Specimen M1323 is exposed only on the ventral region, with its proximal dorsal vertebrae obscured by the sternum and pectoral girdle. Specimen M1328 displays the complete right side of an individual with six fused dorsal vertebrae, of which the first two proximal vertebrae are tightly fused. D1 is 1lmm long, 18mm high, and has an 8mm dorsal spine. D2 is 12mm long, 18mm high, and possesses an exposed 7mm high dorsal spine that is totally fused with its anterior counterpart. D3 is incompletely represented as its anterior end is missing, but the preserved element is 8mm long and 12mm high, with a 6mm dorsal spine, the top of which is missing. D4-D6 are concealed by matrix and the scapula, but they are 31 mm in total length. The exposed portion of the D4 dorsal spine is 8mm. Total length of the notarium is 71 mm. Anteriorly, 20 mm

of the fused dorsal spines are exposed which represent the supraneural plate. Because preservation and preparation are incomplete, a more detailed description and discussion of the articular relationships are not possible here.

On specimen M1328 the notarium is 61mm long with 14mm of dorsal spine and centrum exposed. Centrum boundary relationships are vague due to corrosion and compressional distortion, although it is estimated that there are six vertebrae based upon faint suture lines.

Two dorsal ribs are exposed on specimen M1328, which, according to their location are presumed to be those of fused D3 and D5, although their articular relationship with the centrum are obscured by the scapula and their termini do not reach the ventral region. The proximal surface of the exposed third rib is broad and becomes gracile ventrally. Its broadest point is 7mm with a length of 30 mm. Rib five is distinctly smaller and shorter than its predecessor, is also broad proximally, and gracile distally, being 4mm at its broadest and 27 mm in exposed length. Specimen M1325 displays ribs on its left side that extend slightly posterolaterally from D4 and D5, but the tuberculum-capitulum relationships to the centra are obscured by the scapula and neither extends to the abdominal region. Rib 4 is slightly longer than rib 5, is slender, and only 1.5 mm in breadth. Two articulated dorsal ribs are also visible on the left side of the vertebrae between the notarium and sacrum which are also only 1.5mm in breadth and have shorter lengths than the ribs on the notarium.

The right side of M1238 sacrum of is obscured by the pelvic girdle prohibiting its description, but its length is approximately 57 mm. Specimen M1325 reveals a completely fused sacrum that lacks sutures between centra, but it is estimated that five to six sacral vertebrae are represented. A distinct articular surface is present between the anterior sacrum and posterior dorsal vertebra although posteriorly between the sacrum and first caudal a similar surface is not present. The total length of the sacrum-caudals on M1325 is approximately 60 mm.

Caudal vertebrae of specimen M1238 have separated from the torso and lie in the matrix approximately 15 mm posterior to the sacrum. They are extremely short, being 24 mm in length, with a broad proximal end that attenuates posteriorly. Articular surfaces between centra are absent, but it is estimated that three to four vertebrae are represented. Caudals on specimen M1323 are distinctly robust, but this is actually due to overlapping compressional distortion by the posterior process of the ilium.

Sternum and gastralia.

The sternum of M1323 is a recumbent element with a perfectly preserved ventral region, although a piece of the anterior end is not preserved. It is rectangular, being longer than wide, and both sides of the anterior margins are slightly posteriorly inclined. An anteriorly directed ventrally swollen, and then posteriorly extended process is situated at the center of the element which represents a substantial median keel. The posterior margin is flat and straight, at the center of which also lies a ventral swelling which does not extend beyond the posterior margin. The posterior margin of this swelling facilitates articulation with the medial processes of the gastralia. Both lateral margins of this element have been damaged although two inflations for rib attachment protrude at the center of the left side. Sternum length (from anterior process to posterior margin) is 108 mm, breadth of anterior margin is 32 mm, greatest preserved breadth at center is 48 mm, breadth of posterior margin is 26 mm, and the anterior carina extends approximately 9 mm. The sternum of this genus resembles that on *Nyctosaurus* in shape, but differs by being distinctly longer and broader. Furthermore *Nyctosaurus* possesses a more pronounced anterior carina and the posterior inflation does not extend to the posterior margin.

Six rows of relatively completely preserved gastralia lie between the sternum and the pectoral girdle on M1323 (Fig. 2), with each row consisting of two left and right pairs, and each

pair represented by a medial and lateral element. Medial segments are united to form an inverted "V", are distinctly anteriorly projected, and partially overlap their lateral counterparts with a flattened terminus. The length of each medial segment is approximately 25 mm. Lateral segments are gracile and long, all with equivalent lengths of approximately 15 mm. Medial and lateral termini are slightly pointed. On M1328 most of the gastrailia on the right side are not preserved. The first pair of medial segments is slightly anteriorly projected at the center of each segment to facilitate articulation with the posterior inflation on the sternum, although both lateral terminae are missing. The second pair of medial segments do not demonstrate a conspicuous anterior projection. The third through sixth pairs are tightly constricted due to compressional distortion with both sides gradually diverging. Medial anterior projections are conspicuous on the third pair of medial segments but from the fourth to sixth rows compressional distortion prohibits observation of this feature. The sixth row is obscured by a portion of the pectoral girdle. On specimen M1325 several rows of gastralia are observed compressed beneath the dorsal ribs in an intersecting pattern. It is regrettable they are not more clearly defined to allow measurements.

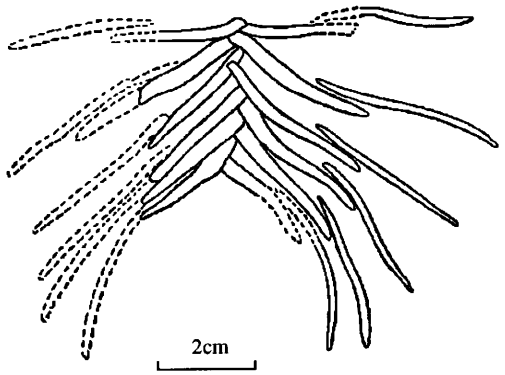

Figure 2. Ventral view of M1323 *Zhejiangopterus linhaiensis* gastralia.

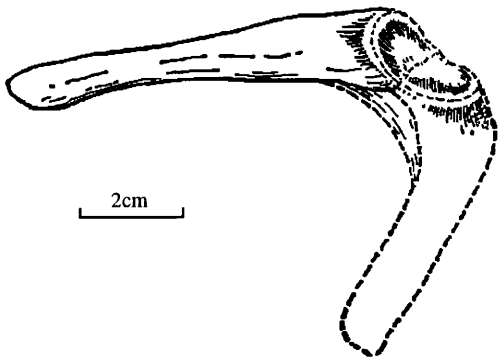

Figure 3. Lateral view of M1328 *Zhejiangopterus linhaiensis* right scapula. Dashed line represents the coracoid of M1328.

Table 1. M1323 gastralia measurements (mm).

	Right medial segment	Left medial segment	Overlap	Left lateral segment
Row I	17 (preserved length)	17 (preserved length)	not preserved	22 (preserved length)
Row II	30	26	10	38
Row III	27	31	11	37
Row IV	28	28	11	30
Row V	26	27	11	36
Row VI	15	8 (exposed)	not exposed	24 (exposed)

Pectoral girdle and fore limbs.

Scapula-coracoids are incomplete on all specimens but M1323 possesses several osteological elements on both sides of the anterior carina of the sternum that should represent these elements. M1328 preserves a relatively complete right scapula, and M1325 preserves both left and right scapulae and a small portion of a dislocated coracoid.

The unified scapula-coracoid forms a completely U-shaped osteological element. On M1325 a glenoid fossa lies at the lateral fusion point of the two elements, although its morphology is obscured by matrix. On M1328 the proximal right scapula is slightly broadened with a small inflation on its dorsal margin, the medial section is slightly constricted, the distal end is flat, and articulation with the humerus occurs proximolaterally (Fig. 3). The M1325 scapula is fundamentally similar, though slightly smaller. The M1323 coracoid is approximately 70 mm in length with a relatively flat and straight axial margin, but a slight inflation on its proximolateral side. A curved V-shaped structure occurs on the right anterior side of the anterior carina. Based upon its location this should represent the scapula-coracoid but compression, rotation, and damage prohibits a precise morphological description.

Several specimens preserve relatively complete, morphologically similar humeri (Fig. 4) which are rather robust and short, but proximal articular surfaces are obscured on all specimens. The deltopectoral crest is extremely large and rather broad on the proximal shaft, while approaching the midpoint it forms into a narrow depression, and at its termini expands and projects laterally to compose a laterally projected arc. The shaft distal to the deltopectoral crest is nearly the same in width but broadens slightly distally. The distal articular surface is unobservable. The shaft itself is pneumatic.

Ulna and radius are nearly parallel, nearly equivalent in length, closely associated, and overlapped. Although these elements are damaged, a relatively good impression remains in the matrix. Shafts are straight and rather flat with expanded termini. M1323, M1328, and M1325 preserve wing fingers that are medially bent. On M1323 the radius-ulna form a nearly 90° angle with the humerus and a 150° angle with the wing metacarpal.

Only M1323 preserves relatively complete right wing metacarpal, pteroid, and carpals, while remaining specimens only preserve the proximal ends of wing metacarpals. Several specimens preserve fused proximal and distal carpal complexes that are slightly larger proximally than distally. A triangular vacuity is present between the carpals and radius-ulna from which the medially directed pteroid projects. This element is extremely slender with a distinct basal expansion. The wing metacarpal is long with an expanded proximal end, a gradually attenuating shaft and an expanded distal end. More detailed descriptions are prohibited due to compressional distortion.

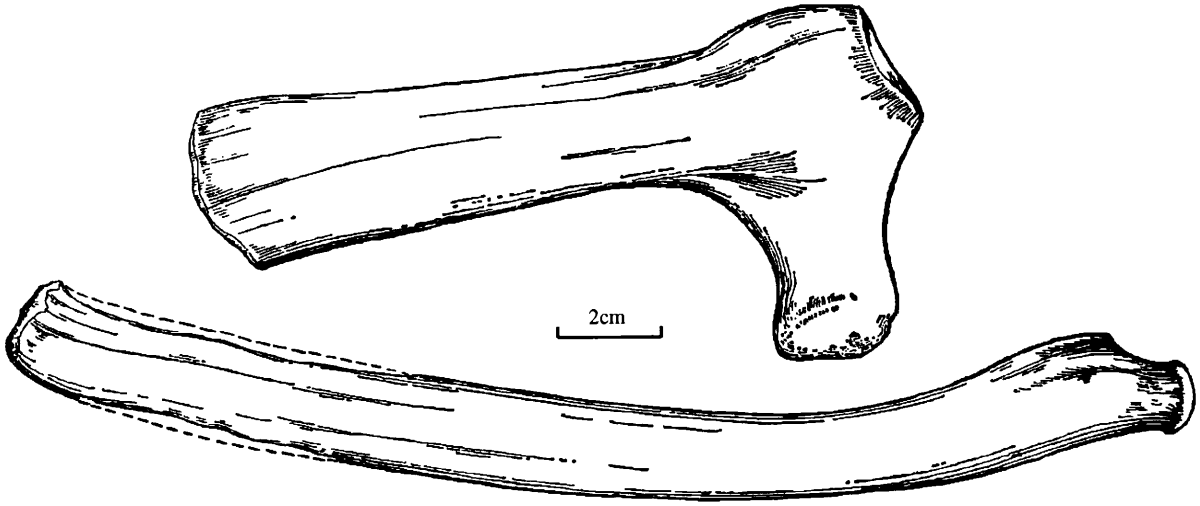

Figure 4. *Zhejiangopterus linhaiensis* (M1323) (left) lateral view of left humerus and (right) left femur

Table 2. Humerus measurements (mm).

	M 1323		M1328	M1325
	Right	Left	Right	Left
Humerus length	137	136	106	90
Prox. breadth	—	32	15	12
Lateral breadth of del. pect. crest	63	68	37	35
Del. pect. crest breath at shaft	41	38	25	26
Mid. sect. breadth of del. pect. crest	24	21	17	15
Distal breadth of del. pect. crest	26	24	—	—
Breadth of shaft	24	25	11	11
Distal breadth	—	~29	24	—

Table 3. Radius-ulna measurements (mm).

	M 1323		M1328	M1325
	Right	Left	Right	Left
Radius-ulna length	~234	234	164	130
Breadth of ulna shaft	13	14	—	—
Breadth of radius shaft	9	10	—	—

Table 4. Metacarpal and pteroid measurements (mm).

	M 1323		M1328
	Right	Left	Right
Pteroid length	124	136	94
Pteroid breadth	5	5	2.5
Metacarpal length	336	—	—
Mc prox. breadth	28	28	—
Mc breadth of shaft	8	—	—
Mc distal breadth	21	—	—

The phalangeal formula (2,3,4,4,0) is consistent with the Pterosauria, with digit IV, or the wing finger, as the longest skeletal element. None of the specimens at hand preserve all the wing bones although M1323 displays a right wing with a large portion of the first and second phalanges, but the third and fourth phalanges still require preparation. The distal end of the wing metacarpal is exposed extending to digits I, II, and III where digit I is represented only by its proximal end, but the three phalanges of digit II and four phalanges of digit III are preserved. Ungual phalanges are all clawed.

Sacral girdle and hind limb.

Although M1323 is preserved in ventral perspective, the ilium, ischium, and pubis are incompletely preserved, overlapped, and compressed to the point that their morphologies are indistinct. The ilium is long with an anterior process that extends beyond the sacrum and curves toward the dorsal vertebrae. The posterior process also extends beyond the sacrum with both anterior and posterior termini being bluntly rounded. Specimen M1325 displays the posterior processes of the left and right ilia as nearly equivalent in length to the caudal vertebrae. Ischium and pubis are fused but their outline is indistinct due to compressional distortion.

Table 5. Measurements of M1323 right wing phalanges (mm).

	Length	Proximal breadth	Shaft breadth	Distal breadth
Phalanx I	322	20	16	16
Phalanx II	220	15	11	10

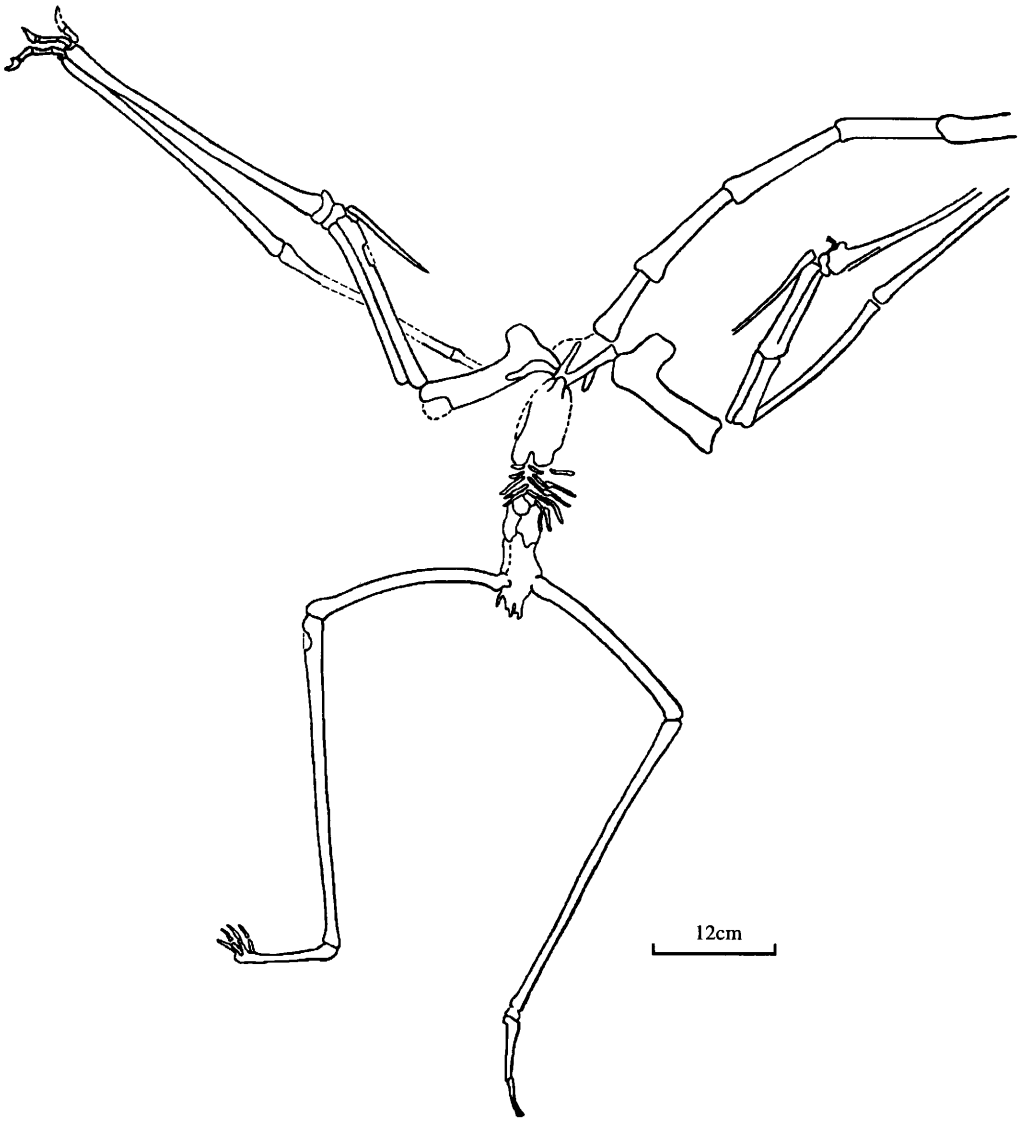

Figure 5. Ventral view of M1323 *Zhejiangopterus linhaiensis*.

Specimen M1323 preserves two opposing thin and flat plates between the pelvic girdle and gastralia that undoubtedly, according to their position, represent prepubi. These elements resemble those on *Pteranodon* but with much broader distal ends.

The femur is long, gracile, and slightly curved with a distinct neck leading to the femoral head (Fig. 4). Although precise morphology of the neck is obscured due to compressional distortion it appears to resemble *Pteranodon* with the distal end of the femur broader than the proximal end. The fibula may be completely fused with the tibia, which is distinctly longer than the femur, more gracile, and gradually attenuates distally. The tarsus is short and composed of

only two elements. M1323 displays a left hind limb with slender and long metatarsals I-IV that are tightly associated proximally, but diverge distally. Phalanges on digits I-IV are well preserved with clawed unguals. Digit V is not preserved.

Table 6. Hindlimb measurements (mm)

	M 1323		M1328	M1325
	Right	Left	Left	Right
Femur length	222	222	122	168
Femur prox. breadth	15	—	9	12
Femur dist. breadth	17	—	13	16
Tibia length	264	265	185	>167
Tibia prox. breadth	14	—	11	13
Tibia dist. breadth	12	—	8	—

Table 7. Osteological measurements (mm).

	M1323	M1330	M1324	M1325	M1328
Length of skull	—	287	430 (as estimated) 203 (as preserved)	—	—
Height of skull	—	45	71	—	—
Nasopreorbital length	—	118	195 (as estimated) 146 (as preserved)	—	—
Depth of mandible	—	19	—	—	—
Cv III length	36	—	50	—	57
CV IV length	114	—	82	—	92
CV V length	142	—	84	—	98
CV VI length	120	—	72	—	81
CVII length	90	—	38	—	56
Notarium length (DI-DVI)	—	—	—	46	71
DVII-DXII length	—	—	—	40	61
Caudal length	—	—	—	—	24
Torso length (~DI-caudal)	310	—	—	140	210
Humerus length	137	—	—	90	106
Radius/ulna length	234	—	—	130	164
Pteroid length	136	—	—	—	94
Metacarpal length	336	—	—	—	—
Wing phalanx I length	322	—	—	—	—
Wing phalanx II length	220	—	—	—	—
Femur length	222	—	—	122	168
Tibia length	265	—	—	185	>167

Diagnosis and Discussion

After his detailed description of Early Cretaceous *Dsungaripterus* from the Xinjiang Autonomous Region of China, C.C. Young (1964) proposed three suborders of Pterosauria: Dsungaripteroidea, Rhamphorhynchoidea, and Pterodactlyoidea. He regarded the Pterodactyloidea as restricted to several Late Jurassic taxa with unfused dorsal vertebrae, while erecting the Dsungaripteroidea as representing large Cretaceous forms with notaria, a superior lamina of the antorbital fenestra, and a supraoccipital crest.

In his summary of the Pterosauria, Wellnhofer (1978) recognized only two suborders while rejecting the characters of the Dsungaripteroidea as being of no taxonomic value as the presence of a supraoccipital crest and superior lamina of the antorbital fenestra are not synapomorphic among enough taxa. Furthermore, he believed the presence of a notarium was functional and not a phylogenetic character, and consequently he rejected the Dsungaripteroidea while erecting a new suborder.

This paper concurs with C.C. Young, recognizing that the presence of a notarium is not merely a character of function but an apomorphy for flight within the Pterosauria, and hence it is recommended that Cretaceous pterosaurs with notaria be retained with in the Dsungaripteroidea. However, a superior lamina in the antorbital fenestra and a supraoccipital crest may only be applied as a basis for generic or familial recognition as they are not synapomorphies for lowest ranks within the suborder

Prior to 1988 only two genera of edentulous pterosaurs were recognized: *Pteranodon* and *Nyctosaurus*, which are extremely lightly structured with notaria and share anterior cranial features including long gracile edentulous beaks. However, these two genera are clearly distinguished by features on their posterior cranium, for *Pteranodon* posseses a well developed crest while *Nyctosaurus* lacks this feature. Other distinguishing characters include the composition of the notarium, sacral vertebral count, and pelvic morphology.

Characters that unite *Zhejiangopteris* with *Nyctosaurus* include the absence of a posterior cranial crest and the distinct deltopectoral crest on the humerus. However the former taxon differs in the presence of a massive antorbital-nasal fenestra that constitutes approximately half the length of the skull, gracile cervical vertebrae, a sternum that is longer than wide, humerus/ulna ratio of 1:1.7, humerus/wing metacarpal ratio of 1:2.5, humerus/first flight phalanx ratio of 1:2.4, humerus/femur ratio of 1:1.5, and humerus/tibia ratio of 1:1.5.

There is controversy regarding whether the crested *Pteranodon* and non-crested *Nyctosaurus* should occupy the same family (Williston, 1903; Young, 1964; Wellnhofer, 1978). This paper regards the presence of a supraoccipital crest as a significant familial synapomorphy, consequently recognizes the independent Nyctosauridae, and furthermore places *Zhejiangopterus* within this family.

Quetzalcoatlus, the gigantic edentulous pterosaur from the Upper Cretaceous Maastrichtian of Brewster Co., Texas, was erected by Lawson (1975). Subsequently Nesov (1984) and Padian (1984,1986) assigned this genus to the family Azhdarchidae. It is regrettable that a more complete description is unavailable for comparison here.

Kellner (1990) erected two edentulous pterosaur genera recovered from the Lower Cretaceous, Aptian, Santana beds in the Araripe Basin, northeast Brazil: *Tupxuara* and *Tapejara* were placed within the newly erected family the Tapejaridae, which, to date, are the oldest known edentulous pterosaurs. Wellnhofer and Kellner (1991) conducted a detailed study of the skull of *Tapejara* and recognized the diagnostic characters of the genus as being small with a short skull, high saggital maxillary crest, with a curved maxilla and mandible which distinguishes it clearly

from other Cretaceous pterosaurs regardless of being edentulous or dentitioned, and is recognized as a morphotype specialized for frugivory. Other pterosaurs with etentulous long, straight and sharp rostra such as *Zhejiangopterus*, or those maintaining long and short randomly arranged dentition represent picivory or pelagic dietary behavior.

IV Discussion of Age

Regional geologic data are used to correlate the calcareous tuffs producing *Zhejiangopterus* at Shangpanzhen to the Cretaceous Tangshang Fm, opinion on the age of which varied based upon two inferences: Some believed the Tanshang Fm. to be an independent early Late Cretaceous unit that unconformably overlies the Jurassic Moshishan Group, while others regarded it as late Early Cretaceous.

The recent discovery of *Zhejiangopterus* has provoked new systematic research into this problem. From a stratigraphic perspective, Yangfan Zheng and Zhonglang He from the Zhejiang Provincial Office of Mines have conducted much regional field work upon igneous rock in the southeast Zhejiang coastal region where the Tangshang Fm. unconformably overlies the Upper Jurassic Moshishan Group in addition to the Lower Cretaceous Guantou and Chaotou formations of the Yongkang Group. The Laijia Fm. unconformably overlying the Tangshang is an independent lithologic unit. These same workers recognize the intercalated calcareous muds underlying the Tangshan Fm. at the type section as the Chawan Fm., which was formerly regarded as a member of the Upper Jurassic Moshi Group but produces pollen including *Taxodiaceaepollenites*, *Carypollenites*, and *Qerlodites*, that reflect a general complexion of early Late Cretaceous. The upper Tangshang Fm. exposed at Shangpanzhen represents a cyclothem of light gray calcareous tuffs, limestones, tuffaceous fine sands, and silts intercalated with ignimbrites which produce the pterosaurs. The lower section consists of gray-banded red ignimbrites, tuffs, and pyroclastic agglomerates which overly the Lower Cretaceous Guangtou Fm. Unconformably overlying the Tangshang Fm. is the Laijai Conglomerate.

Mu (1992) applied potassium-argon dating techniques to the pterosaur bearing sediments and reported that the absolute age should be slightly older than 81.5 Ma. Correlated to the most current international geologic time scale of Cowie and Bassetel (1989) the Late Cretaceous is constrained by dates of 65 Ma and 95 Ma. 81.5 Ma is Late Cretaceous, or possibly correlative to the Santonian Stage. Consequently the upper and lower lithologic boundaries of the Tangshan Fm. are distinct and the age is clearly Late Cretaceous.

To reiterate, with the exception of the Early Cretaceous, Aptian, Tapejaridae, the remaining edentulous pterosaurs are all Late Cretaceous in age. This syapomorphy of *Zhejiangopterus* is shared among *Pteranodon* and *Nyctosaurus* which are derived from Santonian age sediments in the state of Kansas, in the U.S., and is completely correlative to the age of *Zhejiangopterus*.

In conclusion, the age of the Tangshang Fm. in the Shangpan region of Linhai is determined to be early to middle Late Cretaceous based upon stratigraphic, radiometric, and biostratigraphic data.

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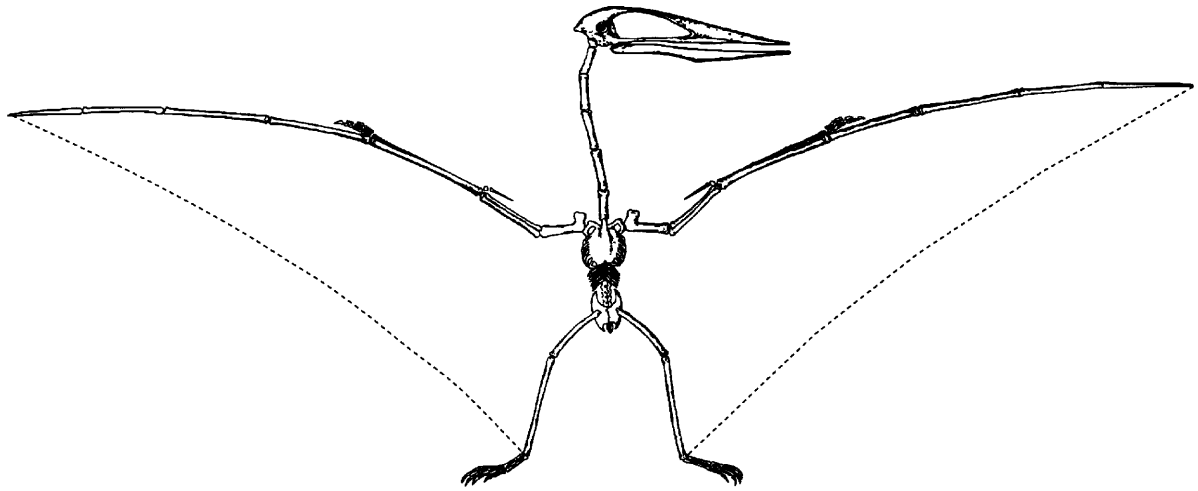

Figure 6. Restoration of *Zhejiangopterus linhaiensis.*

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