

A NEW PTEROSAUR: *BEIPIAOPTERUS CHENIANUS*, GEN. ET SP. NOV. (REPTILIA: PTEROSAURIA) FROM WESTERN LIAONING PROVINCE OF CHINA

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ABSTRACT

Based on an incomplete skeleton, *Beipiaopterus chenianus* gen. et sp. nov. is erected. It is characterized by a wing finger composed of only three wing phalanges with wing phalanx 1 extremely elongate, the scapula is slightly longer than the coracoid, the fifth toe remains in the foot, and a relatively smaller ratio of wing-metacarpal IV to antebrachium. The elongate cervical vertebrae, the ratio of metatarsal III to tibia, and the general shape of the humerus indicate that *Beipiaopterus chenianus* belongs to the Ctenochasmatidae.

Key words: Western Liaoning Province, Early Cretaceous, *Beipiaopterus*, Ctenochasmatidae

INTRODUCTION

Remains of pterosaurs from continental deposits are very rare, compared with those found from marine and marginal marine sediments (Wellnhofer, 1991; Bakhurina and Unwin, 1995). Over 90% of the specimens and about 50% of the pterosaur nominal species come from just a few areas, Solnhofen Limestone (Tithonian, Germany), Santana Formation (Aptian–Albian, Brazil), Cambridge Greensand (Cenomanian, England), and Niobrara Formation (Coniacian–Campanian, Kansas, USA) (Kellner, 1994). In the past several years, numerous pterosaurs found from continental deposits in Mongolia have provided useful information on the distribution, diversity and ecology of pterosaurs (Bakhurina and Unwin, 1995; Unwin et al., 1997, 2000; Unwin and Bakhurina, 2000). Recently, pterosaurs found from the western part of Liaoning Province have made this region important for pterosaurs from continental sediments. At present, seven genera of pterosaurs found from Liaoning Province and its peripheral areas are reported (Ji and Ji, 1997, 1998; Wang and Lü, 2001; Wang et al., 2002; Wang and Zhou, 2002; Wang and Zhou, 2003). Among them, *Jeholopterus* and the herein studied specimen preserve soft tissues (Lü and Wang, 2001; Lü, 2002; Wang et al., 2002). The study of the soft tissues was briefly reported by Lü and Wang (2001), and the detailed study of the soft tissues has been published (Lü, 2002). Although it lacks the skull, the well-preserved soft tissues and the specialized three wing phalanges are significant. The

elongate cervical vertebrae, the ratio of metatarsal III to tibia, and the general shape of the humerus indicate that it represents a new genus of the Ctenochasmatidae.

SYSTEMATIC PALEONTOLOGY

Order PTEROSAURIA Kaup, 1834

Suborder PTERODACTYLOIDEA Plieninger, 1901

Family CTENOCHASMATIDAE Nopcsa, 1928

BEIPIAOPTERUS gen. nov.

Etymology.— *Beipiao* refers to Beipiao City of western part of Liaoning Province, a famous locality with excellent fossils, including insects, plants, amphibians, feathered dinosaurs, birds and mammals.

Diagnosis.— A ctenochasmatoid pterosaur, three sacral vertebrae, length of wing-metacarpal IV approximately equal to that of ulna, highly elongate wing phalanx 1, reaching 53% of the length of the total wing finger, ratio of wing phalanx 2 to wing phalanx 1 of the fourth digit (ph2d4/ph1d4) approximately 0.46, ratio of femur to tibia = 0.41.

BEIPIAOPTERUS CHENIANUS sp. nov.

(Figs. 1, 2)

Holotype.— A partially preserved skeleton with well preserved soft tissues. Beipiao Museum of Liaoning Province (BPM 0002). (SMU: 75565).

Type locality and horizon.— Sihetun, Beipiao City, Liaoning Province; Yixian Formation, middle Barremian



FIGURE 1. The skeleton of *Beipiaopterus chenianus* gen. et sp. nov. (BPM 0002). Scale bar = 5 cm

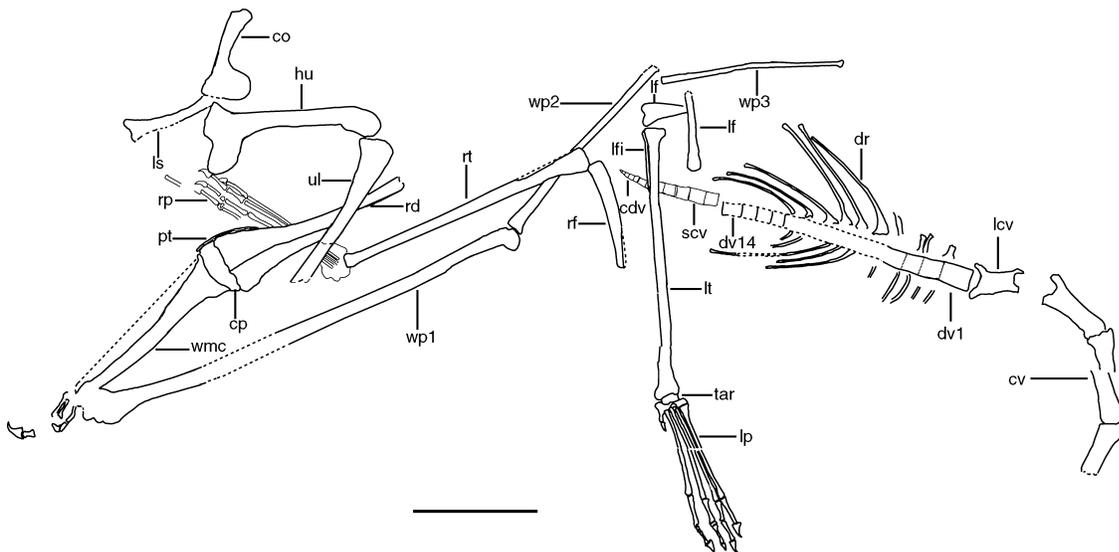


FIGURE 2. Drawings of general disposition of the skeleton of *Beipiaopterus chenianus* gen. et sp. nov. (BPM 0002). **Abbreviations:** **cdv**, caudal vertebrae; **co**, coracoid; **cp**, carpals; **cv**, cervical vertebrae; **dr**, dorsal ribs; **dv1**, the first dorsal vertebra; **dv14**, the 14th dorsal vertebra; **hu**, humerus; **lcv**, the last cervical vertebra; **lf**, left femur; **lfi**, left fibula; **lp**, left pes; **ls**, left scapula; **lt**, left tibia; **wmc**, wing metacarpal IV; **pt**, pteroid; **rd**, radius; **rf**, right femur; **rp**, right pes; **rt**, right tibia; **tar**, tarsals; **ul**, ulna; **wp1**, the first wing phalanx; **wp2**, the second wing phalanx; **wp3**, the third wing phalanx. Scale bar = 5 cm.

(Swisher et al., 1999).

Etymology.—The specific name is in honor of Professor Peiji Chen, a distinguished paleontologist who has made great contribution to the study of Jehol Biota.

Diagnosis.— as for the genus.

DESCRIPTION

Most of the skeleton is preserved, except the skull, right forelimb and pelvic girdle. The specimen is preserved on the bedding plane of a slab of fissile siltstone. Four cervical vertebrae, 14 dorsal vertebrae, 20 dorsal ribs in both sides, three sacral vertebrae, nine small caudal vertebrae, a nearly complete left forelimb, a distal part of the right leg, and a nearly complete left leg are preserved. Soft tissue is preserved as integumentary derivatives in the neck region, as wing membrane near the tip of the left wing and the inner part of the wing, along the right tibia, and integument between the left pedal digits (Lü, 2002).

The cervical vertebrae, anterior dorsal vertebrae are exposed in dorsal aspect, posterior dorsal vertebrae, sacral vertebrae, and the caudal vertebral series are preserved as impressions of their ventral surfaces. Almost all the vertebrae are crushed. The characters of individual vertebrae are unclear.

Cervical vertebrae: Four posterior cervical vertebrae are preserved. The anterior one is missing its anterior part. All the anterior dorsal vertebrae bear ribs, but the anterior ribs are not completely preserved. Therefore, the vertebra without ribs articulated is here inferred as the last cervical vertebra. This vertebra differs greatly from the anterior ones in the shortness of its centrum. But, it is similar to the anterior dorsal vertebrae in length, displaying a gradual change in size from the posterior cervical vertebra to the anterior dorsal vertebrae. The third vertebra from the last cervical, in the anterior direction, is the longest. The ratio of length to narrowest width (middle of the vertebra) of this centrum is 3.4. The ratio of length to width of the last cervical vertebra is 2 (Table 1).

Dorsal vertebrae: Although the boundaries between some vertebrae are not clear, the undisturbed positions of the first ten dorsals with ribs and the last four vertebrae without ribs indicate that the number of dorsal vertebrae is 14. The outlines of last four dorsal vertebrae are clear. They are longer than wide, and of nearly equal length. The outlines of the anterior three dorsal vertebrae are also clear. These vertebrae are short and stouter than the posterior ones. The outlines from the fourth dorsal vertebra to the seventh dorsal vertebra are unclear, but it appears that they are co-ossified. The posterior dorsal vertebrae have round ventral surfaces.

Sacral vertebrae: There are three sacral vertebrae. Their outlines are clear. There is a gap between the anterior end of the first sacral vertebra and the posterior end of the last dorsal vertebra. The first sacral vertebra is preserved as an impression of its ventral surface, showing a round ventral surface, similar

to that of the posterior dorsal vertebrae. The second and third are preserved as small portions of their centra. These sacral vertebrae are fused, but their sutures are traceable. Each sacral vertebra is about 5 mm long.

Caudal vertebrae: There are nine caudal vertebrae. The last six caudal vertebrae are exposed. The second and third caudal vertebrae are partially covered by the left tibia. The anterior four caudal vertebrae are relatively larger than the posterior ones. The posterior caudal vertebrae are small; the combined length of the last five vertebrae is only 11 mm. The ventral surface of the anterior caudal vertebra is round.

From anterior to posterior, the lengths of these caudal vertebrae are nearly equal, but their widths reduce quickly. The distal end of the last caudal vertebra is pointed.

Ribs: 20 dorsal ribs are preserved on each side of the skeleton. Except the well-preserved last six dorsal ribs on the left side and posterior three dorsal ribs on the right side, others are only preserved proximal parts. All the posterior ribs are slender, almost thread-like with slightly expanded distal ends.

Pectoral girdle: The left coracoid and the left scapula are nearly complete. The coracoid is not co-ossified with the scapula. The shaft near the proximal end of the left scapula is narrower than either end. Although its distal end is not well preserved, the impression of the distal end shows no articulation surface. The proximal end of the coracoid is wide. The distal part of the coracoid shows a clear articulation surface for the sternum. The scapula is slightly longer than the coracoid, but it is much less stout. The distal end of the scapula is comparatively thin and slightly expanded.

Humerus: The shaft of the humerus is slightly curved in lateral view. Its deltopectoral crest is slightly expanded, and the distal end of the deltopectoral crest is slightly curved laterally. The anterior margin of the deltopectoral crest is nearly straight, and the lateral margin of the deltopectoral crest is round.

Ulna and radius: The ulna is missing part of its distal end, and the radius is missing part of its proximal end, but their lengths can be inferred. The ulna is wider than the radius.

Carpals: Carpals are poorly preserved. It is difficult to identify their number and shapes of each carpal.

Pteroid: A small pteroid is preserved near the carpals. It is rod-like, and slender, approximately 1/4 the length of the ulna.

Metacarpals and digits: Only metacarpal IV is well exposed. The proximal end of metacarpal IV is wider than its distal end, as in all pterosaurs.

No evidence shows that metacarpals I–III reach the carpals. The finger phalanges of digits I, II, and III are slender. Finger unguals are larger than unguals in the foot.

The fourth wing finger: There are three phalanges preserved in natural position. The first phalanx is highly elongate, reaching 53% of the length of total wing finger. Although a small part near the proximal end is missing, its impression and the articulation with the wing metacarpal indicate that the first phalanx is almost complete. The proximal end is slightly wider

TABLE 1. Measurements of *Beipiaopterus chenianus*, gen. et sp. nov.

(mm).

	Length	Width (middle)	Width (anterior)	Width (posterior)
Cervicals 1, 2, 3, 4	25.0 (pres.), 34.0, 25.0, 19.0	7.5, 10.0, 8.0, 9.5	—, 11.0, 9.0, 14.0	13.0, 10.0, 14.0, 11.0
First dorsal	10.5	7	9	9
Dorsals +sacrals	100	—	—	—
From dorsals to caudals	137	—	—	—
Dorsal ribs 5–7	46	—	—	—
Dorsal ribs 8, 9, 10	40.0, 38.0, 33.0	—	—	—
Scapula	38	—	—	—
Coracoid	36	—	—	—
Humerus	68	7	24	—
Radius	75.0 (pres.)	5	—	20
Ulna	65.0 (pres.), 75 (est.)	7	17	—
Pteroid	24	—	—	—
Carpals	4	—	—	—
Wing-metacarpal	75	—	—	—
Wing-ph4-1, 4-2, 4-3	183.0, 85.0, 77.0	6.0, 3.0, 2.1	12.0, 7.0, 4.5	6.0, —, —
Femur	42	4	—	6
Tibia	102	2	6	6
Fibula	50	—	—	—
Metatarsal I	40	1	—	—
Phalanx 1 of the 1st digit	8	—	—	—
Claw	4	—	2	—
Metatarsal II	40	1	—	—
Phalanges 1, 2 of the 2nd digit	6.0, 6.5	—	—	—
Claw	3	—	—	—
Metatarsal III	38	1	—	—
Phalanges 1, 2, 3 of the 3rd digit	7.0, 1.0, 7.0	—	—	—
Metatarsal IV	34	1	—	—
Phalanges 1, 2, 3, 4 of the 4th digit	11.0, 1.1, 1.1, 4.0	—	—	—
Claw	4	—	2.1	—
Metatarsal V	5	1.5	—	—
Phalanx of the 5th digit	3.5	—	—	—

Pres. preserved; est. estimated; —, un-applicable or not preserved.

than the distal end. There is a clear thin ridge along the middle portion of the dorsal surface. The distal end has a backwardly directed foot. The second phalanx is shorter than the first, approximately 46% length of the first wing phalanx. A small part of its distal end is missing. There is a weak ridge on the middle surface. The impressions of the distal part of the second phalanx show that its ventral surface has parallel thin ridges. The width of the distal part of the second wing phalanx is nearly equal to that of the proximal end of the third. The third phalanx is almost completely preserved except for a small middle portion. The margin of the proximal end is straight. The flattened shaft thins distally to become rod-like. There is a small wing membrane along the distal part of the phalanx. The distal end is slightly expanded, and blunt. It does not show an articulation surface. The wing membrane does not extend to the distal end of the phalanx. The distal end of the wing membrane reaches approximately 89% of the third phalanx. All these features indicate that the third phalanx is the last of the wing phalanges.

Hind limb: An impression of the right femur is preserved. The femur is nearly straight. The distal end of the left femur is also preserved as impression. Two distal condyles are nearly equal in size. The anterior surface of the distal end of the femur is nearly flat. Both ends of the tibia are slightly expanded. The proximal end is flat. The tibia is longer than the femur. The distal end of the left fibula is not fused with the tibia. It is about one half the length of the tibia. The tarsals are poorly preserved and uninformative.

Metatarsals: Metatarsals I and II are equal in length, and metatarsal III is slightly shorter. Metatarsal IV is shorter than metatarsal III. The metatarsals are generally long and slender. Metatarsal V is short. The ratio of metatarsal III to tibia is 0.37

Digits: The second, third and fourth toes are equal in length. The first toe is slightly shorter. All the toes except the fifth have sharp claws. The third and the fourth toes have short central phalanges (Table 2). The fifth toe is short, and consists of only one phalanx, which is reduced to a small nubbin.

COMPARISON AND DISCUSSION

Four genera of pterosaurs from the Early Cretaceous of Yixian Formation and three from the Jiufotang Formation have been reported (Ji and Ji, 1997, 1998; Wang and Lü, 2001; Wang et al., 2002; Wang and Zhou, 2002). *Eosipterus yangi* (Ji and Ji, 1997) was initially identified as a pterodactylid. Later, a morphometric comparison led Ji et al. (1999) to suggest that *Eosipterus* is probably synonymous with *Pterodactylus*. Because the material lacks skull, it is difficult to resolve its relationship. Unwin et al. (2000) noted that *Eosipterus* exhibits proportions that, among ctenochasmatooids, are most similar to those of *Pterodaustro* and *Ctenochasma*. Thus, Unwin et al. (2000) suggest that *Eosipterus* is a ctenochasmatooid and probably belongs within the Ctenochasmatoidae rather than

sharing a close relationship with *Pterodactylus*. *Beipiaopterus* differs from *Eosipterus* in the smaller ratio of wing-metacarpal IV to wing-phalanx 1 and in the relatively longer tibia compared with the femur. The wing finger of *Beipiaopterus* has three phalanges, rather than four as in *Eosipterus*. Wing phalanx 1 is elongate, and the ratio of the length of the wing phalanx 1 to the total length of the wing finger is approximately 53%, while it is only 30% in *Eosipterus*. Although the wing finger consists of only three phalanges in *Beipiaopterus* and four phalanges in *Eosipterus*, the lengths of total wing finger are nearly equal.

Dendrorhynchus curvidentatus (Ji and Ji, 1998) was initially identified as a rhamphorhynchoid, based upon its short wing metacarpal and long tail (Ji and Ji, 1998). Its name was found to be preoccupied and was replaced with *Dendrorhynchoides* (Ji et al., 1999). *Beipiaopterus* differs from *Dendrorhynchoides* in having a relatively long wing-metacarpal compared with the humerus; wing-metacarpal IV attains $1.12 \times$ length of the humerus in *Beipiaopterus*, while it is only $0.33 \times$ length of the humerus in *Dendrorhynchoides*; the pteroid is relatively longer and slender in *Beipiaopterus*, while it exhibits a primitive condition in *Dendrorhynchoides*, where the pteroid is a short, stubby structure (Unwin et al., 2000); the fifth toe is short, consisting of one phalanx in *Beipiaopterus*, while the fifth toe is long, consisting of two phalanges in *Dendrorhynchoides* (Unwin et al., 2000); metatarsals I–III are nearly the same length, showing the primitive condition in *Beipiaopterus*, similar to that of *Dendrorhynchoides* and basal non-pterodactylids (*Preondactylus*, Dimorphodontidae, Anurognathidae) (Unwin et al., 2000).

Haopterus gracilis (Wang and Lü, 2001) is the first well-preserved skeleton with a nearly complete skull from the Yixian Formation. Wang and Lü (2001) attributed *Haopterus* to the family of Pterodactylidae and regarded it as the first indisputable record of Pterodactylidae found from the Yixian Formation. But Unwin (2001) thought that *Haopterus* exhibits two ornithocheiroid apomorphies (coracoid longer than scapula, metatarsal <25% length of humerus), and regarded it as the smallest adult ornithocheiroid known. *Beipiaopterus* is different from *Haopterus* in that *Beipiaopterus* has relatively elongate cervical vertebrae and gradual change in size from posterior cervical to anterior dorsal vertebrae. There is a sharp change from cervical to dorsal vertebrae in *Haopterus* (Wang and Lü, 2001). Metatarsal is greater than 25% (approximately 50%) that of the humerus in *Beipiaopterus*. The wing-metacarpal is nearly $1.9 \times$ the length of the third metatarsal in *Beipiaopterus*, while it is nearly $5.2 \times$ the length of the third metatarsal in *Haopterus*.

Jeholopterus ningchengensis (Wang et al., 2002; Dalla Vecchia, 2002) is the second pterosaur known with soft tissue from the Yixian Formation. It comes from the lower Yixian Formation, Ningcheng City, Nei Mongol. The wing membrane of *Beipiaopterus* attaches to the left leg at the ankle and its webbed foot are characters similar to *Jeholopterus* (Wang et al.,

TABLE 2. Lengths of principal elements (in mm) and ratios of the fore and hind limbs of ctenochasmatooids (the first ten taxa) and some pterosaurs from Liaoning and its peripheral areas. Measurements of *Haopterus gracilis* from Wang and Lü (2001), *Sinopterus dongi* from Wang and Zhou (2002), *Jeholopterus ningchengensis* from Wang et al., (2002), *Chaoyangopterus zhangii* from Wang and Zhou (2003), *Beipiaopterus chenianus* this paper, others are from Unwin et al., (2000). **Abbreviations:** **F:** femur. **L:** length. **Mt3:** the third metatarsal. **Ph1d4:** The first wing phalanx of the fourth digit. **Ph2d4:** The second wing phalanx of the fourth digit. **T:** tibia.

Taxa	Ph1d4 L	Ph2d4 L	Ph2d4/Ph1d4	Femur L	Tibia L	F/T	Mt3 L	Mt3/T
<i>Cycnorhamphus suevicus</i>	141	115.2	0.82	77	122	0.63	30	0.25
<i>Cycnorhamphus canjuersensis</i>	155	134	0.86	101	138	0.73	35	0.25
<i>Pterodactylus antiquus</i>	48.5	44.2	0.91	34.7	48.3	0.72	19	0.39
<i>Pterodactylus kochi</i>	38.5	36.5	0.95	28.5	38.5	0.74	14.5	0.38
<i>Pterodactylus micronyx</i>	46	28.5	0.62	29	40.5	0.72	8.7	0.21
<i>Pterodactylus longicollum</i>	160	109	0.68	99	149	0.66	30	0.2
“ <i>Pterodactylus</i> ” <i>elegans</i>	19.5	17.8	0.91	12.3	17.6	0.698	5.6	0.32
<i>Ctenochasma gracile</i>	66	57	0.86	35	55	0.64	21	0.38
<i>Pterodaustro guinazui</i>	116	112	0.97	60	90	0.67	50	0.56
<i>Eosipterus yangi</i>	96	95	0.99	60	96	0.63	38.5	0.4
<i>Haopterus gracilis</i>	141	119	0.84	?	?	?	17	?
<i>Sinopterus dongi</i>	121	88	0.73	74	104	0.71	21	0.2
<i>Jeholopterus ningchengensis</i>	93	82	0.88	40	50	0.8	22	0.44
<i>Chaoyangopterus zhangii</i>	199	120	0.6	131	208	0.63	44	0.21
<i>Beipiaopterus chenianus</i>	183	85	0.46	42	102	0.41	38	0.37

2002; Lü, 2002). *Beipiaopterus* is different from *Jeholopterus* in the relatively long wing-metacarpal, and reduced fifth toe. *Jeholopterus* is a rhamphorhynchoid pterosaur while *Beipiaopterus* is pterodactyloid pterosaur, showing more advanced characters.

Beipiaopterus differs from *Sinopterus* (Wang and Zhou, 2002; Li et al., 2003) in that *Beipiaopterus* has elongated cervical vertebrae and three wing-phalanges.

Beipiaopterus differs from *Chaoyangopterus* (Wang and Zhou, 2003) in that highly elongate wing phalanx 1, lower ratio of femur to tibia (0.41), it is about 0.63 in *Chaoyangopterus*, higher ratio of metatarsal III to tibia (0.37), it is approximate 0.21 in *Chaoyangopterus*. *Chaoyangopterus* was referred to the Nyctosauridae by Wang and Zhou (2003), but none of the apomorphies of the Nyctosauridae, such as a hatchet-shaped

deltopectoral crest of the humerus, a short, broad sternum with the width of sternal plate over 1.5 the length, mid-notarial vertebrae with T-shaped neural spines in anterior view (Williston, 1903; Bennett, 1989, 1994), was mentioned in the text. However, *Chaoyangopterus* shares one character with Pteranodontidae, that is, the mandibular symphysis is at least 30% length of mandible (Unwin and Lü, 1997) and the ratio of tibia to femur of *Chaoyangopterus* falls within the range (1.325–1.515) of *Pteranodon* (Eaton, 1910: It is 1.5 in Cat. No. 2493, this is exactly same to that of *Chaoyangopterus*), and the sternum is longer than wider in *Chaoyangopterus* (Wang and Zhou, 2003). Thus, *Chaoyangopterus* is proposed be reassigned to the Pteranodontidae. The small sized individual of *Chaoyangopterus* may indicate a primitive form.

Among the known genera of ctenochasmatooids and some

pterosaurs from western Liaoning and its peripheral areas, the ratio of ph2d4/ph1d4 and the ratio of femur/tibia are smallest, while the ratio of mt3/tibia of *Beipiaopterus* is similar to these of *Pterodactylus kochi* and *Ctenochasma gracile* (Table 2). Although the ratio of the mt3/tibia is relatively close to *Eosipterus*, which comes from the same strata, the ratio of femur to tibia and the ratio of ph2d4 to ph1d4 are clearly different. *Beipiaopterus* represents a new taxon differing from *Eosipterus*.

The short tail, the third and the fourth toe having short central phalanges, and the reduced fifth toe (Wellnhofer, 1991) make *Beipiaopterus* attributable as a pterodactyloid pterosaur. The ossified short central phalanges in the third and the fourth toes indicate that it is not a very young individual (see Wellnhofer, 1991). According to Kellner and Tomida (2000) and Wellnhofer (1975), the fusion of pectoral and pelvic girdles occurred later in ontogeny. Therefore, the unfused scapula with coracoid further supports that this is a young individual.

The nearly complete left forelimb shows that the wing-finger has three phalanges. Among pterodactyloids at present, only *Nyctosauridae* (Brown, 1986; Wellnhofer, 1991) and *Anurognathus* (Bennett, 2002) have been reported with three wing-phalanges on the fourth wing-finger. *Beipiaopterus* is distinguished from *Nyctosaurus* in that the deltopeccoral crest of the humerus is not hatchet-shaped, and wing phalanx 1 is elongate; *Beipiaopterus* is distinguished from *Anurognathus* in the relatively longer metacarpals, pedal digit V bears only one short phalanx.

CONCLUSION AND SUMMARY

The elongate cervical vertebrae, the coracoid and the scapula of similar length, wing phalanx 1 longer than the ulna, pes with a single short phalanx in digit five, shorter tail, and greater ratio of metatarsal III to tibia (37%) indicate that *Beipiaopterus* is a pterodactyloid pterosaur. *Beipiaopterus* exhibits proportions, such as the ratio of metatarsal III to tibia, the ratio of the total length of the wing finger to the wing metacarpal that are similar to those of *Eosipterus* (Unwin et al., 2000). But *Beipiaopterus* is different from *Eosipterus* in that it has three phalanges of the wing finger and an extremely elongate wing phalanx 1. It represents a new ctenochamatoid pterosaur, which is close to *Eosipterus*. The reduced number of the wing finger phalanges from four to three occurs in at least three different genera: *Nyctosaurus* (Brown, 1986), *Anurognathus* (Bennett, 2002) and *Beipiaopterus*, so it is a convergent character, not a unique character to *Nyctosaurus* as thought before (Brown, 1986; Wellnhofer, 1991).

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