

A New Pterodactyloid Pterosaur from the Early Cretaceous of the Western Part of Liaoning Province, Northeastern China

LÜ Junchang^{1,*}, LIU Cunyu², PAN Lijun² and SHEN Caizhi¹

¹ Institute of Geology, Chinese Academy of Geological Sciences, Beijing 100037, China

² Beipiao Pterosaur Museum of China, Beipiao County, 122100, China

Abstract: *Pangupterus liui* gen. et sp. nov. from the Jiufotang Formation of Sihedang, Lingyuan City, Liaoning Province is erected based on a nearly complete lower jaw. It is characterized by having a total of 36 slender curved teeth with sharp tips, forming a distinct fish-grabbing mechanism; the teeth are well-spaced and are circular in section; the length ratio of the mandibular symphysis to the whole jaw is 20%; and the ratio of the tooth root width to tooth length is 12%. Toothed pterosaurs make up about 56.3% of the pterosaur assemblage from the Jiufotang Formation, which indicates that toothed forms played a key role in the ecosystem.

Key words: Pterosauria, *Pangupterus*, Jiufotang Formation, western Liaoning

1 Introduction

Pterosaurs are some of the most fascinating and enigmatic reptiles among the extinct creatures. They are a group of flying reptiles that originated in the Late Triassic (about 230 million years ago), at almost the same time as the dinosaurs. They began to adapt for a life in the skies and were the first vertebrates to gain powered flight in earth history. They lived about 160 million years on the earth, and went extinct at the end of the Cretaceous (about 66 Mya) with other groups such as dinosaurs and mosasaurs.

In the last 15 years, many well-preserved pterosaurs from the Lower Cretaceous Yixian and Jiufotang formations of western Liaoning have played a key role in our understanding of pterosaur reproductive biology, evolution, identification of sex, and their diversity. At present, more than 40 new species of pterosaur have been found from western Liaoning and its surrounding areas (Lü et al., 2006a; Lü, 2010a; Lü et al., 2013). Compared with the toothless pterosaurs from the Jiufotang Formation, most toothed pterosaurs from the Jehol Biota were discovered from the Lower Cretaceous Yixian Formation, and include *Eosipterus* (Ji and Ji, 1997; Lü et al., 2006b), *Haopterus* (Wang and Lü, 2001), *Beipiaopterus* (Lü, 2003), *Ningchengopterus* (Lü, 2009), *Zhenyuanopterus* (Lü, 2010b, Teng et al., 2014), *Elanodactylus* (Andres and Ji, 2008), *Boreopterus* (Lü and Ji, 2005a), *Feilongus* (Wang et al., 2005), *Gegepterus*

(Wang et al., 2007), *Yixianopterus* (Lü et al., 2006c), *Cathayopterus* (Wang and Zhou, 2006), *Pterofiltrus* (Jiang and Wang, 2011), *Gladocephaloideus* (Lü et al., 2012a), and *Moganopterus* (Lü et al., 2012b). Only one toothless form has been named, *Eopteranodon* (Lü and Zhang, 2005). At the generic level, the toothed pterosaurs make up about 93% of the pterosaur assemblage from the Yixian Formation. Toothless pterosaurs from the Jiufotang Formation include *Sinopterus* (Wang and Zhou, 2002; Li et al., 2003), *Chaoyangopterus* (Wang and Zhou, 2003), *Jidapterus* (Dong et al., 2003), *Eoazhdarcho* (Lü and Ji, 2005b), *Huaxiapterus* (Lü and Yuan, 2005), *Nemicolopterus* (Wang et al., 2008a), *Shenzhoupterus* (Lü et al., 2008a), and the toothed forms are *Liaoningopterus* (Wang and Zhou, 2003), istiodactylid pterosaurs (including *Nurhachius* Wang and Zhou, 2003; *Longchengpterus* Wang et al., 2006; *Hongshanopterus* Wang et al., 2008b; *Liaoxipterus* Dong and Lü, 2005; Lü et al., 2008b; *Istiodactylus* Andres and Ji, 2006), *Guidraco* (Wang et al., 2012) and *Linlongopterus* (Rodrigues et al., 2015). Toothed pterosaurs form about 53% (not including the new taxon here) of the pterosaur assemblage from the Jiufotang Formation, which is lower than that of the Yixian Formation.

Herein we report another new toothed pterosaur: *Pangupterus liui* gen. et sp. nov. from the Jiufotang Formation of Sihedang, Lingyuan City of Liaoning Province (Fig. 1).

* Corresponding author. E-mail: lujc2008@126.com

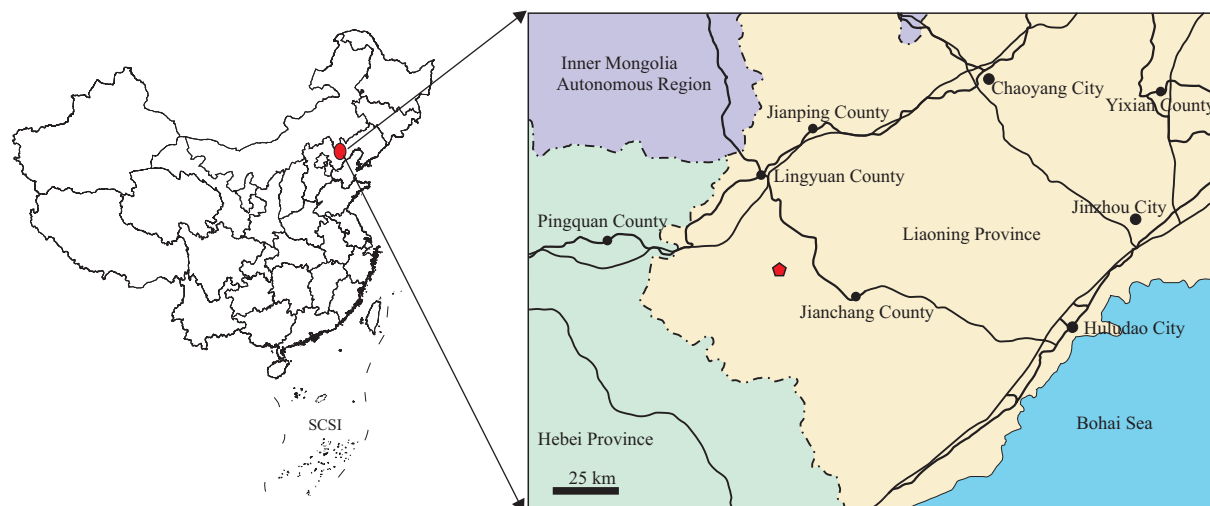


Fig. 1. A map of the new fossil locality in Liaoning Province. Solid pentagon represents the fossil site.

2 Systematic Paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Pangupterus gen. nov.

Etymology: Pangu in Chinese Pinyin, means creator of the universe in Chinese mythology and ‘pterus’ a declension of pteron, the Greek word for wing.

Diagnosis: The same for the type species.

Pangupterus liui sp. nov. (Fig. 2)

Etymology: The specific name is in honor of Jun Liu, who offered the specimen for scientific research.

Diagnosis: A pterodactyloid pterosaur bearing the following combination of characters: a total of 36 slender curved teeth with sharp tips on lower jaw; the teeth are well-spaced with a circular section, the length ratio of mandibular symphysis to the entire jaw is 20%; and the ratio of tooth root width to tooth length is 12%.

Holotype: A nearly complete lower jaw. The specimen is housed at the Beipiao Pterosaur Museum of China (BPMC-0002)

Locality and horizon: Sihedang, Lingyuan County, Liaoning Province; Jiufotang Formation, Lower Cretaceous.

2.1 Description

The lower jaw is nearly complete except for missing their posterior portions. It is exposed its ventral surface (Fig. 2). Although the proximal ends of both rami of the lower jaw are missing, their weak impression in the matrix can be used to measure their lengths, thus the complete length of the lower jaw can be measured (Table 1). The small portion of the distal end of the mandibular

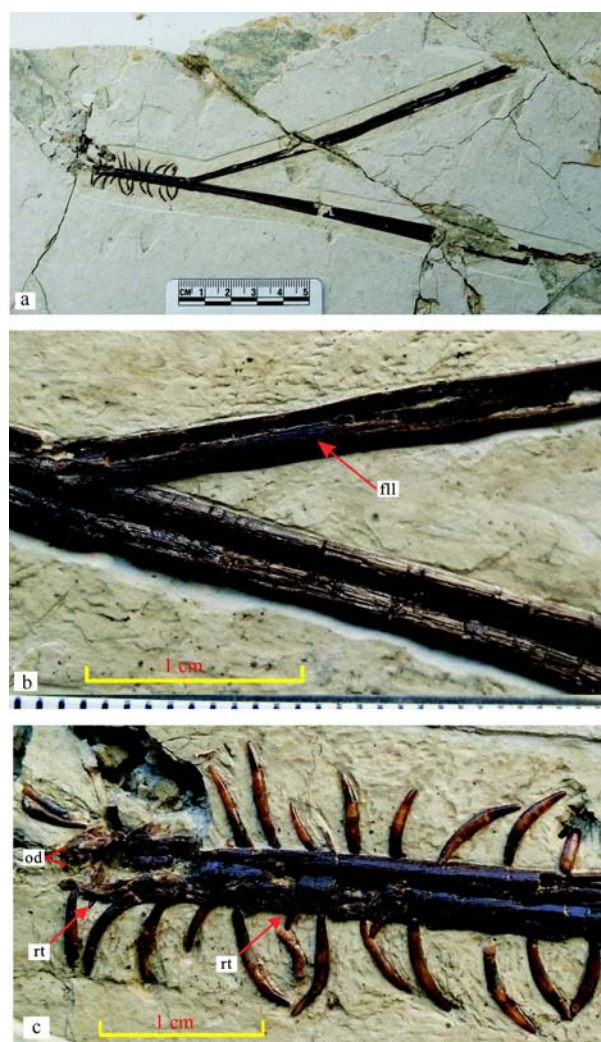


Fig. 2. The lower jaw of *Pangupterus liui* gen. et sp. nov. (BPMC-0002) (a); Close-up of the ventral surfaces of the lower jaw showing fine longitudinal laminations (b); Close-up of a portion of the dentition, showing the replacement teeth (c). Abbreviations: fl, fine longitudinal laminations; rt, replacement teeth; od, odontoid.

Table 1 Measurements (in mm) of *Pangupperus liui* gen. et sp. nov. (BPMC-0002)

	length	width
Lower jaw	188.9 (pres), 195.3	5.8 (widest part)
Mandibular symphysis	39.6	4.1
Tooth row	14.6	-
Tooth	6.7 (longest)	0.8 (widest)

symphysis is missing, but the exact length of the mandibular symphysis can be measured. The angle between the rami of the lower jaw is less than 30 degrees. The ventral surface of the lower jaw is covered with fine longitudinal laminations and small pits (Fig. 2c).

There are at least 12 teeth (excluding tooth sockets) on each side, and most of them are isolated but distributed near their sockets. There is one distinct tooth socket on the right side at the level of the junction of both rami and two tooth sockets posterior to this junction. Three small teeth are still implanted in the tooth sockets on the left side. Another tooth is removed from the tooth socket, which corresponds to the third tooth socket from the junction of both rami. Thus, it is inferred that there are 18 teeth on each side of the lower jaw. Counting from the tip of the rostrum, the second, seventh and tenth teeth are smaller than others on the right side, and they are implanted in tooth sockets; thus they are replacement teeth (Fig. 2b). All the teeth are well spaced. A well-exposed tooth (the left seventh tooth counting from the tip of the rostrum) has a crown length of 4.4 mm, and the length of its tooth root is 2.3 mm. The tooth sockets can be observed in lateral view and they are elongated. The teeth are slender, curved, with sharp tips. The teeth extend laterodorsally, forming a distinct fish-grabbing mechanism.

The distal end of the rostrum is slightly expanded, and although it has been destroyed, it seems to have a bony process in the middle, which is similar to the case in *Longchengpteris* (Wang et al., 2006; Lü et al., 2008b) (Fig. 2b). This kind of process is called an odontoid by Martill (2014).

3 Comparison and Discussion

It is difficult to compare *Pangupperus liui* with the following three ctenochasmatid pterosaurs, *Eosipterus* (Ji and Ji, 1997), *Beipiaopterus* (Lü, 2003) and *Elanodactylus* (Andres and Ji, 2008), because they are only preserved as postcranial skeletons. There are no overlapping elements among them. It is also difficult to compare exactly with *Yixianopterus* (Lü et al., 2006c), in which the lower jaw is not well-preserved, but the teeth of *Yixianopterus* are short and smaller than those of *Pangupperus*.

Pangupperus liui differs from *Gegepterus* (Wang et al., 2007), *Cathayopterus* (Wang and Zhou, 2006) and

Pterofiltrus (Jiang and Wang, 2011) in that there are relatively few (about a total of 36) large, curved and well-spaced teeth in the lower jaws of *Pangupperus*, whilst there are more slender, straight and compacted teeth in the lower jaws of *Gegepterus* (Wang et al., 2007); the tooth number of the lower jaw is about 75, based on equal numbers in both upper and lower jaw, *Cathayopterus* with a total of ~62–66 lower teeth (Wang and Zhou, 2006) and *Pterofiltrus* with about 54 lower jaw teeth (Jiang and Wang, 2011).

Pangupperus liui differs from *Gladocephaloideus* (Lü et al., 2012a) in that its lower teeth are much larger than those of *Gladocephaloideus*. There are a total of 36 lower teeth in *Pangupperus*, compared to 24 in *Gladocephaloideus*.

Pangupperus liui differs from *Feilongus* (Wang et al., 2005) in that the teeth are larger and tooth number is smaller than in *Feilongus*. The teeth are needle-shaped in *Feilongus* and there are a total of 40 lower teeth, whereas this number is 36 in *Pangupperus*.

Pangupperus liui differs from *Moganopterus* (Lü et al., 2012b) in that there are 34 slightly curved lower teeth, with the smaller ones located proximal by in the lower jaw of *Moganopterus*, in contrast to strongly curved lower teeth of almost the same size (except for the replacement teeth) in *Pangupperus*.

Pangupperus liui differs from the boreopterids *Boreopterus* (Lü and Ji, 2005a) and *Zhenyuanopterus* (Lü, 2010b) in having a much smaller number of lower teeth than *Boreopterus* with 54 in total and *Zhenyuanopterus* with 86 in total, and the anterior teeth (rostral portion) are much larger than posterior ones in *Boreopterus* and *Zhenyuanopterus*. However, almost all the teeth are the same in size except for the replacement teeth in *Pangupperus*.

Pangupperus liui differs from *Ningchengopterus* (Lü, 2009) in that the teeth are much larger, curved, and the tooth number is larger than those of *Ningchengopterus* that has a total of 26 lower teeth all of which are small and straight.

Pangupperus liui differs from *Liaoningopterus* (Wang and Zhou, 2003) in that the teeth are different in size, with the anterior teeth larger than posterior ones, and there are only about 13–14 lower teeth in *Liaoningopterus*.

Pangupperus liui differs in tooth morphology from all istiodactylid pterosaurs from the Jiufotang Formation: *Nurhachius ignaciobritoi* (Wang and Zhou, 2005), *Longchengpteris zhaoi* (Wang et al., 2006), *Hongshanopterus lacustris* (Wang et al., 2008b), *Liaoxipterus brachyognathus* (Dong and Lü, 2005; Lü et al., 2008b) and *Istiodactylus sinensis* (Andres and Ji, 2006). All the istiodactylid pterosaurs bear labiolingually compressed and slightly curved lingually, lancet-shaped

teeth and they are closely spaced, often nearly touching one another (Andres and Ji, 2006). The teeth of *Pangupterus liui* are elongated, curved and well-spaced (Fig. 2).

Pangupterus liui differs from *Guidraco* (Wang et al., 2012) in that the first three lower jaw teeth (from first to third) of the latter are robust, large and inclined anteriorly. The length ratio of mandibular symphysis to the entire jaw length is 20% in *Pangupterus liui*, which is much lower than the 54% of *Guidraco*.

Pangupterus liui differs from *Linlongopterus* (Rodrigues et al., 2015) in tooth morphology. The teeth of *Pangupterus* are strongly curved with sharp tips, and are moderately expanded near the crown-root boundary and all the teeth are the same shape. In *Linlongopterus*, however, the first two pairs of lower teeth have gently curved crowns and roots, the crowns of the posterior ones

are slightly smaller and straighter, and below the crown-root boundary, they become swollen (Rodrigues et al., 2015).

At present, there are nine genera of toothed pterosaurs from the Jiufotang Formation, making up about 56.3% of the pterosaur assemblage from this formation. The discovery of this new toothed pterosaur indicates that these forms played an important role in the ecosystem.

4 Conclusions

Pangupterus liui is the ninth toothed pterosaur from the Jiufotang Formation in Liaoning and its surrounding areas. Its long curved, sharp teeth indicate those of a fish-eater (Fig. 3), forming a distinct fish grabbing-like mechanism. The discovery of *Pangupterus* implies that although the numbers of toothless pterosaurs increase in the Jiufotang



Fig. 3. Hypothetical paleoenvironment of *Pangupterus liui* gen. et sp. nov. (drawn by Zhao Chuang).

Formation, the toothed forms undoubtedly played an important role in the ecosystem.

Acknowledgements

We thank Dr. Dale Winkler (Southern Methodist University, Dallas, TX, USA) for providing careful comments on the earlier version of the MS. Mr. Zhang Yuqing (Institute of Geology, Chinese Academy of Geological Sciences) prepared the specimen. This study was supported by the National Natural Science Foundation of China (No. 41272022) and the Central Public-interest Scientific Institution Basal Research Fund for the Chinese Academy of Geological Sciences (No. JB1504) to Junchang Lü.

Manuscript received Feb. 23, 2016

accepted Mar. 21, 2016

edited by Fei Hongcai and Susan Turner

References

- Andres, B., and Ji, Q., 2006. A new species of *Istiodactylus* (Pterosauria, Pterodactyloidea) from the Lower Cretaceous of Liaoning, China. *Journal of Vertebrate Paleontology*, 26: 70–78.
- Andres, B., and Ji, Q., 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology*, 51: 453–469.
- Dong, Z.M., and Lü, J.C., 2005. A new ctenochasmatid pterosaur from the Early Cretaceous of Liaoning Province. *Acta Geologica Sinica* (English Edition), 79(2): 164–167.
- Dong, Z.M., Sun, Y.W., and Wu, S.Y., 2003. On a new pterosaur from the Lower Cretaceous of Chaoyang Basin, Western Liaoning, China. *Global Geology*, 22: 1–7.
- Ji, S.A., and Ji, Q., 1997. Discovery of a new pterosaur in western Liaoning, China. *Acta Geologica Sinica* (English Edition), 71(1): 1–6.
- Jiang, S.X., and Wang, X.L., 2011. A new ctenochasmatid pterosaur from the Lower Cretaceous, western Liaoning, China. *Anais Da Academia Brasileira De Ciencias*, 83: 1243–1249.
- Kaup, J.J., 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. *Isis*, 3: 311–315.
- Li, J.J., Lü, J.C., and Zhang, B.K., 2003. A new Lower Cretaceous sinopterid pterosaur from the Western Liaoning, China. *Acta Palaeont. Sinica*, 42(3): 442–447.
- Lü, J.C., 2003. A new pterosaur: *Beipiaopterus chenianus*, gen. et sp. nov. (Reptilia: Pterosauria) from western Liaoning Province of China. *Memoir of the Fukui Prefectural Dinosaur Museum*, 2: 153–160.
- Lü, J.C., 2009. A baby pterodactyloid pterosaur from the Yixian Formation of Ningcheng, Inner Mongolia, China. *Acta Geologica Sinica* (English Edition), 83(1): 1–8.
- Lü, J.C., 2010a. An overview of the pterosaur fossil record in China. *Acta Geoscientica Sinica*, 31 (Suppl. 1): 49–51.
- Lü, J.C., 2010b. A new boreopterid pterodactyloid pterosaur from the Early Cretaceous Yixian Formation of Liaoning Province, northeastern China. *Acta Geologica Sinica* (English Edition), 84(2): 241–246.
- Lü, J.C., and Ji, Q., 2005a. A new ornithocheirid from the Early Cretaceous of Liaoning Province, China. *Acta Geologica Sinica* (English Edition), 79(2): 157–163.
- Lü, J.C., and Ji, Q., 2005b. New azhdarchid pterosaur from the Early Cretaceous of western Liaoning. *Acta Geologica Sinica* (English Edition), 79(2): 301–307.
- Lü, J.C., and Yuan, C.X., 2005. New tapejarid pterosaur from western Liaoning, China. *Acta Geologica Sinica* (English edition), 79(4): 453–458.
- Lü, J.C., and Zhang, B.K., 2005. New pterodactyloid pterosaur from the Yixian Formation of western Liaoning. *Geological Review*, 51(4): 458–462.
- Lü, J.C., Ji, S.A., Yuan, C.X., and Ji, Q., 2006a. *Pterosaurs from China*. Beijing: Geological Publishing House, 147 (in Chinese).
- Lü, J.C., Gao, C.L., Meng, Q.J., Liu, J.Y., and Ji, Q., 2006b. On the systematic position of *Eosipterus yangi* Ji et Ji, 1997 among pterodactyloids. *Acta Geologica Sinica* (English Edition), 80(5): 643–646.
- Lü, J.C., Ji, S.A., Yuan, C.X., Gao, Y.B., Sun, Z.Y., and Ji, Q., 2006c. New pterodactyloid pterosaur from the Lower Cretaceous Yixian Formation of western Liaoning. In Lü, J.C., Kobayashi Y., Huang D., and Lee Y.-N. (eds.), *Papers from the 2005 Heyuan International Dinosaur Symposium*. Beijing: Geological Publishing House, P195–203.
- Lü, J.C., Unwin, D.M., Xu, L., and Zhang, X.L., 2008a. A new azhdarchoid pterosaur from the Lower Cretaceous of China and its implications for pterosaur phylogeny and evolution. *Naturwissenschaften*, 95: 891–897.
- Lü, J.C., Xu, L., and Ji, Q., 2008b. Restudy of *Liaoxipterus* (Istiodactylidae: Pterosauria), with comments on the Chinese istiodactylid pterosaurs. *Zitteliana*, B28, 229–241.
- Lü, J.C., Ji, Q., Wei, X.F., and Liu, Y.Q., 2012a. A new ctenochasmatoid pterosaur from the Early Cretaceous Yixian Formation of western Liaoning, China. *Cretaceous Research*, 34: 26–30.
- Lü, J.C., Pu, H.Y., Xu, L., Wu, Y.H., and Wei, X.F., 2012b. Largest toothed pterosaur skull from the Early Cretaceous Yixian Formation of western Liaoning, China, with comments on the family Boreopteridae. *Acta Geologica Sinica* (English edition), 86(2): 801–840.
- Lü, J.C., Jin, X.S., Gao, C.L., Du, T.M., Ding, M., Sheng, Y.M., and Wei, X.F., 2013. *Dragons of the skies—Recent advances on the study of pterosaurs from China*. Hangzhou: Zhejiang Science and Technology Press, 129 (in Chinese).
- Martill, D.M., 2014. A functional odontoid in the dentary of the Early Cretaceous pterosaur *Istiodactylus latidens*: Implications for feeding. *Cretaceous Research*, 47: 56–65.
- Plieninger, F., 1901. Beiträge zur Kenntnis der Flugsaurier. *Palaeontologica*, 48: 65–90.
- Rodrigues, T., Jiang, S.X., Cheng, X., Wang, X.L., Kellner, A.W.A., 2015. A new toothed pteranodontoid (Pterosauria, Pterodactyloidea) from the Jiufotang Formation (Lower Cretaceous, Aptian) of China and comments on *Liaoningopterus gui* Wang and Zhou, 2003. *Historical Biology*, 27(6): 782–795.
- Teng, F.F., Lü, J.C., Wei, X.F., Hsiao, Y. F., Pittman, M., 2014. New material of *Zhenyuanopterus* (Pterosauria) from the Early Cretaceous Yixian Formation of western Liaoning.

- Acta Geologica Sinica* (English Edition), 88(1):1–5.
- Wang, L., Li, L., Duan, Y., and Cheng, S.L., 2006. A new istiodactylid pterosaur from western Liaoning. *Geological Bulletin of China*, 25: 737–740.
- Wang X L, and Lü J C. 2001. The discovery of a pterodactylid pterosaur from Yixian Formation of western Liaoning, China. *Chinese Science Bulletin*, 46 (13): 1112–1117 (in Chinese).
- Wang, X.L., and Zhou, Z.H., 2002. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. *Chinese Science Bulletin*, 47 (20): 1521–1527 (in Chinese).
- Wang, X.L., and Zhou, Z.H., 2003. Two new pterodactyloid pterosaurs from the Early Cretaceous Jiufotang Formation of western Liaoning, China. *Vertebr Palasiat*, 41: 34–41.
- Wang, X.L., and Zhou, Z.H., 2006. Pterosaur adaption radiation of the Early Cretaceous Jehol Biota. In: Rong, J.Y., et al. (eds.), *Originations, Radiations and Biodiversity Changes - Evidence from the Chinese Fossil Record*. Beijing: Science Press, pp.665–686.
- Wang, X.L., Kellner, A.W.A., Zhou, Z.H., and Campos, D.A., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature*, 437: 875–879.
- Wang, X.L., Kellner, A.W.A., Zhou, Z.H., and Campos, D.A., 2007. A new pterosaur (Ctenochasmatidae, Archaeoptero-dactyloidea) from the Lower Cretaceous Yixian Formation of China. *Cretaceous Research*, 28: 245–260.
- Wang, X.L., Kellner, A.W.A., Zhou, Z.H., and Campos, D.A., 2008a. Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. *Proceedings of the National Academy of Sciences*, 106(6): 1983–1987.
- Wang, X.L., Campos, D.A., Zhou, Z.H., and Kellner, A.W.A., 2008b. A primitive istiodactylid pterosaur (Pterodactyloidea) from the Jiufotang Formation (Early Cretaceous), northeast China. *Zootaxa*, 1813: 1–18.
- Wang, X.L., Kellner, A.W.A., Jiang, S.X., and Cheng, X., 2012. New toothed flying reptile from Asia: close similarities between early Cretaceous pterosaur faunas from China and Brazil. *Naturwissenschaften*, 99 (4): 249–57.

About the first author

LÜ Jun-Chang, Male; born in 1965 in Pingdu City, Shandong Province; doctoral supervisor; professor at Institute of Geology, Chinese Academy of Geological Sciences; He is now interested in the study of Mesozoic reptiles (especially dinosaurs and pterosaurs).
Email: lujc2008@126.com;
phone: 010-68999707, 13717801392.