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张氏格格翼龙(*Gegepterus changae*)新材料及其重要骨骼特征的补充和修订[1)]

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摘要:张氏格格翼龙正型标本(IVPP V 11981)是产自辽西北票四合屯义县组下部的一件保存不完整的梳颌翼龙类化石材料。本文记述的新材料 IVPP V 11972 与正型标本产出于同一地点的相同层位,具有正型标本的3个独有特征,即泪骨前突位于鼻骨之上,额骨前部和侧部边缘处有广泛蚀痕以及颈椎具有高的神经脊且背部有瘤状膨胀,据此将其归入张氏格格翼龙。通过对新材料 V 11972 和进一步修理的正型标本的形态观察,对张氏格格翼龙的特征进行了补充,增加一个属征:鼻骨背腹向具有两个小孔。这一特征在正型标本中同样被观察到,但在其他翼龙中都没有出现,仅在飞龙中观察到一个孔和一个凹陷。同时补充了张氏格格翼龙的椎体和肩带等的一些特征,如背椎没有完全愈合,荐椎数量为3~4枚,尾椎约9枚;肱骨三角嵴不是十分发育,三角嵴颈及其与肩胛乌喙骨相关联的关节窝不发育;具有前端呈扇形的前耻骨,耻骨闭孔有小骨片覆盖等。依据格格翼龙新的特征,将其与我国发现的归于梳颌翼龙科(Ctenochasmatidae)的华夏翼龙(*Cathaypterus*)、环河翼龙(*Huanhepterus*)及鸢翼龙(*Elanodactylus*)进行了对比。依据齿槽处的纵向沟、牙齿分布密度以及吻端的长度比例等,认为格格翼龙和华夏翼龙有一定区别,但亲缘关系较近,同属梳颌翼龙亚科(Ctenochasmaniae),并建议将华夏翼龙的鼻眶前孔较小的属征修订为其吻端较长。格格翼龙的个体远小于环河翼龙,依据牙齿数量和排列的差异推测它们的捕食方式和食物类型存在明显的区别,应不属于同一亚科。新材料与鸢翼龙的明显区别主要在肱骨上,前者肱骨的肩胛骨关节窝不发育,而后者的这一结构明显。由于鸢翼龙没有保存头骨,它的分类位置不是十分确定,同时鸢翼龙具有许多梳颌翼龙类所不具有的特征,如第一翼指骨短于第二和第三翼指骨,掌骨较短等。

关键词:辽宁北票,义县组,早白垩世,梳颌翼龙科,张氏格格翼龙

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IMPORTANT FEATURES OF *GEGEPTERUS CHANGAE* (PTEROSAURIA: ARCHAEOPTERODACTYLOIDEA, CTENOCHASMATIDAE) FROM A NEW SPECIMEN

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Abstract　*Gegepterus changae* is referred to the Ctenochasmatidae based on an incomplete specimen. The new specimen IVPP V 11972 is assigned to *Gegepterus changae* according to the unique features in the skull and cervical vertebrae. V 11972 is a subadult individual and further provides the morphological characteristics as the vertebrae, pectoral girdle, etc. Especially, we add to the diagnosis a unique feature, including the unique presence of two foramens on the nasal.

Key words　Beipiao, Liaoning; Yixian Formation; Early Cretaceous; Ctenochasmatidae; *Gegepterus changae*

1　Introduction

Wang et al. (2007) first described the only specimen of *Gegepterus changae* [nom. correct. Wang & Dong 2008 (pro *Gegepterus changi* Wang et al., 2007)] from the Lower Cretaceous Yixian Formation in Beipiao City, Liaoning, China. The isotope date of the pterosaur-bearing horizon is 125 Ma (Swisher et al., 2001).

IVPP V 11981 is a partial skeleton with a complete skull and mandible, and some postcranial elements (Fig. 1). Based on the holotype, Wang et al. (2007) identified four unique fea-

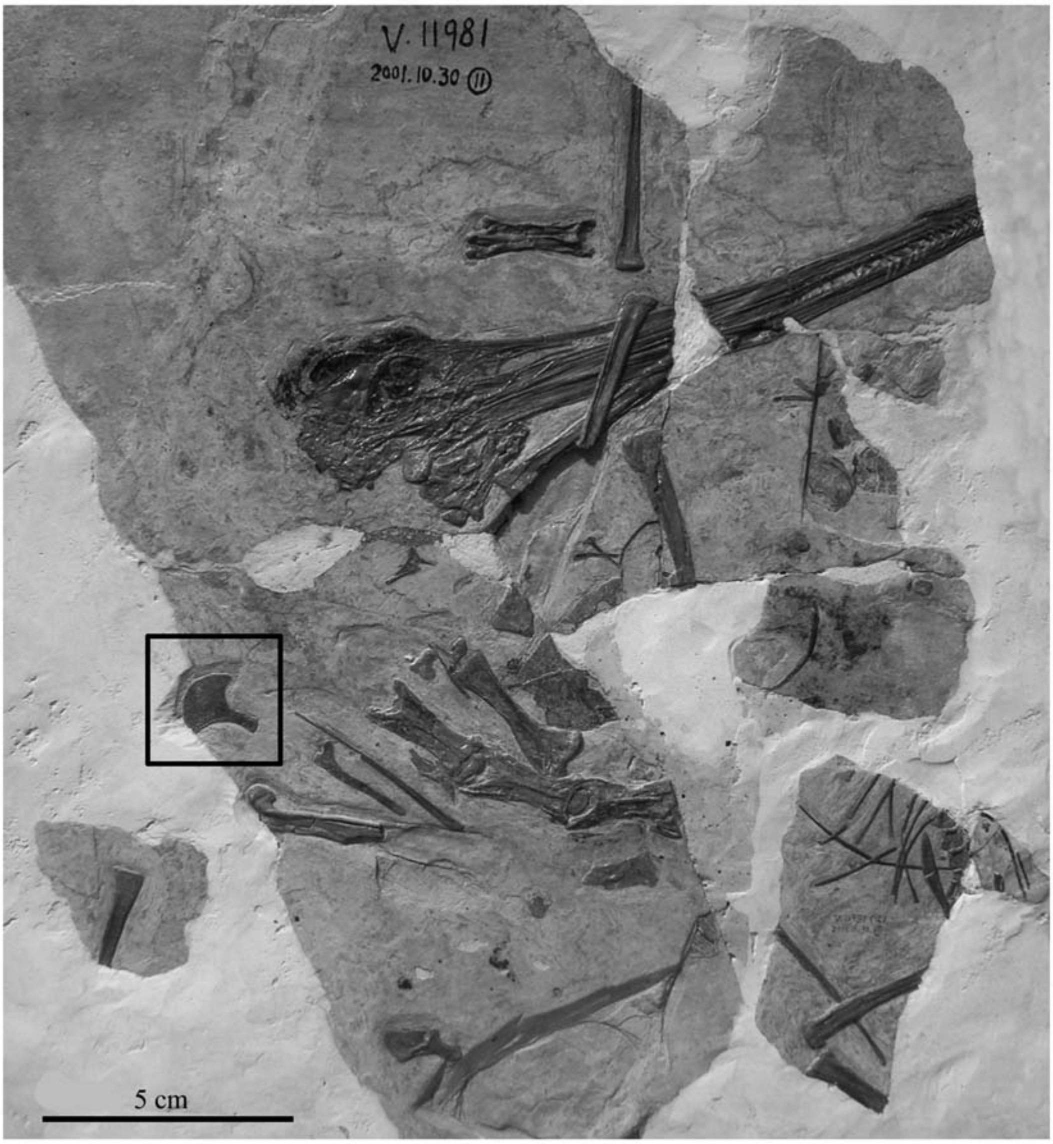

Fig. 1　Holotype of *Gegepterus changae* (IVPP V 11981) with the further preparation (in the black frame)

tures: 1) extensive sculpturing of anterior and lateral margins of frontals; 2) lacrimal with anterior process that overlies nasal; 3) teeth set in alveoli and placed in longitudinal grooves; 4) high neural spine with knob-like dorsal expansion in atlas. They also recognized the following combination of characters: low and thin premaxillary crest confined to anterior portion of skull; about 150 needle-shaped teeth (including upper and lower jaws) that are shorter and fewer than in other ctenochasmatid pterosaurs; presence of cervical ribs; and mid-cervical vertebrae bearing developed postexapophyses.

The new material IVPP V 11972, described here, was unearthed from the same horizon of the holotype (housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences). This specimen is also incomplete, but it preserves the posterior part of the skull and mandible, and the most parts of the postcranial skeleton not preserved in the holotype. Based on the foot and the degree of ossification of the epiphyseal regions of the hindlimb, we suggest that it is an immature or subadult individual (Bennett, 1993; Kellner and Tomida, 2000; Kellner, 2004). Compared with the holotype, V 11972 has the same diagnostic characters 1, 2, and 3 listed above, so it represents a new specimen of *Gegepterus changae*. Meanwhile, the holotype was further prepared, and a new bone, the prepubis, was exposed. As a result, we here revise its diagnosis and discuss its relationship to other ctenochasmatid pterosaurs.

2 Description

The following description is based mainly on information from the new specimen V 11972 (Figs. 2–6; Table 1) and the further prepared holotype (Fig. 1). New and revised anatomical characters are the focus.

Table 1 Measurements of the skulls of IVPP V 11972 and holotype V 11981 (mm)

	V 11972	V 11981 (Wang et al., 2007)
Length of the skull (anterior end to the squamosal)	61.8*	141.0*
Length of the orbit	10.7	16.6
Height of the orbit	10.0	13.7
Length of the nasoantorbital fenestra	32.2	31.0
Height of the nasoantorbital fenestra	5.1	7.0
Rostrum (anterior to the nasoantorbital fenestra)	—	76.2*

* Preserved length.

Skull V 11972 preserved a nearly complete skull except the tip to the anterior margin of the nasoantorbital fenestra (Figs. 2–3; Table 1), though it is not more complete than the holotype. It is laterally compressed, and the right part of the skull has a slight movement from the ventral to the dorsal. The anterior parts of the both dentaries are broken. So, the carcass was probably pushed.

The skull of V 11972 is low and long, a typical feature of archaeopterodactyloids (Kellner, 2003). Its preserved length is 61.8 mm, which is the length from the anterior margin of the nasoantorbital fenestra to the squamosal, and it is subequal to that of the holotype (64.8 mm = 141.0–76.2). Its orbit and nasoantorbital fenestra are also subequal to those of the holotype. So we estimated the length of the skull as 160 mm, because the length of the holotype skull is estimated to be 165 mm (Wang et al., 2007).

Maxilla and premaxilla Only the posterior process of the right premaxilla is preserved, which represents the most dorsal surface from the tip to the posterior of the nasoantorbital fenestra. It is also the anterior third of the dorsal margin of the nasoantorbital fenestra. The process

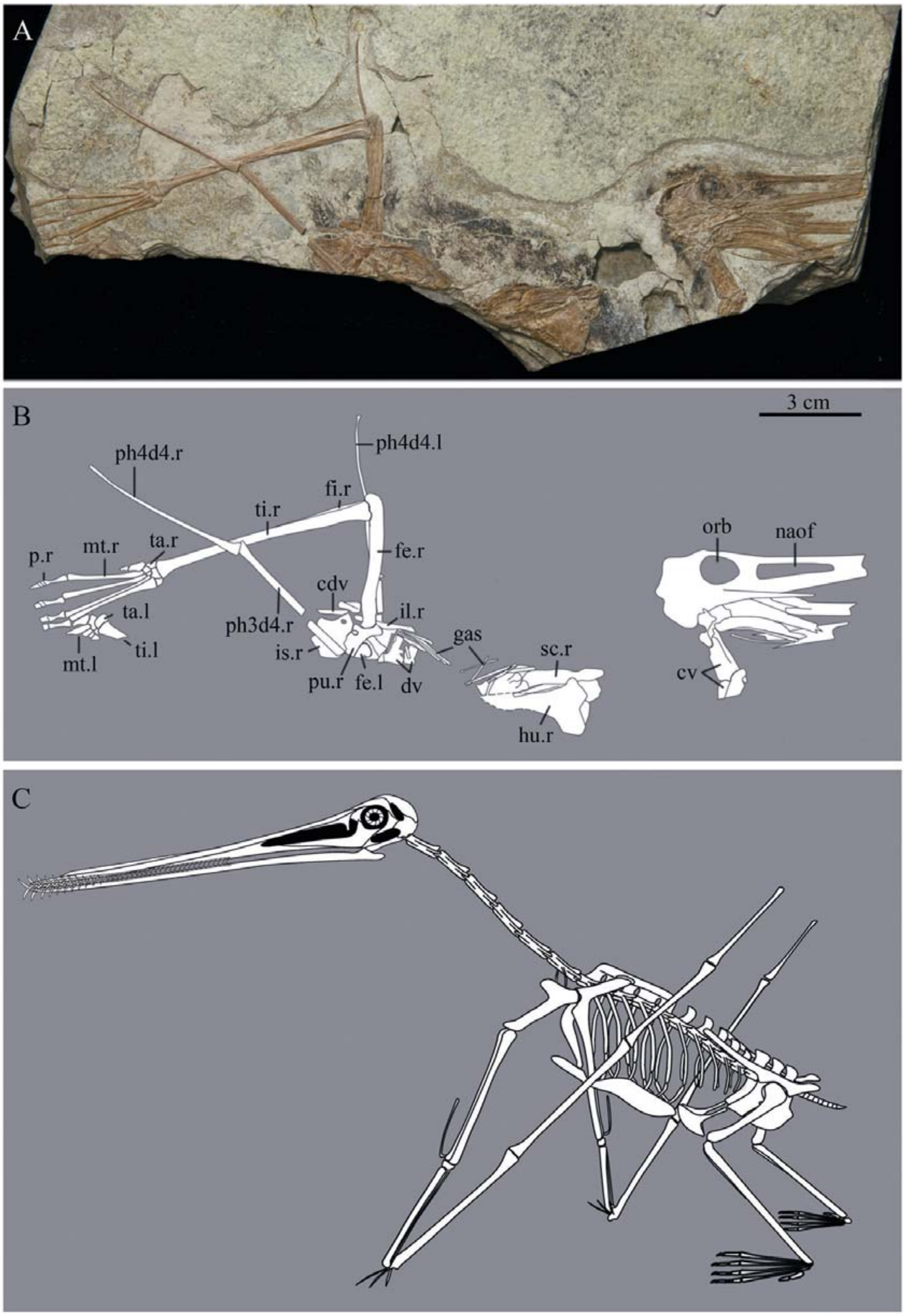

Fig. 2　The photograph（A）, the outline（B）, and the reconstruction（C）of the skeleton of *Gegepterus changae*（IVPP V 11972）

Abbreviations：cdv. caudal vertebra 尾椎；cv. cervical vertebra 颈椎；dv. dorsal vertebra 背椎；fe. femur 股骨；fi. fibula 腓骨；gas. gastralia 腹膜肋；hu. humerus 肱骨；il. ilium 肠骨；is. ischium 坐骨；mt. metatarsal 跖骨；naof. nasoantorbital fenestra 鼻眶前孔；orb. orbit 眼眶；p. pedal digit 趾节；ph3d4. third phalanx of manual digit IV 第 3 翼指骨；ph4d4. fourth phalanx of manual digit IV 第 4 翼指骨；pu. pubis 耻骨；sc. scapula 肩胛骨；ta. tarsus 跗骨；ti. tibia 胫骨；l. left 左；r. right 右

is overlying the nasal, and it is easy to observe the suture between the premaxilla and the nasal, indicating a subadult individual (Kellner and Tomida, 2000). The connection between premaxilla and maxilla is not preserved, and the connection between premaxilla and frontal is also blocked by other bones. The posterior part of the right maxilla is preserved, forming the ventral margin of the anterior part of the skull. It is in the medial side of the right jugal, and the suture of them is obvious, only missing anterior part.

Nasal Both nasals are well preserved. The right one is higher and more exposed than the left one. The part, participating in the dorsoposterior margin of the nasoantorbital fenestra, is compressed dorsoventrally. The nasal is a triradiate bone. The anterior process is extremely elongated, forming the dorsal margin of the nasoantorbital fenestra. The ventral process is nearly vertical to the prolate axis of the nasoantorbital fenestra and shorter than the height. The posterior process is overlaid by the lacrimal, and it is a unique feature as seen in the holotype (Wang et al., 2007).

Wang et al. (2007) described a foramen piercing the left nasal (Fig. 4B), which is not observed on the right one. In the new specimen V 11972, there are two elliptical foramens in the right nasal (Fig. 4A). The anterior one has two openings; the lateral one is bigger than the medial one. And the part of the posterior foramen is overlaid by the lacrimal. In fact, in the left nasal of the holotype, there are also two foramens and most part of the posterior one is invisible because this bone is covered by the right nasal. The foramen has been recorded only in *Feilongus youngi*; however, it bears only one foramen and a depression (Wang et al., 2005). So, the two foramens in the nasal are a new unique feature of *Gegepterus changae*.

Frontal and postfrontal The right frontal and postfrontal are almost completely preserved. The anterior process of the frontal is overlaid by the sclerotic ring and the lacrimal. The postfrontal, being placed ventrally from the frontal, fuses with it and has a ridge. The frontal and postfrontal form the dorsoposterior corner of the orbit. The frontal is a thin bone, its anterior part is narrow, and the rest is extended. The extensive sculpturing of anterior and lateral margins of frontals is a unique feature as recognized in the holotype (Wang et al., 2007). Although the anterior margin of the frontal is invisible in the new specimen, the sculpturing of the lateral margin is still apparent. Except the region mentioned above, the frontal is smooth, and obviously different.

Lacrimal The right lacrimal is complete, and its anterior process overlies the nasal, which is a unique feature as in the holotype. Additionally, a stick-like bone below the lacrimal may represent the ventral process of the nasal, or a process of the jugal, but it is difficult to exactly determine its identification.

The lacrimal foramen in the new specimen is larger than in the holotype. The lacrimal forms the anterior margin and the prefrontal forms the rest of the margin of the lacrimal foramen. A lacrimal foramen exists in the primitive pterodactyloid taxa, such as *Pterodaustro* (Chiappe et al., 2000). However, it is not observed in *Feilongus* (Wang et al., 2005).

Jugal The jugal is a triradiate bone, which has three processes and fuses with the maxilla, lacrimal and postorbital respectively. The anterior process of the jugal is extremely elongated, extending to the anterior margin of the orbit, nearly three quarters length of the jugal. The right anterior process connects with the maxilla, and the left one has a displacement. The posterior process tilts up, and fuses with the postorbital. In the new specimen, the right one is higher than its usual anatomical position in the orbit, and the left one is invisible. The lacrimal processes are not observed, yet we assume the stick-like bone mentioned above might be one of them.

Parietal and squamosal The right parietal is compressed laterally, and the dorsoposterior margin is curved, forming the dorsoposterior corner of the skull. The parietal is connected with the frontal and squamosal anteriorly and ventrally, respectively. In the ventral side of the

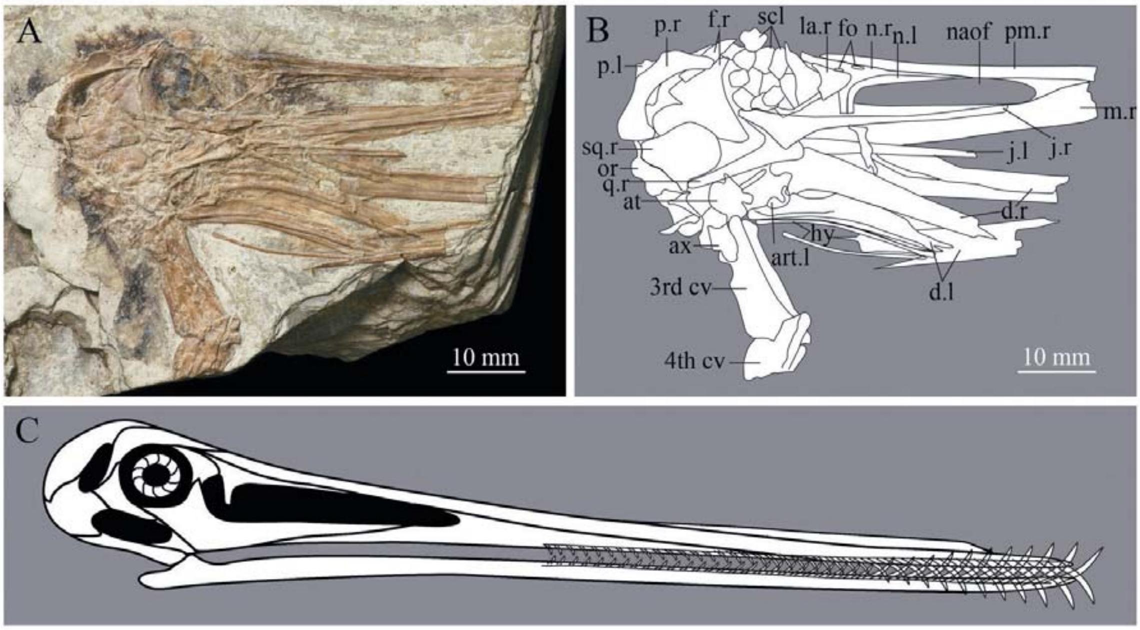

Fig. 3　The photograph (A), the outline (B), and the reconstruction (C) of the skull of *Gegepterus changae* (IVPP V 11972)

Abbreviations: 3rd cv. third cervical vertebra 第 3 颈椎; 4th cv. fourth cervical vertebra 第 4 颈椎; art. articular 关节骨; at. atlas 寰椎; ax. axis 枢椎; d. dentary 齿骨; f. frontal 额骨; fo. foremen 小孔; hy. hyoid 舌骨; j. jugal 轭骨; la. lacrimal 泪骨; m. maxilla 上颌骨; n. nasal 鼻骨; naof. nasoantorbital fenestra 鼻眶前孔; or. occipital region 枕区; p. parietal 顶骨; pm. premaxilla 前上颌骨; q. quadrate 方骨; scl. sclerotic ring 巩膜环; sq. squamosal 鳞骨; l. left 左; r. right 右

Fig. 4　The nasal of *Gegepterus changae* (IVPP V 11972) (A) and the holotype V 11981 (B)
Arrows indicate foramens on the nasal

parietal, there is a low ridge. Below the ridge, a cambered surface forms the medial wall of the upper temporal fenestra. The right squamosal is preserved, but badly crushed. It fuses with the postorbital, parietal, and quadrate to form the ventral margin of the upper temporal fenestra and the dorsal margin of the lower temporal fenestra.

Quadrate and quadratojugal The right quadrate and quadratojugal are preserved and strongly fused, forming a V-shaped structure and no suture between those bones can be identified. The quadrate is nearly parallel to the ventral margin of the skull as a result of the taphonomical displacement of this region of the specimen. Although it cannot be observed directly, we infer that the quadrate is slightly lower than the ventral margin based on the bones around them.

Occipital region The occipital region is completely crushed and individual bones are not distinguishable. From the remaining bones we only can infer the position of the occipital region.

Mandible The posterior parts of the both mandibles are preserved. The right and left can be observed in the lateral and medial aspects, respectively. The mandible consists of the articular, angular, surangular, dentary and splenial. Because of the missing of the anterior parts, the dentaries are lost for the most part. The sutures between the dentary and angular or surangular cannot be observed. The suture between the angular and surangular can be observed in the left one (in lateral view), but not in the right one (in medial view). And the angular rises a little medially.

The outline of the splenial is indistinguishable. And the suture between the articular and other bones is evident. The craniomandibular articulation is very clear, and it rises a little laterally. The retroarticular process is more developed, which is unusual in the primitive pterodactyloids, such as *Gnathosaurus*.

Hyoid The hyoid is incomplete, and only the posterior rami are preserved. The anterior parts of them are separate, and they do not fuse with each other.

Vertebrae In the new specimen the first four cervical vertebrae, the last dorsal vertebra, the first two sacral vertebrae and the last nine caudal vertebrae are preserved (Figs. 2, 3, 5; Table 2).

Cervical vertebrae The atlas and the other three vertebrae are preserved in anterior aspect and lateral aspect, respectively (Figs. 2, 3; Table 2). The atlas is badly crushed, and the wall of the bone is lost. The outline can be identified and inferred to be made of two semicircular neural arches. A unique feature is the atlas with knob-like neural spine. Without the wall of the bone we tentatively suggest that the small convex structure is the knob-like neural spine observed in the holotype. Only partial centrum of the axis is visible.

The third cervical is the most complete one, elongated with a preserved length of 16.3 mm. Although recently a group of non-pterodactyloid pterosaurs also shows the cervical elements rather elongated (Wang et al., 2009; 2010), this feature is predominantly found in archaeopterodactyloids (Kellner, 2003). Due to the compression, it may be slightly longer indeed. The height of the centrum is 3.8 mm at least, and the height of the neural spine is 1.3 mm. The third cervical is elongated, especially the prezygapophysis and postzygapophysis. The fourth cervical preserved its anterior part, with the same elongated prezygapophysis. The prezygapophysis is located in the lateral side of the postzygapophysis of the third cervical, and overlies it.

Dorsal and sacral vertebrae The last dorsal vertebra and the first two sacral vertebrae are incomplete, at the ventral side of the ilium (Fig. 5). The three vertebrae are not long, but with the high neural spine. The sacral vertebra has a wider neural spine than the dorsal one, which are not fused together but have a gap. The connection between the sacral vertebrae can be observed. The prezygapophysis of the second connects with the postzygapophysis of the first dorsolaterally. They fuse together, but the symphysis still exists. In some derived pterodactyloids, such as *Dsungaripterus* and *Dawndraco*, the sacral vertebrae fuse together and form a sacrum. Often the last dorsal vertebra is still included in the sacrum (Young, 1964; Kellner, 2010). In the new specimen, the three vertebrae, though articulated, do not fuse into a sacrum. Due to the distance between the last sacral vertebra and the caudal vertebrae, additional one or two sacral vertebrae may exist. So, *Gegepterus changae* possibly have 3 ~ 4 sacral vertebrae in total.

Caudal vertebrae The caudal vertebrae are small, and most are rectangular, but the last one is triangular (Fig. 5; Table 2). The low neural spine, which is a quarter of the height of the centrum, can be observed in the middle four vertebrae.

Table 2 Measurements of the postcranial bones of *Gegepterus changae* (IVPP V 11972) (mm)

	Length (right, left)	Width (right, left)
axis	5.7*	—
3rd cervical vertebra	16.3	3.8*
4th cervical vertebra	11.2*	—
caudal vertebra	9.8	1.6*
3rd wing phalanx	44.2*, 24.6*	2.1, —
4th wing phalanx	50.7, 49.8	—, —
scapular	23.3, —	3.9, —
humerus	22.4*, —	—, —
femur	39.8, —	3.8, —
tibia	65.0, —	2.9, —
fibula	28.7, —	0.7, —
1st metatarsal	27.5, —	0.7, —
2nd metatarsal	27.7, —	0.6, —
3rd metatarsal	25.8, —	0.6, —
4th metatarsal	22.5, —	0.6, —
5th metatarsal	4.9, 5.1	—, —
1st pedal digit	8.4*, —	—, —
2nd pedal digit	7.4*, —	—, —
3rd pedal digit	8.6*, —	—, —
4th pedal digit	11.8*, —	—, —
5th pedal digit	2.4, —	—, —

* Preserved length.

Pectoral girdle and forelimb V 11972 preserved the right scapular, the proximal end of the right humerus, and the last two phalanges of both wing fingers (Fig. 2; Table 2). The coracoid is not preserved, and it does not fuse with the scapula, either. In the proximal part of the scapular, there is a glenoid fossa for the articulation with the humerus. The articular socket of the humerus, which is in contact with the fossa, is not developed. The right humerus is not complete, and the delto-pectoral crest is not very developed compared with some derived pterosaurs (e. g., *Sinopterus*, Wang and Zhou, 2003) but displaying the typical configuration of the Archaeopterodactyloidae (Costa and Kellner, 2009). It is estimated to be about 30% of the length of humerus, and the neck of this process is not apparent. Although the right humerus is not complete, the fracture of the bone provides some information on the internal structure. The axis of the humerus is concave and the internal surface of the bone wall is observed, suggesting that the shaft of the humerus is hollow, which was previously mentioned in many other pterodactyloids, such as *Dsungaripterus* and *Huanhepterus* (Young, 1964; Dong, 1982).

The last two phalanges of both wing fingers are preserved (Table 2). The third phalanges are not complete, and it is easy to see that the wing fingers are also hollow from the fracture. The articulations of the wing finger phalanges are flat, representing the inflexibility of the wing finger. And the grooves in the wing fingers, to which the wing membranes are attached, are parallel to the axis. All above-mentioned finger characters suggest the pterosaurs with flying ability.

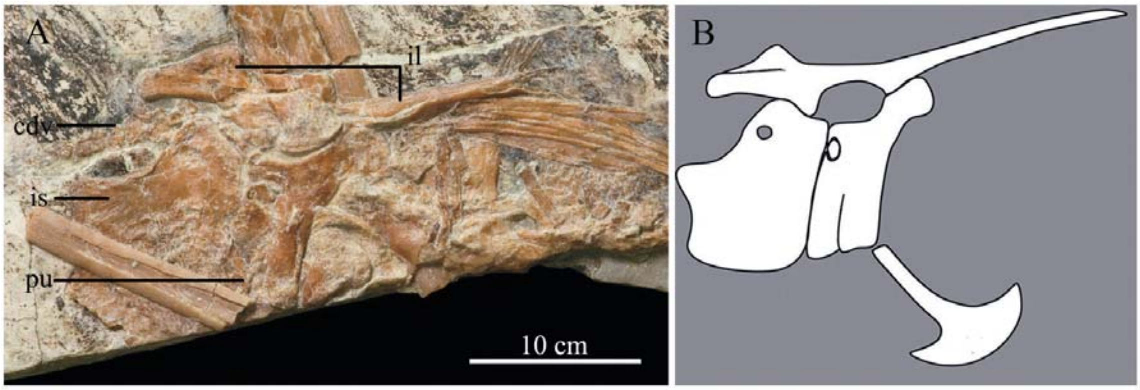

Fig. 5 The pelvis of *Gegepterus changae* (IVPP V 11972)(A), and the reconstruction of the pelvis (B) based on both V 11972 and the holotype
Abbreviations: cdv. caudal vertebra 尾椎; il. ilium 肠骨; is. ischium 坐骨; pu. pubis 耻骨

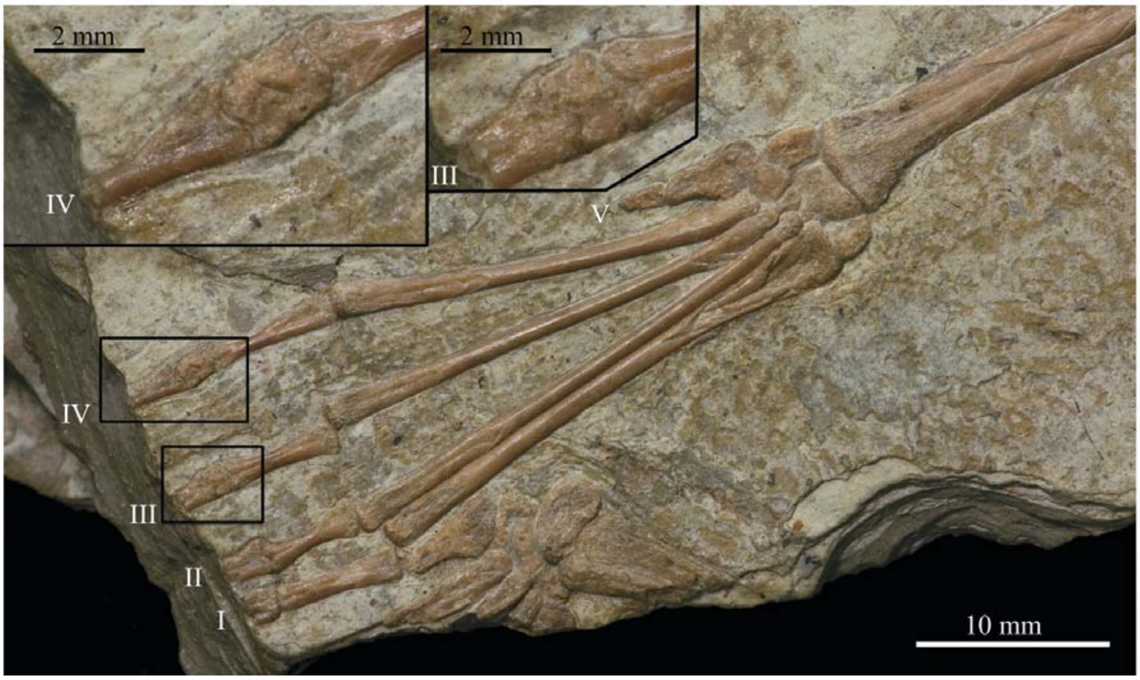

Fig. 6 The metatarsals and pedal digits of *Gegepterus changae* (IVPP V 11972)
I–IV represents pedal digits I–IV

Pelvis and hindlimb V 11972 preserved a nearly complete and articulate right pelvis and hindlimb, and partial left hindlimb (Fig. 5; Table 2). The ilium forms the dorsal margin of the acetabulum. Its anterior process is elongated, and its tip rises slightly. The posterior process is short with a low ridge. The connection between the ilium and the sacral vertebrae is not visible. The pubis and ischium are below the ilium and form the anteroventral and posterior margin of the acetabulum, respectively. The posterior margin of the pubis is straight, in contact with the anterior margin of the ischium. A well-developed obturantor foramen is almost entirely enclosed, and opens to the contact margin with the ischium. Another small rounded bone covering the small foramen is a part of the pubis, which is absent in the holotype. The ischium is an irregular laminal bone, with obvious sculpture on the lateral side. A foramen is in the dorsal part of the ischium, and the dorsoposterior margin is an incisure. After further preparation of the holotype, we recognized another laminal bone, prepubis, which is unusually preserved (Fig. 1, in black frame). Originally, the prepubis is in the anterior portion of the pubis. It consists of two parts: the proximal part is stick-like, which connects but not fuses with the pubis, and the distal part is fanshaped, where the muscle is attached. Both the right and left prepubes are in contact with each other at the distal ends. This kind of prepubis is generally seen in the pterodactyloids.

The right femur curves slightly, and the head of the femur forms an angle with the axis, but the neck is not well developed. The tibia is long and straight, and the fibula is slender and short, only as about 44% of the length of the tibia. The epiphyseal regions of the femur and tibia are pitted and rough, suggesting it is a subadult individual (Bennett, 1993). Five tarsals are preserved completely. The proximal two are big, while the distal three are small. The proximal two are fused with the tibia, a common condition for all in pterodactyloids (Kellner, 2004), with a single suture recognizable. The five tarsals are also fused together with some sutures, indicating it is a subadult individual (Kellner, 2004). The fifth metatarsal is reduced greatly. The other four metatarsals are subequal, with the first being the longest.

The distal ends of the pedal digits are absent (Fig. 6; Table 2). The phalangeal formula for the foot runs 2-3-4-5-1. The fifth digit is reduced and becomes triangular in shape. The third and fourth digits have very short central phalanges, which not ossify in the early growth phase. All these suggest that this individual is a subadult (Kellner and Tomida, 2000; Kellner, 2004). The joint between the phalanx and metatarsal is flat, and suggests the ankle can rotate slightly. However, the joint between two phalanges are flexible. All claws are absent except the first one, whose proximal end is flat. It indicates a limited gripping ability.

Soft tissue　V 11972 preserved a large amount of soft tissue, including the hair-like structure, which has been called pycnofibers (Kellner et al., 2010). It is mainly in the areas of the skull, neck, torso, and tail, and has a similar structure with a few differences. In the neck and partial torso areas, the soft tissue is preserved as a dark mineralized substance on the matrix, and it mostly dose not show any particular structure. In other areas, the soft tissue is fibrous and the single fiber can be distinguished. The fibers are parallel to each other (especially in the tail area), without any branching, and taper off distally. In the skull area, some fibers are more flexible and sinuous, which are similar to the hair-like structure in *Sordes* and *Jeholopterus* (Unwin and Bakhurina, 1994; Bakehurina and Unwin, 1995; Wang et al., 2002; Ji and Yuan, 2002; Kellner et al., 2010).

3　Comparison and discussion

The Ctenochasmatidae are part of the clade known as Archaeopterodactyloidea (Kellner, 2003). There are five genera and species of ctenochasmatids represented only by five specimens from China (Dong, 1982; Lü, 2003; Wang and Zhou, 2006; Wang et al., 2007; Andres and Ji, 2008). *Huanhepterus*, *Cathaypterus*, and *Gegepterus* have partial or nearly complete skulls, whereas *Beipiaopterus* and *Elanodactylus* have only postcranial skeletons. *Huanhepterus* preserved the skull, and most elements of the postcranial skeleton are absent, leaving some three dimensional impression in the sandstone. So, many features of the postcranial skeletons are undefined. In the original paper reporting the holotype of *Gegepterus*, the authors compared it with *Beipiaopterus* (Wang et al., 2007) and *Eosipterus* (Ji and Ji, 1997), the latter was first regarded as a pterodactyloid but later considered as a ctenochasmatid (Unwin and Bakhurina, 2000). In this paper, we will compare the features of the new specimen and the holotype with some other ctenochasmatids in China.

Cathaypterus, preserving part of the skull, differs from *Gegepterus* in the following aspects. First, the skull length of *Cathaypterus*, from the anterior tip to the occipital condyle, is 278 mm, which is much longer than that of *Gegepterus*. Second, *Cathaypterus* (45%, 31 ~ 33 teeth per jaw side) has a similar tooth row and tooth number to that of *Gegepterus* (47%, 35 ~ 37 teeth per jaw side), but the tooth density of *Cathaypterus* is apparently less. The tooth density of *Cathaypterus* is 2.6 teeth/cm, and it is greater in the anterior portion, nearly 3.0 teeth/cm. The tooth densities of the upper and lower jaws in *Gegepterus* are 5.2 teeth/cm and 5.8 teeth/cm, respectively, and they are greater in the anterior portion, nearly 6.0 teeth/cm. This is the most evident difference between these two pterosaurs. Third, the alveoli of *Cathaypterus* are not in the longitudinal grooves, which is a diagnostic of *Gegepterus*. In addition, Wang and Zhou (2006) regarded the small nasoantorbital fenestra as a diagnostic feature, which is 1/5(21%) of the skull length. However, the proportion is slightly lower, and nearly equal to that of *Gegepterus* (19%). In fact, the nasoantorbital fenestra is small because of the extremely elongated rostrum. Comparing the rostrums, we find the proportion of the rostrum in *Cathaypterus* is greater than that in *Gegepterus*. It is regarded as a new diagnostic character of *Cathaypteru*. Thus, all the comparisons above suggest these two pterosaurs are similar and both are members of Ctenochasmaniae, and that they are not the same genus because of some important differences.

Huanhepterus was first described by Dong (1982), and the skull is only prepared recently. *Huanhepterus*, preserving the rostrum and some impression of postcranial skeleton, is very different from *Gegepterus* in the following aspects. First, *Huanhepterus* is much larger than *Gegepterus*, and the rostrum is 330 mm long, so the estimated length of skull must be larger than 500 mm. Second, the tooth number and density of *Huanhepterus* (25 ~ 27 teeth per jaw side, 1.6 teeth/cm) is much smaller and less than those in *Gegepterus*. The tooth shape is also different; the teeth of *Huanhepterus* are shorter and nearly vertical to the axis of the jaws, which is an abnormal feature in ctenochasmatid pterosaurs. The teeth of *Huanhepterus* are much smaller than the gap between two teeth, which is larger than that in *Gegepterus* when the upper and lower teeth interlocks. Third, the cervical vertebrae are more elongated than those in *Gegepterus*. The both ends of the cervical are wider than the middle. The ratio of the length to the middle width reaches 8.8, much larger than that of *Gegepterus* (about 3.4 ~4.5). Considering the ratio from the impression of the cervical, we still regard the cervical vertebrae of *Huanhepterus* to have a specialized feature. So, *Huanhepterus* is considered a member of Gnathosaurinae, because of its fewer teeth, less tooth density, and larger body.

According the initial description of *Elanodactylus*, it differs from *Gegepterus* in blade-shaped and taller neural spines on the mid-cervical vertebrae, postexapophyses forming flanges, presence of cervical ribs, coracoids with a middle constriction and ventral flange, distinct limb ratios, and a much smaller size (Andres and Ji, 2008). Comparing it with the new specimen, we find a new difference in the humerus. The articular socket of the humerus, which is in contact with the scapulocoracoids, is developed in *Elanodactylus*, but not in *Gegepterus*. Considering these differences, we can easily distinguish the two pterosaurs. However, it remains unresolved whether *Elanodactylus* belongs to ctenochasmatids, because of the absence of the skull. The metatarsal is not elongated as in other ctenochasmatids, which is a primitive feature. The first wing phalanx is shorter than the second and third ones, which is absent in ctenochasmatids, but present in *Wukongopterus* and *Darwinopterus* (Lü et al., 2009; Wang et al., 2009). So, we tentatively regard *Elanodactylus* as a primitive ctenochasmatid, a conclusion that awaits more information on cranial features to confirm.

Although other deposits have revealed three-dimensionally preserved soft tissue (e. g., Kellner, 1996), Johel Biota shows much more specimens that preserved the integument covering (e. g. Xu et al., 2009; Zhang et al., 2010). From all material recovered so far, along with *Jeholopterus* (Wang et al., 2002), V 11972 is one of the best preserved pterosaur specimens with soft tissue, which may bear important information on the origin of protofeather. In various hypotheses concerning the origin of feathers (Prum and Brush, 2002; Norell and Xu, 2005; Perrichot et al., 2008; Xu et al., 2009), it is generally agreed that the feather in the first stage should be a single fiber-like structure that lacks any branching and tapers off distally. And it is very similar to the soft tissue in *Gegepterus* and *Jeholopterus* (Wang et al., 2002; Wang et al., 2007). Thus, we propose that the soft tissue in *Gegepterus* might actually represent such a protofeather and the feather we see in birds and many dinosaurs possibly have originated earlier than the first appearance of the dinosaur.

4 Conclusion

The new specimen IVPP V 11972 is recognized as a *Gegepterus changae* based on the unique features in the skull and cervical vertebrae. Based on the phalangeal formula for the foot, we regard V 11972 as a subadult individual. We identified some new features in the vertebrae, pectoral girdle, and other parts of the skeleton. Further, we add a unique feature, two foramens on the nasal, to the diagnosis of *Gegepterus changae*. At present, only specimens with the skull are described, and more complete fossils will be needed in order to determine the phylogenetic position of the species within the archaeopterodactyloid clade Ctenochasmatidae.

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