

A new pterosaur (Ctenochasmatidae, Archaeopterodactyloidea) from the Lower Cretaceous Yixian Formation of China

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Abstract

A partial skeleton (including skull, mandible and soft tissue) of a new archaeopterodactyloid pterosaur, *Gegepterus changi* gen. et sp. nov. from the Lower Cretaceous of Liaoning, northeast China is described. The specimen, IVPP V 11981, was collected from grey shales of the lower Yixian Formation (125 Ma) at the Sihetun locality, near the city of Beipiao. Several elements (cranial bones, scapula-coracoid) are not fused, suggesting that it probably represents a sub-adult individual at the time of death. Soft tissue is found near the posterior region of the skull, inside the orbit and associated with the gastralia. It is formed of an amorphous dark mineralized substance and does not show any particular structure except in an area at the posterior part of the skull where small, dark, unbranched fibres are present. *Gegepterus changi* shows synapomorphies of the Archaeopterodactyloidea sensu Kellner, 2003 (elongated mid-cervical vertebrae with low, blade-like neural spine and strongly inclined quadrate) and shares with the Gallodactylidae and the Ctenochasmatidae a concave dorsal margin of the skull. It further has a large number of thin, needle-like teeth and a long rostrum (anterior to the nasoantorbital fenestra) allowing its allocation to the Ctenochasmatidae, thus making it the first uncontroversial member of this pterosaur clade in the Jehol Group. *Gegepterus changi* is diagnosed by several unique features (e.g., extensive sculpturing of frontals; anterior lacrimal process overlying the nasal; neural spine with knob-like dorsal expansion) and has cervical vertebrae that combine primitive and derived features (e.g., cervical ribs, postexapophyses, lateral pneumatic foramen) that have not been recorded in any member of Archaeopterodactyloidea so far.

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1. Introduction

The Jehol Biota comprises a myriad of exquisitely preserved fossils, from plants and invertebrates to mammals, making it one of the most diverse terrestrial Cretaceous ecosystems known to date (for a review, see Chang et al., 2003 and Zhou et al., 2003). Among the fossils recovered are

pterosaurs, which have been found in increasing numbers in recent years. Since the description of the first species (Ji and Ji, 1997), 16 more have been published, revealing a substantial pterosaur diversity present in the deposits (Dong and Lü, 2005; Lü and Ji, 2005a,b; Lü and Zhang, 2005; Wang et al., 2005a). The first pterosaur eggs (Ji et al., 2004; Wang and Zhou, 2004) and some specimens with preserved integumentary structures (Wang et al., 2002) and other soft tissues (e.g., Lü, 2002) have also been discovered, illustrating the importance of the Jehol material for pterosaur studies in general.

Recently another very interesting specimen was unearthed from the Sihetun locality in Beipiao, Liaoning Province. It

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consists of a partial skeleton (including skull and lower jaw) with some soft tissue and was collected from the Jianshangou Bed of the lower Yixian Formation (Wang et al., 1998). It represents a new genus and species, *Gegepterus changi*, which we describe here. It is the first uncontroversial member of the archaeoptero-dactyloid clade Ctenochasmatidae in the Jehol fauna. Besides its phylogenetic position, *G. changi* shows several morphological features not previously recorded in the Archaeoptero-dactyloidea as briefly mentioned before (Wang et al., 2005b). We also discuss the phylogenetic position of *Eosipterus yangi* Ji and Ji, 1997, previously assigned to the Ctenochasmatidae (Unwin et al., 2000; Lü, 2003).

2. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Archaeoptero-dactyloidea Kellner, 1996

Ctenochasmatidae Nopcsa, 1928

Gegepterus gen. nov.

Derivation of name. *Gege*, meaning princess in the Chinese Qing Dynasty, and Greek, *pterus*, wing.

Type species. *Gegepterus changi*, type by monotypy.

Diagnosis. Archaeoptero-dactyloid pterosaur with the following unique features: extensive sculpturing of anterior and lateral margins of frontals; lacrimal with anterior process that overlies nasal; teeth set in alveoli and placed in longitudinal grooves; high neural spine with knob-like dorsal expansion. It can be further separated from all other archaeoptero-dactyloids by the following combination of characters: low, 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 Ctenochasmatidae (e.g., *Ctenochasma*); presence of cervical ribs; and mid-cervical vertebrae bearing developed postexapophyses.

Gegepterus changi sp. nov.

Figs. 1–11

Derivation of name. In honour of Prof. Dr. Meemann Chang, who fostered the collaboration of scientists from Brazil and China for projects on flying reptiles.

Type specimen. Partial skeleton including an incomplete skull and mandible, vertebrae (cervical, dorsals), a coracoid, elements of the wing, hindlimb and pelvis, housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP V 11981), Beijing, China.

Type locality, stratigraphic horizon and age. Sihetun, Beipiao, western Liaoning, Jianshangou Member, lower Yixian Formation, Early Cretaceous.

Diagnosis. As for the genus.

Description and comparisons

Generalities and taphonomy. The only known specimen of *Gegepterus changi* (Fig. 1) was found in beige coloured shales in the Yixian Formation and was brought to the IVPP in nine pieces. Five of these contained the main part of the skeleton (including the skull and soft tissue) and could be united based on a perfect match of rock and bones (Fig. 2, 1–5). Two contained the preserved part of the pelvis (Fig. 2, 6–7) and could also be pieced together, although their exact position relative to the main portion of the skeleton cannot be established. The two remaining parts, comprising the proximal articulation of a wing phalanx and a small unidentified bone fragment (Fig. 2, 8–9), did not show any contact surface with parts of other portions of the material. However, based on the colour of the matrix, the absence of bone duplication, and the overall preservation of the bones, we confidently assign them all to one individual. It is also clear that more of the skeleton was originally preserved but lost during collection.

Overall the preservation of *Gegepterus changi* is the same as that seen in other Yixian specimens in that the bones are crushed but with a well preserved cortex. Most of the external surface of the bones is formed by longitudinal ridges and grooves, sometimes intercalated with smoother bone (e.g., maxilla, dentary). Soft tissue is found at the back part of the skull, in the orbit and associated with the gastralia (Figs. 1, 2). Several conchostracans are also found along with the pterosaur bones, confirming the freshwater palaeoenvironment that is generally attributed to the layers of the Yixian Formation (e.g., Chang et al., 2003).

The following elements were found articulated: skull and lower jaw; atlas and cervical 3; cervicals 5–8 and their respective ribs; the last three dorsals with the first sacral and the ilia; and the tibia and fibula. Other elements were found in close association: atlas and skull; wing phalanges 2 and 3; right femur, tibia (+fibula) and ilium; and several elements of the gastralia. Other components like the pubes, cervical 4, and carpals are not in their original anatomical position. The skull and lower jaw lie on the left side above the right first wing phalanx, with wing phalanx 3 (perhaps from the left side) above them. Several elements (cranial bones, both dentaries, scapula-coracoid) are not fused, indicating that this skeleton probably represented a sub-adult individual at the time of death.

The features presented above suggest that the carcass was washed into a deep, low-energy freshwater lake. The main part of the carcass of this pterosaur reached the bottom as one unit. Once there it was not immediately buried and decomposition continued, allowing slow currents present at the bottom of the lake (or the action of other animals, such as fishes) to displace and remove some elements from their anatomical position. Soft tissue preservation and the fact that all elements are closely associated (ca. 400 cm²) suggest that the pre-burial time was not very long, possibly in the range of days or a few weeks.

Skull. The skull of *Gegepterus changi* can be observed from the right side (Figs. 3, 4; Table 1). It lies above one wing phalanx and is crossed by another. It is almost complete, lacking the anterior end and part of the middle portion of the jaws, and has an estimated total length of about 165 mm (see Table 1). Several elements were displaced during fossilization, particularly from the left side, and can be observed in medial view. Compression obscured most of the morphological features of the posterior cranial elements making their identification difficult. The same applies to the palatal region and, excepting the palatine, no bones from this area could be confidently identified.

The skull is long and laterally compressed. The dorsal margin is concave, a feature observed in some archaeoptero-dactyloids like *Gallodactylus*, *Ctenochasma* and *Pterodaustro* (Wellnhofer, 1970; Fabre, 1974; Chiappe et al., 2000). Except for the premaxillary crest, the skull becomes progressively thinner dorsoventrally and mediolaterally towards the anterior end. The orbit is large and rounded and occupies most of the posterolateral surface of the skull, a common feature within archaeoptero-dactyloids. The naris and antorbital fenestra are confluent, forming a nasoantorbital fenestra whose anterior margin is obscured by the presence of a wing phalanx, and its exact length cannot be established. It is the longest cranial opening, albeit low and small compared to those in other pterosaurs (height 7 mm; estimated length ca. 31 mm). Based on the estimated length, this opening reaches around 18% of the estimated skull length (from the squamosal to the premaxillary tip), similar to that of *Ctenochasma gracile* and larger than in *Pterodaustro*. The rostral part anterior to the external naris is very elongated, more than half the estimated skull length (69%). The tip of the upper and lower jaw is not preserved, but from the preserved part it is clear that it is not downturned.

Premaxilla. The premaxilla is a long bone that makes most of the dorsal surface of the skull (Fig. 5). This element also participates in the anterior part of the dorsal margin of the nasoantorbital fenestra, overlying the nasal. The suture between the premaxillae is visible as a shallow groove present along most of the length of the skull except for the anterior portion where the bones appear to be already fused. The suture between the premaxilla and the maxilla is also visible, forming a straight, shallow groove that can be followed for virtually the entire preserved parts of the skull. Posteriorly, the premaxilla overlies the nasal and separates the anterior ends of the frontals, reaching the anterior third of the orbit.

At the anterior end, the premaxillae form a low, thin premaxillary crest. The bone surface is rugose, contrasting with the smoother texture of the main part of the premaxilla. The exact anterior extension of the crest is not known, but posteriorly it ends well before the beginning of the nasoantorbital fenestra. There is no indication of a soft extension above the bony portion of the crest, as reported in some primitive (Bennett, 2002) and derived pterodactyloids (e.g., Campos and Kellner, 1997; Kellner, 2006).

Concerning archaeoptero-dactyloids, most lack a premaxillary sagittal crest (e.g., *Pterodactylus*, *Pterodaustro*, *Ctenochasma gracile*, *Gallodactylus*, *Cycnorhamphus*). The premaxillary crest in *Germanodactylus cristatus* is low but displaced backwards, reaching the skull roof above the orbit. *Gnathosaurus* also bears a low premaxillary crest, but it is displaced backwards and grades into the skull roof dorsal to the middle portion of the nasoantorbital fenestra. This same condition is found in “*Ctenochasma*” *porocristata* (Buissonjé, 1981), whose premaxillary crest is apparently very thick and distinct from all other archaeoptero-dactyloids known to date.

Within more derived pterodactyloids (Dsungaripteroidea), most taxa bear a premaxillary sagittal crest but all are different in morphology from that of *Gegepterus changi* (Wellnhofer, 1991; Kellner, 1996, 2003).

Maxilla. The maxilla is a flat, elongated element that forms the ventrolateral part of the skull. Although the anterior margin of the nasoantorbital fenestra cannot be observed, it is clear that the maxilla forms the anterior margin of this cranial opening. The posterior extension of this bone appears to be limited, with most of the ventral margin of the nasoantorbital fenestra made by the jugal, which overlaps the maxilla laterally. Anterior to the nasoantorbital fenestra, the dorsal part of the maxilla shows a smooth wedge-shaped surface about 18 mm long that becomes thinner anteriorly, contrasting with the coarser texture of the ventral portion of this bone and the overlying premaxilla. This feature, which can be observed in other archaeoptero-dactyloids, such as *Pterodactylus*, suggests that this part of the bone might be somewhat displaced medially relative to the lateral surface of the skull.

The dentigerous part of the maxilla has a very peculiar construction. Teeth are set in alveoli that are placed in a longitudinal groove bordered by the maxilla. The borders are made of thickened bone, with the lateral margin thicker than the medial one. The same construction is found in the dentary (see below).

The peculiar dentigerous portion of the maxilla of *Gegepterus* has not been reported in any other pterosaur. *Pterodaustro* lacks alveoli in the maxilla and the numerous teeth must have been connected to the lateral margin of the jaw by soft tissue (Chiappe et al., 2000). In *Ctenochasma* the presence of alveoli has been reported (Wellnhofer, 1970; Buissonjé, 1981), but there is no sign of a longitudinal groove.

Nasal. Both nasals can be observed. This bone is positioned at the dorsoposterior corner of the nasoantorbital fenestra. Anteriorly it has a thin, long process that extends for almost the entire dorsomedial surface of the nasoantorbital fenestra and is anteriorly overlain by the premaxilla. Posteriorly this bone is partially overlain by the lacrimal and sends a thin process that contacts the prefrontal. The nasal contacts neither the frontal laterally nor the supraorbital. It bears a long nasal process that starts at a thickened lateral margin of the nasal, indicating that it is positioned slightly medially relative to the lateral surface of the skull. The nasal process is directed subvertically, with a slight posterior



Fig. 1. *Gegepterus changi* gen. et sp. nov., IVPP V 11981. Note the soft tissue posterodorsal to the skull, in the orbit and associated with the gastralia. Arrows indicate conchostracans. Scale bar represents 50 mm.

inclination, and reaches the lower portion of the nasoantorbital fenestra, contacting but not fused to the bony bar formed, medially, by the maxilla and, laterally, by the jugal. This process is not pierced by foramina, as is the case in some more derived pterodactyloids such as *Anhanguera* (Kellner and Tomida, 2000). Opposite nasal processes are also not fused in the midline.

The left nasal is displaced inside the nasoantorbital fenestra and shows the medial anatomy of this bone. It preserves an elongated depression dorsal to the nasal process that bears an elliptical foramen that pierces the bone (Fig. 10). Such

a foramen is not evident on the right nasal (exposed in lateral view), possibly owing to its extensively fragmented external surface.

A foramen in the dorsal part of the nasal is not common in pterosaurs (e.g., Wellnhofer, 1978). The nasal in the new species is long, more so than in any other pterosaur reported to date, including the archaeopterygoids *Pterodactylus*, *Germanodactylus*, *Ctenochasma* and *Pterodaustro*. Those two features, however, have been recorded in *Feilongus youngi* from the Yixian Formation (Wang et al., 2005a) and are not unique to *Gegepterus changi*.

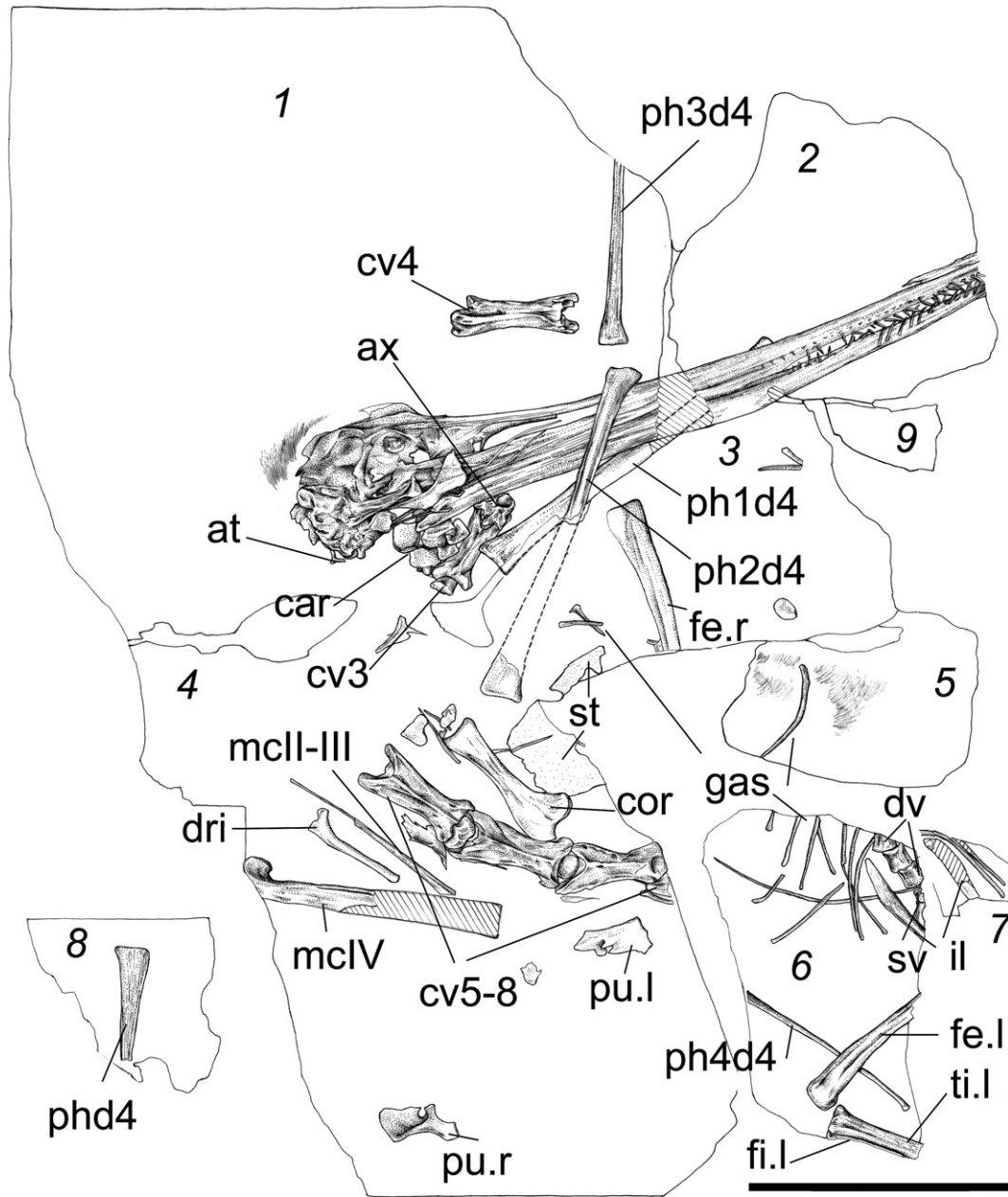


Fig. 2. Drawing of the preserved elements of *Gegepterus changi*, IVPP V 11981 with indication of the broken parts of the slab. Note that the exact position of parts 6–9 are not known. Abbreviations: at, atlas; ax, axis; cor, coracoid; cv3–8, cervical vertebrae 3–8; car, carpus; dri, dorsal rib; dv, dorsal vertebra; fe, femur; fi, fibula; gas, gastralia; il, ilium; mcII–III, metacarpal II–III; mcIV, metacarpal IV; phd4, indeterminate wing phalanx; ph1d4, first phalanx of manual digit IV; ph2d4, second phalanx of manual digit IV; ph3d4, third phalanx of manual digit IV; ph4d4, fourth phalanx of manual digit IV; pu, pubis; st, sternum; sv, sacral vertebra; ti, tibia; l, left; r, right. Scale bar represents 50 mm.

Prefrontal, supraorbital and postfrontal. The prefrontal is a dorsoventrally flattened bone whose posterior contacts with the frontal cannot be established, possibly due to fusion. Anteriorly, it overlaps the lacrimal, and ventrally, the supraorbital.

Besides the bony plates of the sclerotic ring, two additional elements are preserved inside the orbit, close to the dorsal border. The more anterior one is interpreted as the supraorbital and can be distinguished from the sclerotic elements by having

a more rugose surface. It is a thin lamina of bone incomplete posteriorly. It is conceivable that it extends much further posteriorly, connecting the postfrontal.

The second element is an elongated bone positioned at the dorsoposterior corner of the orbit and is here interpreted as the postfrontal. It is positioned ventral to the right frontal and is slightly displaced inside the orbit relative to the lateral surface of the skull. It is a thin flat bone with a semicircular shape and a rugose external surface.

Table 1
Measurements of the skull (in mm)

Preserved length
frontal-premaxilla: 137.0
squamosal-premaxilla: 141.0
quadrate-premaxilla: 114.0
rostrum (anterior to the nasoantorbital fenestra): ca. 76.2
premaxillary crest: 14.2
orbit: 16.6
Estimated length
squamosal-premaxilla: ca. 165.0
quadrate-premaxilla: ca. 138.0
rostral end (anterior to the nasoantorbital fenestra): ca. 14.0
nasoantorbital fenestra: ca. 31.0
Height
above craniomandibular articulation – frontal: 16.6
maximum preserved above premaxillary crest (anterior end): 3.2
nasoantorbital fenestra: 7.0
premaxillary crest: 2.0
orbit: 13.7

Frontal. Post-mortem compaction has resulted in a dorsolateral exposure of both frontals. It is a large bone and forms the majority of the skull roof dorsal to the braincase and orbit. The suture between the frontals is obliterated, showing that they are fused in the midline forming a ridge that can be followed until the contact with the premaxillae. No frontal crest is present.

Overall, the frontal is dorsally convex, forming a subtriangular element that has a large anterior process which extends dorsally over the orbit, anteromedially contacting the posterior end of the premaxilla and fusing laterally with the prefrontal (no suture is visible). The posterior end is much shorter and is wedged between the parietals. At the most posterior end, the frontal and parietal are separated (owing to disarticulation) and their anterior contact surface forms a low ridge. The external surface of the frontal is smooth in the middle region, but towards the lateral and anterior margins it becomes rugose and irregular, showing small pits, ridges and grooves, particularly on the part adjacent to the postorbital.

The most interesting feature of the frontal in *Gegepterus changi* is the extensive sculpturing of the lateral and anterior part of this bone, which has not been reported in any other pterosaur.

Parietal and squamosal. The bones of the posterior region of the skull cannot be delimited with precision because of the crushing of the posterior region of the skull. The parietals form the medial wall of the upper temporal fenestra. Although slightly projected posteriorly, there is no evidence of a sagittal parietal crest such as found in *Gallodactylus* and *Cycnorhamphus* (Wellnhofer, 1978; Kellner, 2003).

The squamosal is damaged and the limits of this bone cannot be recognized. It forms the posterior margin of the upper temporal fenestra. Notwithstanding its preservation, it is clear that this bone was situated very low in the skull, a common feature among archaeoptero-dactyloids (e.g., Wellnhofer, 1991; Kellner, 2003).

Lacrima. The right lacrimal is well preserved, participates in the posterior margin of the nasoantorbital fenestra, and forms the anterodorsal margin of the orbit (Fig. 10). It contacts the nasal anterodorsally, the prefrontal posteriorly and the jugal ventrally. The contact with the nasal is rather unusual and formed by two parts. Anteriorly, the lacrimal has a short process that overlies the nasal. Dorsally, it is overlain by the posterior process of the nasal, and shows a depressed area at the nasolacrimal contact surface. Posteriorly, the lacrimal is overlain by the prefrontal. Ventrally, it sends a broad process that overlies the jugal. A small foramen is observed close to this contact area.

A large lacrimal foramen, whose posterior margin is not preserved, is present. The posterodorsal margin of this foramen is formed by the prefrontal. Inside the foramen, close to the anterior margin, several bone struts are observed. This bone further carries a posteroventrally directed short lacrimal process that overlies the anterior margin of the orbit.

A lacrimal foramen is observed in some archaeoptero-dactyloids, such as *Pterodactylus antiquus*, *Pterodactylus kochi* (Kellner and Tomida, 2000) and *Germanodactylus cristatus* (pers. obs.), but not in others, such as *Pterodaustro* (Chiappe et al., 2000) and *Ctenochasma* (pers. obs.). However, the fact that this foramen is observed in *Gegepterus changi*, in some other undescribed archaeoptero-dactyloids from the Yixian formation, and in *Feilongus* (Wang et al., 2005a), suggests that this feature might have been more widespread among primitive pterodactyloid taxa than previously thought.

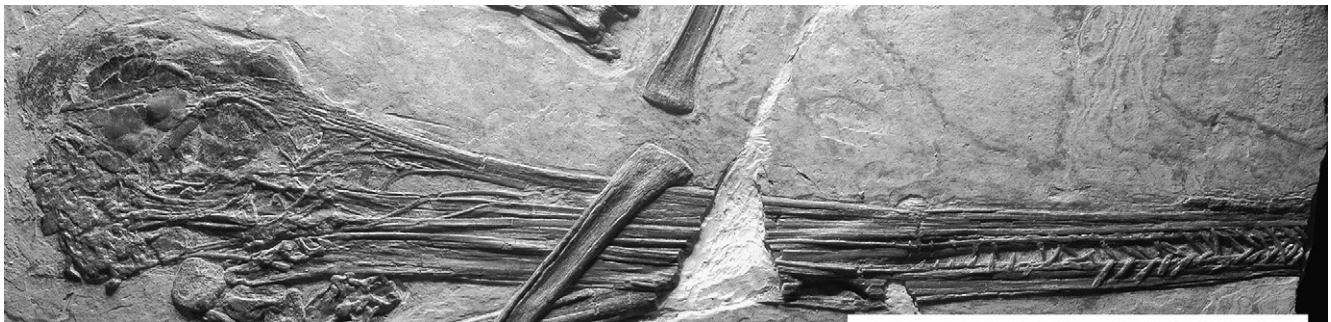


Fig. 3. *Gegepterus changi*, IVPP V 11981, photograph of the skull and lower jaw. Scale bar represents 50 mm.

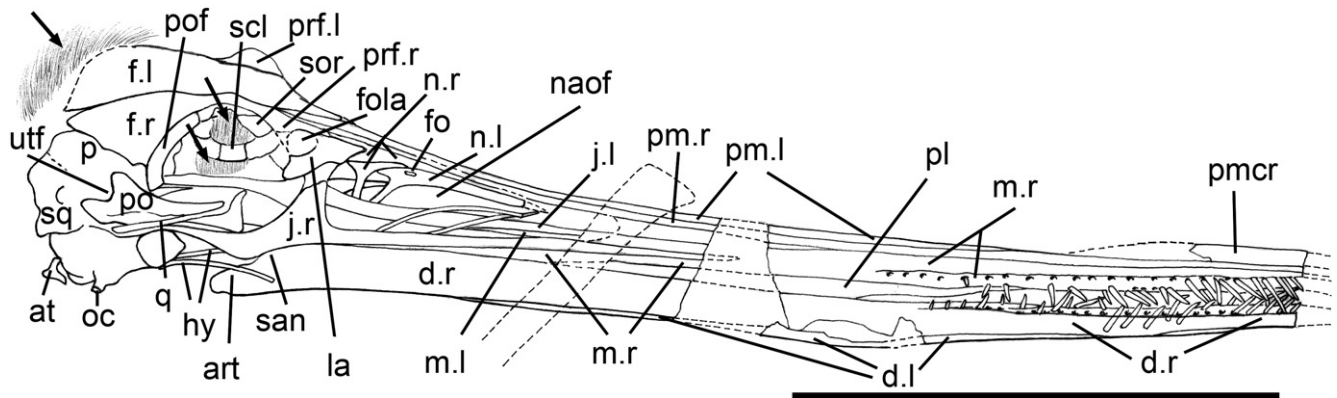


Fig. 4. *Gegepterus changi*, IVPP V 11981, drawing of the skull. Soft tissue posterior to the skull and inside the orbit indicated by arrows. art, articular; at, atlas; d, dentary; f, frontal; fo, foramen; fola, foramen lacrimale; hy, hyoid bone; j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; oc, occipital condyle; p, parietal; pl, palatine; pm, premaxilla; pmcr, premaxillary crest; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; san, surangular; scl, sclerotic ring; sor, supraorbital; sq, squamosal; utf, upper temporal fenestra; l, left; r, right. Scale bar represents 50 mm.

The posteriorly orientated, short process of the lacrimal that overlies the anterior margin of the orbit in *Gegepterus changi* is observed in some archaeoptero-dactyloids, such as *Pterodactylus* and *Gallodactylus* (e.g., Wellnhofer, 1970; Fabre, 1974), but is apparently absent in *Pterodaustro* (Chiappe et al., 2000). The condition of this feature in *Ctenochasma*, *Gnathosaurus* and *Germanodactylus* is presently unknown.

The most unusual feature of the lacrimal in *Gegepterus changi* is the anteriorly projecting process that overlies the nasal, not reported in any pterosaur before.

Postorbital. The postorbital is damaged and the limits of this bone are difficult to establish. It is a triradiate element that participates in the posteroventral margin of the orbit and the anterior margin of the upper temporal fenestra. In other pterodactyloids this bone also forms the dorsoventral margin of the lower temporal opening, but this part of the skull is flattened. The anteroventral process of this bone is very long, more than in most other archaeoptero-dactyloids such as *Ctenochasma* and *Pterodactylus* (Wellnhofer, 1970, 1978).

Jugal. The jugal is a triradiate bone with maxillary, lacrimal and postorbital processes. The right jugal is observed in lateral view while the left one is displaced inside the nasoantorbital fenestra and only exposed for a section of its medial surface. The long anterior maxillary process forms most of the ventral margin of the nasoantorbital fenestra, tapers anteriorly, and overlaps the maxilla. The lacrimal ramus is broad, inclined dorsoanteriorly, forms the posteroventral margin of the nasoantorbital fenestra and the anteroventral margin of the orbit, and is overlain by the lacrimal. It lacks a ventral ridge observed in more derived pterodactyloids such as *Anhanguera* (Kellner and Tomida, 2000), *Pteranodon* (Bennett, 2001), *Tapejara* (Kellner, 1989) and *Thalassodromeus* (Kellner and Campos, 2002). The third ramus of this bone is directed posteriorly, gradually becomes thinner, and is overlain by the postorbital, forming the ventral margin of the orbit. Apparently the jugal does not take part in the lower temporal

fenestra. The jugal border of the orbit is very thick, contrasting to the thinner border of the nasoantorbital fenestra.

A triradiate jugal is present in several pterodactyloid pterosaurs. Within the Archaeoptero-dactyloidea, the main exception is *Pterodaustro* in which this bone is tetra-radiate (Chiappe et al., 2000).

Other bones that are usually in contact with the jugal could not be observed in detail. One long element, possibly the right quadrate, became displaced dorsally during fossilization. Nevertheless, it is clear from the posterior process of the jugal that the quadrate must have been strongly inclined relative the ventral margin of the skull, as observed in the members of the Archaeoptero-dactyloidea (e.g., Kellner, 1996, 2003).

Palatine. Part of the right palatine is the only bone of the palate that could be identified. It is dorsoventrally compacted and brighter in colour than the surrounding elements, suggesting that it was thinner. The bone surface is smooth and the contact with the maxilla is marked by a faint line. No palatal ridge could be observed.

Occipital region. The occipital region is completely crushed and individual bones are not distinguishable. The only discernible element is the occipital condyle that has a rounded shape and shows a long, comparatively robust neck.

Mandible. The mandible is almost complete, lacking the anterior end and part of the middle portion of the dentary (Figs. 3, 4; Table 2). It is exposed on the right side, in close contact with the skull, and is slightly displaced anteriorly (ca. 1–2 mm) from the natural articulation with the quadrate. As with the skull, the mandible also overlies, and is overlain by, wing phalanges. Some parts of the left lower jaw can be seen ventral to the right dentary. The posterior end of the lower jaw is crushed and occasionally covered by bony fragments, hindering the observation of the limits between mandibular elements.

Table 2
Measurements of the mandible and other elements (in mm)

Mandible preserved length: 118.0
Mandible estimated total length: 142.0
Retroarticular process: 4.6
Sternum, posterior margin: ca. 28.3
Coracoid, length: 28.7
Pubis (right), anterodorsal-posteroventral height: 16.0
Wing metacarpal, length: ca. 52.7
First wing phalanx, preserved length: 69.3
First wing phalanx, estimated length including the extensor tendon process: ca. 0.8
Second wing phalanx, length: 68.3
Fourth wing phalanx, preserved length: +38.0

Dentary. The dentary is the largest bone in the lower jaw. It is long and shows a concave dorsal and a convex ventral margin in lateral view. Towards the anterior part, it turns slightly upwards, following the general pattern of the upper jaw. Towards the anterior region it becomes progressively thinner, similar to the upper jaw. Most of the bone surface is decorated with longitudinal ridges and shallow grooves. In contrast, the middle and lateral part shows a smooth surface for an area that starts almost at the posterior end and tapers anteriorly (ca. 65 mm). The bone in this region is thinner and apparently displaced medially, suggesting that the lateral surface of the dentary was longitudinally concave.

Ventral to the right dentary a longitudinal strip of bone can be followed for almost its entire length and is here interpreted as the left dentary. This suggests that, although the contact surface between both dentaries is long, these bones have not yet fused, at least in the ventral portion. Nevertheless, it is likely that in more mature individuals these bones would indeed fuse, forming an extensive mandibular symphysis, as reported in many pterodactyls (e.g., Kellner, 2003).

As in the maxilla, the dentigerous portion of the dentary is formed by a longitudinal groove bordered by thick margins that enclose the alveoli. The contact of the dentary with the posterior mandibular bones cannot be determined since this region is crushed and partially covered by bone fragments. There are no signs of a dentary sagittal crest.

The particular configuration of the dentigerous portion of the dentary in *Gegepterus* has not been reported in any other pterosaur. The most similar condition to that of *Gegepterus* is observed in the dentary of *Pterodaustro*, where teeth are also set in a longitudinal groove, but only the more anterior ones are set in small, shallow alveoli (Chiappe et al., 2000). The teeth in *Ctenochasma* are set in alveoli (Wellnhofer, 1970; Buissonjé, 1981) but not in longitudinal grooves.

Articular. The only other mandibular bone that can be recognized with confidence is the articular (Fig. 10). It bears a well-developed retroarticular process whose dorsal margin is slightly concave. The suture with the surangular, which forms the anterior part of the craniomandibular articulation, is partially visible.

Compared to other archaeopterygoids (e.g., *Gnathosaurus*), the retroarticular process of *Gegepterus changi* is more developed.

Sclerotic ring. The sclerotic ring is preserved inside the orbit (Figs. 3, 4, 10). About ten elements could be recognized although the total number is unclear. Several elements have shifted from their original anatomical position. Each consists of a thin bony plate that has a smooth, convex external surface, with the medial portion projected laterally relative to the borders. The dorsal part of each plate is smaller than the ventral component.

Ceratobranchial (Hyoid). Two thin, rod-like bones are preserved ventral to the posterior margin of the skull and are regarded as ceratobranchials (Figs. 3, 4). Both elements are incomplete. The shorter is preserved in an almost horizontal position and lies dorsal to the external surface of the posterior end of the lower jaw. The second runs from the ventral margin of the skull between the jugals and reaches the internal part of the nasoantorbital fenestra.

Dentition. The teeth are regularly spaced, curved, thin, and needle shaped (Figs. 3–5). Several have fallen out of their alveoli, particularly in the lower jaw. The larger teeth are positioned anteriorly and gradually become smaller towards the posterior end. The diameter of the basal portion of the largest preserved teeth is around 0.45 mm while the tip is around 0.20 mm. The spaces between the alveoli are slightly larger than the diameter of the alveoli themselves. Anterior teeth are more closely spaced than the posterior ones. A total of 24 and 25 teeth (or alveoli) were found respectively on the preserved portion of the right maxilla and right dentary. The distance from the last tooth to the anterior preserved end of the premaxilla/maxilla is 4.57 cm, producing a tooth density in the upper jaw of 5.25 teeth/cm. The distance from the last dentary tooth to the preserved anterior portion of the mandible is 4.3 cm, giving a tooth density of about 5.8 teeth/cm. Measurements in the upper and lower jaw indicate that in the anterior preserved region, the tooth density is slightly higher, with at least 6 teeth/cm. This provides a total estimated tooth number of about 150. Teeth of both jaws tend to interlock, but in the posterior part the spaces between alveoli are sometimes larger in the upper jaw than those in the lower jaw. Several replacement teeth were found in the same alveoli right behind the preceding tooth. The last maxillary tooth is located posteriorly relative to the last dentary tooth, and about 31 mm before the anterior margin of the nasoantorbital fenestra. Despite the fact that the jaws are flattened laterally, it is clear that the teeth are directed anterolaterally.

Of all of the pterosaurs, the dentition of *Gegepterus changi* is more similar to that of *Ctenochasma gracile* and “*Ctenochasma*” *porocristata*. The total estimated number of teeth in *Gegepterus* (about 150) is more than in *Gnathosaurus* (128–136) but less than in *Ctenochasma* (200–360) (Wellnhofer, 1978; Buissonjé, 1981). Although the lack of the distal ends of the jaws in *Gegepterus* makes size comparisons of the teeth between this taxon and others difficult, judging from the preserved parts the teeth in the new Chinese species are shorter than in both *Gnathosaurus* and *Ctenochasma*. Other differences between these taxa are that in *Gegepterus* the dentition stops comparatively well before the nasoantorbital fenestra and the tooth density (5–6 teeth/cm) is less than in *Ctenochasma gracile*

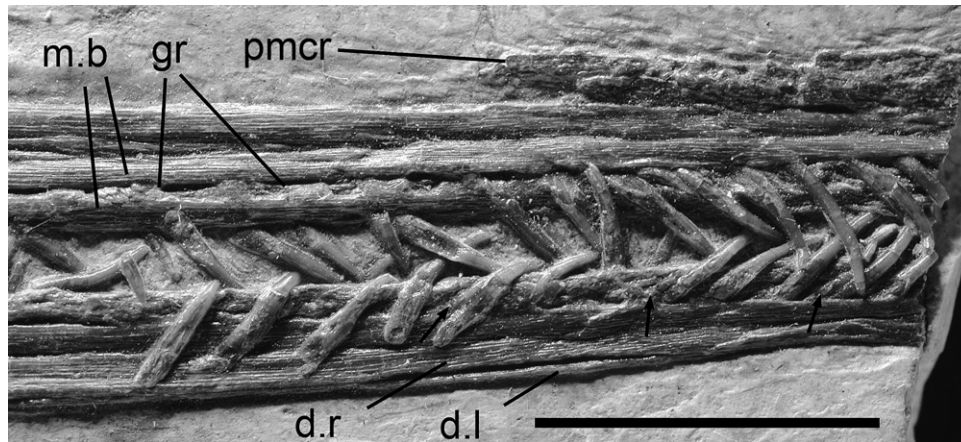


Fig. 5. *Gegepterus changi*, IVPP V 11981, detail of the anterior part of the skull showing the dentition. Arrows indicate replacement tooth set behind the older tooth in the same alveoli. Abbreviations: d, dentary; gr, groove; m.b, thickened borders of the maxilla; pmcr, premaxillary crest; l, left; r, right. Scale bar represents 10 mm.

(+10/cm, pers. obs.) and “*Ctenochasma*” *porocristata* (8–9/cm; Buisonjé, 1981). The dentition of the Gallodactylidae (*Gallodactylus* + *Cynorhamphus*) also differs in not extending so far along the jaws, in containing fewer teeth, and in being confined to the anterior part of the rostrum.

Atlas and axis. A comparatively small element situated on the posteroventral margin of the skull is tentatively interpreted as the atlas. It is incomplete and partially overlain by the crushed occipital region of the skull. The preserved dimensions are 3.8×2.5 mm. The preserved part consists of the left half of the neural arch, formed by a semicircular element surrounding the neural canal. It bears a thin, flange-like dorsal projection (neural spine?) and a laterally placed process. This element is not fused with the axis.

The axis is dislocated from its original anatomical position, next to the ventral margin of the mandible (Figs. 1, 2, 6). It is still attached to cervical 3 and can be observed in dorsal view. The neural spine is high and shows a distinct knob-like dorsal expansion. The postzygapophyses are directed lateroposteriorly. Anterior to the centrum of the axis, there are two distinct ossifications, similar to those observed in *Anhanguera piscator* (Kellner and Tomida, 2000). They are paired structures (anteroposterior length ca. 7.2 mm) the exact shape and extension of which cannot be determined.

The atlas and axis are rarely observable in pterosaurs and there is little information available. The axis of *Gegepterus changi* differs from that of the comparatively more derived pterodactyloids *Anhanguera* (Kellner and Tomida, 2000) and *Pteranodon* (Bennett, 2001) in having a distinct knob-like expansion on the neural spine, not previously reported in any pterosaur.

Cervical vertebrae 3–8. The remains of cervicals 3–8 are dislocated from their original anatomical position (Figs. 1, 2; Table 3). All centra appear to be fused with the neural arches. Cervical 3 is connected to the axis, and both are preserved close to the ventral margin of the mandible (Fig. 6). Cervical 4, the only one exposed ventrolaterally, drifted away and is

found isolated above the skull. Cervicals 5–7 are on the lower part of the slabs, close to some elements of the wing and the pectoral girdle (Fig. 8). Curiously, they are in about the correct anatomical position relative to the skull if the other cervicals were in place (Figs. 1, 2). Only the left prezygapophysis (associated with the corresponding cervical rib) of the anterior portion of cervical 8 was preserved (in articulation with the previous vertebrae). It is clear that more of the neck (and perhaps other parts of the vertebral column) was preserved in this specimen but probably lost during collection.

The morphology of cervicals 3–7 is very similar in being strongly procoelous and possessing an elongate, low, blade-like neural spine. Their length increases toward cervicals 4 and 5 and decreases thereafter (Table 3). All show concave

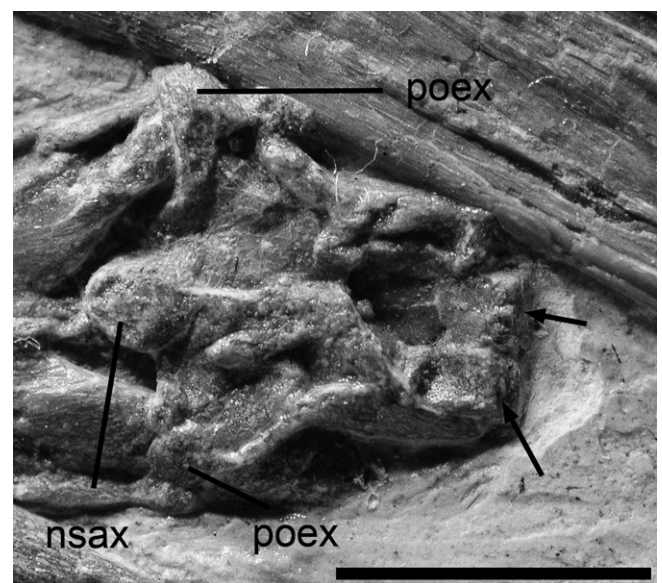


Fig. 6. Photograph of the axis of *Gegepterus changi*, IVPP V 11981. Note the unusual knob-like expansion of the neural spine and the two ossifications anterior to the centrum, indicated by the arrows. Abbreviations: nsax, neural spine of axis; poex, postexapophysis. Scale bar represents 5 mm.

Table 3
Measurements of cervical vertebrae (in mm)

	Length centrum	Length prez-poz	Width prez	Width poz	Minimum width of the centrum
Axis	6.3	X	X	7.2	X
Cervical 3	~17.5	17.2	~7.2	7.9	3.9
Cervical 4	21.3	21.3	6.7	X	4.8
Cervical 5	21.3	21.0	9.2	9.6	5.8
Cervical 6	20.5	20.8	~9.5	~10.2	6.0
Cervical 7	16.4	~20	~10.2	X	~5.7

The measurements were taken as follows: length of centrum: ventral anterior margin of cotyle to condyle; length zygapophyses: between external anterior and posterior margins; width zygapophyses: between external lateral margins of both sides; minimum width of centrum: between lateral margins.

lateral margins with the minimum width situated in the posterior half (i.e., not in the exact mid point) of the vertebra. The pre- and postzygapophyses are projected anterolaterally and ventrolaterally, respectively, with the postzygapophyses more divergent. Cervicals 3 and 4 show well-developed postexapophyses, which in the remaining cervicals are not exposed or were broken (e.g., cervical 7). The posterior end, corresponding to the condyle (and the postexapophyses) extends posteriorly. Cervical 4 shows a well-developed hypapophysis in the midline, close to the cotyle. Furthermore, this vertebra also has a small lateral pneumatic foramen situated in the probable contact region of the centrum and the neural arch. Whether the remaining cervicals also bear such a foramen is not known since they all are exposed in dorsal view. Starting with cervical 4 at least, all bear cervical ribs that are articulated at the lateroventral margin of the neural arch, close to the prezygapophysis. Whether the axis and cervical 3 also bear ribs cannot be established in this specimen.

The cervical vertebrae of *Gegepterus changi* are more derived than in any other archaeopteroactyloid. They have postexapophyses, a feature previously regarded as synapomorphic of the Dsungaripteroidea (sensu Kellner, 1996, 2003). Furthermore, at least cervical 4 shows a lateral pneumatic foramen (Fig. 7), a feature common to derived pterosaurs but not reported in any primitive pterodactyloid so far. These features distinguish the cervicals of *Gegepterus* from those of all other members of the Archaeopteroactyloidea.

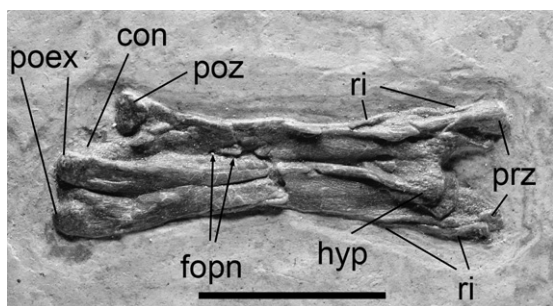


Fig. 7. Cervical vertebra 4 of *Gegepterus changi*, IVPP V 11981, in lateroventral view. Abbreviations: con, condyle; fopn, foramen pneumaticum; hyp, hypapophysis; poex, postexapophysis; poz, postzygapophysis; prz, prezygapophysis; ri, rib. Scale bar represents 10 mm.

Dorsal and sacral vertebrae. Only the remains of the last three dorsal and first sacral vertebrae are preserved. They are articulated, associated with the ilia, and exposed from the dorsal side. Regarding the dorsals, only the centrum is preserved. Apparently they were not fused to the respective neural arches, another feature suggesting that this was a young animal at the time of death. Their interior is hollow, indicating that they were lightly built. The anterior margin, corresponding to the cotyle, is very thick. All dorsals are slightly procoelous and are not fused with the sacral to form a synsacrum. There are two bony fragments on the lateral side of the last dorsal that could be the remains of the transverse processes. If this interpretation is correct, they do not contact the ilia.

Only a fragment of the left side of the first sacral vertebra is preserved. It has a posterolaterally directed sacral transverse process which is apparently fused to the sacral rib, forming a broad sacral process that contacts the ilium.

Ribs. Starting at cervical 4, all cervical vertebrae bear laterally placed ribs, which are better preserved on the left side (Figs. 7, 8). The left rib of cervical 4 is about 5.7 mm long and has a broad articulation with a comparatively thick shaft that thins abruptly in its posterior segment. The left ribs of cervical 5 and 6 extend for about 11.5 mm and differ from others by thinning more uniformly. The remaining cervical ribs are incomplete.

Only one complete dorsal rib was found. It is isolated and double-headed with a length of 20.4 mm. The shaft is almost straight with sub-parallel anterior and posterior margins, and ends in a slightly rounded posterior tip.

The occurrence of cervical ribs in *Gegepterus changi* is an interesting novelty. The absence of cervical ribs was previously considered a synapomorphy of the Pterodactyloidea (Howse, 1986; Kellner, 2003; Unwin, 2003). Its presence in *Gegepterus* shows that this feature is still retained in some primitive pterodactyloids.

Sternum. Only the right lateral part and the posterior edge of the sternum are preserved (Figs. 1, 2; Table 2). It is a broad, thin, dorsoventrally flattened bone that has a slightly convex posterior edge. The portion closer to the midline tends to have a smoother surface compared to the lateral parts. Although the right lateral edge is incomplete, the remains of at least three costal articulations could be identified.

The sternum in most pterosaur taxa is unknown. This element in *Gegepterus changi* has a slightly convex posterior edge, differing from the more rounded distal part present in archaeopteroactyloids such as *Pterodactylus*, *Cynorhamphus* and *Germanodactylus rhamphastinus* (Wellnhofer, 1978).

Gastralia. Several gastralia are preserved. Most are incomplete and associated with the remains of the pelvis. Some drifted away and are clearly displaced from their original anatomical position. The preserved elements are slender and flat, with slightly expanded medial articulations. One incomplete V-shaped medial element was found close to the posterior edge of the sternum.

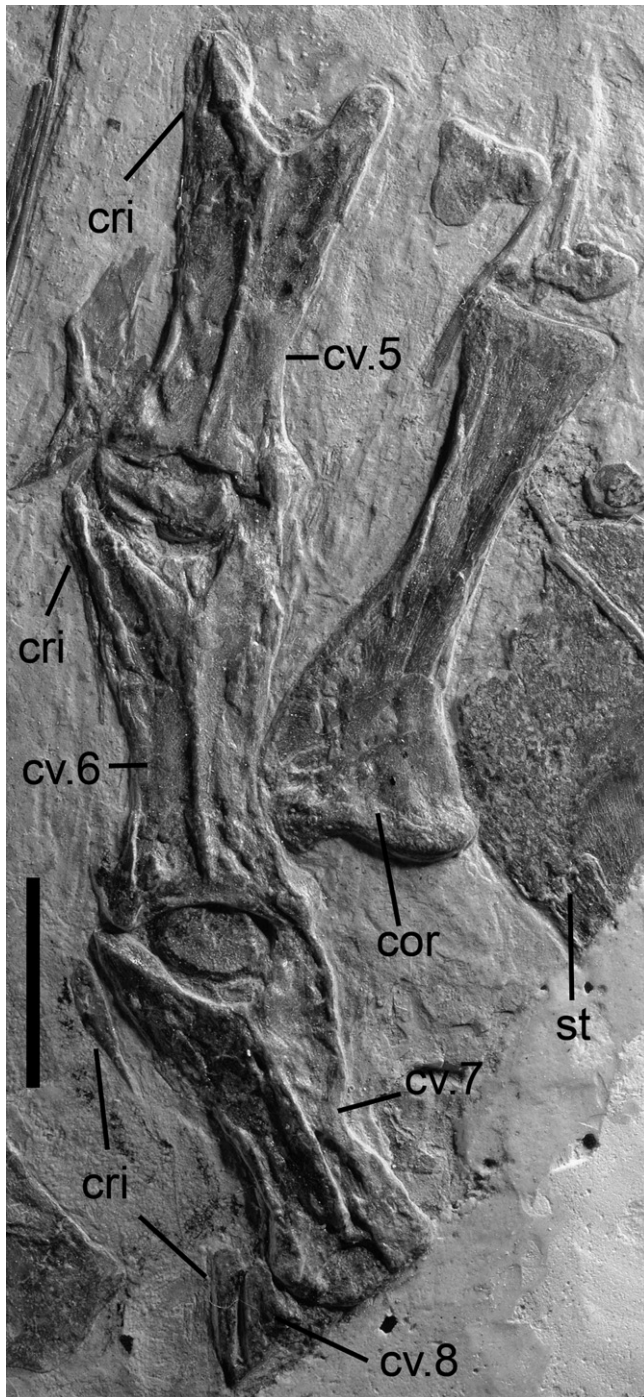


Fig. 8. Cervical vertebrae 5–8 (plus their respective ribs), and coracoid of *Gegepterus changi*, IVPP V 11981. Abbreviations: cor, coracoid; cri, cervical rib; cv, cervical vertebra 5–8, st, sternum. Scale bar represents 10 mm.

Coracoid. The only preserved element from the pectoral girdle is the left coracoid, exposed in anterior view (Fig. 8; Table 2). No sign of the scapula or breakage of the glenoid portion of the coracoid is observed, indicating that these bones were not fused. The coracoid has a constricted shaft and expanded ends. The articulation with the sternum is flattened dorsoventrally and slightly concave. The glenoid part of the coracoid is expanded both anteroposteriorly and dorsoventrally,

and has thickened anterior borders. Ventral to the glenoid surface, the coracoid expands, forming a coracoidal flange. Close to the ventral border of this expansion the bone surface is rugose, possibly for muscle attachments.

Overall, the coracoid of *Gegepterus changi* is similar to that of other archaeopterydactyloids such as *Pterodactylus antiquus* and *Germanodactylus rhamphastinus*. The coracoidal flange is less developed than in *Beipiaopterus* (Lü, 2003), neither the condition in this taxon nor that in *Gegepterus* approaching the expanded, deep condition observed in the more derived pterodactyloid *Quetzalcoatlus* (Kellner and Langston, 1996).

Carpus. At least part of one carpal region is preserved, and is displaced to the ventral margin of the lower jaw. The proximal and distal carpal series is composed of several elements that are unfused and mixed, making it difficult to tell them apart. There are at least five elements of different size and morphology. No pteroid or sesamoids were identified.

Metacarpus. The metacarpal region is incomplete with three elements preserved. Only the most distal part of the right wing metacarpal (mcIV) can be observed, while the proximal end is impressed into the sediment (Figs. 1, 2; Table 2). It is a long bone that has a distinct depression on the surface close to the distal articulation.

Two other thin, elongated bones are interpreted as metacarpals II and III. They are incomplete, but the preserved extension indicates that metacarpal III was articulated with the carpus and this was also likely the case of metacarpal II. In all archaeopterydactyloids, the metacarpals articulate with the carpus (e.g., *Pterodactylus*, *Cynorhamphus*), a primitive condition within Pterosauria (Kellner, 2003).

Wing phalanges. The remains of five wing phalanges are preserved (Figs. 1, 2; Table 2). One long element whose proximal articulation is partially preserved lies underneath the skull. This bone is interpreted as the right first wing phalanx, exposed in ventral view. Partially lying above the skull is the second wing phalanx, closely associated with an incomplete third wing phalanx. Near the pelvic region, overlain by the left femur, is a long, thin, incomplete bone interpreted as the fourth wing phalanx. A proximal part of an indeterminate wing phalanx is also preserved.

Pelvis. The pelvis is represented by incomplete ilia and pubes. The ilia comprise the preacetabular portion, with the left one complete and the right one mostly preserved as an impression in the matrix. It is a thin, dorsoventrally flattened lamina of bone. A marked ridge that extends for a short distance is observed close to the lateral margin of the left ilium.

Both pubes are complete. The right one is exposed laterally while the left one can be observed from the medial side. The pubis is a laterally compressed bone with the main axis orientated dorsoventrally (Fig. 9; Table 2). It forms the anteroventral part of the acetabulum and its lateral surface can be divided into two parts. The dorsoanterior portion is broad, and merges into a dorsoventrally aligned thickened ridge that runs along

the anterior margin of the bone. Posterior to this process the pubis forms a laterally compressed lamina that almost entirely encloses a well-developed obturator foramen. The latter is open towards the contact surface with the ischium (not preserved). The ventral margin of the pubis is sigmoid, with the postero-ventral corner rounded. The contact surface with the ischium is straight. Medially the pubis is flat.

Hindlimb. Only the distal half of the left femur is preserved and the length of this bone cannot be established. It is closely associated with the tibia and fibula. The preserved portion indicates that the femur was bowed. An incomplete bone, positioned close to the first wing phalanx, is here interpreted as the distal portion of the left femur.

Only the proximal parts of the left tibia and fibula are preserved. The tibia is a robust bone whereas the fibula is far thinner and rod-like. Both are unfused.

Soft tissue. Besides the skeletal elements, three areas with soft tissue could be identified: at the posterior part of the skull, around the sclerotic ring inside the orbit and in association with the gastralia (Figs. 10, 11). The soft tissue is preserved as a dark mineralized substance “staining” the matrix. In some areas it forms a thin layer covering the bone. Mostly it is amorphous and does not show any particular structure. On the posterior part of the skull there are a few areas where small, dark, unbranched fibres were found. They are very similar to the hair-like structures reported in other pterosaurs from Liaoning (e.g., Wang et al., 2002).

The soft tissue inside the orbit is surrounded or positioned above the bony plates that form the sclerotic ring. No

particular structure could be identified. Although this soft tissue might be related to the eyeball, the only difference between this and the soft tissue associated with the posterior part of the skull is that, in the orbit, it tends to be more massive, less fibrous and concentrated in places.

3. Comments on *Eosipterus yangi*

The first pterosaur to be described from the Liaoning deposits was *Eosipterus yangi*. The specimen was found in the Shangyuan region, Beipiao, western Liaoning (Ji and Ji, 1997), in the lower part of the Yixian Formation, and consists of a partial skeleton (without skull and lower jaw) now housed in the Geological Museum of China (GMV2117).

To date, three papers have focused on this taxon. Ji and Ji (1997) described the species without assigning it to a particular pterodactyloid clade. Later, Ji et al. (1999) reanalyzed the material and, based on morphometric studies, regarded *Eosipterus* as a member of the Pterodactylidae, a pterodactyloid clade (member of the Archaeopterygoidea) well known from tens of specimens from the Solnhofen limestones (Wellnhofer, 1991). These authors also pointed out that *Eosipterus* might be synonymous with *Pterodactylus*. This assignment was contested by Unwin et al. (2000), who recognized the pterodactyloid nature of the Chinese taxon, but regarded it as more closely related to *Ctenochasma* and *Pterodaustro* than to *Pterodactylus*. The two latter studies are based essentially on bone ratios of different pterosaur taxa and how they might relate to the phylogenetic placement of *Eosipterus*.

Our examination of the type and only known specimen of *Eosipterus yangi* clearly showed that it is still unprepared. Apparently the original specimen was found in several slabs that had been put together by its discoverer. The limits of many elements have been artificially added impeding accurate measurements (e.g., most of the wing elements). This includes the thoracic area: a mishmash of bones present on one slab should be continuous with the other side, but instead just stops at the contact with the next part of the slab. This suggests that the latter does not belong with the adjacent part of the specimen. The pelvic region is severely damaged and the exact length of the femur cannot be established. No caudal vertebrae are preserved. The few prepared bones that were exposed mostly seem to belong to the left side, and not to the right, as had been thought in previous studies (Ji and Ji, 1997; Unwin et al., 2000).

Notwithstanding these observations, some anatomical features of *Eosipterus* are worthy of note. The specimen represents a sub-adult individual since several bones are unfused, including the left proximal tarsals and tibia, and the left extensor tendon process and the first wing phalanx. Both fibulae are preserved (the left one being more complete) as splint-like elements that apparently do not reach the tarsus. The first wing phalanx has a concave anterior margin, a feature reported in *Dsungaripterus* (Young, 1964).

Not previously reported is that the specimen includes well-preserved soft tissue, particularly along the left wing finger and close to the gastralia. The soft tissue associated with the

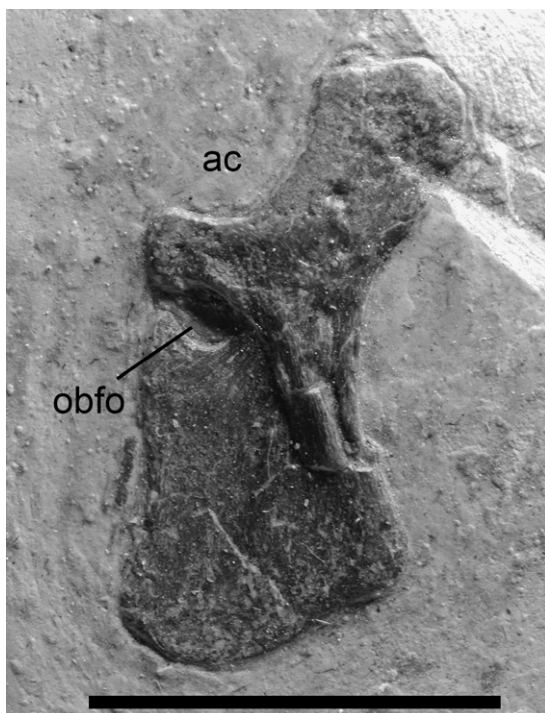


Fig. 9. Right pubis of *Gegepterus changi*, IVPP V 11981. Abbreviations: ac, acetabulum; obfo, obturator foramen. Scale bar represents 10 mm.

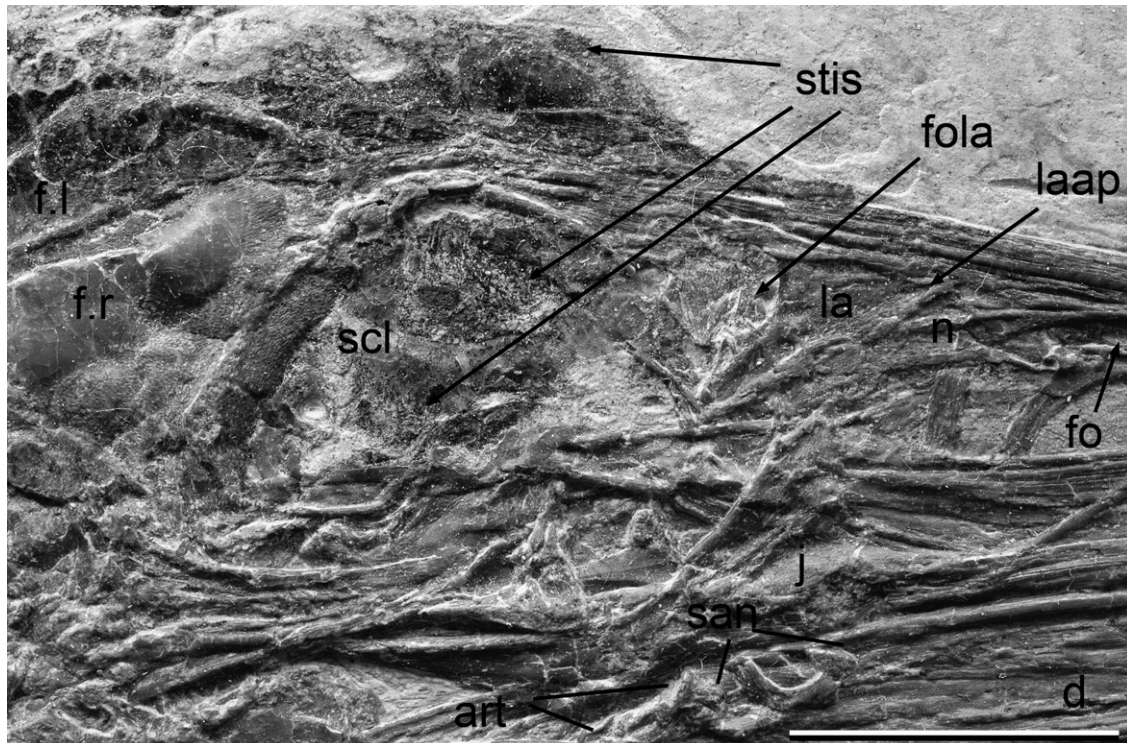


Fig. 10. Orbital region of *Gegepterus changi*, IVPP V 11981, with associated soft tissue. Abbreviations: art, articular; d, dentary; f, frontal; fo, foramen; fola, foramen lacrimale; j, jugal; la, lacrimal; laap, anterior process of lacrimal; n, nasal; san, surangular; scl, sclerotic ring; stis, soft tissue; l, left; r, right. Scale bar represents 10 mm.

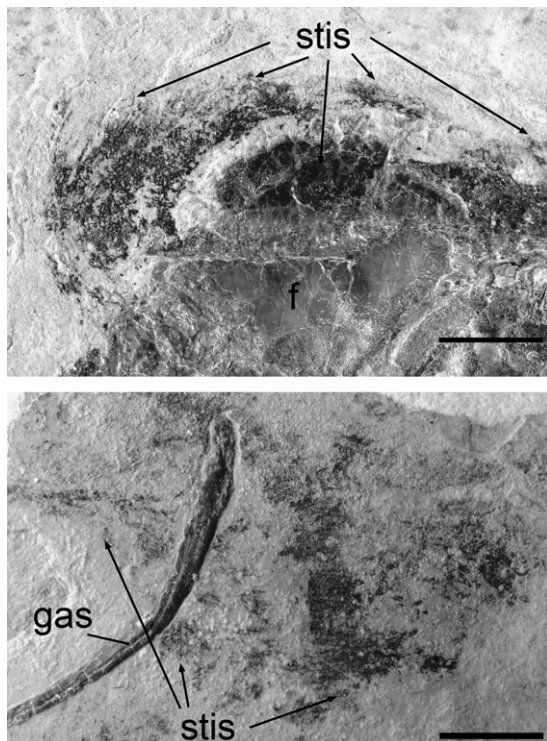


Fig. 11. Mineralized soft tissue of *Gegepterus changi*, IVPP V 11981, near the back of the skull and associated with the gastralium. Note the sculpturing of the frontal. Abbreviations: f, frontal; gas, gastralium; stis, soft tissue. Scale bar represents 5 mm.

wing elements show the typical pattern of parallel to sub-parallel fibres (“actinofibrils”) reported in a variety of specimens (e.g., Padian and Rayner, 1993), some connecting the first and second left wing phalanges. The soft tissue associated with the gastralium lacks this pattern and shows a rugose texture probably representing the abdominal skin of this pterosaur. No stomach contents could be identified.

Another interesting feature that was correctly illustrated in the original description of *Eosipterus* (Ji and Ji, 1997) is the broken right first wing phalanx. Although some artificial material was added to the proximal part, the relationship between the two halves of this bone suggests that it was naturally broken before the carcass became buried. Wellnhofer (1970) described two *Pterodactylus* specimens with broken wing metacarpals and suggested that this might have been the *causa mortis* of these two individuals. This is also a possible scenario for the *Eosipterus yangi* holotype, though involving a different wing element.

Ji and Ji (1997) listed several features as diagnostic for this species, but most are either common to a wide range of pterosaurs (e.g., wing phalanx joints, reduced pedal phalanx V), not preserved (e.g., tail), or cannot be established with certainty (relationship of several wing elements). The main reasons that led Unwin et al. (2000) to consider *Eosipterus* more closely related to *Ctenochasma* and *Pterodaustro* than *Pterodactylus* were the proportions of some bones, whose exact length cannot be determined at present (e.g., ulna, second wing phalanx). Unwin (2003) also listed the relative size of metatarsal III, it being longer than one-third of the length of

the tibia, as diagnostic of the Ctenochasmatidae, but according to the data presented by Unwin et al. (2000) this feature is widespread among non-pterodactyloid pterosaurs (e.g., *Preondactylus*, “*Eudimorphodon*” *rosenfeldi*, *Dorygnathus*) and also present in several species of *Pterodactylus*.

To conclude, *Eosipterus yangi* is indeed a pterodactyloid as originally established by Ji and Ji (1997) based on at least one synapomorphic feature of this group: the reduced fifth digit of the left foot (Kellner, 2003), as correctly pointed out by Unwin et al. (2000). Based on other faunal components of the Yixian deposits, this species is very likely to be a member of the Archaeopterodactyloidea (abundant in this deposit), but its phylogenetic position within that clade has yet to be established.

4. Discussion

In recent years, several pterosaurs from different clades have been unearthed in the deposits that comprise the Yixian and Jiufotang formations (Chang et al., 2003; Kellner, 2004; Wang et al., 2005a). This includes basal non-pterodactyloids (Wang et al., 2002), as well as primitive and derived pterodactyloids (e.g., Lü, 2003; Wang and Lü, 2001; Wang and Zhou, 2003a,b), demonstrating the richness of the pterosaur fauna from these terrestrial Cretaceous Lagerstätten (Kellner, 2006).

The new species described here, *Gegepterus changi*, can be confidently assigned to the Pterodactyloidea based on the confluent naris and antorbital fenestra (Wellnhofer, 1991; Kellner, 2003; Unwin, 2003). It further shows the following features of the Archaeopterodactyloidea (sensu Kellner, 1996, 2003): laterally placed nasal process; posterior region of the skull rounded with the squamosal displaced ventrally; strong inclination of the bones made by the quadrate and jugal relative to the ventral margin of the skull; elongated mid-cervical vertebrae; and neural spines of mid-cervical vertebrae low and blade like. It further shares with the archaeopterodactyloid clades Ctenochasmatidae and Gallodactylidae a skull with a concave dorsal margin (Kellner, 2003). The dentition of the new taxon, composed of numerous long, slender teeth, and the large rostrum, are synapomorphies of the Ctenochasmatidae, indicating that *Gegepterus* is a member of that clade. The fact that it lacks all synapomorphies of the Gallodactylidae, such as a parietal crest, reduced nasal process, and teeth confined to the anterior part of the jaws, also supports this phylogenetic placement.

According to Kellner (2003), two genera are presently classified in the Ctenochasmatidae: *Pterodaustro* and *Ctenochasma*. *Pterodaustro* has a unique dentition in which upper and lower jaw teeth differ markedly. In the upper jaw hundreds of small teeth, each with a thin, conical base and a broad, spatulate crown, are connected with the jaw by soft tissue. The lower dentition consists of hundreds of long, closely spaced teeth set in a longitudinal groove. Except for a few shallow alveoli in the anterior portion of the lower jaw, *Pterodaustro* lacks alveoli. *Ctenochasma* also has hundreds of teeth which, according to the published studies, are all placed in alveoli (e.g., Wellnhofer, 1978; Buissonjé, 1981). In this respect, the dentition of *Gegepterus* is more similar to that of *Ctenochasma*

and it is here regarded to be most closely related to this taxon among archaeopterodactyloids (including *Pterodaustro*). The main dental differences between *Gegepterus* and *Ctenochasma* are the marked longitudinal groove where the alveoli are set and the overall smaller teeth observed in the Chinese species.

Within *Ctenochasma* three species were recognized: *Ctenochasma roemeri* Meyer, 1852, *Ctenochasma gracile* Oppel, 1862 and “*Ctenochasma*” *porocristata* Buissonjé, 1981. More recently Jouve (2004) has reviewed the taxonomic validity of some European ctenochasmatids and regarded *Ctenochasma gracile* and “*Ctenochasma*” *porocristata* as senior synonyms of *Pterodactylus elegans*. This implies that the number of teeth grew significantly during ontogeny in these pterosaurs. Since we agree with Jouve (2004) that, if correct, this phenomenon is a considerable biological anomaly, we prefer to consider the original interpretations of the taxa as separate species pending a thorough restudy of the available material.

Ctenochasma roemeri is known from a lower jaw that is apparently lost (Wellnhofer, 1978). *Ctenochasma gracile* is known from five specimens: three skulls and two almost complete skeletons (Wellnhofer, 1970; Buissonjé, 1981). The third species, “*Ctenochasma*” *porocristata*, is known from a partial skull, lacking the braincase (Buissonjé, 1981). The dentition of all three species is very similar. In *Ctenochasma gracile* and “*Ctenochasma*” *porocristata* (the condition in *Ctenochasma roemeri* is not known), the toothed part of the upper jaw extends posteriorly to the ventral margin of the skull under the beginning of the nasoantorbital fenestra (Wellnhofer, 1978). In *Gegepterus changi*, the dentition does not extend as far to the posterior; it also has a lower tooth density. These are the reasons why the number of teeth in *Gegepterus changi* is estimated to be fewer than in *Ctenochasma*.

“*Ctenochasma*” *porocristata* shows a well-developed premaxillary crest, starting between the tip of the premaxillae and the anterior margin of the nasoantorbital fenestra, which is not present in *Ctenochasma gracile* (the condition of *Ctenochasma roemeri* is unknown). Overall the skull of “*Ctenochasma*” *porocristata* is more strongly built, wider, and probably pertains to a genus different from, but closely related to, *Ctenochasma*. In any case, the premaxillary crest of “*Ctenochasma*” *porocristata* is reported to have a comparatively thick base (Buissonjé, 1981) and differs in both position and thickness from the premaxillary crest of *Gegepterus changi*. The number of teeth and their density in the Chinese form is also less than that of “*Ctenochasma*” *porocristata*.

Compared to other pterosaurs from the Jehol Biota, *Gegepterus* can easily be separated from the more primitive Anurognathidae (Ji and Ji, 1998; Wang et al., 2002), supposed rhamphorhynchids (Czerkas and Ji, 2002), *Feilongus youngi*, which is closely related to the Gallodactylidae (Wang et al., 2005a), and the more derived pterodactyloids represented by several distinct clades of the Dsungaripteroidea (sensu Kellner, 1996, 2003), such as tapejarids (Wang and Zhou, 2003a; Li et al., 2003), anhanguerids (Wang and Zhou, 2003b; Lü and Ji, 2005a), possible pteranodontids (Dong et al., 2003; Wang and Zhou, 2003b; Wang et al., 2005a), azhdarchids (Lü and Ji, 2005b), and istiodactylids (Wang et al., 2005a). Lü and

Zhang (2005) also described *Eopteranodon*, supposedly closely related to *Pteranodon*, from the Niobrara Formation (Santonian, North America). Despite possibly being a dsungaripteroid pterodactyloid, this species lacks a warped deltopectoral crest and is unlikely to be related to *Pteranodon* or *Pteranodontoidea* sensu Kellner (1996, 2003). As pointed out above, comparisons with *Eosipterus yangi* cannot be made at the moment owing to lack of preparation. The skull and dentition of *Haopterus gracilis* is distinct from the ctenochasmatid condition and, although its phylogenetic position has yet to be established among the Pterodactyloidea (Wang et al., 2005a), it clearly differs from *Gegepterus changi*.

Two other taxa need to be compared with *Gegepterus changi* because they were also classified in the Ctenochasmatidae. The first is *Beipiaopterus chenianus* Lü, 2003, recovered from the same locality as *Gegepterus*. The holotype consists of a partial skeleton with soft tissue, lacking the skull, housed at the Beipiao Paleontological Museum of Liaoning (BPM 0002; SMU 75565) (Lü, 2002, 2003). The available illustrations of *Beipiaopterus chenianus* show that the material was also found broken into several pieces and that the specimen has undergone some reconstruction, particularly at the middle part of the first wing phalanx. In addition, the contacts between some bones are not clear, particularly between the first, second and third wing phalanges (some clearly incomplete), which could reflect on the diagnosis of this taxon. We agree that *Beipiaopterus* is a member of the Pterodactyloidea since it possesses, for example, a reduced pedal digit V. Based on the elongated mid-cervical vertebrae it is probably an archaeopterodactyloid, but its phylogenetic position still needs to be clarified. The main problem is the lack of a skull, since the synapomorphies of most archaeopterodactyloid clades are found in the skull and dentition (e.g., Ctenochasmatidae, Galodactylidae; see Kellner, 2003).

In any case, based on the published information, *Gegepterus* is about one-third smaller than *Beipiaopterus* and differs from it in a number of features. The most striking of these is the relationships of the wing phalanges, with *Beipiaopterus* having a comparatively large first wing phalanx. Other differences can be seen in the cervical vertebrae, e.g., *Beipiaopterus* lacks cervical ribs and postexpophyses. Furthermore, the coracoid of *Beipiaopterus* has a deep ventral extension (a potential autapomorphy), in contrast to the more reduced condition in *Gegepterus*.

The last putative member of the Ctenochasmatidae from the Jehol Biota is *Liaoxipterus brachyognathus*, described by Dong and Lü (2005). The holotype is a lower jaw found in the Jiufotang Formation near Chaoyang. Based on the published illustrations, it is quite clear that *Liaoxipterus brachyognathus* has a small mandibular symphysis and closely spaced, short teeth with a triangular crown, quite distinct from the condition reported in all ctenochasmatids known to date. It is, therefore, unlikely to be a member of that group of pterosaurs. Although the phylogenetic position of *Liaoxipterus* is beyond the scope of this paper, it is possibly a member of the Istiodactylidae, perhaps closely related to *Nurhachius*, differing only in the degree of lateral expansion and number of teeth.

It is interesting to note that the neck of *Gegepterus changi* shows a remarkable combination of derived and primitive features. It shows well-developed postexpophyses, a feature previously regarded as a synapomorphy of derived pterodactyloids (Dsungaripteroidea). At least one cervical shows a pneumatic foramen on the lateral surface, a feature previously regarded as restricted to more derived pterodactyloids (Kellner, 2003). At the same time, *Gegepterus changi* shows well-developed ribs on the mid-cervical vertebrae, a feature unknown in any other pterodactyloid but common in more basal pterosaurs.

5. Conclusions

Although pterosaurs from Liaoning and similar deposits in China have been reported for less than a decade, their diversity in both the Yixian and Jiufotang formations is clearly indicated. *Gegepterus changi* is a new taxon and the first Liaoning pterosaur unequivocally attributed to the Ctenochasmatidae (sensu Kellner, 1996, 2003), previously recorded in Europe (*Ctenochasma*) and South America (*Pterodaustro*). This indicates a greater diversity in the Jehol pterosaur fauna. The Chinese deposits contain the best preserved record of pterosaurs from deep inside the Asian continent; this is significant because the pterosaur fossil record tends to be biased towards coastal deposits (Kellner, 1994, 2006). The new discovery provides further evidence of the presence of cosmopolitan groups in the Jehol Biota, a fact that might have resulted from the disappearance of biogeographic barriers between East Asia and Europe by the Early Cretaceous (Zhou et al., 2003).

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