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LETTERS

Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China

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New specimens and an analysis of the Jehol pterosaur faunae of northeastern China show an unexpected diversity of flying reptile groups in terrestrial Cretaceous ecosystems[1–4]. Here we report two new pterosaurs that are referred to European groups previously unknown in deposits of northeastern China. *Feilongus youngi*, from the Yixian Formation[1,3], is closely related to the Gallodactylidae[5–6] and is distinguished by the presence of two independent sagittal crests and a protruding upper jaw. *Nurhachius ignaciobritoi*, from the Jiufotang Formation[2,3], has teeth formed by labiolingually compressed triangular crowns, only previously reported in *Istiodactylus latidens*[7] from England. With these new discoveries, the Jehol pterosaurs show a wide range of groups including both primitive and derived forms that are not matched by any other deposit in the world. The discoveries also document the turnover of pterosaur faunae, with the primitive Anurognathidae and early archaeopterodactyloids being replaced by derived pterodactyloids. Furthermore, these deposits offer an opportunity to examine the interaction and competition between birds and pterosaurs—it indicates that the avian fauna during the Lower Cretaceous (and possibly most of the Mesozoic) dominated terrestrial, inland regions, whereas pterosaurs were more abundant in coastal areas.

The record of pterosaurs is strongly biased towards ancient coastal environments[5,8], and species from terrestrial deposits are rare, showing little diversity[9]. The Jehol Group, comprising the Yixian and Jiufotang formations, is an exception. The myriad of well-preserved fossils from these deposits is known as the Jehol biota, with some taxa—such as fishes (*Peipiaosteus*, *Sinamia*, *Protopsephurus* and *Yanosteus*), the dinosaur *Psittacosaurus* and the birds *Confuciusornis*[3,4] and *Jeholornis* (undescribed species)—found (at a generic level) in both formations. Recent dating indicates that the main portion of these terrestrial ecosystems existed 125–120 million years ago[2].

Although pterosaurs have only been reported in the past decade[10–13], extensive collecting in the deposits of northeastern China shows that their diversity rivals that of other important lagerstätten, such as the Upper Jurassic Solnhofen limestones[5] and the Lower Cretaceous Santana Formation[14], providing a unique insight into the pterosaur fauna that lived far within the interior of the continent, away from the ancient coastlines.

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Archaeopterodactyloidea Kellner, 1996
Feilongus youngi gen. et sp. nov.

Etymology. *Feilongus* from the Chinese spelling feilong, meaning flying dragon; *youngi*, in honour of the late Chinese palaeontologist C. C. Young, who described the first pterosaur from China.

Holotype. Skull and mandible deposited at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China (IVPP V-12539; Fig. 1).

Locality and horizon. Jianshangou Bed, lower Yixian Formation at Heitizigou in Beipiao, Liaoning Province, China.

Diagnosis. Large archaeopterodactyloid pterosaur (wing span $\sim$2.4 m) that can be differentiated from all other members of the Archaeopterodactyloidea by the following unique features: combination of two sagittal cranial crests (a low premaxillary crest positioned in the middle segment of the rostrum, ending well before the anterior margin of the nasoantorbital fenestra, and a short, bony parietal crest); parietal crest with a rounded posterior margin; protruding upper jaw that is about 10% longer than the lower jaw.

The specimen consists of an almost complete skull and mandible that is lying on its right side (Fig. 1a, b). Several cranial elements are unfused, indicating that this specimen probably represents a subadult individual at time of death[14,15]. The length of the skull is between 390–400 mm (tip of premaxilla to squamosal is 390 mm).

The presence of a confluent naris and antorbital fenestra allows the classification of *Feilongus youngi* within the Pterodactyloidea[5,6,16]. This new species also shows a laterally placed nasal process and a strongly inclined quadrate relative to the ventral margin of the skull, indicating that it is a member of the Archaeopterodactyloidea (*sensu* Kellner[6]), and is therefore compared with other members of this clade. The nasoantorbital fenestra of *Feilongus youngi* occupies 28.7% of the cranial length between the squamosal and the premaxilla, which is larger than in the Ctenochasmatidae (*Pterodaustro* and *Ctenochasma*[6]) and *Gnathosaurus* but smaller than in all other archaeopterodactyloids (for example, *Pterodactylus* and *Germanodactylus*). The rostrum (that is, the cranial part anterior to the nasoantorbital fenestra) is more elongated than in other pterosaurs with the exception of the Ctenochasmatidae. *Feilongus youngi* has a concave dorsal margin of the skull, a feature that it shares with *Ctenochasma*, *Pterodaustro*, *Gallodactylus* and *Cycnorhamphus* (Fig. 1c).

A low sagittal crest formed by the premaxillae starts at the region corresponding to the ninth tooth and extends posteriorly, finishing well before the anterior margin of the nasoantorbital fenestra (Fig. 1). A distinct rugose area is present on most of the sagittal crest, indicating that it was covered by a soft extension, as has been reported in some other pterosaurs[14,17,18]. The premaxillary crest in *Feilongus youngi* differs by being positioned in the middle portion of the rostrum, not extending above the nasoantorbital fenestra and by having a very low bony part. A second sagittal crest is observed on the posterior part of the skull, formed mainly by the parietals (Fig. 1c). This structure is thin and shows a rugose surface, indicating that it probably also bore a soft extension. A parietal crest is also observed in *Gallodactylus* and *Cycnorhamphus*, suggesting that they are closely

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related to *Feilongus*. In *Feilongus*, however, the bony part of the crest is much shorter and has a distinctive rounded posterior end.

The lower jaw is complete, with a total length of 334 mm (tip to craniomandibular articulation is 321 mm). The anterior end is slightly turned upward. Compared to the upper jaw, the lower jaw is about 27 mm shorter, a unique feature among toothed pterosaurs (Fig. 1c). Only the toothless and more derived pterodactyloid *Pteranodon*[15] has the upper jaw longer than the lower jaw, which was achieved independently in both taxa.

The dentition of *Feilongus youngi* consists of elongated, strongly curved needle-shaped teeth that are confined to the anterior third of the skull and mandible (Fig. 1). On the left side, the upper and lower jaws have 18 and 20 alveoli, respectively, indicating that the total number of teeth is 76, less than in *Gnathosaurus* and the Ctenochasmatidae but more than in *Germanodactylus* and *Cycnorhamphus* (and probably also *Gallodactylus*). In comparison with other archaeopterodactyloids, *Feilongus youngi* had an estimated wing span of around 2.4 m, making it the largest member of this group known so far.

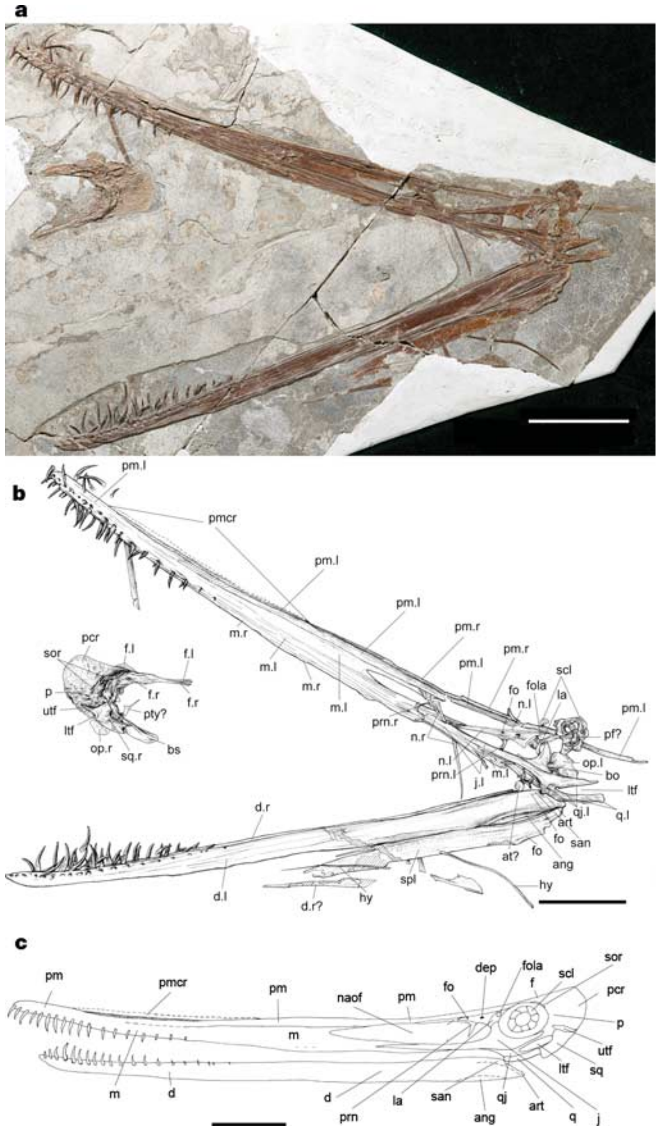

Figure 1 | ***Feilongus youngi*** **gen. et sp. nov., a new archaeopterodactyloid from the Yixian Formation.** **a**, Skull. **b**, Drawing showing the contact of cranial bones (the posterior part of the skull is rotated for clarity). **c**, Reconstruction. Scale bars, 50 mm. ang, angular; art, articular; at, atlas; bo, basioccipital; bs, basisphenoid; d, dentary; dep, depression; f, frontal; fo, foramen; fola, foramen lacrimale; hy, hyoid bone; j, jugal; la, lacrimal; ltf, lower temporal fenestra; m, maxilla; n, nasal; naof, nasoantorbital fenestra; op, opisthotic; or, orbit; p, parietal; pcr, parietal crest; pf, prefrontal; pl, palatine; pm, premaxilla; pmcr, premaxillary crest; prn, processus nasalis; pty, pterygoid; q, quadrate; qj, quadratojugal; san, surangular; scl, slerotic ring; sor, supraorbital; spl, splenial; sq, squamosal; utf, upper temporal fenestra. l indicates left and r indicates right.

Dsungaripteroidea Young, 1964
Istiodactylidae Howse, Milner & Martill, 2001
Nurhachius ignaciobritoi gen. et sp. nov.

Etymology. *Nurhachius* from Nurhachi, the name of the founder of the Ch'ing Dynasty in China; *ignaciobritoi*, in honour of the late Brazilian palaeontologist Ignacio M. Brito, who has fostered palaeontological studies in Brazil.

Holotype. A partial skeleton deposited at the IVPP (IVPP V-13288; Fig. 2).

Locality and horizon. Jiufotang Formation (Aptian) at Gonggao, Chaoyang, western Liaoning, China.

Diagnosis. An istiodactylid pterodactyloid that can be differentiated from *Istiodactylus latidens* (the only other member of this clade) by the following unique characters: low skull; absence of a suborbital vacuity; jugal with short lacrimal process; teeth labiolingually compressed with triangular roots subequal to or larger than crowns; alveolar margin of the lower jaw slightly bent upward.

This specimen (Fig. 2a) shows a tightly connected scapula–coracoid and an open suture between the extensor tendon process and the first phalanx, representing a subadult individual[14,15]. The confluent nasoantorbital fenestra and the proportions of several postcranial elements (for example, humerus, metacarpal IV) indicates that *Nurhachius ignaciobritoi* is a member of the Pterodactyloidea[6,16]. Other features, such as the presence of a notarium (formed by six fused dorsal vertebrae), allow its classification in the Dsungaripteroidea[6] (Fig. 2a).

The skull of *Nurhachius ignaciobritoi* is visible from the left side and lacks the posterior end, including the braincase (Figs 2a and 3). The preserved part is 315 mm long, with an estimated total length of 330 mm (premaxilla to squamosal is ~320 mm). The most outstanding cranial feature is the nasoantorbital fenestra, which is very long, occupying approximately 58% of the skull length (premaxilla to squamosal). The lacrimal process of the jugal is thin, similar to the members of the Tapejaridae, but is more inclined posteriorly. According to the cranial reconstructions of *Istiodactylus latidens*[5,7], this taxon also shows a jugal with a thin and strongly posteriorly inclined lacrimal process, but in *Nurhachius ignaciobritoi* this process is shorter.

The lower jaw of *Nurhachius ignaciobritoi* is observed from the right side (Fig. 2a). It is long (291 mm) and thin, slightly deeper at the posterior region. The dentition comprises 14 teeth on each side of the upper jaw and 13 on the lower jaw, totalling 54 teeth. Except for two tiny anteriorly projected teeth on the tip of the lower jaw, all teeth are labiolingually compressed, with pointed triangular crowns (Fig. 2b). A marked constriction is present at the limit between root and crown. Better preserved ones show sharp anterior and posterior carinae and lack any ridges. This kind of dentition is only observed in *Istiodactylus latidens*[5,7], albeit fewer in number (49).

The postcranial skeleton of *Nurhachius ignaciobritoi* shows almost all parts except for some cervical vertebrae, ribs, the tail and the third and fourth wing phalanges. It presents several postcranial features unique to the Pteranodontoidea (*Pteranodon* plus *Istiodactylus* plus Anhangueridae[6]) such as: tall and spike-like neural spines of the mid-cervical vertebrae, scapula shorter than coracoid, and warped deltopectoral crest of the humerus (Fig. 2a). *Nurhachius ignaciobritoi* also shares with *Istiodactylus* and the Anhangueridae a stout scapula with a marked constricted shaft. As in *Anhanguera*[14], metacarpal III of *Nurhachius* articulates with the carpal region whereas metacarpals I–II are reduced, another feature separating istiodactylids and anhanguerids from *Pteranodon*. The phylogenetic analysis presented here shows that *Nurhachius ignaciobritoi* is closely related to *Istiodactylus*, both

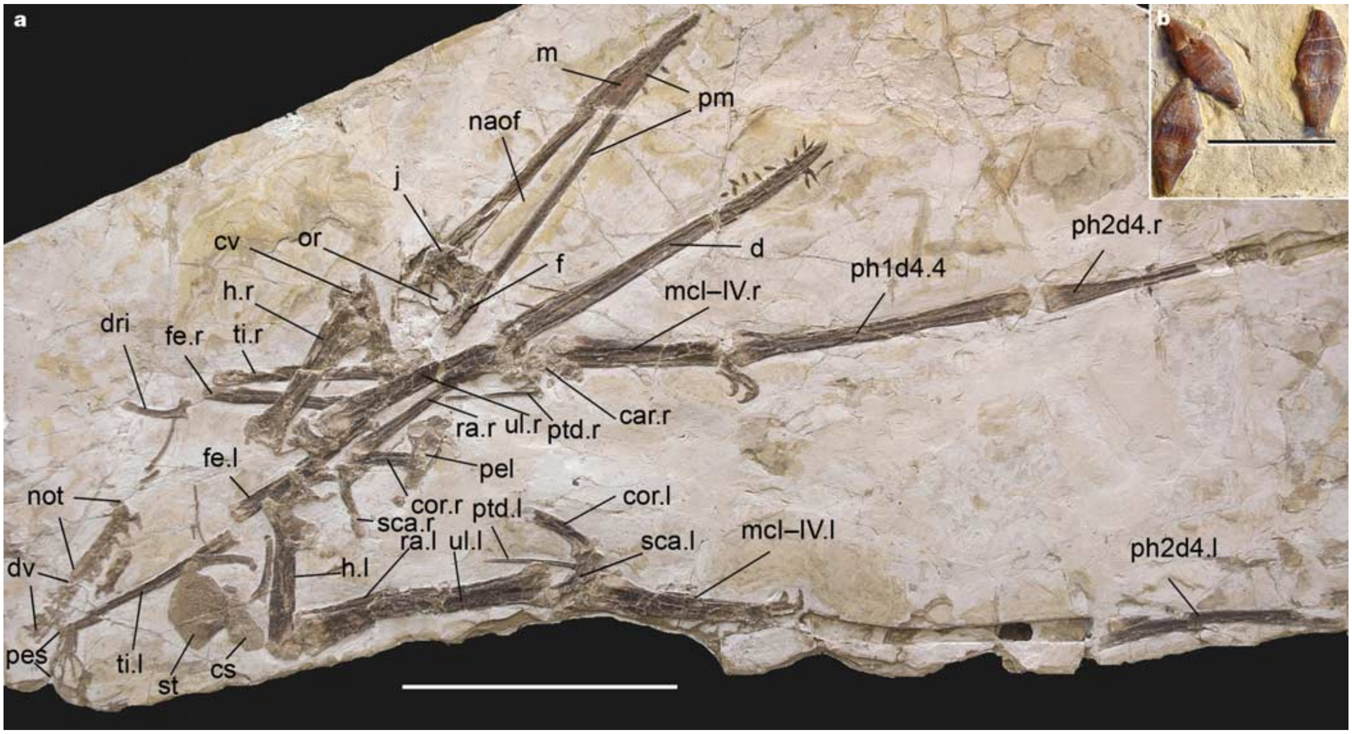

Figure 2 | ***Nurhachius ignaciobritoi* gen. et sp. nov., a new istiodactylid from the Jiufotang Formation.** **a**, Complete skeleton. Scale bar, 200 mm. **b**, Detail showing isolated teeth (crown and root). Scale bar, 10 mm. Abbreviations are the same as for Fig. 1 and also include: car, carpus; cor, coracoid; cs, cristospine; cv, cervical vertebra; dri, dorsal rib; dv, free dorsal vertebrae; fe, femur; hu, humerus; mcI–IV, metacarpal 1–4; not, notarium (fused dorsal vertebrae); pel, pelvis; pes, foot; ph1d4, first phalanx of manual digit IV; ph2d4, second phalanx of manual digit IV; ptd, pteroid; ra, radius; sca, scapula; st, sternum; ti, tibia; ul, ulna.

sharing at least two unique derived features: the particular dentition and the strongly posteriorly oriented lacrimal process of the jugal (see Supplementary Information).

The postcranial elements of *Nurhachius ignaciobritoi* indicate a wing span between 2.4 and 2.5 m. Direct comparisons with the European *Istiodactylus latidens* indicate a wing span of 4.2 m for the latter, about 20% less than previously thought[7].

Including the new taxa, 13 species have been reported from the Jehol Group. The basal Yixian Formation has yielded seven species, including the anurognathids *Dendrorhynchoides curvidentatus*[10,19] and *Jeholopterus ningchengensis*[11], which we show to be more closely related to *Batrachognathus* (from Kazakhstan) than to *Anurognathus* (from Solnhofen limestones; Fig. 4a). *Pterorhynchus* is referred to the Rhamphorhynchidae[20] and represents the sole long-tailed pterosaur from the Jehol fauna. The remaining species were referred to the archaeopterodactyloid clades Ctenochasmatidae and Pterodactylidae (*Eosipterus yangi*, *Haopterus gracilis* and *Beipiaopterus chenianus*[10,21,22]) but their exact phylogenetic position has yet to be determined. The case of *Eosipterus*, the first described pterosaur from the Jehol Group, is particularly problematical, because it is still unprepared and several parts were artificially reconstructed (for example, wing elements), casting doubt upon published morphometric studies[11,19]. Recently, the tapejarid *Sinopterus* was also recorded (specimen IVPP V-14191; X.W., A.W.A.K., Z.Z. & D.dA.C., unpublished material). *Feilongus youngi* is the first archaeopterodactyloid from this deposit to show a close relationship with the Gallodactylidae (*Gallodactylus* plus *Cycnorhamphus*; Fig. 4a).

The overlying Jiufotang Formation has furnished six derived pterodactyloids. Two species (*Sinopterus dongi* and *Sinopterus gui*) are referred to the Tapejaridae[13,23], a clade previously known only from the Santana Formation (Brazil[24]) and Cretaceous deposits of Morocco[25]. *Liaoningopterus gui* is an anhanguerid[12] and *Chaoyangopterus zhangi* was referred to the Nyctosauridae[12], but is more closely related to *Pteranodon* from the Santonian Niobrara Chalk of North America. The same is apparently the case for '*Jidapterus edentus*'[26], which might be congeneric (or even conspecific) with *Chaoyangopterus*. *Nurhachius ignaciobritoi*, described here, is the first istiodactylid from this deposit (Fig. 4).

Despite the recognized difficulties in using pterosaurs in palaeobiogeographic studies, it is interesting to note that the two new taxa—*Feilongus* and *Nurhachius*—have their closest relatives in Europe (Fig. 4). Evidence for broad faunal exchanges between Europe and Siberia/East Asia at this time also comes from other groups, such as iguanodontian ornithopods, dromaeosaurid theropods, enantiornithine birds, discoglossid frogs, paramacellodid lizards, crocodyliforms and gobiconodontid mammals[3,4,27,28]. Other taxa, such as *Sinopterus* and *Liaoningopterus*, however, have their closest relatives in the Early Cretaceous deposits of Brazil[12,13,23], demonstrating that the palaeobiogeographic history of the Jehol biota is very complex[4].

Despite being two strongly connected deposits (for example, geographical location, age, lithology and depositional environment), the Jehol Group comprises two distinct pterosaur faunae. The Yixian Formation contains the primitive Anurognathidae and

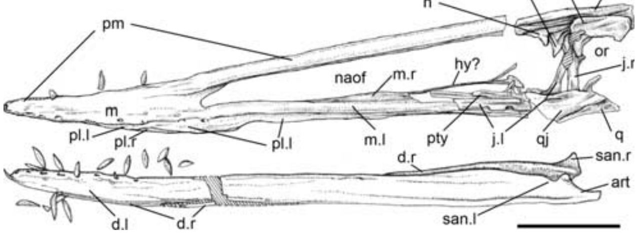

Figure 3 | **Drawing of the skull and lower jaw of *Nurhachius ignaciobritoi* gen. et sp. nov.** Scale bar, 50 mm. Abbreviations are the same as for Fig. 1.

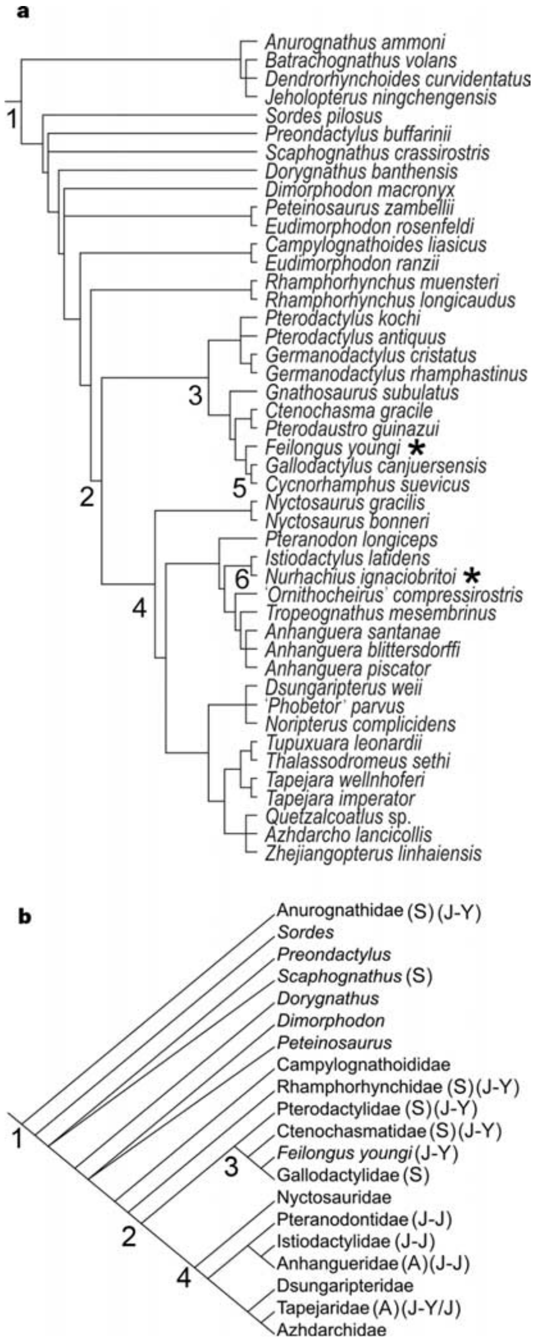

Figure 4 | Cladistic analyses of the new pterosaur species and others from the Jehol Biota. a, Cladogram showing the phylogenetic position of *Feilongus youngi* gen. et sp. nov. and *Nurhachius ignaciobritoi* gen. et sp. nov. (see Supplementary Information). **b**, Simplified cladogram showing the relationships of the most important pterosaur groups, including several taxa reported from the Jehol Group (based on this study and information from the literature). A, Araripe Basin (Santana Formation, Aptian–Albian); J-J, Jiufotang Formation of the Jehol Group (Barremian–Early Aptian); J-Y, Yixian Formation of the Jehol Group (Barremian–Early Aptian); S, Solnhofen limestones (Early Tithonian); 1, Pterosauria; 2, Pterodactyloidea; 3, Archaeopterodactyloidea; 4, Dsungaripteroidea; 5, Gallodactylidae; 6, Istiodactylidae.

Rhamphorhynchidae, several archaeopterodactyloids and one derived pterodactyloid (the tapejarid *Sinopterus*), which is a very unusual mixture of faunal elements. The Jiufotang Formation comprises derived pterodactyloids such as Istiodactylidae, Tapejaridae, Anhangueridae and possible pteranodontids (*Chaoyangopterus* and '*Jidapterus*'). Combined, the Jehol Group shows a wide range of pterosaur groups (Fig. 4b), a diversity not matched by any other region. The Solnhofen limestones, where fossils have been collected for over two centuries, has yielded primitive forms (Anurognathidae and Rhamphorhynchidae) and members of the Archaeopterodactyloidea, but lacks more derived species[5]. The Santana Formation, where pterosaurs are also found in large numbers, only contains members of the derived Tapejaridae and Anhangueridae (or closely related species[14,17]). Perhaps the time span encompassing the existence of the Jehol biota—around 5 million years[1,2]—might explain this diversity, showing a succession from a more archaic pterosaur fauna of the Yixian Formation (with the appearance of some derived forms such as the Tapejaridae) to a more advanced assemblage of the Jiufotang deposits. This time span is greater than the range of the Solnhofen limestones (0.5 million years[29]) but less than the estimates for the total time of deposition of the Santana Formation (around 8 million years[30]). It is possible that the Jehol biota documents a worldwide trend in changes of pterosaur faunae, with more primitive forms such as Anurognathidae, Rhamphorhynchidae and early archaeopterodactyloids being replaced by more derived pterodactyloids such as Anhangueridae and probably Pteranodontidae. This unexpected mixture of different pterosaur groups in these Chinese deposits indicates a very complex evolutionary history of pterosaurs in general, which is just beginning to be deciphered.

The Jehol deposits constitute an opportunity to examine the question related to the interaction (and competition) between pterosaurs and birds. The Yixian Formation has furnished an estimated 40 pterosaur remains and more than 1,000 birds. The Jiufotang Formation recorded about 100 pterosaur remains compared with the remains of more than 1,000 birds. Overall, there are 21 avian species described and we know of at least five more. Including the two new pterosaurs described here, there are 13 described and 3 undescribed species. This preliminary analysis clearly shows that birds are more diverse and outnumber pterosaurs (in both the Yixian and Jiufotang formations[3,4]). This information and comparisons with other deposits[5,8] leads to the hypothesis that the avian fauna of the Lower Cretaceous—and perhaps most of the Mesozoic era—was more confined to terrestrial, inland regions, whereas pterosaurs dominated the coastal areas. The Jehol deposits are unique Cretaceous terrestrial ecosystems where this question can be refined in the future with more precise stratigraphic information regarding the co-occurrence of these volant creatures.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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