

and the Darwin rise are the sites of most Pacific hotspots over the past 120 Myr (ref. 14) and correspond to a prominent, long-wavelength geoid high¹⁸ and to a zone of low seismic velocities extending to the lower mantle¹⁹. The Superswell may thus be located over a stable, persisting zone of upwelling from the lower mantle^{7,20} which may have been acting as a barrier since at least Cretaceous times, separating two large mantle domains with different convecting histories.

We discuss two interpretations of the above three observations. (1) The pollution hypothesis: the data can be interpreted in terms of the southern N-MORB being polluted by sources having a HIMU (that is, 'high μ ', where $\mu = {}^{238}\text{U}/{}^{204}\text{Pb}$) end component affinity (high ${}^{206}\text{Pb}/{}^{204}\text{Pb}$, low ${}^{87}\text{Sr}/{}^{86}\text{Sr}$), where the northern N-MORB would be polluted by sources having an EM (enriched mantle) end component affinity (high ${}^{87}\text{Sr}/{}^{86}\text{Sr}$). This view is supported by the observation that the 25° S boundary coincides with the SOPITA (Fig. 1), which has its northern part dominated by EM (Samoa, Societies and Marquesas) whereas its southern part is dominated by HIMU (Cook-Austral and Foundation chains)^{14,21,22}. An alternative view, based on the observation that the relative slopes are indistinguishable in Pb–Pb plots²³, would be that the northern province has experienced more pollution by EM sources on a time-integrated basis than the southern province. (2) Melting hypothesis: according to the "plum-pudding" model²⁴, the MORB mantle source is composed of small-scale, uniformly distributed mantle heterogeneities which are expected to have high ${}^{87}\text{Sr}/{}^{86}\text{Sr}$ (relative to ${}^{143}\text{Nd}/{}^{144}\text{Nd}$ or ${}^{206}\text{Pb}/{}^{204}\text{Pb}$). These heterogeneities would be preferentially sampled^{25,26} by the low extents of melting which may prevail beneath the axis of the deeper, northern province. The higher extents of melting expected in the shallower, southern province would average the properties of mantle components, resulting in lower (${}^{87}\text{Sr}/{}^{86}\text{Sr}$)/(${}^{143}\text{Nd}/{}^{144}\text{Nd}$) and (${}^{87}\text{Sr}/{}^{86}\text{Sr}$)/(${}^{206}\text{Pb}/{}^{204}\text{Pb}$). However, the differences of mantle temperatures and melt parameters between the two provinces are not resolved by a petrological model²⁷ based on Na₈ data (Na normalized to 8% MgO).

These two hypotheses may be reconciled by considering the link between the chemical characteristics of the mantle and its physical properties (thermal state) as expressed at the surface by the bathymetry of the ridge. To summarize, the Pacific mantle displays at the same time large-scale variation of composition and temperature.

The rather sharp bathymetric²⁸ and geochemical²⁹ transition at 25° S indicates a superficial origin, whereas the cluster of hotspots constituting the Pacific Superswell suggests the existence of a deep-mantle process. This apparent paradox requires some interactions between the deeper and the shallower layers of the mantle. We propose that the lower-mantle upwelling suspected to be present near 25° S could have contributed to the isolation of two large-scale, deep-mantle domains with their own convective histories, producing slight differences in their chemical properties, thus influencing differently the thermal structure of the overlying MORB mantle source layer. □

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A therizinosauroid dinosaur with integumentary structures from China

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Therizinosauroida ('segnosaurs') are little-known group of Asian dinosaurs with an unusual combination of features that, until recently, obscured their evolutionary relationships. Suggested affinities include Ornithischia¹, Sauropodomorpha^{2,3}, Theropoda^{4–11} and Saurischia *sedis mutabilis*¹². Here we describe a new therizinosauroid from the Yixian Formation (Early Cretaceous, Liaoning, China)¹³. This new taxon provides fresh evidence that therizinosauroids are nested within the coelurosaurian theropods^{8–11}. Our analysis suggests that several specialized therizinosauroid characters, such as the Sauropodomorpha-like tetradactyl pes^{1,2}, evolved independently within this group. Most interestingly, this new dinosaur has integumentary filaments as in

Sinosauropteryx^{14,15}. This indicates that such feather-like structures may have a broad distribution among non-avian theropods, and supports the hypothesis that the filamentous integumentary structures may be homologous to the feathers of birds^{14,15}.

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria *sensu* Gauthier 1986

Therizinosauroida Russell and Dong 1993

Beipiaosaurus inexpectus gen. et sp. nov.

Etymology. Beipiao: the city near the locality where the specimen was found; saurus: lizard; inexpectus: referring to the surprising features in this animal.

Holotype. IVPP V11559 (Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China; see Fig. 1).

Locality and horizon. Sihetun locality near Beipiao, Liaoning, China. The lower part of the Yixian Formation, probably from the Lower Cretaceous based on latest radiometric evidence¹³.

Diagnosis. *Beipiaosaurus inexpectus* differs from other therizinosauroids in having shorter and more bulbous tooth crowns, a larger skull, a tridactyl pes with a splint-like proximal first metatarsal, a shallow anterior iliac process, a long manus (10% longer than a femur), a long tibia (275 mm > 265 mm of the femur), an elongated lateral articular surface on the palmar side of manual phalanx I-1, and proximally compressed metatarsals III and IV.

Beipiaosaurus is the largest known theropod from the Yixian Formation, with an estimated length of 2.2 m. It has a relatively large skull compared to other therizinosauroids (preserved dentary is 65% of femur length). The anterior end of its dentary is downturned. The dentary has a lateral shelf, similar to other therizinosauroids and ornithischians¹. *Beipiaosaurus* has a large number of teeth (more than 37, inferred from the preserved alveoli in the broken dentary). They resemble those of *Protarchaeopteryx*¹⁶, but have larger serrations (3 serrations per mm) as in other therizinosauroids and troodontids⁹. Replacement teeth developed in oval resorption pits next to the roots of erupted teeth (Fig. 2a), as in *Archaeopteryx*¹⁷. Dorsally pointed, triangular interdental plates are present.

The cervical vertebrae bear low, anteroposteriorly short neural spines. Lateral depressions are present on the lateral sides of the centra of the fused posterior dorsals.

The coracoid is subrectangular, as in some maniraptoran theropods, with a pronounced coracoid tubercle. Exquisite impressions show that the furcula is a widely arched bone, oblate-shaped in cross section, without a hypocleidium. Compared to the short and stout hindlimb, the forelimbs are relatively long. The elongate hand is longer than the foot, as in dromaeosaurids and primitive *Avialae*¹⁸. As in other therizinosauroids, the humerus has a pointed internal tuberosity on its proximal end, and anteriorly positioned radial and ulnar condyles on its distal end. A depression on the proximal surface of the humerus separates the head and internal tuberosity, as in other therizinosauroids and *Mononykus*¹⁹. Five carpals are preserved. The largest distal carpal, the semilunate (Fig. 2c, d), is smaller than but otherwise identical to that of *Deinonychus*²⁰. It primarily contacts metacarpal II but also touches metacarpal I (Fig. 2d), unlike the condition in *Alxasaurus*, in which the largest carpal is the distal carpal I⁸. Distal carpal I is large and oval (Fig. 2c). The proximal carpals are represented by a V-shaped radiale in close contact with the radius, and a small rounded carpal between the distal ends of the radius and ulna (Fig. 2c, d). The manus is slender and elongate, proportionally similar to that of *Deinonychus*²⁰. Metacarpal I has a pronounced distal flange, as in *Deinonychus*. The proximal parts of metacarpals I and II are closely appressed. Metacarpal III is slender and slightly bowed. The combined lengths of phalanges III-1 and III-2 are equal to the length of phalanx III-3, as in advanced theropods². There are well developed ligament pits on the lateral sides of the distal ends of the phalanges. The manual unguals are laterally compressed and strongly curved. As in other

therizinosauroids⁸, their proximal ends are deep but taper to needle-sharp points. The second manual claw is slightly longer than the first, resembling those of *Archaeopteryx* and *Protarchaeopteryx*²¹.

The ilium is shaped like a parallelogram, similar to those of dromaeosaurids and basal birds, but unlike the sauropod-like ilia of derived therizinosauroids^{1,22}. The posterodorsal margin of the ilium curves ventrally in lateral view. The anterior and posterior processes are almost the same length. The posteroventral margin of the ilium is deflected laterally at a right angle to the vertical ramus, and has a shallow brevis fossa similar to those of other coelurosaurians²³. The partial pubic peduncle of the ilium is longer than the ischiadic peduncle, similar to those of therizinosauroids, dromaeosaurids and *Archaeopteryx*²³. Both the pubic and the ischial shafts are more rounded than flattened, unlike those of *Alxasaurus* and *Segnosaurus*. As in some theropods, the pubic apron is compressed and positioned more distally. The femur of *Beipiaosaurus* has a wing-like lesser trochanter, a cleft between the greater trochanter and the lesser trochanter, and a crest-like fourth trochanter. The tibia has a fibular crest, a feature of theropods². The fibula is very slender compared to the tibia, especially the distal half. As in *Alxasaurus*⁸ and the *Avialae*²⁴, the medial surface of the fibula is flat, lacking the medial fossa of some theropods. As in other therizinosauroids, the astragalus has a tall ascending process and reduced condyles that only partly cover the distal end of the tibia. The calcaneum is sub-oval and disk-shaped. The metatarsus is 39% of the length of the tibia, larger than in known therizinosauroids but less than in other theropods (>45%)⁸. The proximal end of metatarsal I is flattened and tapered and, as in most maniraptorans, does not contact the tarsus (Fig. 2e, f). The proximal ends of both metatarsals III and IV are compressed, especially on the medial side. Metatarsal V is slender and strap-like, being only half the length of the other metatarsals. One pedal ungual is preserved, and is shorter than any manual unguals.

Large patches of integumentary structures were found in close association with the ulna, radius, femur and tibia, as well as with pectoral elements. The filamentous structures are best preserved near the ulna, almost perpendicular to the bone (Fig. 3). They are similar to the integumentary structures of *Sinosauropteryx*¹⁵ in their parallel arrangement. Unlike those of *Sinosauropteryx*, the integumentary structures of *Beipiaosaurus* contact the ulna. They are densest close to the bone. Most of the integumentary filaments are about 50 mm long, although the longest is up to 70 mm. Some filaments have shallow and faint median grooves, possibly indicating hollow cores that had collapsed, and have indications of branching distal ends as in *Sinosauropteryx*¹⁵. As in *Sinosauropteryx*¹⁵ and birds from the same locality, it is difficult to isolate a single filament and thus difficult to describe the branching pattern of the integumentary filaments.

Therizinosauroida has many perplexing features for a theropod, such as a very small head, a sauropod-like ilium and a short and broad tetradactyl pes with rudimentary metatarsal V^{1,2,12,22}. Until now, no cladogram has been proposed for the relationships and morphological evolution of therizinosauroids. We ran a phylogenetic analysis with an 84-character dataset (see Supplementary Information for the character list and matrix). We left out the unnamed 'segnosaur' from the Early Jurassic Lower Lufeng Formation²⁵ as it is too incomplete. Using PAUP (3.1.1. Exhaustive search, Deltran optimization; Swofford, 1993), we obtained a single most parsimonious tree (tree length, 133; consistency index, 0.707; retention index, 0.645; rescaled consistency index, 0.456). Our analysis (Fig. 4) places *Beipiaosaurus* as a basal taxon within Therizinosauroida. *Beipiaosaurus* has a relatively large skull (1.0) among therizinosauroids, a tridactyl pes (79.0) and a fibular crest on the tibia, all of which are primitive theropod features. The pelvic elements are also very similar to those of other coelurosaurians. These characteristics support the hypothesis that therizinosauroids (including *Beipiaosaurus*) are nested within the coelurosaurian

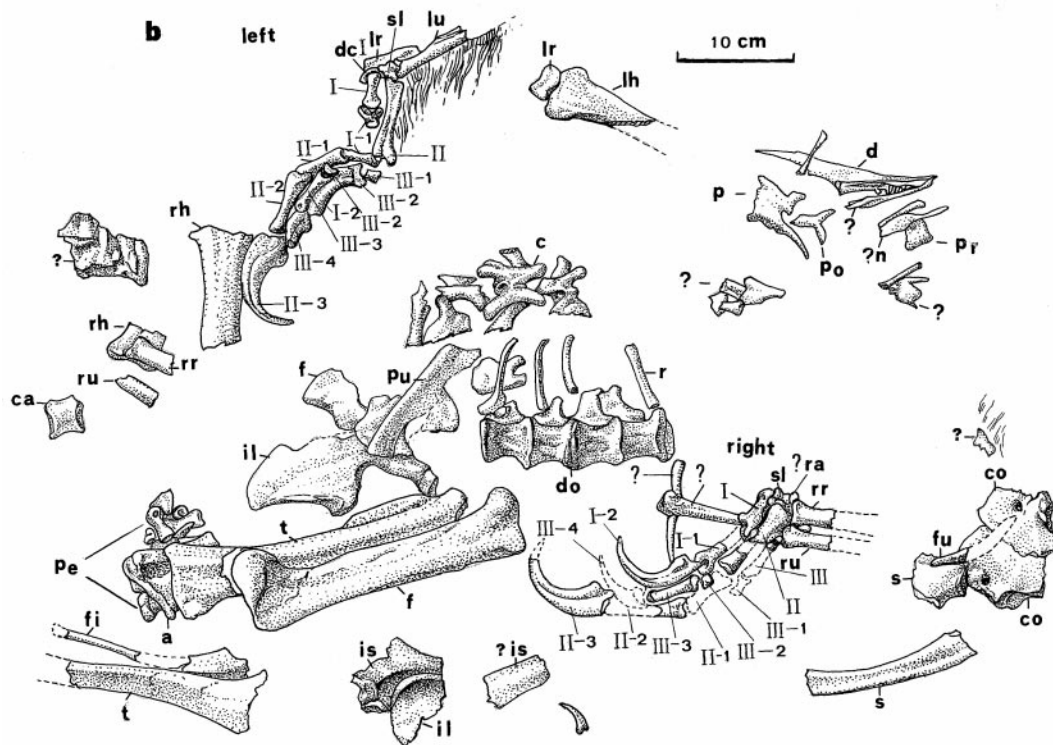


Figure 1 *Beipiaosaurus inexpectus* (V11559, holotype). Photograph (a) and outline (b) of the skeleton (broken lines indicate features preserved in impressions). The holotype was collected in 1996 by a farmer, Li Yinxian, from the famous Sihetun locality. It was later (1997) determined to be from the lower part of the Yixian Formation. According to communication with the collector, and consistent with the close proximity, preservation and proportions of the elements, all elements (including the integumentary structures) are from a single individual. V11559 includes the partial right dentary with dentition, right postorbital, right parietal, right nasal?, right prootic, a few cervicals and dorsals, an incomplete caudal, incomplete ribs, partial scapula, coracoids and furcula, partial humerus,

radius and ulna, nearly complete hands, partial ilium, pubis and ischium, complete right femur, right tibia and right fibula, incomplete left femur, tibia and fibula, incomplete right foot. Some elements are represented by impressions. Sacral and most caudal vertebrae are missing. a, astragalus; c, cervical vertebra; ca, caudal vertebra; co, coracoids; d, dentary; dcl, distal carpal I; do, dorsal vertebra; f, femur; fi, fibula; fu, furcula; I-III, metacarpals I-III, I-1 to III-4, manual phalanges I-1 to phalanges III-4; il, ilium; is, ischium; lh, left humerus; lr, left radius; lu, left ulna; ?n, ?nasal; p, parietal; pe, pes; po, postorbital; pr, prootic; pu, pubis; r, rib; ?ra, ?radiale; rh, right humerus; rr, right radius; ru, right ulna; s, scapula; sl, semilunate distal carpal; t, tibia.

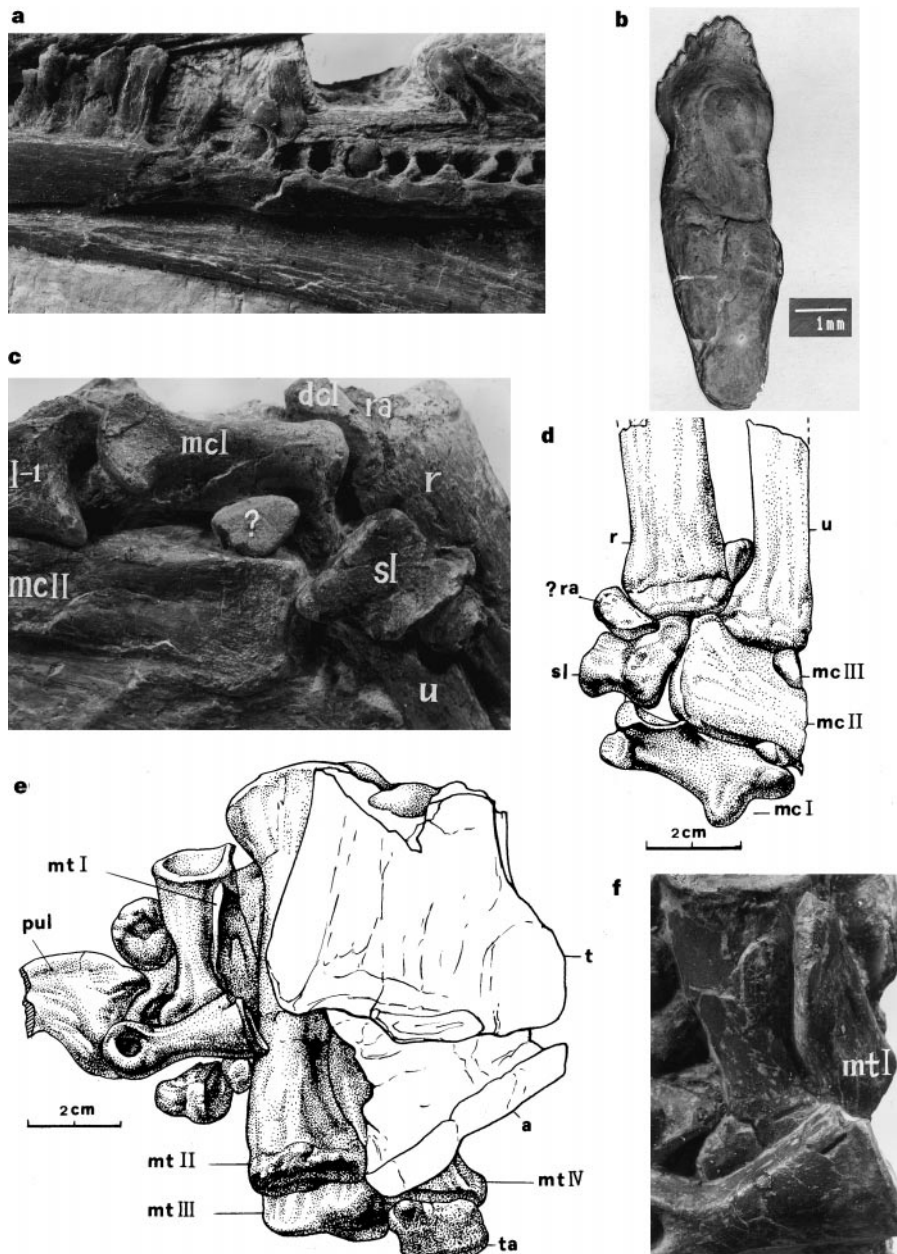


Figure 2 *Beipiaosaurus inexpectus*. **a**, Nine right dentary teeth in medial view. Note the resorption pits and replacement teeth. **b**, A dentary tooth in lateral view. **c**, Close-up of the left semilunate carpal of V11559. **d**, Drawing of part of the right manus of V11559. Note the shape and position of the semilunate, which is very similar to that of birds¹⁷. **e**, Drawing of the partially preserved right pes of V11559.

f, Close-up of the first metatarsal of V11559. Note the proximally pinched theropod first metatarsal. The theropod first metatarsal is absent in other therizinosauroids, which has been argued as being strong evidence against the theropod affinities of therizinosauroids¹. Additional abbreviations: mc I-III, metacarpals I-III; mt I-IV, metatarsals I-IV; pul, pedal ungual; r, radius; ra, radiale; ta, tarsal; u, ulna.

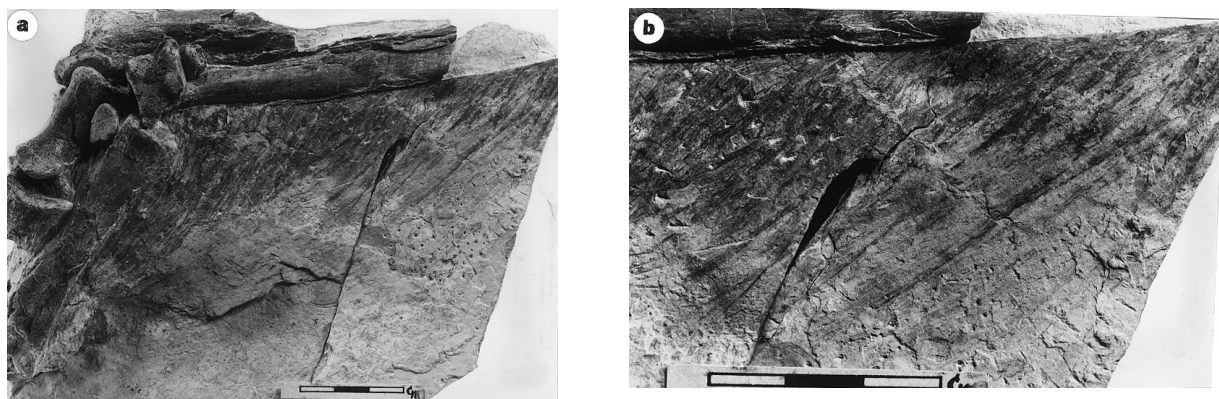


Figure 3 *Beipiaosaurus inexpectus*. **a**, Partially preserved forelimb with unusual integumentary impression. **b**, Close-up of the integumentary impression.

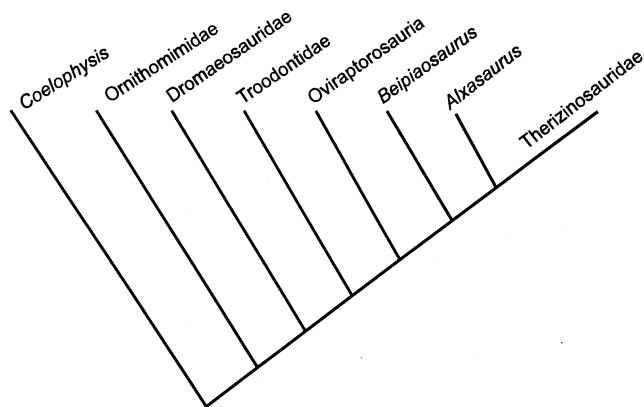


Figure 4 Phylogenetic relationships of *Beipiaosaurus inexpectus*. *Beipiaosaurus* and other therizinosauroids share 18 synapomorphies, including the following unique characters: a prominent dorsolateral shelf on the dentary (21.1), teeth that increase in size anteriorly (25.1), tooth crowns with sub-circular basal cross-sections that lack mediolateral compression (27.1), anteroposteriorly narrow and dorsoventrally deep pubic peduncle of ilium (46.1 and 47.1), very deep proximal end of manual unguals (70.1), short metatarsus (78.1) and reduced main body of astragalus (82.1). It is less derived than other therizinosauroids because it lacks 13 characters of Therizinosauridae (1.1, 36.1, 38.0, 43.0, 48.1, 49.1, 51.1, 52.1, 58.1, 60.0, 66.0, 77.1, 79.1), including the following unusual characters: a very small head (1.1), the long and deep preacetabular portion of ilium (48.1 and 49.1) and absence of the theropod first metatarsal (79.1).

theropods^{8–11}. Given this phylogeny (Fig. 4), some derived characters of therizinosauroids other than *Beipiaosaurus* are most parsimoniously interpreted as having evolved convergently with some other dinosaur groups, sauripodomorphs in particular. Thus, therizinosauroids re-evolved a robust first digit in which the proximal end of metatarsal I articulates with the tarsals (79.1).

Feathers are complex structures. Their abrupt appearance in the bird fossil record has been difficult to explain, mainly because no intermediate structures are preserved in the related theropod taxa. The integumentary filaments of *Sinosauropteryx* have been considered to be 'proto-feathers' by some, but this idea has been rejected by others²⁶. Such structures have not been preserved with any other theropods²⁶ until the discovery of *Beipiaosaurus*. The filamentous structures in *Beipiaosaurus* are similar to, but longer than, those of the compsognathid *Sinosauropteryx*. They are perpendicular to the limb bones, and are unlikely to be muscle fibres or frayed collagen²⁷. Their presence in both therizinosauroids and compsognathids indicates that there may be a broader distribution of similar structures in theropod dinosaurs. This supports the idea that these simple integumentary filaments may represent an intermediate evolutionary stage to the more complex feathers of *Protarchaeopteryx*, *Caudipteryx*¹⁶ and more derived Avialae. The absence of such structures in most theropod fossils is probably attributable to the lack of such ideal preservation as is found in the Yixian Formation. This again indicates that feathers preceded flight¹⁶, because both therizinosaurids and compsognathids apparently could not fly and did not descend from flying animals. □

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Complex dynamics and phase synchronization in spatially extended ecological systems

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Population cycles that persist in time and are synchronized over space pervade ecological systems, but their underlying causes remain a long-standing enigma^{1–11}. Here we examine the synchronization of complex population oscillations in networks of model communities and in natural systems, where phenomena such as unusual '4- and 10-year cycle' of wildlife are often found. In the proposed spatial model, each local patch sustains a three-level trophic system composed of interacting predators, consumers and vegetation. Populations oscillate regularly and periodically in phase, but with irregular and chaotic peaks together in abundance—twin realistic features that are not found in standard ecological models. In a spatial lattice of patches, only small amounts of local migration are required to induce broad-scale 'phase synchronization'^{12,13}, with all populations in the lattice phase-locking to the same collective rhythm. Peak population abundances, however, remain chaotic and largely uncorrelated. Although synchronization is often perceived as being detrimental