The research area is located at 34.5° N, 82° W. Annual precipitation averages 1,170 mm (1950–87) and temperature 16 °C. In the early 1800s, primary deciduous forests at the site were cleared, mainly to grow cotton, and the site was managed for row crops, hay and pasture until the mid-twentieth century[7,16]. Soils are acidic Ultisols, classified as the Appling series (fine, kaolinitic, thermic Typic Kanhapludults). The Appling soil is a common soil of southeastern North America, and is formed from granitic gneiss, the bedrock from which about half the soils in the southern Piedmont region are derived.

In 1957, 16 permanent plots were installed on two cotton fields at the Calhoun Experimental Forest, eight of which are used in these carbon analyses. The mineral soils of these eight plots were sampled in 1962, 1968, 1972, 1978, 1982, 1990 and 1997. At each collection, each plot was sampled at least 20 times with a 2-cm-diameter punch tube in a systematic random fashion at four soil depths: 0–7.5, 7.5–15, 15–35 and 35–60 cm. Within each plot, the $\geqslant$20 samples per soil depth were composited, that is, in one sample per depth.

Soil archive, radiation and total carbon. The Duke Soil Archive stores air-dried soil samples at room temperature in sealed glass containers. Total soil carbon was analysed in powdered samples with a Perkin-Elmer CHN combustion instrument. Radiocarbon was measured by accelerator mass spectrometry (AMS) on graphite targets prepared from soil organic matter and is reported as Δ^{14}C, the per mil deviation of ^{14}C/^{12}C compared with a decay-corrected oxalic acid standard[27]. Positive values of Δ^{14}C indicate presence of bomb-produced ^{14}C, and negative values indicate predominance of old soil organic matter with ^{14}C that has experienced significant radioactive decay (half-life is 5,730 yr). Radiocarbon was estimated using AMS of composite samples made from soil from the eight plots at each depth. Analysis of variance and means separation tests were used to test effects of time on soil carbon accumulation.

Soil carbon inputs. To estimate carbon inputs to soils, carbon in litterfall, fine roots, and soil water were estimated. Litterfall was sampled in each of the eight permanent plots with five collectors (each 0.72 m^2 in area) per plot. Canopy litterfall was collected monthly during 1991–92[28].

Fine roots were sampled volumetrically using a 6-cm-diameter corer that collected undisturbed cores of O horizon and mineral soil from 0–15 and 15–30 cm depths. Soil cores were taken every three weeks for 18 months in 1994–95. Samples were returned to the laboratory where fine roots ($<$2-mm) were separated from soil by wet-sieving and hand picking. Live roots were separated from dead, and the former were ashed to estimate carbon contents (taken as half the loss on ignition). Only the live fraction of the fine roots is reported here, and carbon inputs from fine-root turnover were simply estimated as 50% of live fine-root carbon in forest floor, or mineral soil at 0–15 and 15–30 cm depth. This factor (50%) is taken to be a conservative estimate of carbon inputs from rhizo-deposition.

DOC was determined in atmospheric precipitation (wet deposition), canopy throughfall, and solutions draining forest floor and several depths of mineral soils to 60 cm (ref. 19). Wet-only precipitation was collected by an Aerochem Metric sampler. Throughfall was collected in three bulk precipitation collectors in each of 8 plots using 16-cm-diameter funnels that were continuously open. Gravitational lysimeters were used to collect water from below O horizons and at 15-cm depth. Tension lysimeters of porous Teflon-quartz design collected solutions at 60-cm depths. Solutions were collected every two or three weeks over two years, 1992–94, and solutions were estimated for DOC concentration by combustion and infrared analysis, after purging solutions of CO_2 and H_2CO_3 by acidification and sparging with N_2 gas.

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Cretaceous age for the feathered dinosaurs of Liaoning, China

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The ancient lake beds of the lower part of the Yixian Formation, Liaoning Province, northeastern China, have yielded a wide range of well-preserved fossils: the 'feathered' dinosaurs *Sinosauropteryx*[1], *Protarchaeopteryx* and *Caudipteryx*[2], the primitive birds *Confuciusornis*[3] and *Liaoningornis*[4], the mammal *Zhangheotherium*[5] and the reportedly oldest flowering plant, *Archaefructus*[6]. Equally well preserved in the lake beds are a wide range of fossil plants, insects, bivalves, conchostracans, ostracods, gastropods, fish, salamanders, turtles, lizards, the frog *Callobatrachus*[7] and the pterosaur *Eosipterus*[1,8]. This uniquely preserved assemblage of fossils is providing new insight into long-lived controversies over bird–dinosaur relationships[1,2], the early diversification of birds[3,9,10] and the origin and evolution of flowering plants[6]. Despite the importance of this fossil assemblage, estimates of its geological age have varied widely from the Late Jurassic to the Early Cretaceous. Here we present the first ^{40}Ar/^{39}Ar dates unambiguously associated with the main fossil horizons of the lower part of the Yixian Formation, and thus, for the first time, provide accurate age calibration of this

important fauna. The results of this dating study indicate that the lower Yixian fossil horizons are not Jurassic but rather are at least 20 Myr younger, placing them within middle Early Cretaceous time.

The bulk of the fossils from the lower part of the Yixian Formation come from a small region surrounding the village of Sihetun, located about 20–25 km south of the city of Beipiao (Fig. 1). Fossils in this area occur primarily at two horizons separated stratigraphically by about 30–40 m (ref. 11). Most of the vertebrate fossils listed above come from an interval of a few metres, designated as Bed 6 in our Fig. 2. The angiosperm *Archaefructus* and the pterosaur *Eosipterus*, as well as other well preserved fossils, are known from the stratigraphically higher fossiliferous level, here referred to as Bed 8 (Fig. 2). Some confusion surrounds the reported occurrence of the dinosaurs *Protarchaeopteryx* and *Caudipteryx*. These dinosaurs were reported as coming from a 'Chaomidianzi' Formation in the Sihetun area. This formally unpublished formation consists of layers that are also known as the 'Jianshangou' beds and are here considered to be equivalent to Beds 1–9 of the lower part of the Yixian Formation, following the terminology in ref. 11. The designation of a separate formation for these beds has not gained wide acceptance in China.

Palaeontologists focusing on various aspects of the fossil assemblage have considered the fauna to be Late Jurassic[3,4,12–17], Late Jurassic to Early Cretaceous[1,2] or Early to late Early Cretaceous[18–20] in age. Unfortunately, many of these ages are based on comparisons of freshwater invertebrates from sites that are also poorly dated. The Jurassic age for the *Archaefructus* site was based on comparisons of fossil insects from sites in Siberia and Kazakhstan[16]. However, the ages of these sites are equally poorly known, lacking any independent isotopic age control. Looking at the vertebrate fauna, comparison of *Sinosauropteryx* and *Confuciusornis* with *Compsognathus* and *Archaeopteryx*, respectively, from the Solnhofen Limestone of Europe[3,21], led some workers to argue for a Late Jurassic (Tithonian) age or an age near the Jurassic/Cretaceous boundary. However, derived features noted in some of the bird fossils (for example, in comparison with *Archaeopteryx*, *Confuciusornis* lacks teeth, possesses a beak, has a much shorter tail and so on), and the occurrence of the ceratopsian dinosaur *Psittacosaurus*[22], have led others to argue for a younger Cretaceous age. A Cretaceous Valanginian age has also been proposed, based on pollen and spores associated with the fossil birds *Sinornis*, *Cathyornis* and *Chaoyangia* from the overlying Jiufotang Formation[10].

Isotopic dates on volcanics from the Yixian Formation have not helped to resolve the controversy. Proponents of a Jurassic age for the Lower Yixian Formation refer to a K–Ar date of 137 ± 7 Myr and a Rb–Sr date of 143 ± 4 Myr (refs 23, 24) (these uncertainties are 2 standard deviations (s.d.), all others in this report are 1 s.d.). These workers propose an age of around 135 Myr for the Jurassic/Cretaceous boundary, although most workers now accept an age for the boundary of around 144 Myr (ref. 25). Most of the younger age estimates for a Jurassic/Cretaceous boundary are based on low-temperature glauconite dates which we consider to be unreliable. Although the boundary is still not well calibrated, for the purposes of this study we defer to the discussion within ref. 25 and adopt their age of 144 Myr.

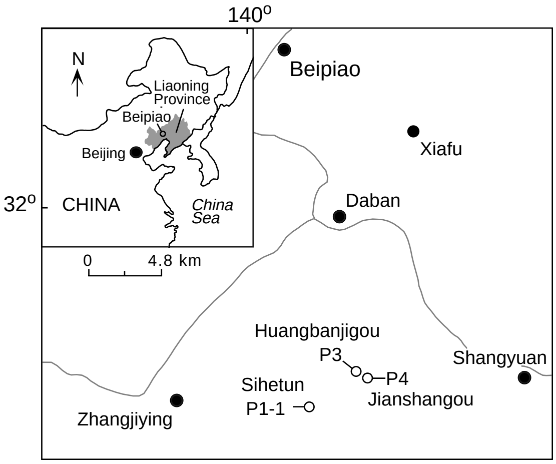

Figure 1 Map of the Sihetun area, Liaoning Province, northeastern China. Locations of stratigraphic sections and sites discussed in the text and in Fig. 2 are shown.

^{40}Ar/^{39}Ar dates on a volcanic breccia and diabase from the upper part of the Yixian at Jingangshan have been used to argue for a Cretaceous age for the underlying fossils[26]. The average age of 121.1 ± 0.2 Myr for these dates suggests correlation with the Cretaceous Aptian. ^{40}Ar/^{39}Ar dates have also been obtained from volcanic rocks from the lower part of the Yixian Formation. An andesite from Daxinfangzi has been dated at 122.9 ± 0.3 Myr and a basalt from Beipiao at 121.2 ± 0.3 Myr (ref. 26). However, the relationship of these dated volcanics to fossil-bearing horizons has recently come into question. Additional data indicates that the basalt from Beipiao may be an intrusive sill rather than an interbedded flow within the lake beds of the Yixian Formation. Dated volcanics at Jingangshan and Daxinfangzi are geographically distant from the 'feathered' dinosaur and *Confuciusornis* sites and precise stratigraphic relationships are uncertain and require further investigation.

During stratigraphic studies of the Sihetun area in 1997–98, volcanic layers were found interbedded within the main fossiliferous horizons of Bed 6 (Fig. 2). To try and resolve the age of the fossils of the lower Yixian Formation, two tuffs were collected for ^{40}Ar/^{39}Ar dating. Dates on these tuffs are potentially better than previous dates for two reasons. First, given the proximity of the tuffs to the fossiliferous layers, problems with correlation and provenance are obviated. Second, the tuffs are pristine water-lain tephra that contain abundant euhedral sanidine feldspars. Sanidine, because of its argon retentivity and potential reproducibility (as established from previous dating studies on replicate analyses of single crystals), is considered to be one of the most reliable materials for ^{40}Ar/^{39}Ar dating[27,28].

The tuffs were collected from Bed 6 at two sites, about 4 km apart,

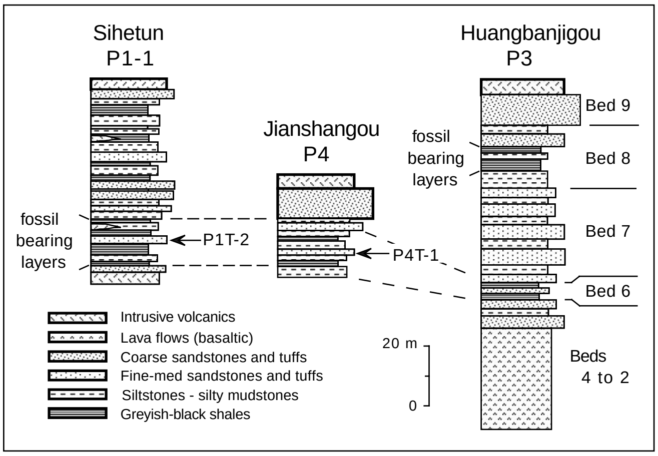

Figure 2 Stratigraphic correlation of the main fossil-bearing layers of the lower Yixian Formation. Arrows show stratigraphic locations of dated tuff samples P1T-2 and P4T-1. Precise stratigraphic relationship of key vertebrate fossils from Bed 6 to the dated tuff layers are reported in the text. The *Archaefructus* and *Eosipterus*-bearing layers of Bed 8 are located about 30 m stratigraphically above the dated tuff layers. The stratigraphic sections and correlations are modified slightly from those reported in ref. 11 as a result of additional geological field mapping in Autumn of 1998.

in the main fossil-bearing region of Sihetun (Fig. 1, 2). Tuff P4T-1 is from the Jianshangou section (Fig. 2) and occurs about 50 cm above the type specimen of *Zhangheotherium quinquecuspidens*[5,11]. The second tuff (PIT-2) is from the Sihetun section (Fig. 2), located 3.40 m above the layer bearing the type specimen of *Confuciusornis sanctus*[3,11]. Bed 6 at Sihetun has also yielded well-preserved specimens of *Sinosauropteryx*, *Protarchaeopteryx* and *Liaoningornis*[11]. The Sihetun and Jianshangou tuffs are stratigraphically within a metre of each other, and may represent the same tuff, although changes in depositional facies preclude this determination. The reportedly oldest flowering plant, *Archaefructus*, comes from approximately 30 m above this level in Bed 8 at Huangbanjigou (Fig. 1, 2).

^{40}Ar/^{39}Ar dating of the P4T-1 and P1T-2 tuffs was done by replicate Ar-ion-laser total-fusion analyses of single crystals of sanidine and CO$_2$-laser incremental-heating of a bulk sanidine separate. Thirty-four single sanidine crystal dates obtained on Tuff P4T-1 (Fig. 3a) give a mean age of 124.6 ± 0.2 (s.d.) ± 0.03 Myr (s.e.) Thirty-five single sanidine crystal dates on Tuff P1T-2 (Fig. 3a) give an age of 124.6 ± 0.3 (s.d.) ± 0.04 Myr (s.e.), an age indistinguishable from that of P4T-1. The radiogenic ^{40}Ar yields from all of the sanidines were greater than 99%, indicating little alteration. No crystals of significantly older age that might suggest reworking or detrital contamination were found in either tuff. A few additional crystals that were dated gave lower radiogenic yields, but were determined subsequently to be plagioclase crystals based on their measured ^{37}Ar/^{39}Ar (Ca/K) ratios. These lower radiogenic plagioclase analyses gave a wider variance in age distribution (122.5 Myr to 125 Myr) than the sanidine, considered here to be a result of various alteration of the plagioclase. These analyses are omitted from the calculation of the age of the tuffs.

To address the possibility of argon loss and/or trapped excess argon, CO$_2$-laser incremental-heating of the sanidine of P4T-1 was also undertaken (Fig. 3b). The release profile (Fig. 3b) was relatively flat with only a slight deviation from a plateau occurring at the lowest three temperature increments. All of the 24 increments that formed the plateau yielded over 95% radiogenic ^{40}Ar and totalled more than 90% of the ^{39}Ar released from the sample. The calculated age for the plateau is 124.6 ± 0.1 Myr (Fig. 3b). The uniformly high radiogenic yields of all 24 increments resulted in a small cluster of points when plotted on an inverse (^{36}Ar/^{40}Ar vs ^{39}Ar/^{40}Ar) isochron, making any fit unreliable. If we include the three lower radiogenic steps that fell outside the plateau in the isochron, an age of 124.6 ± 0.1 Myr (MSWD (mean sum of weighted deviates) = 1.48) is obtained. The ^{40}Ar/^{36}Ar intercept of 286.2 ± 10.7 is not distinguishable from the air ratio. The incremental-heating and single-crystal experiments indicate little alteration of the sanidine, no discernible excess argon and no apparent detrital contamination of the sanidine.

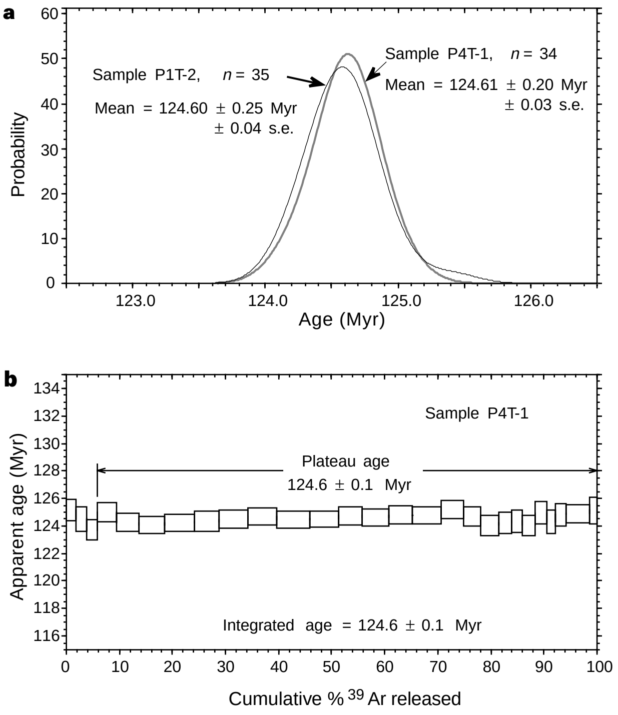

Figure 3 ^{40}Ar/^{39}Ar dating results. **a**, Age probability diagram for single sanidine crystal dates; **b**, incremental-heating spectrum on sanidine.

The dates reported here are the first ^{40}Ar–^{39}Ar analyses on tuffs interbedded directly in the fossiliferous horizons of the lower Yixian Formation. Our ^{40}Ar/^{39}Ar ages for Tuffs P4T-1 and P1T-2 from the Bed 6 fossil-bearing levels are about 10% younger than the previously reported K/Ar and Rb/Sr dates[23,24]. Although we are unaware of the precise stratigraphic and geographic location of these dated samples, the dates are accompanied by large uncertainties and are generally not considered reliable owing to probably alterations and/or contamination. Our sanidine dates, although 2% older, are more consistent with the ^{40}Ar/^{39}Ar dates on andesites and basalts of the Yixian Formation reported in ref. 26. However we consider our dates to be a more accurate calibration of the fossils from the lower Yixian Formation. We base this on the superior argon retentivity of sanidine versus the whole rock and biotite[27,28] used in their dating study[26] and on the unambiguous relationships of our dated tuffs to fossiliferous levels. We also note the possibility of some ^{40}Ar loss and/or ^{39}Ar recoil during irradiation that accompanies some of the ^{40}Ar/^{39}Ar release spectra shown for those dates[26], which may indicate that those samples are altered. At least a percentage of the age difference can be attributed to the age of Hb-3gr, the standard used in ref. 26. We can make a second-order comparison of our dates with those in ref. 26 using the interlaboratory standard MMHb which has been intercalibrated with both Hb-3gr[29] and our standard Fish Canyon Sanidine[27]. Compared with our age for Fish Canyon Sanidine, we obtain ages of 122–124 Myr for the dates in ref. 26, bringing them into close agreement with our sanidine dates for tuffs P4T-1 and P1T-2.

The new dates reported here, in conjunction with the results of ref. 26, indicate that the 'feathered' dinosaurs of Liaoning, although primitive in appearance, are not Late Jurassic or even earliest Cretaceous in age. Compared with the geologic timescale of ref. 25, the dates indicate a correlation with the middle Barremian (mid-Early Cretaceous), at least 20 Myr younger than *Archaeopteryx* from the Late Jurassic (Tithonian) Solnhofen Limestone of Europe. Given the similarities already noted with the Solnhofen and Liaoning fossils, it would appear that aspects of the terrestrial fauna were part of a long-lived chronofauna, persisting across the Jurassic–Cretaceous boundary. However, the ages of many of these sites worldwide are poorly known and, in light of the new dates for the lower Yixian fauna reported here, their ages may need re-examination. A final outcome of the new dates is that *Archaefructus*, although remarkably well preserved, cannot be considered as early as originally thought[5]. Depending on the accuracy in dating of other fossil sites worldwide, *Archaefructus* appears to be comparable in age with early angiosperm evidence from the Barremian of China, Europe, Russia and eastern North America[30]. ☐

Methods

^{40}Ar/^{39}Ar dating of the P4T-1 and P1T-2 tuffs follow procedures described in ref. 27 and references therein. Sanidine from the tuffs and multiple samples of the monitor mineral Fish Canyon Sanidine (to determine lateral flux gradients during irradiation) were co-irradiated for 20 h in the cadmium-lined core (CLICIT) facility of the Oregon State University TRIGA reactor. Nucleogenic interference corrections are those previously reported[27]. Mass discrimination was monitored before and after measurement of the sanidines using an on-line air pipette system. The P4T-1 and P1T-2 dates are referenced to the Fish Canyon Sanidine monitor mineral using the published age of 28.02 Myr (ref. 27). The ages reported are arithmetic means of the individual dates based on total fusion analyses of single sanidine crystals. We report one standard deviation (s.d.) and standard error of the mean (s.e.) uncertainties with the mean ages to document crystal-to-crystal age variation. Individual crystal dates are presented in the Supplementary Information, Table 1.

In the incremental-heating experiment, 15 handpicked euhedral sanidine crystals were laid flat on the bottom of a 2-cm-diameter well of a copper sample disk. The crystals were heated by a CO_2 laser beam directed through an integrator lens that produces relatively even and uniform heating. Twenty-seven discrete temperature increments based on a controlled stepwise increase in power of the CO_2 laser were obtained. The heating time for each increment was 60 s. Incremental heating data are supplied in the Supplementary Information, Table 2.

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Hydrologically defined niches reveal a basis for species richness in plant communities

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Species-rich plant communities are prized repositories of biodiversity and a dwindling resource, but how the large numbers of species that characterize such communities are able to coexist is poorly understood. Resource-based competition theory predicts that stable coexistence between species depends on each being a superior competitor in its own niche[1]. The theoretical problem is that plants all require the same resources and acquire them in a very limited variety of ways, so observed niche overlaps are high[2,3] and exclusion of all but the best competitor is the predicted result. This problem, central to community ecology, has elicited a variety of theoretical solutions[4–7], several of which invoke some degree of niche separation in time or space[8,9]. The signature of niche separation in the field is to be found in community structure, which should indicate (i) smaller than expected niche overlaps on relevant niche axes and (ii) a trade-off between species' resource use on orthogonal axes. Here we provide evidence for the existence of both these conditions in a species-rich plant community.

We sampled two English meadow plant communities (flood-plain meadows, NVC MG8 and MG4 (ref. 10)), at Tadham Moor, Somerset, UK, and at Cricklade, Wiltshire, UK. The percentage abundance of all species present was estimated in 844 1-m^2 quadrats within a 22-ha area at Tadham and in 641 quadrats within a 44-ha area at Crickdale. Species' tolerances were estimated from the range of hydrological conditions in which they were recorded growing in the field. Soil moisture conditions in each quadrat were determined from quadrat locations in relation to surrounding water courses by using two hydrological models parameterized with 15 years of data on meteorological inputs and weekly water levels in the surrounding rivers and ditches. The models were verified against water-table depths measured in dip-wells located at a subset of quadrat locations[11,12]. Two sum exceedence parameters[13] were derived from the modelled water-table depths and were used as niche axes. A sum exceedence value (SEV) for soil drying was cumulated during periods in which the moisture tension of the surface soil exceeded 5 kPa, which could potentially induce stomatal closure[14]. An SEV for aeration was cumulated during periods in which the soil air-filled porosity fell below 10% by volume, which is assumed to preclude the free diffusion of oxygen in the topsoil[15]. High aeration SEVs indicate waterlogging. The water-table depths that, under average summer evaporative demand, gave rise to (i) a surface tension of 5 kPa and (ii) an air-filled porosity of 10% were calculated for each of the soil types. These depths were then used as maximum and minimum thresholds, respectively. Each SEV gives the number of weeks for which the relevant threshold was exceeded multiplied by the vertical distance by which the water-table exceeded it, measured in units of metre weeks. SEVs have the advantage that they incorporate a measure of long-term temporal variation in soil moisture at a scale relevant to the physiological tolerances of plants.

Quadrat sampling locations were distributed randomly throughout the available niche space, as defined by the two SEV axes (Fig. 1). The Tadham site (Fig. 1a) is topographically very flat, whereas