

# An exceptionally preserved Lower Cretaceous ecosystem

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**Fieldwork in the Early Cretaceous Jehol Group, northeastern China has revealed a plethora of extraordinarily well-preserved fossils that are shaping some of the most contentious debates in palaeontology and evolutionary biology. These discoveries include feathered theropod dinosaurs and early birds, which provide additional, indisputable support for the dinosaurian ancestry of birds, and much new evidence on the evolution of feathers and flight. Specimens of putative basal angiosperms and primitive mammals are clarifying details of the early radiations of these major clades. Detailed soft-tissue preservation of the organisms from the Jehol Biota is providing palaeobiological insights that would not normally be accessible from the fossil record.**

The Yixian and Jiufotang Formations of northeastern China have yielded a huge variety of exceptionally well-preserved fossils that comprise the ‘Jehol Biota’<sup>1–8</sup>. Recent discoveries of spectacular vertebrate specimens, particularly of theropod dinosaurs, birds and mammals with associated integumentary structures and other soft tissues, and of putative early angiosperms have established the global significance of this Lower Cretaceous biome<sup>9–16</sup>. The Jehol Biota includes representatives of almost all of the major clades of Lower Cretaceous terrestrial and freshwater vertebrates, a wide variety of invertebrates and a diverse flora. It is unique in terms of its species richness, exceptional preservation and in the sheer numbers of specimens of many of the species present. The combination of these factors means that the Jehol Biota provides a rare, incredibly detailed picture of an intact Early Cretaceous terrestrial ecosystem. Here, we present a synthetic overview of the entire biota, emphasising its impact on wide-ranging evolutionary, palaeoecological and phylogenetic questions, including the origin of birds, the evolution of feathers and flight, the early diversification of angiosperms, and the timing of the placental mammal radiation.

## Geological, palaeoenvironmental and preservational setting

The Jehol Group comprises the Yixian and Jiufotang Formations, which crop out in western Liaoning, northern Hebei and south-eastern Inner Mongolia (Figs 1 and 2). Lateral equivalents of these units, with similar biotas, are found in adjacent areas of eastern and central Asia, including Kazakhstan, Mongolia, Siberia, Japan and Korea (Fig. 1)<sup>3–4</sup>. The Yixian and Jiufotang Formations are conformable, lithologically similar deposits of weakly laminated to finely bedded siliciclastic sediments, mainly low-energy sandstones and shales, intercalated with extrusive basalts and tuffs and cross-cut by occasional dykes and sills<sup>17</sup> (Fig. 2). Jehol Group sediments represent freshwater lacustrine environments, and lack the laterally variable features of other freshwater settings such as rivers and deltas<sup>17</sup>, a reconstruction that is consistent with the mixed terrestrial/freshwater fossil assemblage. Eastern Asia was a fully emergent landmass during the late Mesozoic era<sup>18</sup>, and this terrestrial depositional setting contrasts with those of most other penecontemporaneous biotas, which show evidence of greater marine influence or are exclusively marine. For example, the sediments of the Santana and Crato Formations of Brazil (Aptian/Albian) represent saline

lagoons, whereas the Spanish locality of Montsec (Berriasian/Valanginian) was deposited under peritidal conditions<sup>19</sup>. Extensive volcanism, resulting from increased tectonic activity along the Pacific Rim at this time<sup>20</sup>, is apparent from the conformable deposition of tuffaceous sediments within the Jehol Group. Volcanic activity was most frequent during deposition of the Yixian Formation, but became progressively less pronounced in Jiufotang times<sup>17</sup>. Regional volcanism, in combination with the presence of numerous shallow lakes, provided ideal environments for the exceptional preservation of the Jehol Biota and has also permitted high-resolution dating of the fossiliferous horizons (see below). Palaeobotanical and sedimentological evidence indicate seasonal climatic fluctuations between semi-arid and mesic conditions<sup>4,21</sup>.

Freshwater and terrestrial organisms from the biota usually occur together within the same sedimentary horizon (Fig. 2). Preservation of complete articulated shells, arthropod exoskeletons, vertebrate skeletons and terrestrial plant stems with associated leaves, rootlets and other structures, indicates that all of these specimens originated in close proximity to low-energy lacustrine depositional sites and were not transported over extensive distances. Individual elements are generally unbroken and display little or no abrasion<sup>6,22</sup>.

Dead organisms entered the lakes, were buried rapidly and encased in fine-grained sediments. The most productive horizons are beneath ash tuff falls, which would have entombed most of the organisms present in the water column—the tuff layers are strongly correlated with mass mortality events<sup>6,22,23</sup>. Tuff deposition effectively sealed the fossil-bearing sediments, creating microenvironments around the organisms that promoted anoxic conditions and halted bacterial decay of soft tissues. Moreover, tuffs prevented burrowing organisms from disturbing organic remains within the sediment, eliminating bioturbation and scavenging. The combination of these factors resulted in the formation of *Konservat-Lagerstätten* conditions<sup>19</sup>, permitting exceptional preservation of many original soft-tissue features. Integumentary structures (filaments, feathers and fur) are known from pterosaur<sup>24</sup>, dinosaur<sup>13,14,25–30</sup>, bird<sup>31,32</sup> and mammal<sup>33</sup> specimens: preservation of other soft tissues (skin impressions, cartilaginous elements, keratinous beaks) and stomach contents is also common and has been reported for a wide variety of taxa<sup>7</sup>. Preservation of wing membranes, hairs and colour patterning have been recorded from insects and other invertebrates<sup>4,7</sup>. The gross morphology of Jehol plants is often well preserved, but fine anatomical detail and cuticular material are usually lacking. Consequently, anatomical features that are generally not preserved in fossils are often found in the Jehol material. Three-dimensionally

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preserved specimens of dinosaurs<sup>34–37</sup>, mammals<sup>38,39</sup>, frogs and lizards have been recovered from the Lujiatun locality in the Yixian Formation near Beipiao, western Liaoning Province. The fossil-bearing tuffs at this locality lack obvious bedding planes, suggesting that this deposit resulted from a single, catastrophic mass mortality event.

**Age of the deposits**

The dating of the Yixian and Jiufotang Formations has proved to be contentious<sup>4,5,8,40–42</sup>, and many biostratigraphical correlations and radiometric dates have been published that support the Jehol Biota being either Late Jurassic or Early Cretaceous in age<sup>5,8,42</sup>. Establishing the age of these units is critical for evaluating the evolutionary significance of the biota, as the Late Jurassic/Early Cretaceous interval is an important time in Earth history, during which major changes in the composition and dynamics of terrestrial ecosystems occurred<sup>5</sup>. For example, if a Late Jurassic age were accepted, this would suggest that the phylogenetic and ecological radiations of birds, placental mammals and angiosperms began significantly earlier than current palaeontological evidence indicates.

Most of the evidence supporting a Late Jurassic age for the Jehol Group is either equivocal or flawed<sup>5,8,42,43</sup>. Many proposed Late

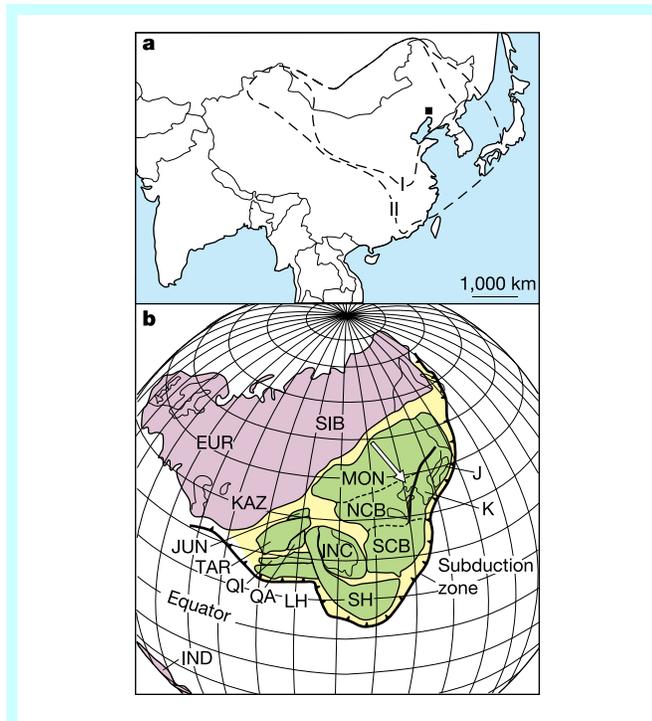
Jurassic biostratigraphical correlations are based on taxa with low stratigraphical resolution, use taxa that are difficult to diagnose or differentiate from each other, or depend on vertebrates of limited biostratigraphical utility<sup>5,8</sup>. <sup>40</sup>K–<sup>40</sup>Ar and <sup>87</sup>Rb–<sup>87</sup>Sr dates of  $137 \pm 7$  Myr ago and  $143 \pm 4$  Myr ago, from the Yixian Formation, have been advanced in favour of a Late Jurassic age<sup>44</sup>. However, this conclusion depends on the adoption of a chronological framework in which the Jurassic/Cretaceous boundary occurred at about 135 Myr: in contrast, most geochronologists regard the latter as unreliable, accepting a slightly older age (approximately 144 Myr) for the boundary<sup>5,8</sup>. Consequently, these <sup>40</sup>K–<sup>40</sup>Ar and <sup>87</sup>Rb–<sup>87</sup>Sr dates actually support an Early Cretaceous age when the older boundary age is applied<sup>5,8,42</sup>. <sup>40</sup>Ar–<sup>39</sup>Ar dating of biotite crystals from a tuff in the Yixian Formation suggested a Late Jurassic age, producing an overall mean age of  $145.3 \pm 4.4$  Myr and a combined isochron date of  $147.1 \pm 0.18$  Myr<sup>45</sup>. However, these results are subject to doubt as some evidence suggests that the samples used were either altered diagenetically or contained trapped argon, either of which could adversely affect the results of the analyses<sup>42</sup>.

Current evidence indicates that the Jehol Biota is of late Early Cretaceous age<sup>5,8,41–43,46</sup>. <sup>40</sup>Ar–<sup>39</sup>Ar dates of  $124.6 \pm 0.1$  Myr and  $125.0 \pm 0.18$  Myr obtained from total fusion and incremental heating analyses of sanidine and biotite crystals from three different tuff layers in the ‘Jianshangou beds’ of the Yixian Formation indicate referral to the Barremian stage<sup>41,42</sup>, whereas a <sup>40</sup>Ar–<sup>39</sup>Ar date of  $128.4 \pm 0.2$  Myr from a basalt capping the lowermost ‘Lujiatun beds’ suggests a Hauterivian age for the base of the formation<sup>46</sup>. A <sup>235</sup>U–<sup>207</sup>Pb zircon date of  $125.2 \pm 0.9$  Myr for the Jianshangou beds is in close agreement<sup>46</sup>, and a mean age of  $121.1 \pm 0.2$  Myr obtained from overlying lava layers and intrusive volcanics<sup>47</sup> adds support to this conclusion<sup>41,42</sup>. Moreover, <sup>40</sup>Ar–<sup>39</sup>Ar dates of  $139.4 \pm 0.19$  Myr obtained from the underlying Tuchengzi Formation (demonstrating an earliest Cretaceous, Berriasian age for this unit)<sup>42</sup> confirm that the succeeding Jehol Group was deposited during the Cretaceous period. An Early Cretaceous age is also supported by numerous biostratigraphical correlations<sup>5,8,43</sup>, although some of these present minor conflicts with radiometric dating, placing the deposits in the basalmost Cretaceous (Berriasian/Valanginian stages). An <sup>40</sup>Ar–<sup>39</sup>Ar date of  $110.59 \pm 0.52$  Myr has been obtained from an intrusive basalt within the Jiufotang Formation of Inner Mongolia, indicating an Aptian age for this formation in an adjacent region of northeast China<sup>48</sup>. Consequently, we regard the Jehol Biota as Late Hauterivian to Early Aptian in age, and to have existed for a minimum of 18 Myr.

**Vertebrate palaeontology**

The vertebrate fauna includes osteichthyan fish<sup>4,49</sup>, lissamphibians (discoglossid anurans<sup>50</sup>, various urodeles<sup>51</sup>), chelonians (sinemydids<sup>4</sup>), choristoderes<sup>52,53</sup>, squamates<sup>54</sup>, pterosaurs (anurognathids<sup>24,55</sup>, pterodactylids<sup>56</sup>, ctenochasmatids<sup>55</sup>) and dinosaurs (undescribed sauropods<sup>22</sup>, ornithopods<sup>36,57</sup>, ceratopians<sup>30,35,58</sup> and an ankylosaur<sup>59</sup>). Some species (birds, choristoderes, salamanders and fishes) are known from hundreds of specimens. The most significant discoveries are undoubtedly the non-avian coelurosaurian theropods, the diverse avifauna and a variety of mammals, all of which have impacted on wide-ranging evolutionary debates.

Material from the Jehol Biota has greatly augmented and strengthened the hypothesis that birds are direct descendants of theropod dinosaurs, and has provided new insights into the origin of feathers and of flight, as well as the physiological status of dinosaurs and early birds<sup>60,61</sup>. Its diverse theropod fauna spans the phylogenetic transition from basal coelurosaurians to ornithurine birds (Figs 3 and 4). The basal coelurosaur *Sinosauropteryx* possesses an extensive covering of filamentous integumentary structures<sup>13</sup> (Fig. 4), which are considered to be the precursors of true feathers<sup>27</sup>. Identical structures are also known in the therizinosauroid *Beipiao-*



**Figure 1** Palaeogeographical setting of the Jehol Biota. **a**, Modern-day map showing different geographical extents of the Jehol Biota through time. I, Yixian Formation and its lateral equivalents (Late Hauterivian/Barremian); II, Jiufotang Formation and its lateral equivalents (Early Aptian); modified from ref. 4. The filled square marks the position of the major vertebrate-bearing sites in Liaoning Province. Insect faunas from penecontemporaneous units in Kazakhstan are remarkably similar to those from the Jehol Biota, and may indicate a westward extension of these ranges<sup>71</sup>.

**b**, Palaeogeographic map of eastern Asia in the Lower Cretaceous, showing major regional tectonic features (modified from ref. 99). The arrow indicates the approximate position of outcrop of the Yixian and Jiufotang Formations in northeastern China. This region would have occupied a palaeolatitude of approximately 40–45° N during the late Mesozoic era<sup>18,99</sup>. Abbreviations refer to major tectonic divisions: EUR, Europe; INC, Indo-China; IND, India; J, Japan; JUN, Junggar; K, Korea; KAZ, Kazakhstan; LH, Lhassa; MON, Mongolian; NCB, north China; QI, Qiangtang; SCB, south China; SH, Shan Thai; SIB, Siberian; TAR, Tarim.

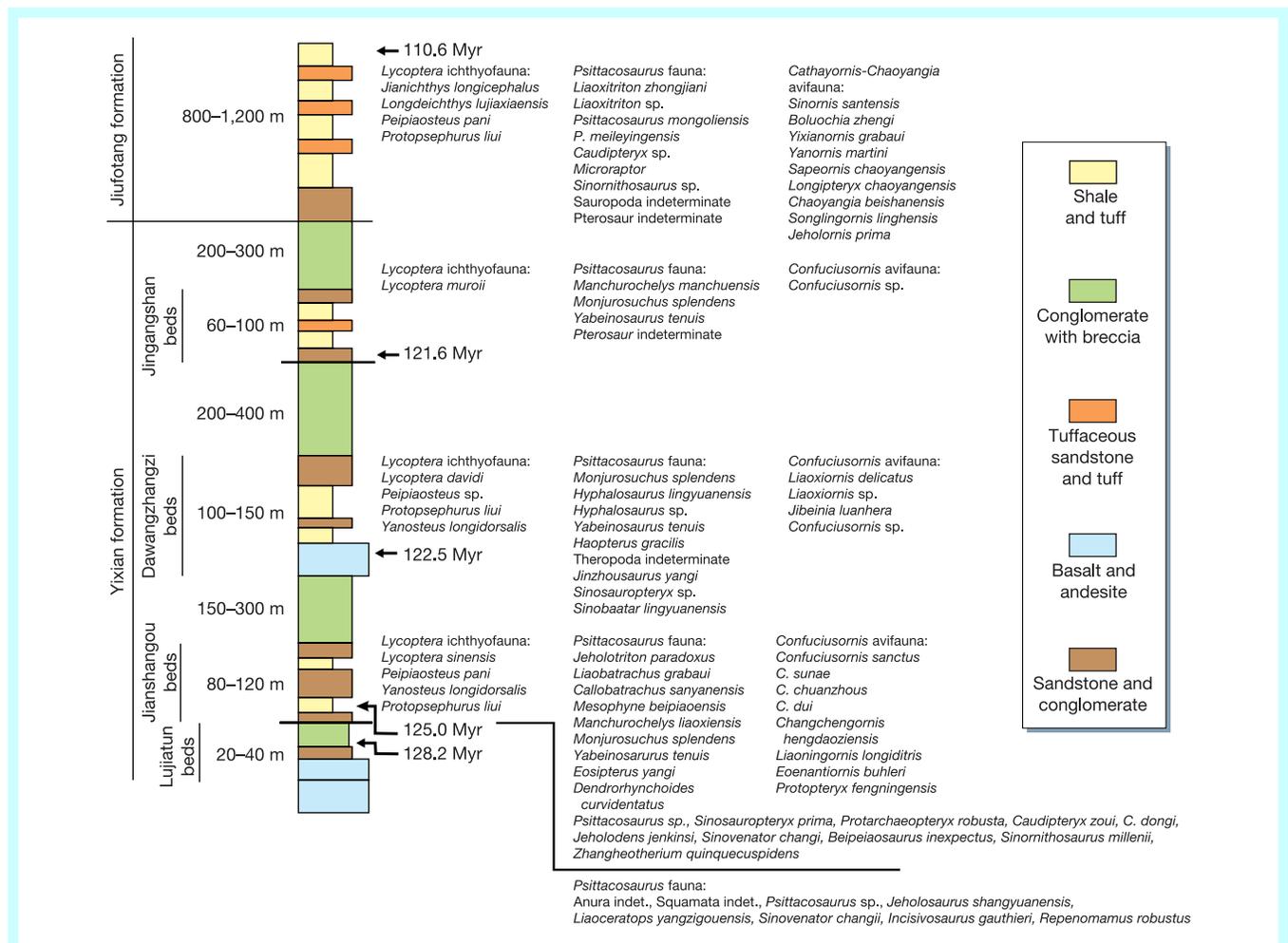
saurus<sup>25</sup>. In contrast, the basal oviraptorosaurian *Caudipteryx* and the enigmatic coelurosaur *Protarchaeopteryx* definitely bear feathers of modern appearance<sup>14</sup>, in which a central rachis supports a branching pattern of barbs (Fig. 4). Similar feathers are present in Jehol dromaeosaurs, including *Sinornithosaurus*<sup>26,27</sup> and several undescribed taxa<sup>28,29</sup>. All of these animals lacked flight specializations, and most were ground-dwelling cursorial animals, indicating that the selective pressures responsible for initiating the development of feathers were imposed before the origin of flight<sup>60,61</sup>. This conclusion is underlined by the appearance of ‘protofeathers’ in basal coelurosaurians that were distant relatives of birds<sup>13,27,61</sup> (Fig. 3). Increasing feather complexity in oviraptorosaurians and dromaeosaurids accords well with their status as progressively more derived avian outgroups (Figs 3 and 4). Recognition of true feathers in these non-avian dinosaurs demonstrates that feathers are not unique to birds, but had a broader phylogenetic distribution within Theropoda<sup>60,61</sup>.

As the origin of feathers is not correlated with the origin of flight, other functions must be sought for protofeathers and the earliest true feathers<sup>61</sup>. Sexual display, camouflage, species recognition and thrust generation during running/jumping are plausible hypotheses that may account for the origin of varied feather types, although all of these suggestions are difficult to test on the basis of palaeontological evidence<sup>61</sup>. These integumentary structures would certainly have had a considerable effect on the thermoregulatory strategies of

these animals, and may have had an important role in the evolution of brooding behaviour<sup>61</sup>.

The presence of feathers in *Caudipteryx* and *Protarchaeopteryx* has been dismissed as a vestige of secondary flightlessness, and the identification of these structures as integumentary features has been questioned<sup>62</sup>, but these interpretations have not been supported by other studies. Phylogenetic evidence demonstrates emphatically that these animals were primarily flightless non-avian theropods, not secondarily flightless basal birds, and detailed anatomical observations confirm the integumentary derivation of these structures<sup>61</sup>. Moreover, the feathers of *Sinornithosaurus* and integumentary structures of *Sinosauropteryx* are consistent with models of feather evolution and development based on neontological evidence<sup>27</sup>.

*Microraptor*, another Jehol theropod with true feathers, is the smallest known dromaeosaurid (trunk length approximately 50 mm)<sup>63</sup>. It exhibits several pedal characteristics that have been suggested as potentially consistent with a climbing/perching mode of life, whereas other features of the skeleton demonstrate that it was not a volant or secondarily flightless animal. The discovery of this possibly arboreal dromaeosaurid has contributed to the debate over the origin of flight, and has been cited as evidence for the now heterodox view that flight originated from the trees down (by gliding and jumping down from trees), rather than from the ground up (by running and leaping for prey)<sup>63</sup>. However, detailed



**Figure 2** Composite stratigraphic log of the Yixian and Jiufotang Formations in Liaoning Province, showing the positions of radiometrically dated horizons. Vertebrate faunas are listed for each horizon (modified from ref. 6). The Yixian Formation reaches a

maximum thickness of 4,700 m, whereas the less extensive Jiufotang Formation reaches 1,650 m<sup>17</sup>.

functional morphological studies on *Microraptor* have not yet been attempted and are needed to test its proposed arboreal mode of life.

The high diversity and abundance of birds in the Jehol fauna provides a unique window onto the adaptive radiation and palaeoecology of early avians<sup>64–67</sup>. Body size and locomotory differences between sympatric Jehol taxa indicate that a rapid ecological diversification of avian taxa occurred during the Early Cretaceous<sup>66,67</sup>. Several taxa (*Jeholornis*, *Sapeornis* and *Confuciusornis*) lie outside Ornithothoraces (Fig. 3) and help to determine the sequence of acquisition of typical avian features, such as cranial kinesis, the horny beak, and the pygostyle (Figs 3 and 4)<sup>31,64,67</sup>. *Confuciusornis* is represented by hundreds of specimens from the same locality, suggesting a mass mortality event and/or gregarious behaviour, and allowing the potential for studies of sexual dimorphism and population structure<sup>31</sup>. *Sapeornis* is the largest Early Cretaceous bird and its extremely elongated forelimbs suggest that it may have been a soaring form<sup>64</sup>. Enantiornithine birds are common and are represented by the basal form *Protopteryx*<sup>32</sup>, with its unusual scale-like tail feathers, and *Longipteryx*, which possessed much longer wings than other known enantiornithines, which suggest a rather different ecology<sup>65</sup>. Ornithurine birds are generally diverse but numerically rare, and included the basalmost ornithurine *Liaoningornis*, a small perching form, and the larger *Yixianornis* and *Yanornis*<sup>66</sup>. The latter possessed an advanced flight apparatus, including an elongated, deeply keeled sternum and a coracoid of ‘modern’ appearance, both of which indicate strong flight capability (Figs 3 and 4). The presence of an intact seed mass in the preserved stomach contents of *Jeholornis* provides a specific instance of plant–animal interaction and indicates that frugivory appeared early in avian history<sup>67</sup>.

The Jehol Group also yields important evidence on the evolutionary history of Cretaceous mammals. Six genera are known,

including basal forms (the eutriconodont *Jeholodens*<sup>68</sup> and the gobiconodontids *Repenomamus*<sup>38,39</sup> and *Gobiconodon* sp.<sup>38</sup>) and more derived taxa (the symmetrodont (basal therian) *Zhangheotherium*<sup>15</sup>, the multituberculate *Sinobaatar*<sup>69</sup> and the basal eutherian *Eomaia*<sup>33</sup>). Each genus provides many character states amenable to phylogenetic analyses that in turn have elucidated sequences of character acquisition in Theria and Eutheria. For example, *Jeholodens* exhibits a mosaic of therian and non-therian character states<sup>68</sup>, *Repenomamus* provides new information on the evolution of the mammalian middle ear and feeding apparatus<sup>38</sup>, and *Zhangheotherium* demonstrates that a parasagittal gait was not characteristic of basal therians<sup>15</sup>. Of equal importance, the occurrence of *Eomaia* extends the range of eutherians into the Early Cretaceous, and indicates a pre-Barremian origin for the group that is much earlier than the origination dates posited by previous palaeontological and molecular clock studies<sup>33</sup>. These fossils also offer a rare glimpse into the functional morphology and palaeoecology of Cretaceous mammals, which are usually known solely from dental material. *Eomaia* has limb and phalangeal proportions that are characteristic of extant arboreal and scansorial mammals<sup>33</sup>, whereas *Zhangheotherium* and *Jeholodens* lack these specializations and were probably ground dwellers<sup>15,68</sup>. The presence of epipubic bones in *Eomaia* suggests that it carried its young in a pouch, much like extant marsupials<sup>33</sup>. The dentitions of all six taxa are consistent with insectivory or carnivory, and the animals ranged in size from *Jeholodens* (snout–vent length of about 50 mm)<sup>68</sup> to *Repenomamus* (skull length of 110 mm)<sup>38</sup>, one of the largest Mesozoic mammals. These differences in body size and locomotory features indicate that mammals had diversified into a number of ecological roles by the late Early Cretaceous.

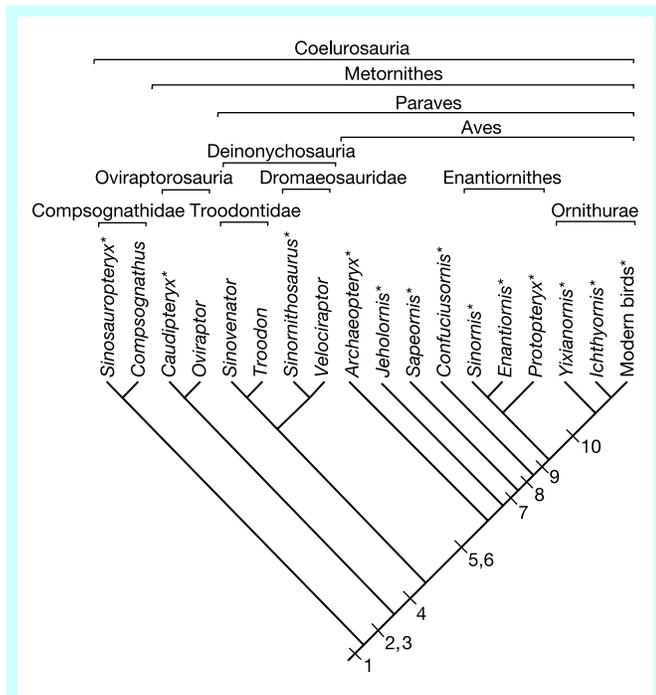
### Invertebrate palaeontology

Invertebrates are the most abundant elements of the biota (Fig. 5)<sup>4</sup>. Nevertheless, although several groups have been studied intensively by biostratigraphers and taxonomists (for example, conchostracans), this work has had only limited effects on more general phylogenetic and palaeobiological issues. Much of the invertebrate material has yet to be described in detail and remains poorly known. Preliminary studies indicate that the diverse invertebrate fauna (Fig. 5) contained insects (Ephemeroptera, Odonata, Blattoidea, Hemiptera and Diptera)<sup>4,70,71</sup>, spiders, crustaceans (Ostracoda, Notostraca, Conchostraca, Decapoda, Peracarida)<sup>4,72</sup>, bivalves<sup>4</sup> and gastropods<sup>4</sup>. The discovery of brachyceran flies with long tubular mouthparts suggests the presence of nectar-producing angiosperms in the Jehol flora<sup>71</sup>, provides circumstantial support for the suggestion that pollinating insects might have had an important role in the origin and early evolution of flowering plants, and may suggest long-lived plant–insect associations<sup>71,73</sup>.

### Palaeobotany

The Jehol flora is abundant, diverse and conifer dominated. It also contains bryophytes, lycopsids, sphenopsids, ferns, bennettitaleans, czekanowskialeans, ginkgoaleans, gnetaleans<sup>4,21</sup> and enigmatic plants including putative early angiosperms<sup>16,21,74</sup>. The latter, although rare, have been proposed as the oldest flowering plants<sup>16,21,74</sup> and have received disproportionate attention owing to their possible relevance to the origin and early radiation of angiosperms. Most of these ‘angiosperms’ have now been discredited<sup>21</sup>, and only *Archaeoartus*<sup>16,21,74</sup> is currently thought to represent a stem-group flowering plant. In our view, however, the affinities of this taxon remain controversial.

*Archaeoartus* contains three species: *A. liaoningensis*<sup>16,21,74</sup>, *A. sinensis*<sup>74</sup> and a third unnamed species<sup>21</sup>. ‘Flowers’ of *Archaeoartus* contain male and female reproductive organs on the same shoot (Fig. 6). Male organs comprise paired, bilaterally symmetrical shoot stamens with slender filaments and long anthers, apparently containing two pollen sacs with monosulcate pollen. Stamens occur



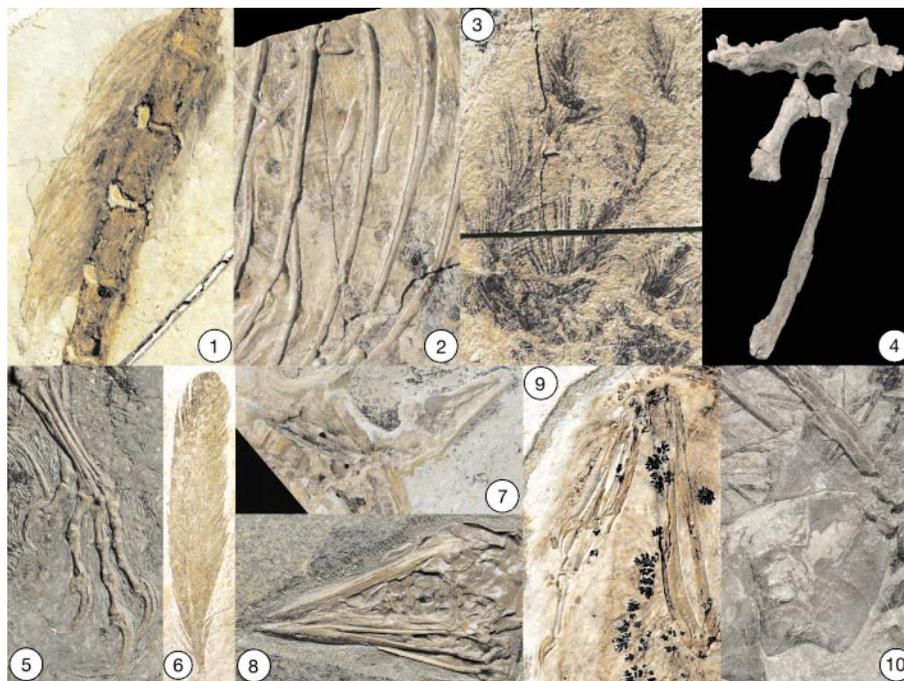
**Figure 3** Cladogram illustrating the relationship of birds with major clades of non-avian coelurosaurian theropods (based on refs 34, 64, 67). The numbers in circles at each branching node indicate the first appearance of key morphological characters. 1, unbranched feathers; 2, uncinat processes on ribs; 3, true branched feathers; 4, retroverted pubis; 5, reversed hallux; 6, asymmetrical flight feathers; 7, pygostyle; 8, horny beak; 9, alula (bastard wing); 10, large, keeled sternum. Taxa indicated with an asterisk are known to have possessed either protofeathers or true feathers.

below the female organs, mature first, and are abscised through ontogeny<sup>21,74</sup>. Female organs are interpreted as stalked conduplicate carpels with adaxially elongated stigmatic crests. Carpels contain numerous obliquely oriented ovules (*A. liaoningensis*, 2–4; *A. sinensis*, 8–12)<sup>21,74</sup>. Leaves are pinnately compound, highly divided and may be abscised<sup>21,74</sup>. *Archaeofructus* lacked petals, sepals and other organs associated with stamens and carpels<sup>16,21,74</sup>. Its flowers, therefore, are unlike those of both extant basal angiosperms<sup>74,75</sup> and those Lower Cretaceous basal forms (in some cases referable to Nymphaeales) that possess small, compact flowers<sup>75,76</sup>. The absence of these floral features, noted in most *bona fide* angiosperms<sup>75,76</sup>, demonstrates that *Archaeofructus* does not belong within the angiosperm crown group, although it is conceivable that it lies on the angiosperm stem lineage. *Archaeofructus* shares several similarities with other Mesozoic seed plants such as *Caytonia*<sup>74</sup>, from which it is apparent that its inferred phylogenetic position remains weakly supported<sup>77</sup>. This problem is compounded by a lack of unambiguous anatomical data supporting key features in *Archaeofructus*. Specifically, we regard the presence of two pollen sacs in each of the thecae as unproven, and although it was suggested that the ovules of *Archaeofructus* were enclosed in a carpel<sup>16,21,74</sup>, the description of this structure lacks sufficient detail to identify synapomorphic characters that would link it specifically with angiosperms. This is important as carpel-like structures are known in other seed plants that are distantly related to angiosperms, such as caytonialeans<sup>75,78,79</sup>. On the basis of available published data, it is currently impossible to determine whether the ovule-enclosing structure in *Archaeofructus* is a carpel, or merely carpel-like. Several other important features that would influence the phylogenetic position of *Archaeofructus* (such as cuticular structure, shoot anatomy

and ovule histology) are also unknown. Therefore, we cannot unquestioningly accept *Archaeofructus* as an angiosperm.

If *Archaeofructus* is a stem-group angiosperm, the Late Hauterivian/Early Aptian age of the deposits indicates that it significantly post-dates the first appearance of crown-group angiosperms<sup>5</sup>. Consequently, *Archaeofructus* cannot represent the oldest known flowering plant. It would, however, offer insights into the origin of the crown group and of the character states associated with it. For example, its morphology suggests it to have been herbaceous and aquatic, indicating that flowering plants might have evolved in riparian environments where competition with other seed plants was, perhaps, less intense<sup>74,77</sup>. The apparently paired stamens in *Archaeofructus* could indicate that basal flowering plants bore male and female organs on separate shoots and that these later evolved into shorter bisexual flowers<sup>74,77</sup>, and that stamens are remnants of earlier branching systems<sup>74</sup>. Ideally, *Archaeofructus* needs to be included in more exhaustive cladistic analyses with wider taxon sampling of fossil plants (Bennettitales, Caytoniales and extinct Gnetales) that are known to be of relevance to angiosperm origin<sup>75,79</sup>, and using a greater range of morphological characters<sup>79</sup>. Although *Archaeofructus* may be the sister clade of crown-group angiosperms<sup>74</sup>, the possibility that it represents a previously unrecognized group of seed plants cannot at this stage be excluded.

Non-angiosperms in the flora have received little attention so far, but several studies have attempted to place the Jehol plants within wider biostratigraphical, regional and phylogenetic contexts. For example, Jehol gnetaleans contribute significantly to our knowledge of the evolutionary history of this paucispecific group. These plants possess features that allow them to be affiliated with extant genera: for example, three *Ephedrites* species (see Fig. 6 for an example)



**Figure 4** Vertebrate fossils from the Jehol Biota, illustrating key morphological changes during the transition from non-avian coelurosaurs to modern birds. Numbering of the following figures corresponds to the sequence of acquisition of the various character states shown on the cladogram in Fig. 3: 1, unbranched, filamentous integumentary structures associated with the tail of *Sinosauropteryx* sp. (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP) V12415); 2, *Caudipteryx dongi* (IVPP V12344), showing the presence of uncinata processes on the

dorsal ribs; 3, feathers of modern, branched appearance from *Caudipteryx* sp. (IVPP V12430); 4, retroverted pubis of *Sinovenator zhangii* (IVPP V12615); 5, pes of *Confuciusornis sanctus* (IVPP V12352) showing reversed hallux; 6, asymmetrical flight feather of *Archaeopteryx lithographica* (Tithonian, Germany); 7, pygostyle of *Sapeornis chaoyangensis* (IVPP V13275); 8, *Confuciusornis sanctus*, showing preservation of a horny keratinous beak (IVPP V12352); 9, the alula of *Protopteryx fengningensis* (IVPP V11665); 10, keeled sternum of *Yixianornis graubi* (IVPP V12631).

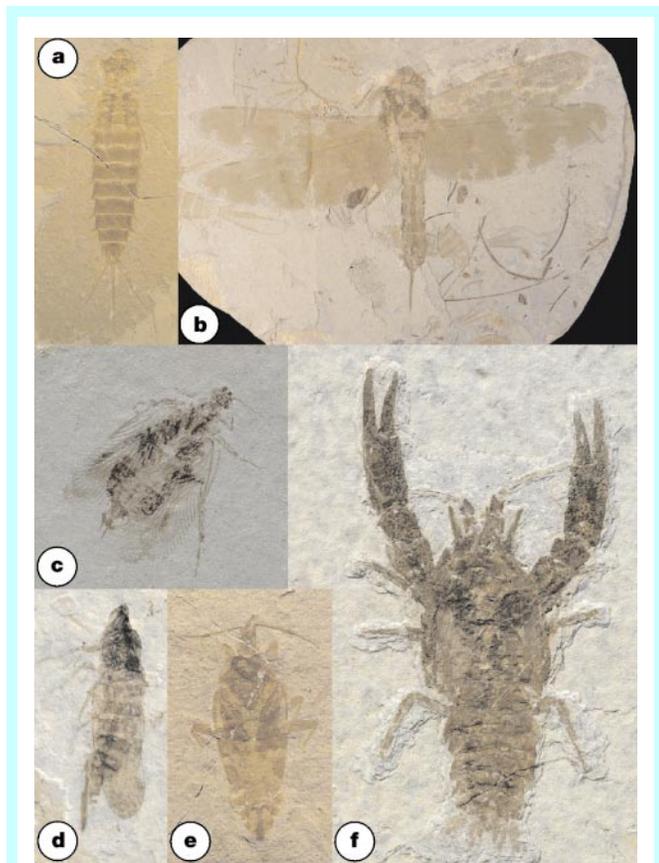
are closely related to living *Ephedra*<sup>21</sup>. Similarly, the Jehol form *Gurvanella* (see Fig. 6 for an example) is reproductively similar to extant *Welwitschia*<sup>21</sup>, but resembles extant *Ephedra* in its vegetative features. These observations support a closer relationship between *Ephedra* and *Welwitschia* than usually proposed<sup>80</sup>, and suggest a relatively recent, pre-Barremian, divergence of families including extant genera<sup>79</sup>. The vegetative morphology of *Gurvanella* (Fig. 6) is typical of most gnetaleans, but differs radically from that of closely related extant *Welwitschia*, supporting the hypothesis that the latter is highly derived and adapted to extreme environmental conditions. Most Jehol conifers represent typical Mesozoic forms (Fig. 6), although some have been considered to be equivalents of living genera (*Podocarpites*, *Araucarites*<sup>4,21</sup>). Similarly, the Jehol sphenop-sid *Equisetites* bears a strong resemblance to the living horsetail *Equisetum*<sup>4,21</sup>. In both cases, the similarity of these plants to extant genera, in combination with the age of the deposits, suggests that Jehol plants bridge chronological and evolutionary gaps between Mesozoic plants and their living relatives. As a result, they should be able to contribute significantly to debates on conifer phylogeny and the origin of modern horsetails.

**Palaeobiogeography: a refugium, a cradle or both?**

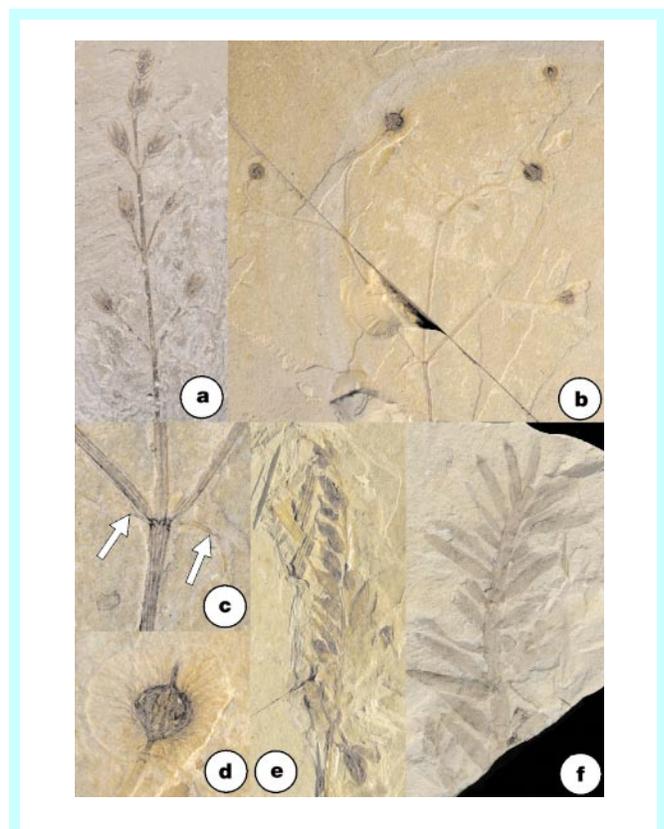
Although radiometric dating and biostratigraphical correlations provide overwhelming evidence for an Early Cretaceous age, the

closest relatives of several Jehol taxa are from Late Jurassic, or older, deposits. This pattern has prompted the hypothesis that east Asia acted as a refugium for some of these more typically ‘Jurassic’ taxa in the Lower Cretaceous<sup>81</sup>. Such ‘relicts’ include the theropod dinosaur *Sinosauropteryx* (sister taxon of the Upper Jurassic *Compsognathus*) and the anurognathid pterosaur *Dendrorhynchoides* (no other post-Jurassic anurognathids are known currently). Palaeogeography and the composition of terrestrial vertebrate faunas provide some support for this hypothesis, as eastern Asia seems to have been isolated from the rest of Laurasia during Middle Jurassic to Early Cretaceous times<sup>82–84</sup>. Potential isolating mechanisms included the Mongol–Okhotsk Sea between eastern Asia and Siberia, the epicontinental Turgai Sea between Europe and Central Asia, and breaches in the tenuous Junggar–Tarim–Mongolian land bridge, which had linked east Asia with the rest of Laurasia during the Triassic and Early Jurassic<sup>82,83</sup>. The occurrence of a relict tritylodontid synapsid (a group thought to have become extinct at the end of the Middle Jurassic) in the Early Cretaceous of Japan<sup>85</sup> adds some support to the refugial hypothesis, as does the presence of several endemic plant and vertebrate clades in eastern Asia at this time, including *Archaeofructus*, psittacosaurid dinosaurs, testudinoid turtles, and sinamiid and peipiaosteiid freshwater fishes<sup>4,16,30,58,86,87</sup>.

The palaeobiogeographical history of this region was complex, and the composition of the Jehol Biota is only partly explained by



**Figure 5** Selected invertebrates from the Jehol fauna. **a**, A larval specimen of the biozonal ephemeropteran insect *Ephemeropsis trisetalis* (IVPP I0237). **b**, Adult specimen of *Aeschnidium heishankowense* (Insecta: Odonata) (Nanjing Institute of Geology and Palaeontology (NIGP) B930042-2). **c**, Undescribed cockroach (Blattoidea) referable to the Mesoblattinidae (IVPP I0076). **d**, An undescribed procercopid (Hemiptera) insect (IVPP I0050). **e**, Hemipteran insect (*Mesanthocoris* sp.: NIGP, uncatalogued specimen), note the well-preserved stylus. **f**, The crayfish *Cricoidoselosus aethus* (IVPP I0041).



**Figure 6** Selected plants from the Jehol flora. **a**, Fertile shoot of the gnetalean *Ephedrites* sp. (IVPP B0129). **b**, Fertile branching system of the gnetalean *Gurvanella* (holotype of *Chaoyangia liangii* Duan 1998; specimen 9341). **c**, Branching structure of *Gurvanella* sp. demonstrating ribbed stem, nodal architecture and small leaves originating at the level of branching (arrowed), consistent with gnetalean affinities. **d**, Seed of *Gurvanella* sp. with delicate wing and *Welwitschia*-like morphology. **e**, Fertile shoot of the putative basal angiosperm *Archaeofructus liaoningensis* with ovulate units distal on the shoot, and male organs proximal (IVPP B0161). **f**, Broad-leaved conifer, *Cephalotaxopsis* sp. (IVPP B0048).

the refugium hypothesis<sup>88</sup>. In addition to the various relict and endemic taxa listed above, east Asian Lower Cretaceous faunas also contained early, and in many cases basal, representatives of dinosaur clades that are more often associated with Upper Cretaceous biomes (for example, tyrannosauroid<sup>89</sup>, therizinosauroid and oviraptorosaurian theropods<sup>14,25,37,88</sup>, and neoceratopians<sup>35</sup>), suggesting that this region could also be regarded as a centre of diversification for some of these taxa<sup>88</sup>. These faunas also include members of several clades that have a more cosmopolitan Early Cretaceous distribution, including various dinosaurs (iguanodontian ornithopods<sup>57</sup>, titanosauriform sauropods<sup>90</sup>, nodosaurid ankylosaurs<sup>59</sup>, dromaeosaurid theropods<sup>26–29</sup>), discoglossid frogs<sup>50,91</sup>, paramacellodid lizards<sup>91</sup>, ctenochasmatid pterosaurs<sup>55</sup>, enantiornithine birds<sup>32,65</sup> and an eobaatarid multituberculate mammal<sup>69</sup>. The flora is closely comparable with that from other Lower Cretaceous sites in Mongolia and northern China<sup>92,93</sup> and is broadly similar to contemporaneous floras from other regions. In particular, the Jehol gnetaleans are very similar to those from coeval formations in southern Russia<sup>21</sup> and Brazil<sup>94</sup>. Indeed, in these respects the Jehol Biota can be regarded as a ‘typical’ Early Cretaceous biome, and is broadly comparable to penecontemporaneous terrestrial biomes from western Europe, North and South America, Africa and Australia. Most palaeobiogeographical models suggest that Asian isolation ended close to the end of the Early Cretaceous, sometime during either the Aptian or Albian stages<sup>82–84</sup>. However, the presence of titanosauriform, dromaeosaurid and iguanodontian dinosaurs in the Jehol Biota and in other east Asian faunas (from the Berriasian/Barremian of China, Japan, Korea and Thailand) indicates that isolation must have ended earlier in the Cretaceous, perhaps in the Berriasian<sup>90</sup>.

Why did east Asia host a combination of relicts, cosmopolitan taxa and endemics at this time? The temporal proximity of the Jehol Biota to the time when east Asian isolation ended may offer a partial explanation for the mixed composition of the biome. The presence of relict taxa may simply reflect the long period of isolation through the Middle Jurassic to the earliest Cretaceous, whereas the arrival of more cosmopolitan forms probably signalled the breaching of various palaeogeographical barriers (such as regression of the Turgai Sea)<sup>82–84,88,90</sup>. The Jehol Group can be viewed as a window on succession in an Early Cretaceous terrestrial biome, in which an established biota merged with and was partially replaced by a novel biota composed of immigrants and new taxa that were evolving *in situ*. The high degree of endemism is probably explicable in terms of east Asian isolation generally and, more specifically, in the isolation of the Jehol Biota within eastern Asia by additional local palaeogeographical barriers (such as the Qing and Dabieshan Mountains<sup>7</sup>).

### Collection strategies and associated problems

Advances in our understanding of the Jehol Biota have been hampered by illegal collecting<sup>95</sup>, manufacture of faked and composite specimens (as in the ‘*Archaeoraptor*’ debacle<sup>95,96</sup>), illegal sale and export of fossils<sup>97,98</sup>, and difficulties in the acquisition of specimens by international scientific institutions bound by ethical collecting standards<sup>98</sup>. Currently, the main problem for legitimate scientific investigation is collection by private individuals. Such collectors do not record the contextual information of locality, stratigraphy and sedimentology essential for placing the organisms within their palaeoenvironmental and taphonomic settings. To bypass these problems, and to advance research on this important biome, excavations sponsored by research institutes, under the supervision and guidance of local authorities, must become the norm. Systematic, responsible collecting and vigilant site management are needed to stop the loss of important and unique specimens.

### Conclusions

The spectacular fossils of the Jehol Group have already provided many important insights into the evolution of birds, angiosperms

and mammals. Nevertheless, the rate of fossil discovery presently outstrips the rate of description, and detailed monographic treatments of all species from the biota are needed if the full potential of these deposits is to be realized. The Jehol Biota currently represents our best chance of viewing the composition and dynamics of an intact Early Cretaceous terrestrial ecosystem: continuing study of the fauna, flora, taphonomy and palaeoenvironment is likely to yield exciting new results for years to come.

*Note added in proof:* New material of the dromaeosaurid theropod *Microraptor* indicates that this animal possessed wing-like arrays of asymmetrical feathers<sup>100</sup> on both its fore- and hindlimbs. This observation provides additional support for the hypothesis that this taxon was an arboreal glider. □

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