age of the last common ancestor of lorisiforms and lemuriforms ranged from 49.7 to 53.3 Myr ago (95% confidence interval = 46.9–57.3 Myr ago).

Given that molecular dating has consistently supported an earlier origin for crown lemuriforms than for crown lorisiforms[1,3,6], and that palaeontological sampling of the early crown strepsirrhine radiation remains woefully inadequate[8,28], it is remarkable that such early dates are likely to considerably underestimate the true antiquity of the lemuriform–lorisiform split. Nevertheless, by doubling the previous minimum paleontological estimate for the age of crown Lorisiformes, *Karanisia* and *Saharagalago* provide the first convincing fossil evidence attesting to such an ancient origin for crown Strepsirrhini, and further bolster the hypothesis that that clade originated on the Afro-Arabian landmass[1,3]. These taxa also help to inform at least one other major outstanding issue within the clade—the timing of the lemuriform colonization of Madagascar[9]. Although Marivaux *et al.*[7] have recently suggested that early Oligocene *Bugtilemur* from Pakistan is a cheirogaleid lemur specifically aligned with extant *Cheirogaleus* (a conclusion that we must view with skepticism given *Bugtilemur*'s location and age), the current restriction of lemurs to Madagascar would, nevertheless, still be most parsimoniously explicable as the result of a single invasion[1,3]. As molecular data suggest that *Daubentonia* diverged from other crown lemuriforms very shortly after the appearance of crown strepsirrhines[1,3,6], and before the divergence of galagids from other lorisiforms, it is now reasonable to infer that, at the very latest, lemurs reached Madagascar by the late middle Eocene. □

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Earliest known crown-group salamanders

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Salamanders are a model system for studying the rates and patterns of the evolution of new anatomical structures[1–4]. Recent discoveries of abundant Late Jurassic and Early Cretaceous salamanders are helping to address these issues[5–8]. Here we report the discovery of well-preserved Middle Jurassic salamanders from China, which constitutes the earliest known record of crown-group urodeles (living salamanders and their closest relatives). The new specimens are from the volcanic deposits of the Jiulongshan Formation (Bathonian)[9–13], Inner Mongolia, China, and represent basal members of the Cryptobranchidae, a family that includes the endangered Asian giant salamander (*Andrias*) and the North American hellbender (*Cryptobranchus*). These fossils document a Mesozoic record of the Cryptobranchidae, predating the previous record of the group by some 100 million years[14–17]. This discovery provides evidence to support the hypothesis that the divergence of the Cryptobranchidae from the Hynobiidae had taken place in Asia before the Middle Jurassic period.

Amphibia Linnaeus, 1758
Lissamphibia Haeckel, 1866
Caudata Scopoli, 1777
Urodela Dumeril, 1806
Cryptobranchoidea Dunn, 1922
Cryptobranchidae Fitzinger, 1826
Chunerpeton tianyiensis gen. et sp. nov.

Holotype. Chinese Academy of Geological Sciences (CAGS)-IG-02051, natural mould of dorsal and ventral aspects of an articulated

skeleton including the cranium and postcranium (Figs 1 and 2).
Etymology. Chu (Pinyin) meaning early and herpeton (Greek) meaning creeping animal; tianyi, ancient country name for Ningcheng.
Locality and horizon. Daohugou, Ningcheng County, Inner Mongolia, China; Middle Jurassic Jiulongshan Formation (Bathonian, 161 million years (Myr) ago)[9–13].
Referred material. Peking University Palaeontology Collections

(PKUP) V0210-0212, specimens preserved as natural moulds of articulated skeletons.
Diagnosis. *Chunerpeton tianyiensis* shares with living cryptobranchoids derived characters including: presacral vertebrae bearing unicapitate ribs; reduction in the number of rib-bearing anterior caudal vertebrae reduced to two or three. *Chunerpeton tianyiensis* shares with cryptobranchids derived characters such as: nasal much
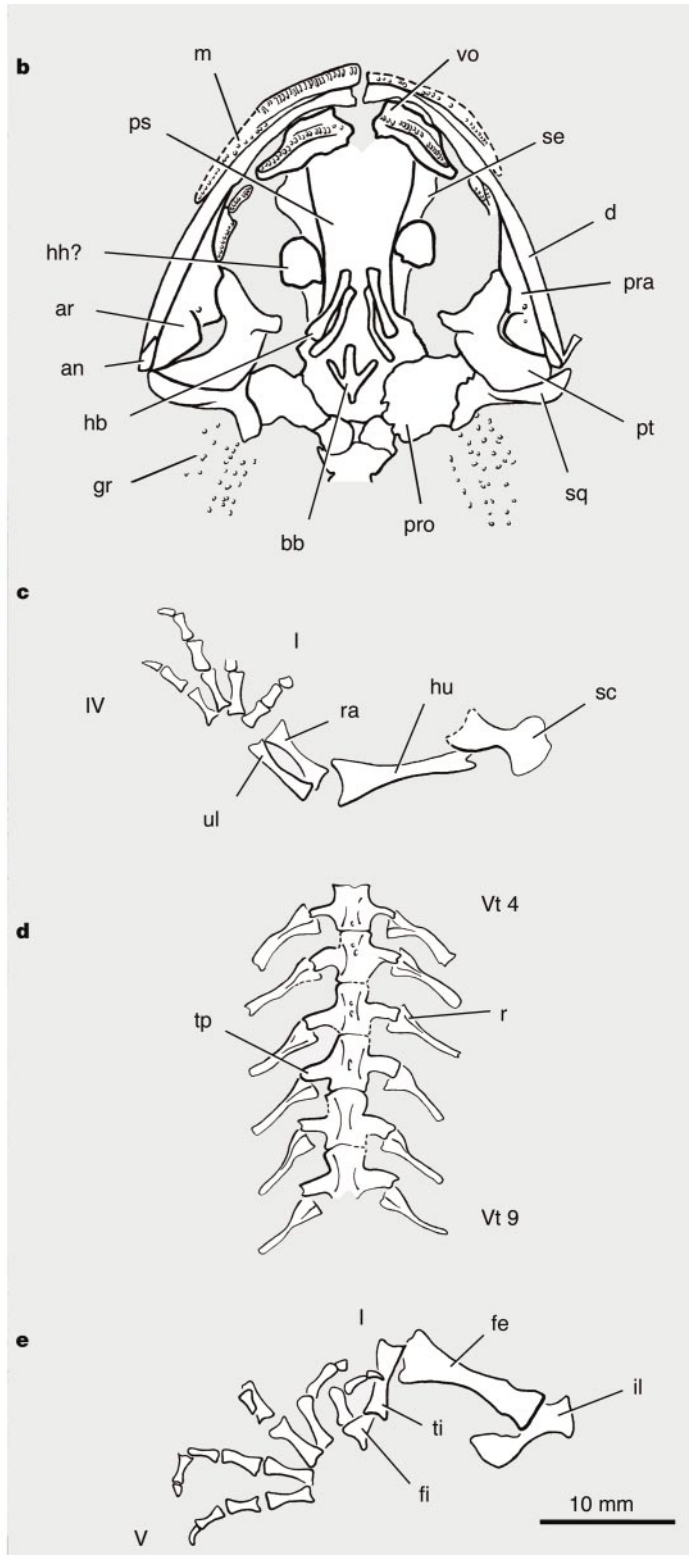

Figure 1 Holotype (CAGS-IG-02051) of *Chunerpeton tianyiensis* gen. et sp. nov. **a**, Natural mould of ventral aspect of entire specimen. **b**, Line drawing of skull in palatal view. **c**, Line drawing of left pectoral girdle and forelimb. **d**, Ventral aspect of anterior trunk vertebrae. **e**, Details of left pelvis and hindlimb. See Fig. 2 for abbreviations.

narrower than interorbital width; nasal–prefrontal contact absent; frontals extend anteriorly to lateral border of nasal; lachrymal absent; anterolateral process of parietal extends along lateral border of frontal; internal carotid foramina penetrate palatal surface of parasphenoid. *Chunerpeton tianyiensis* differs from extant crypto-branchids in lacking midline contact of dorsal processes of pre-maxillae; frontal–maxillary contact absent; absence of contact between anterolateral process of parietal and prefrontal; vomers without posterior extension; retention of palatal fenestra between

vomers; presence of distinct medial process of pterygoid; pterygoid–parasphenoid contact absent; basibranchial II ossified and trident-shaped; first three pairs of ribs with spatulate distal end; phalangeal formula of 2-2-3-(3/4)-3 in pes.

The new salamander fossils were recovered from volcanic depos-its of pale-grey shales and tuffs at Daohugou Village, Inner Mon-golia, China. Virtually all of the 200 specimens recovered from the site are larval or subadult individuals with articulated skeletons, many of which preserve evidence of soft tissues. The assessment of
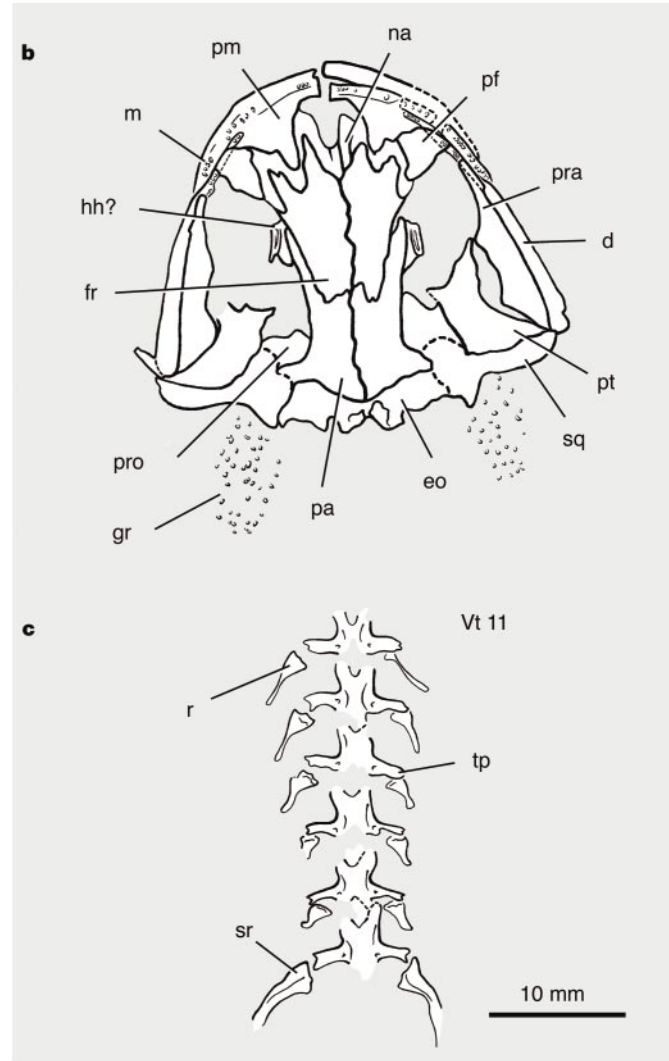

Figure 2 Holotype (CAGS-IG-02051) of *C. tianyiensis* gen. et sp. nov. **a**, Natural mould of dorsal aspect of entire specimen. **b**, Line drawing of skull in dorsal view. **c**, Line drawing of posterior trunk vertebrae in dorsal view. an, angular; ar, articular; bb, basibranchial; d, dentary; eo, exoccipital; fe, femur; fi, fibula; fr, frontal; gr, gill rakers; hb, hypobranchial; hh?, hypohyal?; hu, humerus; il, ilium; m, maxilla; na, nasal; pa, parietal; pf, prefrontal; pm, premaxilla; pra, prearticular; pro, pro-otic; ps, parasphenoid; pt, pterygoid; r, rib; ra, radius; sc, scapula; se, sphenethmoid; sq, squamosal; sr, sacral rib; ti, tibia; tp, transverse process; ul, ulna; vo, vomer; vt, vertebra.

the Middle Jurassic (Bathonian) age of the fossil beds is based on biostratigraphic analysis of insect and vertebrate assemblages[9–13]. Therefore, these fossils represent the earliest known relatives of living salamanders, as other Middle Jurassic forms (such as *Kokartus* and *Marmorerpeton*) lie outside the crown group[18,19].

The holotype of the new taxon has a total length of approximately 180 mm. Despite its large size, this specimen retains juvenile features such as incomplete ossification of the nasals and the presence of short external gills. Impressions of the gill rakers are preserved in the gill chamber (Figs 1 and 2). These features indicate that the holotype was probably a neotenic form like its extant cryptobranchid relatives. Details of the body wall and tail are preserved. All of the bony tissues have been largely dissolved during fossilization; consequently, the skeleton is preserved as a natural mould that includes such details as sculptured surfaces on the parietals, squamosals, and the dorsal aspect of the pterygoids. The exceptional preservation of the specimen provides a variety of osteological and soft tissue characters to refer it to the Cryptobranchidae.

In addition, the new fossil assemblage includes a small larval specimen that shows remarkable preservation of soft tissues, with evidence of eyes, gill filaments, tail keel, tail seam, and notochord (Fig. 3). Also, there is incomplete ossification of the skull, vertebral column and phalanges. Abundant intact conchostracans in the gut cavity indicate recent feeding behaviour for this individual. Although the lack of specific adult features makes it difficult to refer the larval form to the new taxon, the presence of unicapitate ribs supports its definitive inclusion in the Cryptobranchoidea.

Most phylogenetic hypotheses recognize that the Cryptobranchidae and the Hynobiidae form a monophyletic basal clade, the Cryptobranchoidea[5,20–22]. The split between the two groups is an important historical event in salamander evolution. Unfortunately, little is known about when and where this event took place. Until now, the earliest record of hynobiids was in the Miocene epoch (about 5.2 Myr) of Europe[23], and that of cryptobranchids in the Palaeocene epoch (about 56 Myr) of both Asia and North America[14–16]. The presence of *Chunerpeton* in the Middle Jurassic of China implies that the split between hynobiids and cryptobranchids occurred before that time in Asia (Fig. 4). The hypothesis of an Asian origin of cryptobranchoids[20] is further supported by the Jurassic age and Asian distribution of stem caudates (such as *Karaurus*, *Kokartus*)[24–26] and other cryptobranchoid outgroups (for example, *Laccotriton*, *Sinerpeton*, *Jeholotriton*)[5–7]. The only exception to this palaeogeographic pattern is *Marmorerpeton*, a Jurassic stem caudate from Europe with uncertain affinities[27]. With an Asian origin of cryptobranchids, their extension to North
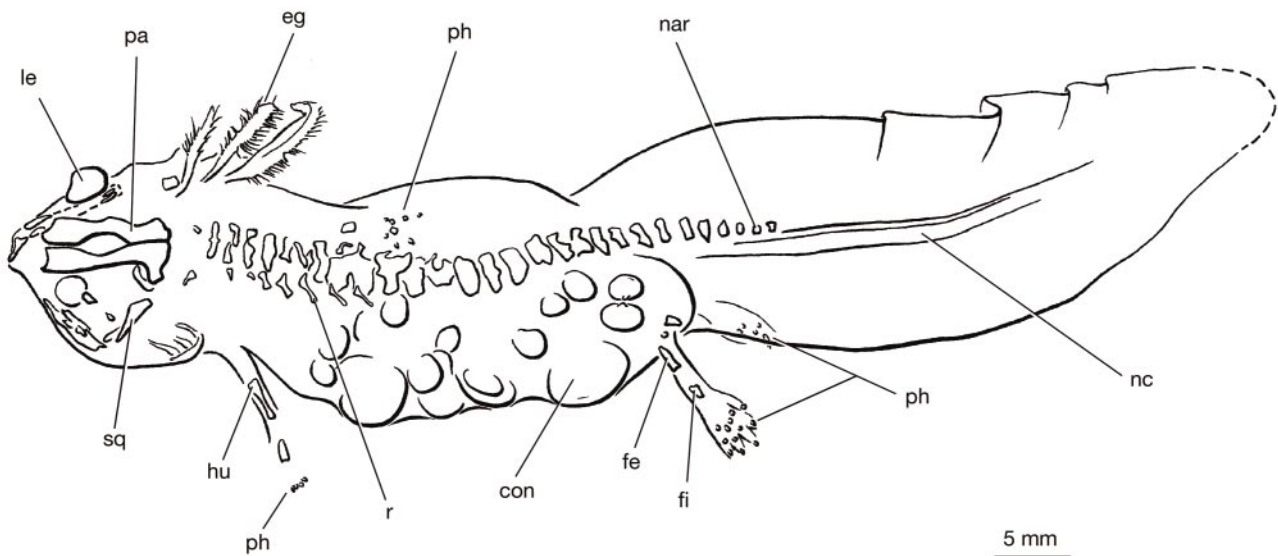

Figure 3 A small larval cryptobranchoid showing exceptional preservation of soft tissues. The presence of unicapitate ribs supports its referral to the Cryptobranchoidea. con, conchostracans; eg, external gills; le, lens; nar, neural arch; nc, notochord; ph, phalanges.
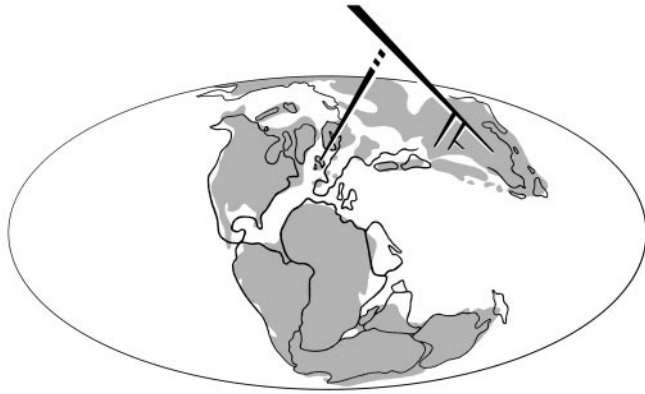
Figure 4 Map of Jurassic continental configuration (modified from ref. 29) with cladogram showing relationships and provenance of known Jurassic caudates. The taxa at the tips of the cladogram are, from left to right: (1) *Marmorerpeton*; (2) *Karaurus* and *Kokartus*; (3) *Laccotriton* and *Sinerpeton*; (4) *Jeholotriton*; and (5) *Chunerpeton*. The dotted line indicates the uncertainty of the phylogenetic position of *Marmorerpeton*. The shaded area represents the extent of continents.

America represents a more recent dispersal, perhaps associated with the development of a land bridge[19,20]. Hynobiids, on the other hand, underwent a range contraction. As hynobiid fossils are known from the Miocene and Pleistocene of Europe[23], this group probably extended its range out of Asia only to be limited to that continent by the Holocene epoch.

Despite its Bathonian age, the new cryptobranchid shows extraordinary morphological similarity to its living relatives. This similarity underscores the stasis within salamander anatomical evolution[28]. Indeed, extant cryptobranchid salamanders can be regarded as living fossils whose structures have remained little changed for over 160 million years. Furthermore, the new material from China reveals that the early diversification of salamanders was well underway by the Middle Jurassic; several extant taxa including hynobiids and cryptobranchids had already appeared by that time. Notably, this ancient pattern of taxonomic diversification does not correlate to any great disparity in anatomical structure. □

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Ecological and immunological determinants of influenza evolution

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In pandemic and epidemic forms, influenza causes substantial, sometimes catastrophic, morbidity and mortality. Intense selection from the host immune system drives antigenic change in influenza A and B, resulting in continuous replacement of circulating strains with new variants able to re-infect hosts immune to earlier types. This 'antigenic drift'[1] often requires a new vaccine to be formulated before each annual epidemic. However, given the high transmissibility and mutation rate of influenza, the constancy of genetic diversity within lineages over time is paradoxical. Another enigma is the replacement of existing strains during a global pandemic caused by 'antigenic shift'—the introduction of a new avian influenza A subtype into the human population[1]. Here we explore ecological and immunological factors underlying these patterns using a mathematical model capturing both realistic epidemiological dynamics and viral evolution at the sequence level. By matching model output to phylogenetic patterns seen in sequence data collected through global surveillance[2], we find that short-lived strain-transcending immunity is essential to restrict viral diversity in the host population and thus to explain key aspects of drift and shift dynamics.

The surface glycoprotein haemagglutinin of influenza is under strong selection by the human immune system as the primary antibody target[2]. Figure 1a–c shows phylogenies constructed using