# A Cretaceous symmetrodont therian with some monotreme-like postcranial features

Gang Li[1] & Zhe-Xi Luo[2,3]

A new spalacotheriid mammal preserved with a complete postcranium and a partial skull has been discovered from the Yixian Formation[1–3] of Liaoning, China. Spalacotheroid symmetrodonts[4–11] are relatives to modern therians (combined group of marsupials and placentals) and are characterized by many skeletal apomorphies of therians. But unlike the closely related spalacotheroids and living therians, this new mammal revealed some surprisingly convergent features to monotremes in the lumbar vertebrae, pelvis and hindlimb[12,13]. These peculiar features may have developed as functional convergence to locomotory features of monotremes, or the presence of lumbar ribs in this newly discovered mammal and their absence in its close relatives might be due to evolutionary developmental homoplasy. Analysis including this new taxon suggests that spalacotheroids evolved earlier in Eurasia and then dispersed to North America, in concordance with prevailing geodispersal patterns of several common mammalian groups during the Early Cretaceous period.

Class Mammalia
Clade Trechnotheria
Family Spalacotheriidae
Akidolestes cifellii gen. et sp. nov.
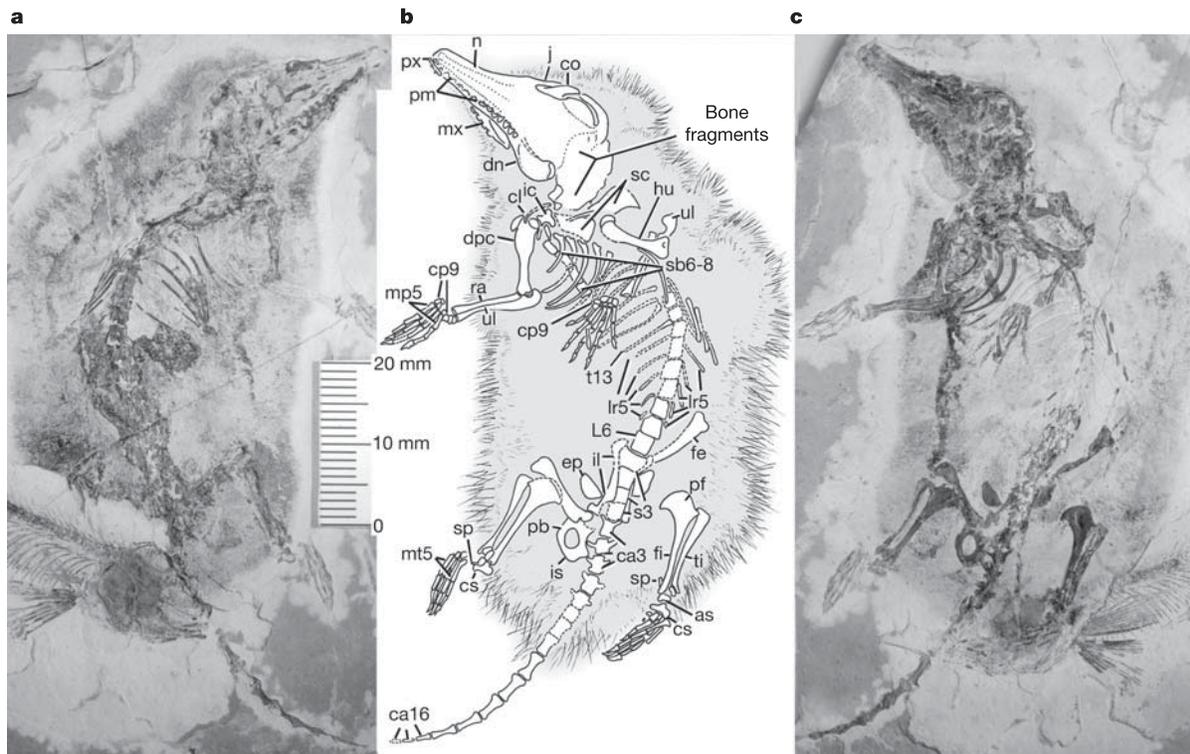
Figure 1 | *Akidolestes cifellii.* **a**, **c**, Counterpart (**a**) and main part (**c**) of the holotype (Nanjing Institute of Geology and Palaeontology, Academia Sinica, NIGPAS139381A, B). **b**, Skeletal features and fur outline of NIGPAS139381A. Abbreviations: as, astragalus; ca3, caudal vertebrae 1 through 3; ca16, caudal vertebrae 14 through 16; cl, clavicle; cp9, carpals 1 through 9; co, coronoid process of the dentary; cs, calcaneus; dn, dentary; dpc, deltopectoral crest (humerus); ep, epipubis; fe, femur; fi, fibula; hu, humerus; ic, interclavicle; il, ilium; is, ischium; j, jugal; L6, lumbar vertebrae 1 through 6; lr5, lumbar ribs 1 through 5; mp5, metacarpals 1 through 5; mt5, metatarsals 1 through 5; mx, broken and separated maxilla with upper molars; n, nasal; pb, pubis; pf, parafibular process of fibula; pm, lower premolars; px, broken and separated premaxilla with incisors; ra, radius; s3, sacral vertebrae 1 through 3; sc, scapula; sp, extratarsal 'poison' spur including os calcaris and cornu calcaris; sb6-8, sternebrae 6 through 8 (including xiphoid); ti, tibia; t13, the 13th thoracic rib (left); ul, ulna.

[1]Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. [2]Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213, USA. [3]Department of Earth Sciences, Nanjing University, Nanjing 200017, China.

Holotype. Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGPAS) 139381A, B (Fig. 1), a skeleton with partial skull and dentition preserved in part and counterpart.

Etymology. Akidolestes: *akido-* (Greek) for point, for the pointed rostrum of this new mammal; *-lestes* (Greek), for thief, a common suffix for the name of fossil mammals; *cifellii*, in honour of Richard L. Cifelli, for his pioneering studies of symmetrodont mammals.

Locality, age and associated fauna. Yixian lacustrine beds at the Dawangzhangzi Locality, Lingyuan, Liaoning, China. The locality is correlated with other localities in Liaoning dated to be 124.6 Myr of the Barremian stage of the Lower Cretaceous[1,2], although there is no universal agreement on correlating the Yixian Formation to the European marine stages[3]. Other mammals of this formation include eutriconodontans[14,15], multituberculates[4], symmetrodonts[5–7], metatherians[16] and eutherians[17].

Diagnosis. Symmetrodont with dentition of I4.C1.P5(?).M5(?)/i4.c1.p5.m6, with successively more acute angles of cusps from posterior premolars to posterior molars, in which cusp angles are less than 50° (Fig. 2). Molars with acute-triangulation of cusps and other features are typical of spalacotheroids that include zhangheotheriids[5–7] and spalacotheriids[8–11]; differs from *Zhangheotherium*[5,6] and *Maotherium*[7] of the Yixian Formation in having higher protocristid on molars, longer (larger) posterior premolars than anterior molars, and more premolars; from *Symmetrolestes*[9] in having more molars; from older *Spalacotherium*[10] and younger *Spalacolestes*[8] and *Heinshanlestes*[11] in having a gracile coronoid process of the mandible (although similar to zhangheotheriids in this feature). *Akidolestes* is more primitive, in retaining distinctive cusps on the ultimate lower molar with symmetrical crown, than the geologically younger and derived spalacolestines, which lack cusp separation on an asymmetrical ultimate lower molar[8,9,11]. *Akidolestes* is also distinguishable from all other Mesozoic mammaliaforms, including the paraphyletic "obtuse-angled symmetrodonts"[4,18], in a combination of primitive and derived features to be described below (see also Supplementary Information).

Description. The mandible of *Akidolestes cifellii* is nearly identical to those of *Zhangheotherium*[5,6] and *Maotherium*[7] in having an elongate and gracile coronoid process and a mediolaterally compressed dentary condyle. However, the anterior portion of the mandible is more gracile, corresponding to the anteriorly narrow upper jaws and rostrum (Fig. 1), and differing from the broader rostrum of these zhangheotheriids[7]. The lower molar has a lower, continuous prevallid shearing surface between the protoconid and the paraconid and a higher, continuous postvallid shearing surface between the protoconid and metaconid. This is more derived than zhangheotheriids with the interrupted prevallid and postvallid surfaces, but similar to spalacotheriids[8–11]. *A. cifellii* differs from zhangheotheriids but is very similar to spalacotheriids[8–11] in having large posterior premolars that are longer than molars (Fig. 2). *Akidolestes* is unequivocally placed within the family Spalacotheriidae by dental characteristics (Fig. 3b, node 7).

The shoulder girdle and forelimb are similar to those of zhangheotheriids[5–7]. However, *Akidolestes* differs from zhangheotheriids but is similar to monotremes in many features in the posterior part of the skeleton[12,13] (Figs 1, 2, 4). Of the six lumbar vertebrae, five have unfused ribs (Fig. 2d, e), similar to the condition of monotremes, the eutriconodont *Repenomamus*[15], *Fruitafossor*[19] and many premammaliaform cynodonts[20,21]. The presence of mobile lumbar ribs differs conspicuously from the absence of these ribs in the closely related zhangheotheriids[5–7] and some Mesozoic mammals, or their fusion to the lumbar centra in other Mesozoic mammals[4,14,16,17,22–24].
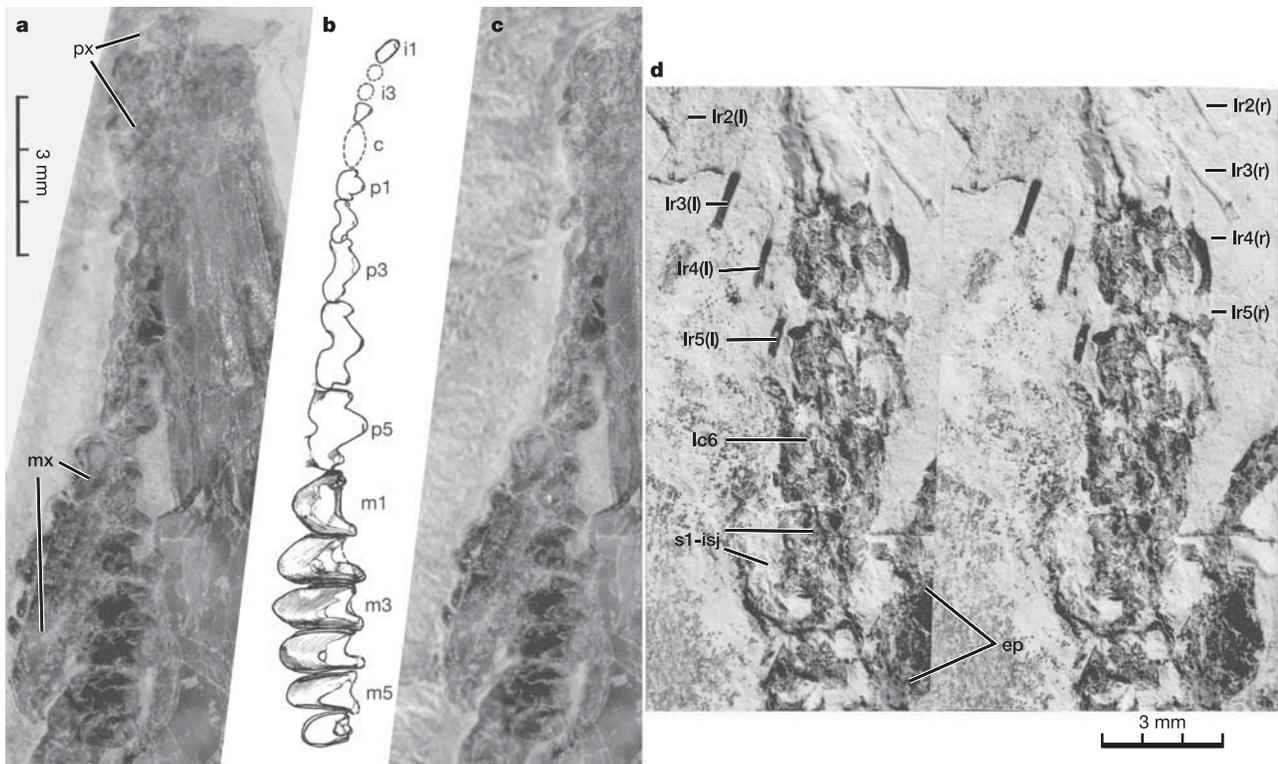
Figure 2 | Dentition of *Akidolestes cifellii*. a, **c**, Stereo photograph of the left lower teeth (**a**) and incomplete upper teeth (**c**) of NIGPAS139381A. **b**, Composite reconstruction of the lower teeth on the main part (NIGPAS139381A) and impression on the counterpart (NIGPAS139381B). **d**, Mobile lumbar ribs (stereo photograph of NIGPAS139381A; preserved on NIGPAS139381B but not illustrated). Abbreviations: ep, plate-like epipubis; lc6, lumbar centrum 6; lr2–5(l), left lumbar ribs 2–5; lr2–5(r), right lumbar ribs 2–5; mx, broken maxilla with five preserved molars; px, broken premaxilla with upper incisors and incisor alveoli (maxilla and premaxilla are separated from cranium by the lower jaw); s1-isj, sacral vertebra 1 and ilio-sacral joint (outline on NIGPAS139381A, broken bone on NIGPAS139381B).
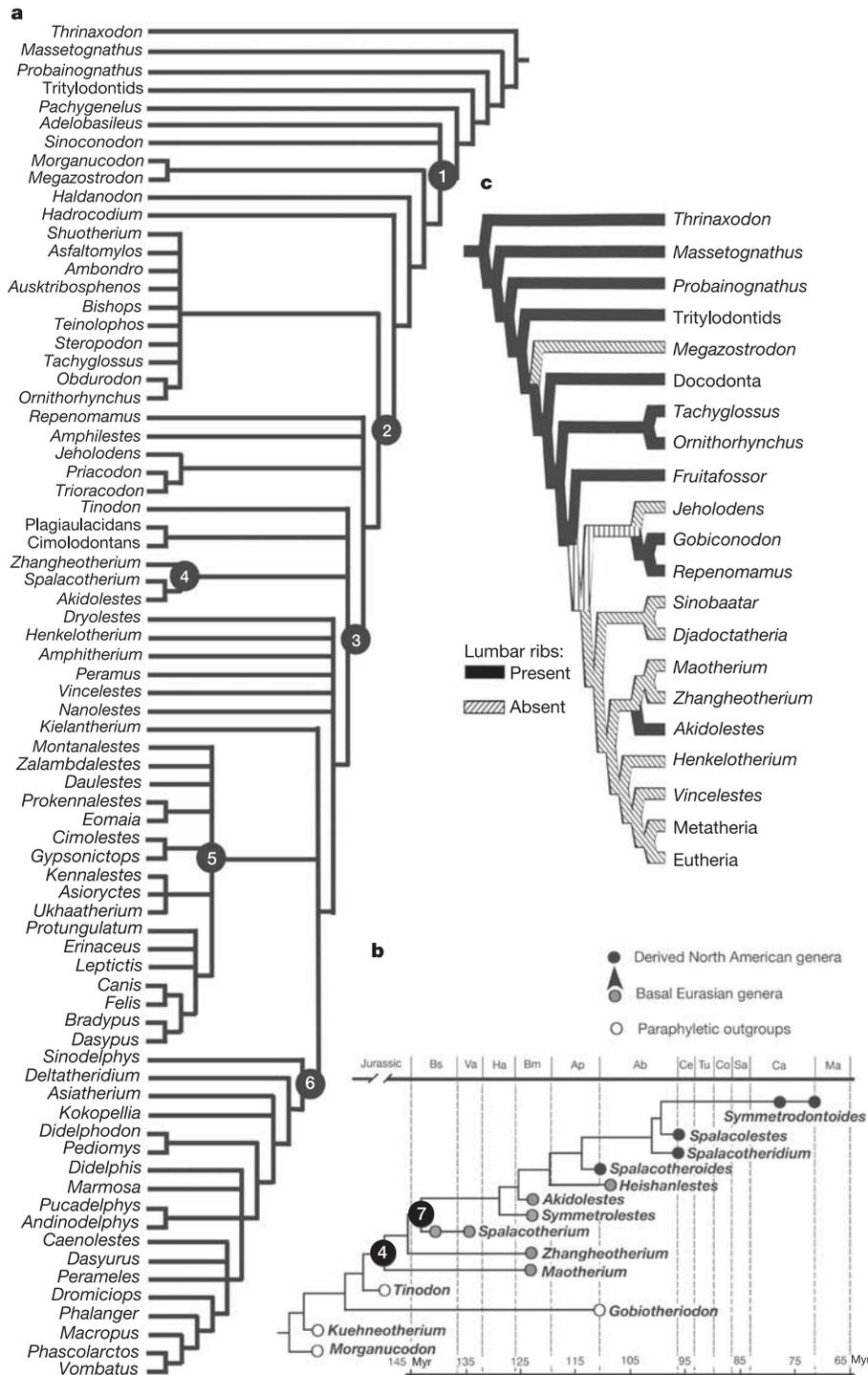
Figure 3 | Phylogenetic relationships of *Akidolestes cifellii*. a, Relationship of *A. cifellii* to major mammaliaform clades. **b**, Relationship of *A. cifellii* to other spalacotheroids (= basal trechnotherians). **c**, Hypothesis on homoplasy of lumbar ribs among mammaliaforms in which the intact lumbar region is preserved (tree simplified from **a** with data from ref. 19). Black branches, lumbar ribs present; hatched branches, lumbar ribs absent. The mammaliaform phylogeny is based on the strict consensus of 200 equally parsimonious and shortest trees (tree length 1,819, consistency index 0.426, retention index 0.794) from a PAUP analysis (version 4.0b; 1,000 runs of heuristic search with unordered multistate characters) of 413 morphological characters (from refs 16–19) that can be scored for the 74 comparative clades (including 5 pre-mammaliaform cynodont as outgroups and 17 extant mammal genera). Placement of *Akidolestes* within

spalacotheroids (node 4) and spalacotheriids (node 7) is based on a single shortest tree from 28 dental and mandibular characters of 10 spalacotheroid genera[8,9] (tree length 47, consistency index 0.702, retention index 0.821, PAUP branch and bound search). Tree nodes: 1, Mammaliaformes; 2, Mammalia; 3, Theriiformes; 4, Spalacotheroidea; 5, Eutheria; 6, Metatheria; 7, Spalacotheriidae. Temporal distribution of spalacotheroids follows refs 4–11; the pattern of the geodispersal of spalacotheroids is consistent with Eurasia–North America dispersal patterns of all major groups that are common in Eurasian and North American Cretaceous faunas[9,28,29]. Cretaceous stages shown in **b**: Ab, Albian; Ap, Aptian; Bm, Barremian; Bs, Berriasian; Ca, Campanian; Ce, Cenomanian; Co, Coniacian; Ha, Hauterivian; Ma, Maastrichtian; Sa, Santonian; Tu, Turonian; Va, Valanginian.

On the pelvis (Fig. 4), the epipubic bone is a broad plate, similar to that of *Ornithorhynchus* but different from the narrow epipubes of *Tachyglossus* and other Mesozoic mammals[4–7,16,17]. The pubis has a prominent tubercle for the psoas minor muscle (Fig. 4a), a feature otherwise present only in living monotremes[13] but absent in living therians and all other Mesozoic mammals for which the pelvis is known. In the head, neck and trochanteric area of the femur, *Akidolestes* is most similar to morganucodontans[24], eutricono-dontans[14,15] and monotremes (although to a smaller extent for the latter), but different from the closely related zhangheotheriids (Fig. 4), multituberculates and cladotherians[4,16,17]. A striking feature of *Akidolestes* is a hypertrophied parafibular process of the fibula. The parafibula is a homoplastic feature, formed from a small ossification independent of the fibular diaphysis in some marsupials; it shows

variation in multituberculates[22,23] but the parafibula is hypertrophied and fused completely to the fibula in living monotremes.

Akidolestes is similar to monotremes in the hindlimb. During the entire propulsive phase of locomotion in extant monotremes, the femur is horizontal and abducted, with a flexed knee joint[12,13]. This sprawling posture is correlated with the hypertrophied parafibular process, which is so large so that it constrains the knee joint to be permanently flexed in abducted position[12,13] (Fig. 4j). The sprawling posture is also correlated with a short femoral neck and a curved tibia with a distal malleolus for an asymmetrical upper ankle joint (Fig. 4d, dtm). We postulate that *Akidolestes* had a sprawling hindlimb posture from the similar osteological correlates of the sprawling posture of monotremes (Fig. 4i, j).

By contrast, the hindlimb posture of *Zhangheotherium* is more
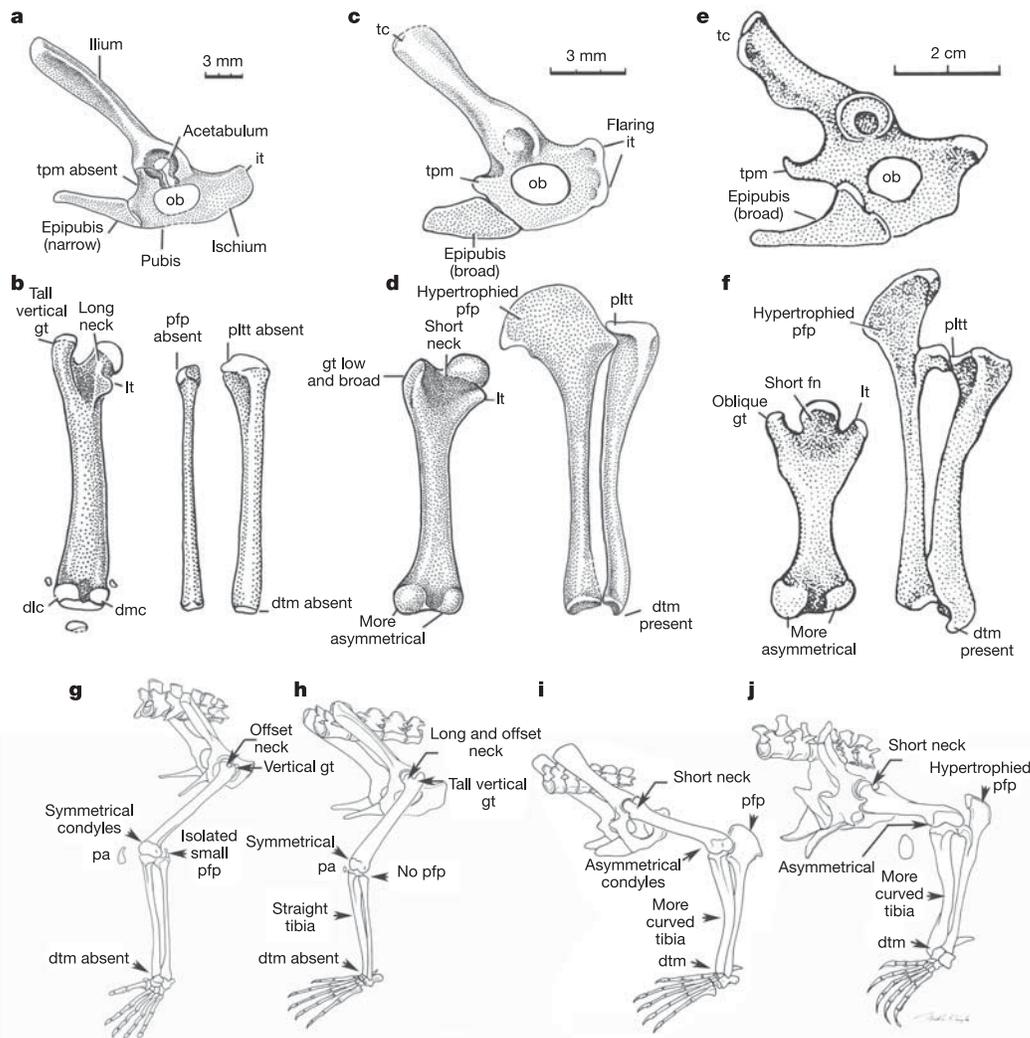
Figure 4 | Comparison of pelvic and hindlimb features of the spalacotheroids *Akidolestes* and *Zhangheotherium*, and hindlimb posture of *Didelphis* and *Ornithorhynchus*. a, **b**, *Zhangheotherium*: left pelvis (ventrolateral view) (**a**); left femur (posterior view), right fibula and tibia (lateral to anterolateral view) (**b**). **c**, **d**, *Akidolestes*: pelvis (ventrolateral view) (**c**); femur (posterior view), fibula and tibia (both in lateral view) (**d**). **e**, **f**, *Ornithorhynchus*: pelvis (ventrolateral view) (**e**); femur (posterior view), fibula and tibia (lateral view) (**f**). **g**, Near-parasagittal hindlimb posture of the opossum *Didelphis* (anterolateral view of the pelvis and hindlimb; arrows indicate the key characters for a more erect posture). **h**, Hindlimb posture of *Zhangheotherium* (more similar to opossum than to monotremes). **i**, Hindlimb posture of *Akidolestes* (more similar to monotremes than to opossum). **j**, *Ornithorhynchus*: anterolateral view of the pelvis and hindlimb; arrows indicate the key characters for sprawling posture). Abbreviations: dlc, distal lateral condyle; dmc, distal medial condyle (of femur); dtm, distal tibial malleolus; ep, epipubis; neck, femoral neck (distinctive and angled in *Zhangheotherium*; short and indistinct in *Akidolestes*); gt, greater trochanter (high and vertical in *Zhangheotherium*; triangular and broad in *Akidolestes*); it, ischial tuberosity; lt, lesser trochanter; ob, obdurator foramen; pfp, parafibular process (hypertrophied, fused in *Akidolestes* and *Ornithorhynchus*; small and isolated in *Didelphis*; absent in *Zhangheotherium*); pa, patella (relocated in illustration to show the distal femur); pltt, proximolateral tuberosity of tibia (large in *Akidolestes*); tpm, tubercle for M. psoas minor (on pubis); tc, tuber coxae (of ilium). For comparison of these pelvic and hindlimb features see Supplementary Information.

similar to that of *Didelphis* (Fig. 4g, h), on the basis of many osteological correlates for a more erect or parasagittal posture (Supplementary Information). The femur has a high and vertical greater trochanter, and a more distinctive neck, offset from the shaft (Fig. 4b, g). The distal femoral condyles are nearly equal; the fibula lacks the parafibular process; the tibia is straight. The long bones in zhangheotheriids[5–7] would be oriented as in the extant *Didelphis* and derived cladotherians.

The phalangeal length ratios in each digit and profile of the terminal phalanx of *Akidolestes* differ from those of fossorial and semi-aquatic mammals so it would be unlikely to have had a fully fossorial adaptation[19], or a fossorial and semi-aquatic adaptation[25]. It lacks the phalangeal characteristics of scansorial mammals[16,17]. On the basis of the structure of manus and pes, *Akidolestes* was most probably a generalized terrestrial mammal, like zhangheotheriids[5–7] and morganucodontans[24].

The complete fossil of *Akidolestes* made it possible to evaluate these 'exceptional' features in the context of global parsimony (Fig. 3c). Our analyses of all features of *Akidolestes* have unequivocally placed it in the spalacotheroid clade within the trechnotherian group (Fig. 3a, b). Although 'unusual' for all theriiform mammals that are close relatives to *Akidolestes*, the lumbar ribs (Fig. 4) are clearly atavistic reversals to the primitive condition of the successively more distant groups of some (but not all) eutriconodontans, monotremes and nonmammalian cynodonts; the hypertrophied parafibula is convergent to those of distantly related monotremes. The mobile lumbar ribs are plesiomorphies of nonmammalian synapsids[20,21]. Presence of these lumbar ribs in *Akidolestes*, which is nested deeply inside successive ranks of clades that do not have lumbar ribs (Fig. 3c), can be proposed as a phylogenetically homoplastic and functionally convergent feature or as the result of evolutionary development.

In extant monotremes, the posterior thoracic and anterior lumbar ribs provide attachment for many muscles of locomotory and respiratory functions[13], including the following: the lumbar portion of the diaphragm for breathing; the psoas minor muscle inserting on the psoas minor tubercle for flexing the lumbars and pelvis; the psoas major muscle inserting on the lesser trochanter of the femur for rotating the femur; the quadratus lumborum muscle for flexing the lumbar and pelvic region; and the longissimus dorsi and iliocostalis lumborum muscles for extension of the lumbar and pelvic region[13].

The presence of long lumbar ribs, a large psoas minor tubercle and the expanded anterior end of the ilium in *Akidolestes* indicate that the flexor and extensor muscles of the lumbar and pelvic region are well developed in this spalacotheriid, as in the extant monotremes, and more so than in *Zhangheotherium*, which is more similar to the marsupial *Didelphis* (Fig. 4, and Supplementary Information). The hypertrophied parafibula in *Akidolestes* would provide an expanded origination for several enlarged muscles for flexing the upper ankle joint and pedal digits, as in monotremes[13]. Given these many similarities, we infer that *Akidolestes* had a strong capacity for flexion and extension of the lumbar–pelvic region of the skeleton, for rotation of the femur, and for strong flexion of the pes, in convergence to the locomotory function of modern monotremes. The presence of the epipubic bone is correlated with the cross-couplet hypaxial muscle function in plesiomorphic locomotory pattern of basal mammals[26]. However, it is difficult to interpret the homoplastic variation of the epipubic bone (large and broad versus gracile and small) in *Akidolestes* and other spalacotheroids in terms of convergent evolution of functionally adaptive features.

Within eutriconodontans, lumbar ribs are present in gobiconodontids but not in the related *Jeholodens*. Within spalacotheroids, these are present in *Akidolestes* but absent in zhangheotheriids. Outside the crown mammals, lumbar ribs are absent in morganucodontans[24] but variably present in many advanced cynodonts[20,21]. It is possible that this rampant homoplasy of the lumbarosacral vertebral ribs is patterned by developmental genes that are deeply conserved in widely separated mammalian taxa that lacked a recent common history[27]. However, homoplastic development of the lumbar ribs is not mutually exclusive of the interpretation that these ribs and related features also have convergent function to extant monotremes.

Mammalian biogeography of Laurasia during the Early Cretaceous is characterized by iterative dispersals of major clades from their ancestral area of Asia to North America, where arrival of immigrant lineages is correlated with rapid turnover of the mammalian faunas. The phylogeny of spalacotheroids, including newly discovered taxa such as *Akidolestes*, suggests that basal spalacotheroid taxa are entirely Eurasian during the Berrasian–Barremian ages of the Cretaceous[5–11,28] (Fig. 3b), and younger and more derived taxa are North American[8]. This geodispersal is consistent with palaeobiogeographical patterns of the main clades of Cretaceous mammalian faunas of Eurasia and North America, including multituberculates[4], eutriconodontans[28], eutherians[17,28,29] and metatherians[16,28]. The concordant geodispersal patterns[30] of unrelated lineages suggests that during the Early Cretaceous (Fig. 3b), Asia was a source area for the origination and emigration of the main mammalian groups that became the major elements in North American faunas of the Late Cretaceous[6,16,17,28,29].

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