# ARTICLES

# A new eutriconodont mammal and evolutionary development in early mammals

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Detachment of the three tiny middle ear bones from the reptilian mandible is an important innovation of modern mammals. Here we describe a Mesozoic eutriconodont nested within crown mammals that clearly illustrates this transition: the middle ear bones are connected to the mandible via an ossified Meckel's cartilage. The connected ear and jaw structure is similar to the embryonic pattern in modern monotremes (egg-laying mammals) and placental mammals, but is a paedomorphic feature retained in the adult, unlike in monotreme and placental adults. This suggests that reversal to (or retention of) this premammalian ancestral condition is correlated with different developmental timing (heterochrony) in eutriconodonts. This new eutriconodont adds to the evidence of homoplasy of vertebral characters in the thoraco-lumbar transition and unfused lumbar ribs among early mammals. This is similar to the effect of homeobox gene patterning of vertebrae in modern mammals, making it plausible to extrapolate the effects of *Hox* gene patterning to account for homoplastic evolution of vertebral characters in early mammals.

Class Mammalia
Order Eutriconodonta (ref. 1)
**Family Jeholodentidae (nov.)**
*Yanoconodon allini* gen. et sp. nov.

**Etymology.** *Yan* is for the Yan mountains in Northern Hebei Province; *conodon* is Latin for 'cuspate tooth', a common suffix for mammalian taxonomic names; *allini* refers to Edgar Allin's studies on mammalian ear evolution.

**Holotype.** Nanjing University - Paleontology Laboratory NJU-P 06001, preserved on a slab (NJU-P06001A, shown in Fig. 1) and counter-slab (NJU-P06001B, shown in the Supplementary Information) of laminated siltstones.

**Locality and horizon.** Yixian Formation at Daluozigou locality (41° 49′ N and 116° 31′ E) in Fengning County in Hebei Province, China. Equivalent beds in the western Liaoning Province were dated to 125 to 122 million years ago[2–4].

**Diagnosis.** Dental formula $I^2.C^1.P^2.M^3/I_2.C_1.P_2.M_3$, with plesiomorphic 'triconodont' molars having three laterally compressed main cusps in straight alignment. Among mammaliaforms with 'triconodont-like' postcanines, it differs from *Sinoconodon* and morganucodontans in its absence of a post-dentary trough[1,5,6]. Among eutriconodontans, it differs from all known 'amphilestids' and gobiconodontids in its absence of lower cingular cuspules e and f and the upper lingual cingulum[1,5–12]. *Yanoconodon* and *Jeholodens*[13] are identical in molar characteristics and clustered in one clade (Fig. 2)[14–16]. *Yanoconodon allini* differs from *Jeholodens jenkinsi* in having a triangular outline of scapula and several differences in thoracolumbar vertebrae (full diagnoses of *Y. allini* and the family Jeholodentidae are given in the Supplementary Information).

## Description

The last molariform in the holotype of *Yanoconodon* has partially erupted (Fig. 3b), similar to the condition in *Jeholodens*[13]. However, the exposed interior of the lower and upper jaws shows no replacement at any tooth loci and its functional teeth (including the last tooth) are all permanent. The holotype is either a late-stage subadult or an adult with a delayed eruption of the last molar. It differs from gobiconodontids in the absence of replacements at the anterior molariform loci, although it shares this delayed eruption of the ultimate molariform with older gobiconodontid individuals[8–12].

*Yanoconodon* is preserved with the middle-ear bones (except the stapes), an ossified Meckel's cartilages, and the associated (although disarticulated) hyoid elements (Fig. 1; also Supplementary Information). The malleus has a manubrium that is similar to (although more robust than) that of the adult monotreme *Ornithorhynchus*[17–19], and the goniale element ('prearticular') is also present (Fig. 3). Similarly to modern mammals, the incus has a crus longum (stapedial process) and a crus breve (for basicranial articulation). The ectotympanic ring ('reflected lamina of angular') forms an arc of about 90°. The dorsal crus of the ectotympanic and the prearticular element of the malleus are fused to each other and both are connected anteriorly with the ossified Meckel's cartilage (Fig. 3b, g). The Meckel's cartilage has a mediolaterally compressed anterior (mandibular) limb, and a dorsoventrally compressed posterior (tympanic) limb. These two limbs are twisted relative to each other and curved at the mid-length of the cartilage (red arrow in Fig. 3). By comparison to *Yanoconodon*, we recognize that an ossified Meckel's cartilage is also preserved, although it is detached from the mandible in *Jeholodens*[13]. The Meckel's cartilage is similar to those preserved in several gobiconodontids (Fig. 3e, 3f)[9–12] but adds new information on its structural connection with the middle-ear bones, which are as yet unknown in gobiconodontids.

### Limb and foot structure

*Yanoconodon* has a triangular outline of the scapula, and a gracile and slightly curved clavicle that lacks a rigid articulation to the interclavicle, it therefore has a mobile and 'therian-like' shoulder girdle (Fig. 1). However, the humerus resembles those of mammaliaforms or cynodonts[20–25] in a spindle-shaped (instead of spherical) head, a broad and shallow intertubercular groove, broad ect- and entepicondyles, and a proximo-distal torsion. The femur is similar to those of

cynodonts in that the femoral head is not spherical and has no neck; the greater trochanter has no vertical process. Gobiconodontids and jeholodentids lack the epiphyseal growth plates between the epiphyses (growth caps) and diaphysis (shaft) of long bones, a plesiomorphy of mammaliaforms and cynodonts[20–25]. But such growth plates are typical in multituberculates, extant monotremes, and therians[26–33]. Many modern therians have relatively rapid early skeletal growth, but terminate this growth upon the fusion of the epiphyses to the diaphysis. By contrast, eutriconodonts lacked a similar mechanism for terminating skeletal growth that would presumably slow down (although not stop completely) in the adult, because of the absence of the epiphyseal growth plates. The astragalus is oblong in outline without a distinctive neck or a pulley-like articulation for the upper ankle joint. The calcaneus has a broad peroneal shelf and a short tuber. *Yanoconodon* and *Jeholodens* lack a long list of apomorphies of limb and foot bones of multituberculates and therian mammals[26–35]. The fore- and hind-limbs both have sprawling posture (Fig. 1b). The metacarpals, metatarsals, and all phalanges are short and stout, which are primitive features also of cynodonts, mammaliaforms, gobiconodontids and *Jeholodens*[12,13,20–25], for either terrestrial or fossorial habits.

The vertebral column of *Yanoconodon* (NJU-P06001A and B) has seven cervical vertebrae with unfused ribs. Components of the atlas and axis are not co-ossified (Fig. 1). Owing to a gradational transition from thoracics to lumbars (Figs 1 and 5), designation of the 18 thoracic versus eight lumbar vertebrae is somewhat arbitrary, based on the criterion that lumbars tend to have larger and more robust centra and wider rib 'plates'. *Yanoconodon* is similar to gobiconodontids[12,36] but different from closely related *Jeholodens* in having these primitive features. Similar to many cynodonts and some mammaliaforms[20–25], the anterior seven lumbar vertebrae have mobile ribs, several with an expanded proximal portion of the rib as in (but less developed than) the plated lumbar ribs of many cynodonts and the docodont *Castorocauda*[22–25]. *Yanoconodon* and *Repenomamus*[36] have 26 thoracolumbar vertebral segments, an exceptional number if compared to the 22 thoracolumbars of *Jeholodens*, and 19 or 20 thoracolumbars in most Tertiary and modern mammals[37].

## Implications for mammalian ear evolution

The rare preservation of Meckel's cartilage in association with the ectotympanic, malleus and incus in *Yanoconodon* provides the following new observation of the middle ear and its relationship to the mandible. The outline and proportion of the ectotympanic, malleus and incus of *Yanoconodon* are similar to their homologues in adult *Ornithorhynchus* (except for the gracile tips of the manubrium and ectotympanic in the latter) (Fig. 3c, 3h)[17–19]. *Yanoconodon* is far more derived than mammaliaforms (Fig. 3a)[5,6,22] in that its middle-ear bones are mediolaterally separated from the pterygoid part of the mandible (Fig. 3b, 3h), despite the plesiomorphic similarity in retaining the Meckel's connection to the mandible.

The homology of post-dentary elements of non-mammalian tetrapods with the mammalian middle-ear bones has long been established[38–44]. Long before the current fossil evidence was discovered, it was hypothesized that the migration of middle-ear bones from the
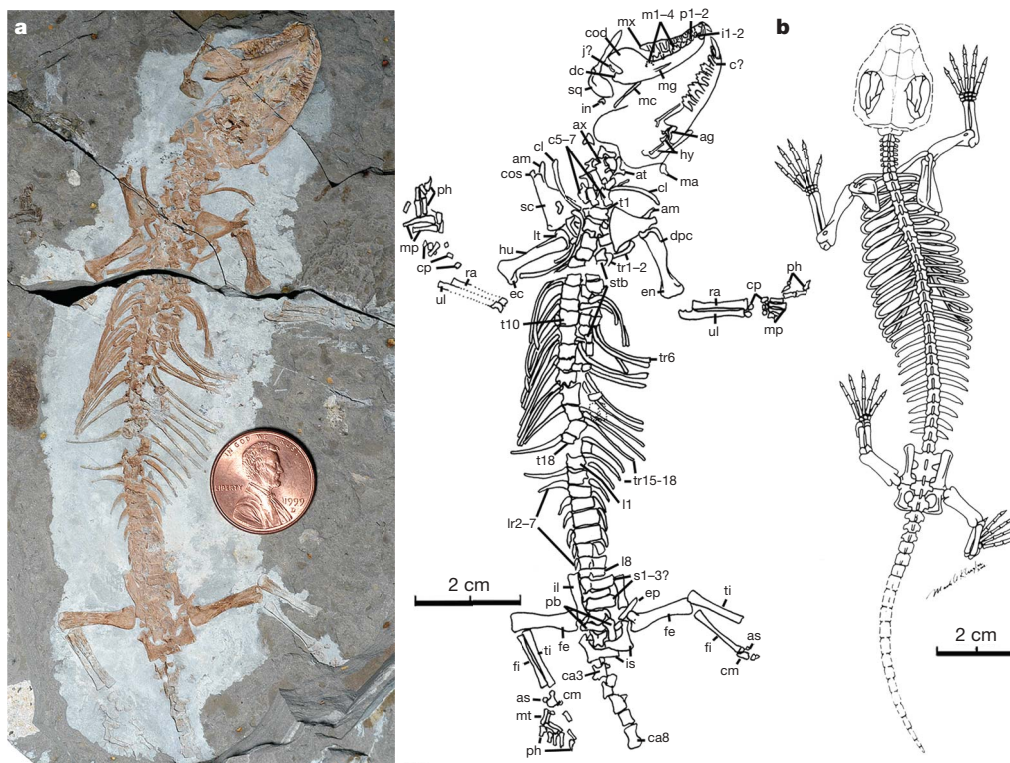


**Figure 1 | New mammal *Yanoconodon allini*. a**, Main part of the holotype (Nanjing University-Paleontology NJU-P06001A; the counterpart NJU-P06001B is illustrated in the Supplementary Information). **b**, Skeletal restoration (dorsal view). Abbreviations: ag, angular (ectotympanic ring); am, acromion (scapula); as, astragalus; at, atlas (cervical vertebra, c1); ax, axis (c2); c?, canine?; c5–7, cervical vertebrae 5–7; ca3 and ca8, caudal vertebrae 3 and 8 (distal caudals are missing); cl, clavicle; cm, calcaneum; cod, coronoid process (dentary); cos, coracoid process (scapula); cp, carpals; dc, dentary condyle; dpc, deltopectoral crest (humerus); ec, ectepicondyle (humerus); en, entepicondyle; ep, epipubis; fe, femur; fi, fibula; hu, humerus; hy, hyoid elements; i1–2, incisors 1 and 2; il, ilium; in, incus; is, ischium; j?, jugal?; l1 and l8, lumbar vertebrae 1 and 8; lr2–7, lumbar ribs 2–7; lt, lesser tubercle (humerus); m1–4, lower molars 1–4; ma, malleus; mc, Meckel's cartilage (ossified); mg, Meckel's groove (dentary); mp, metacarpals; mt, metatarsals; mx, maxillary; p1–2, premolars 1 and 2; pb, pubic; ph, phalanges; ra, radius; sc, scapula; sq, squamosal; stb, sternum and sternabrae; s1–3?, sacral vertebrae 1 and 2 (and possibly sacral vertebra 3?); t1, t10 and t18, thoracic vertebrae 1, 10 and 18; ti, tibia; tr1–2, tr6 and tr15–18, thoracic ribs 1, 2, 6 and 18; ti, tibia; ul, ulna.

mandible in cynodont–mammal evolution underwent an intermediate stage in which these bones would be anteriorly connected to the lower jaw, but suspended medial to (and free of) the mandibular pterygoid region (ref. 43 and Fig. 28.11 of ref. 44). *Yanoconodon* corroborates Allin's hypothetical model of an intermediate evolutionary stage. Newly discovered fossils of *Yanoconodon* (Fig. 1) and gobiconodontids[9–11], preserved in multiple specimens from two different fossil sites, add some crucial and previously unknown structural elements to this 'transitional' middle-ear model:

(1) The anterior (mandibular) limb and the posterior (tympanic) limb of Meckel's cartilage are twisted and curved relative to each other at the mid-length of the cartilage (red arrow in Fig. 3). (2) The mid-length twist and curvature of Meckel's cartilage made it feasible for the anterior limb of the cartilage to be nestled in the Meckel's groove on the mandible[9–11], while the tympanic limb of the cartilage and its associated ectotympanic and prearticular are separated mediolaterally from the pterygoid region of the mandible (Fig. 3f, g), as

postulated by Allin[43]. The tympanic membrane suspended by the ectotympanic ring and malleus manubrium would be re-oriented more mediodorsally (see red arrows in b-1 and b-2 of Fig. 3b), similar to the ectotympanic's migratory path during ontogeny in the marsupial *Monodelphys*[41], leaving a space between the pterygoid region of the mandible and the tympanic membrane for access of the external auditory meatus and for pterygoid muscle. (3) Owing to the curvature of Meckel's cartilage, the basicranial articulation of the incus is nearly co-axial with the fulcrum for movement around the dentary-squamosal jaw hinge, so the jaw movement had little impact on the middle ear function. (4) The middle ear and the ossified Meckel's cartilage in late-stage subadult or adult of *Yanoconodon* (Fig. 3g) show a similar structural pattern to the embryos of monotreme (Fig. 3i) and placental mammals. The middle ear is anteriorly connected to a curved Meckel's cartilage, which is in turn connected to the mandible. In the meantime, the embryonic middle-ear bones are mediolaterally separated from the pterygoid region[17,18,39,40].
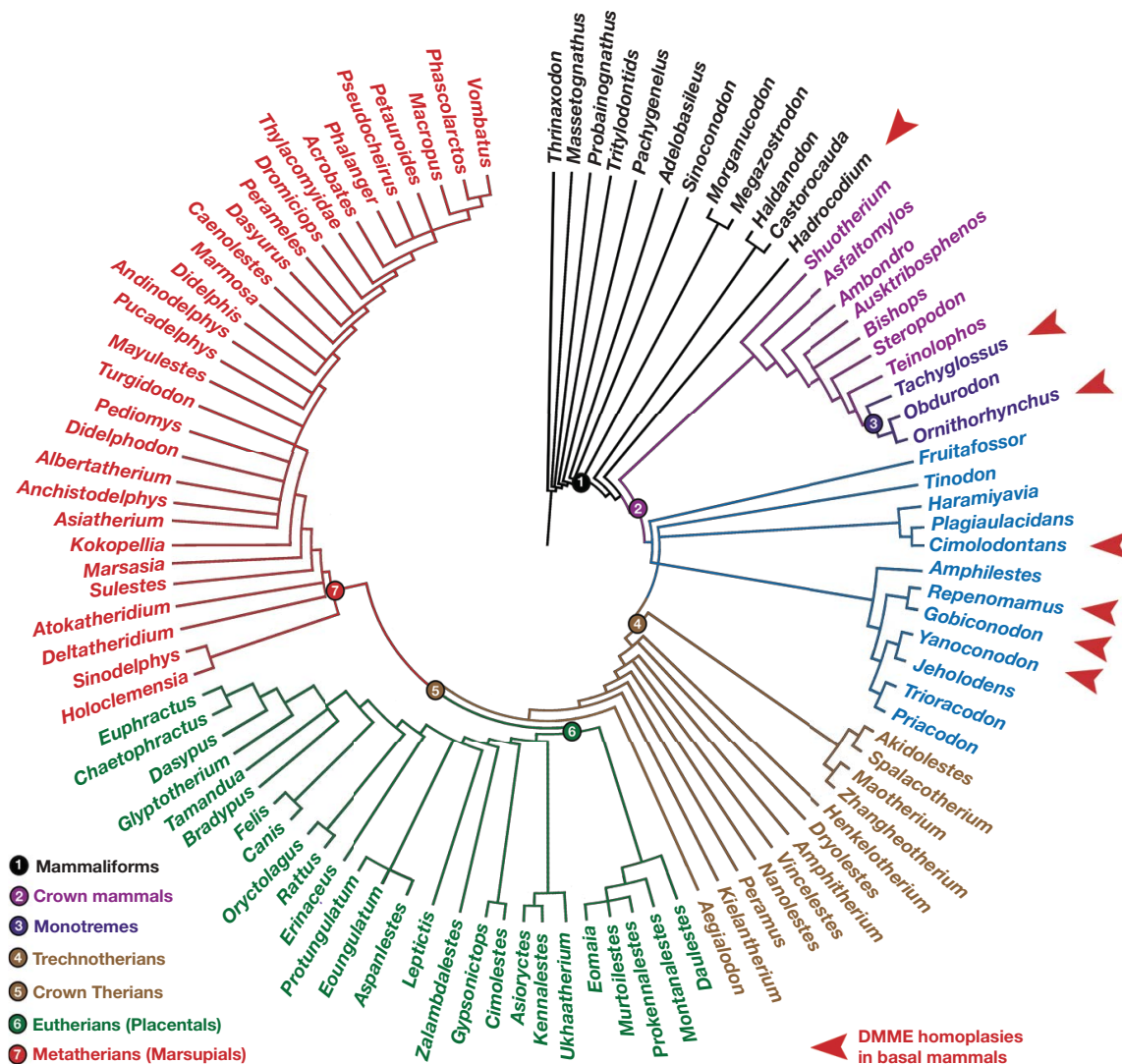


**Figure 2 | Relationship of *Yanoconodon allini*.** Analysis of all dental and skeletal characters of *Yanoconodon* places it as a close relative of *Jeholodens*, in the Jeholodentidae among eutriconodontans. This is based on the strict consensus of 218 equally parsimonious trees of PAUP (Phylogenetic Analysis Using Parsimony and Other Methods, version 4.0b) analysis of 436 characters (1,000 heuristic runs with unordered multi-state characters) that can be scored for 102 comparative taxa (97 mammaliaforms including 25 extant mammals, plus three cynodonts as outgroups). For each equally parsimonious tree, tree length = 2,188, consistency index = 0.375, retention index = 0.803. Characters are based on refs 1, 14–16, 22, 33 and this study. Graphic produced by M. Klingler.
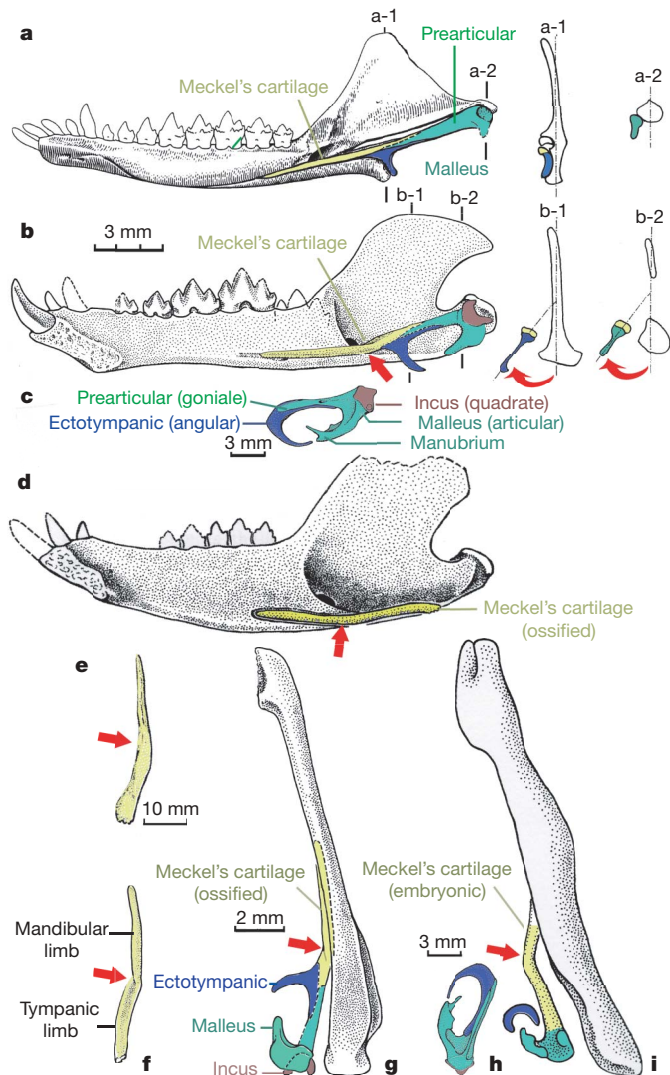
**Figure 3 | Comparison of mandible and middle ear of *Yanoconodon*.**
**a**, Mammaliaform *Morganucodon* (medial view); a-1 and a-2 label schematic transverse sections at the levels of the malleus and the ectotympanic[5–7]. In *Morganucodon*, the middle ear maintains both an anterior connection to the mandible via the Meckel's cartilage, and a mediolateral contact to the mandible. **b**, Euriconodont *Yanoconodon* (medial view, composite restoration of mandible and middle ear from NJU-P06001A and B). b-1 and b-2 label transverse sections at the levels of the malleus and the ectotympanic. The middle ear retains the anterior connection to the mandible via ossified Meckel's cartilage (yellow), but is mediolaterally separated from the posterior part of the mandible because of the twist and curvature of Meckel's cartilage (red arrows in **b**). **c**, the ectotympanic (blue), malleus (green) and incus (brown) of modern *Ornithorhynchus*[18]: the shape and proportion of the ear bones are similar in *Ornithorhynchus* and *Yanoconodon*. **d**, Euriconodont *Repenomamus*[9–11]: ossified Meckel's cartilage connected anteriorly to the mandible (similar to *Yanoconodon*). **e**, Ossified Meckel's cartilage of *Repenomamus* (ventral view, isolated, redrawn from Fig. 1 of ref. 9). **f**, Ossified Meckel's cartilage of *Yanoconodon* (ventral view, isolated, composite restoration of both the left and the right elements). **g**, Middle ear of *Yanoconodon* (composite restoration, ventral view): the ectotympanic and malleus are connected anteriorly to the mandible via ossified Meckel's cartilage; but these are mediolaterally separated from the posterior part of mandible, facilitated by curvature of the Meckel's cartilage (yellow). **h**, Middle ear bones of adult *Ornithorhynchus* (ventral view) and similarity to those of *Yanoconodon*. **i**, Embryonic *Ornithorhynchus*[17]: the tympanic ring and the partially developed manubrium and goniale ('prearticular') of the malleus are anteriorly connected via Meckel's cartilage to the mandible, but separated mediolaterally from the posterior region of mandible, facilitated by the curved cartilage (red arrow). *Yanoconodon* retains the embryonic pattern of *Ornithorhynchus* owing to the timing change of earlier ossification of Meckel's cartilage, but otherwise its ectotympanic, malleus and incus are nearly the same as in adult *Ornithorhynchus*.

Overall, *Yanoconodon*'s middle ear shows a paedomorphic resemblance to the embryonic pattern of modern mammals. All that is necessary for adult *Yanoconodon* to retain this paedomorphic (albeit permanent) connection of the middle ear to the mandible is a relatively earlier timing in (premature) ossification of the Meckel's cartilage and its fusion with the ectotympanic (Fig. 3c–g).

## Developmental heterochrony and evolutionary homoplasy

A definite mammalian middle ear (DMME)[43,44] is accomplished by two ontogenetic steps in extant monotremes and placentals: first, a mediolateral separation of the middle ear bones from the mandible in early embryonic stages (secondary mediolateral contact in marsupials due to inflected mandibular angle; see Fig. 12.10 of ref. 40), and second, a loss of anterior connection to the mandible owing to the reabsorption of Meckel's cartilage in the subadult. In *Yanoconodon* and gobiconodontids (and by inference also *Jeholodens*), the former step of mediolateral separation of the middle ear from the mandible has already occurred. But reabsorption of Meckel's cartilage did not happen, resulting in the retention in *Yanoconodon* of the middle-ear connection to the mandible, otherwise seen only in the early embryonic or fetal stage of extant mammals[17,18,39–42].

*Yanoconodon* and its euriconodontan kin are nested within the crown Mammalia (Fig. 2) by the parsimony of all characters[14–16]. The absence of DMME in euriconodonts, an in-group of crown Mammalia, is in sharp contrast to modern monotremes and therians that have DMME. This phylogeny requires one of the following two evolutionary scenarios: either (1) DMME was present in the common ancestor of monotremes, euriconodonts and therians; but euriconodonts re-evolved the middle ear attachment to mandible, or (2) DMME was absent in the common ancestor of monotremes, euriconodonts and therians, and this is retained as a paedomorphosis in euriconodonts; but DMME evolved in extant monotremes[44–47], and separately in therians[39]. Paedomorphosis, or retention of fetal or juvenile characteristics of ancestors and relatives through developmental heterochrony, is a common phenomenon in vertebrate evolution. The heterochronic ('premature') ossification of Meckel's cartilage in euriconodonts is the immediate cause for this paedomorphic connection of middle ear and mandible, and is why there is an overall homoplastic distribution among therians (with DMME), euriconodonts (without DMME), monotremes (with DMME) and pre-mammalian relatives (without DMME) (triangles in Fig. 2). The paedomorphic connection of the middle ear to mandible of euriconodonts and mammaliaforms is consistent with their lack of the long-bone epiphyses for terminating skeletal growth, as seen in modern mammals.

## *Hox* gene patterning of axial skeleton in extinct mammals

Modern mammals have a highly conserved pattern of vertebral identities: seven cervical, 13 to 14 thoracic, and five or six lumbar vertebrae (without separate lumbar ribs) for a combined 19 or 20 thoracolumbar vertebrae[37]. These regional vertebral identities are patterned by homeobox genes[37,48–50]. Homeotic changes in vertebral identities, such as shift of the thoracolumbar boundary or gradational transition, are now correlated with the loss and gain of *Hox* genes function in mice[48]. The distinctive boundary of thoracic versus lumbar regions and the absence of lumbar ribs are patterned by the *Hox10* paralogues in modern placental mammals (Fig. 4)[48]. The triple knockout of *Hox10* paralogues can alter the thoracic versus lumbar boundary, and triple knockout of *Hox11* can alter lumbar versus sacral vertebral identities. A loss of *Hox10* gene function can regenerate the lumbar ribs and a more gradational thoraco-lumbar transition in laboratory mice (Fig. 4)[48].

*Yanoconodon* and *Repenomamus* both have 26 thoracolumbar vertebrae, and these euriconodontans represent a high variation for the highly conserved 19 to 20 thoracolumbar vertebrae of crown Mammalia. By contrast, *Jeholodens* lost lumbar ribs and achieved a
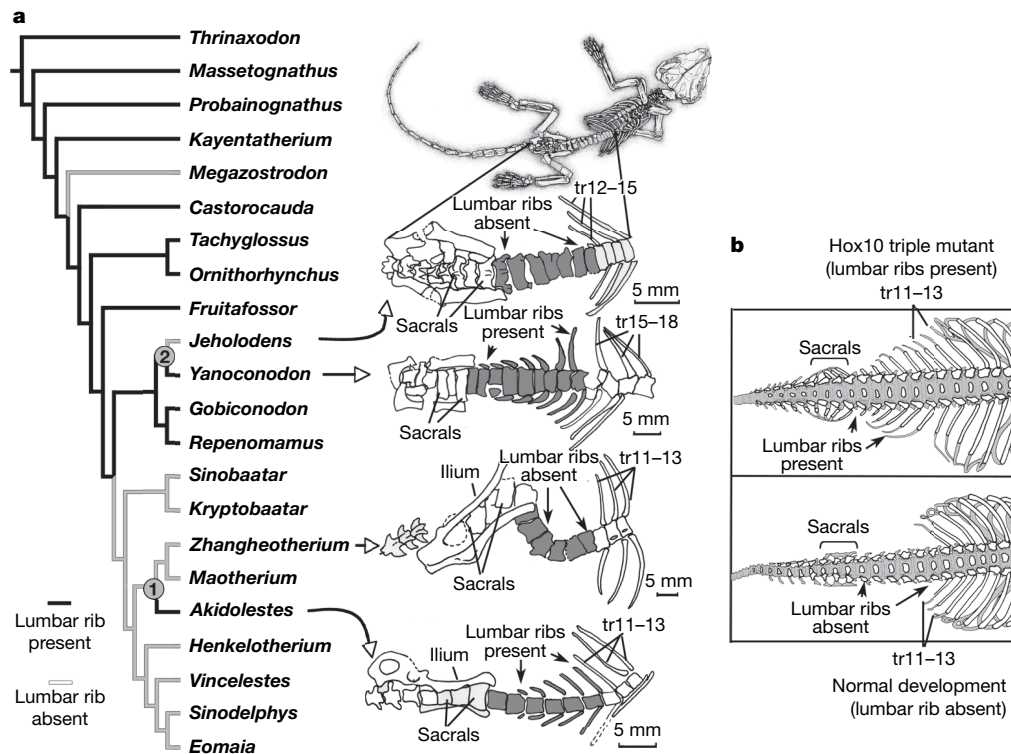
**Figure 4 | Homoplastic evolution of lumbar ribs among Mesozoic mammals and patterning of vertebral and rib development by *Hox10* gene in extant mammals. a**, Homoplastic distribution of lumbar ribs in Mesozoic mammal taxa preserved with vertebral column (topology from Fig. 2): lumbar ribs are present in gobiconodontids and *Yanoconodon* but absent in closely related *Jeholodens* (node marked 2), present in *Akidolestes* but absent in closely related *Zhangheotherium*[33] and the more inclusive theriiforms (node 1). **b**, Patterning of vertebral structure (development of lumbar ribs) in modern laboratory mice by *homeobox* genes (redrawn and flipped from Fig. 1 of ref. 48). A separate loss of lumbar ribs in *Jeholodens* among eutriconodontans is hypothesized to be correlated with an independent activation of *Hox10* patterning of thoracolumbar vertebrae (node 2). An isolated occurrence of lumbar ribs in *Akidolestes* among most spalacotheroids without lumbar ribs is hypothesized to be the effect of an independent loss of *Hox10* gene function. The loss or gain of *Hox* gene function to pattern the vertebral identities is a plausible mechanism for homoplasy of lumbar ribs in early mammals, and for variation of thoracolumbar vertebral counts among eutriconodontans. tr, numbered thoracic ribs.

distinctive boundary between the thoracic and lumbar regions (Fig. 4: node 2); its 15 thoracic and 7 lumbar vertebral counts are more comparable to modern mammals. These derived lumbar features of *Jeholodens* evolved from within eutriconodontans, convergent to those in theriiform mammals (node 1 in Fig. 4), and may be hypothesized as an independent activation of *Hox10* gene patterning[48].

Homoplasy of mobile lumbar ribs also occurs in symmetrodonts (Fig. 4)[33]. The presence of primitive lumbar ribs in *Akidolestes* is best hypothesized as an atavistic reversal because its related spalacotheroids show the derived therian condition without lumbar ribs[29,32,33]. Given that the regeneration of lumbar ribs in mutant mice is correlated with loss of function of *Hox10* paralogues (Fig. 4b), it is plausible that a similar mutation (that is, triple knockout of *Hox10* paralogues or a similar developmental event) was correlated with the 'reappearance' of lumbar ribs in *Akidolestes*, whose immediate relatives in successive ranks of theriiform mammals (node 1 in Fig. 4) all lack lumbar ribs.

Shifts in the thoracolumbar boundary and homoplasy of their vertebral identities are primarily correlated with mutation in *Hox* genes for their patterning[37,48–50]. This provides a plausible mechanism for the evolutionary patterns in lumbar ribs and the thoracolumbar transition in Mesozoic mammals (Fig. 4). This developmental mechanism for evolutionary homoplasy of thoracolumbar structure is mutually compatible with one of the two functional interpretations: either the lumbar ribs in *Akidolestes* had a function similar to that in primitive mammals and cynodonts with similar ribs[23–25], or the separate loss of lumbar ribs in *Jeholodens* was an adaptation convergent to most theriiform mammals. Reciprocally, homoplastic thoraco-lumbar characters within eutriconodontans and symmetrodonts[29,32,33] provide two cases for extrapolating the *Hox* gene

patterning of laboratory mice to early mammal phylogeny on a grand evolutionary scale.

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