ARTICLE

Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodont

Jin Meng[1,2], Yuanqing Wang[2] & Chuankui Li[2]

The transference of post-dentary jaw elements to the cranium of mammals as auditory ossicles is one of the central topics in evolutionary biology of vertebrates. Homologies of these bones among jawed vertebrates have long been demonstrated by developmental studies; but fossils illuminating this critical transference are sparse and often ambiguous. Here we report the first unambiguous ectotympanic (angular), malleus (articular and prearticular) and incus (quadrate) of an Early Cretaceous eutriconodont mammal from the Jehol Biota, Liaoning, China. The ectotympanic and malleus have lost their direct contact with the dentary bone but still connect the ossified Meckel's cartilage (OMC); we hypothesize that the OMC serves as a stabilizing mechanism bridging the dentary and the detached ossicles during mammalian evolution. This transitional mammalian middle ear narrows the morphological gap between the mandibular middle ear in basal mammaliaforms and the definitive mammalian middle ear (DMME) of extant mammals; it reveals complex changes contributing to the detachment of ear ossicles during mammalian evolution.

The lower jaw of non-mammalian amniotes is composed of the tooth-bearing dentary and several post-dentary bones; that of mammals is formed by the dentary alone. In contrast, there is only one ossicle, the columella auris (or stapes), in the middle ear of non-mammalian amniotes, but there are multiple ossicles in mammals, including the malleus, incus, stapes and ectotympanic[1–4]. Fossils have shown a series of reductions of the post-dentary bones during synapsid evolution towards mammals[1,2,4–6], and developmental studies have demonstrated homologies of mammalian middle ear ossicles with their reptilian precursors, including the malleus (=articular plus prearticular), incus (=quadrate) and ectotympanic (=angular)[7–9]. In basal mammaliaforms, such as *Morganucodon*, the post-dentary bones have greatly reduced but still attach to the dentary, serving a dual function for hearing and feeding[2,4,5,10,11]. The mandibular middle ear of *Morganucodon*[12] is regarded as the prototype that gives rise to the definitive mammalian middle ear (DMME) in which the angular, articular plus prearticular, and quadrate are strictly auditory structures and fully divorced from the feeding apparatus[2,4]. Incorporation of the lower jaw elements and the quadrate into the middle ear on the cranium represents an innovative feature of mammals and has been regarded as a classic example of gradual evolution in vertebrates, a subject that has attracted enormous attention[1–19]. Conventional research on the evolution of the mammalian middle ear has focused primarily on detachment of the post-dentary bones[2–4,10,11,14,16–18,20], in which transitional changes are often inferred from grooves on the medial surface of the dentary[4,6] or from fragmentary specimens[18]. The key questions still remain: what has happened, and how did it happen, during the transference from the mandibular middle ear to the DMME?

In view of the middle ear from the new Cretaceous eutriconodont mammal reported here, we hypothesize that the ossified Meckel's cartilage (OMC) serves as a stabilizing mechanism for the post-dentary bones during their evolutionary departure from the dentary. We define the transitional mammalian middle ear (TMME) as a distinct stage in the evolution of the mammalian middle ear and characterize the transference with a suite of morphological changes.

Mammalia Linnaeus, 1758
Euticonodonta Kermack *et al.*, 1973
***Liaoconodon hui*, gen. et sp. nov.**

Etymology. *Liao*, the short form for Liaoning Province; *conodon*, Latin, 'cuspate tooth', a common suffix for generic names in 'triconodonts'; *hui*, after Yaoming Hu, a student dedicated to the study of Mesozoic mammals.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V16051, a skeleton preserved on one slab of laminated siltstone (Figs 1 and 2 and Supplementary Figs 1–6).

Locality and horizon. Xiao-tai-zi, La-ma-dong, Jianchang, Liaoning, China; Jiufotang Formation. Early Cretaceous, Aptian, 120 Myr (ref. 21) (Supplementary Information part A).

Diagnosis. A medial-sized eutriconodont with a body length of 195 mm (from the tip of the rostrum to the hip) or 357 mm including the tail (Fig. 1). Dental formula I3.C1.P2.M3/i2.c1.p2.m4, with molariform teeth having three main cusps mesiodistally arranged and laterally compressed, and a dentary lacking an angular process and post-dentary trough. Differs from all known eutriconodonts in having the lower incisors, canine and first premolariform proportionally enlarged, similar in shape, and closely packed in space, and in having a deep trench along the ventral border of the masseteric fossa. Further differs from triconodontids in having the main cusp A/a distinctively higher and more inflated than other cusps; from 'jeholodentids'[18,22] in being larger and having relatively smaller (shorter) molariforms and a different dental formula; from gobiconodontids[12,23,24] in having fewer molariforms and in lacking a proportionally enlarged first incisor and the interlocking mechanism between successive lower molariforms; from *Repenomamus*[25,26] in being considerably smaller, having a different dental formula and less inflated cusp A/a in molariforms; from 'amphi-lestids' in having fewer molariforms and cheek teeth asymmetrical in labial view. Phylogenetic analyses place *Liaoconodon* between triconodontids and paraphyletic 'jeholodentids' (Supplementary Information and Supplementary Fig. 8).

Description

The description focuses on the middle ear region (Fig, 2, Supplementary Information part B and Supplementary Figs 2–6). The mandibular condyle is robust but not rounded. The glenoid fossa is well defined.

[1]Division of Paleontology, American Museum of Natural History, Central Park West at 79th street, New York, New York 10024, USA. [2]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China.
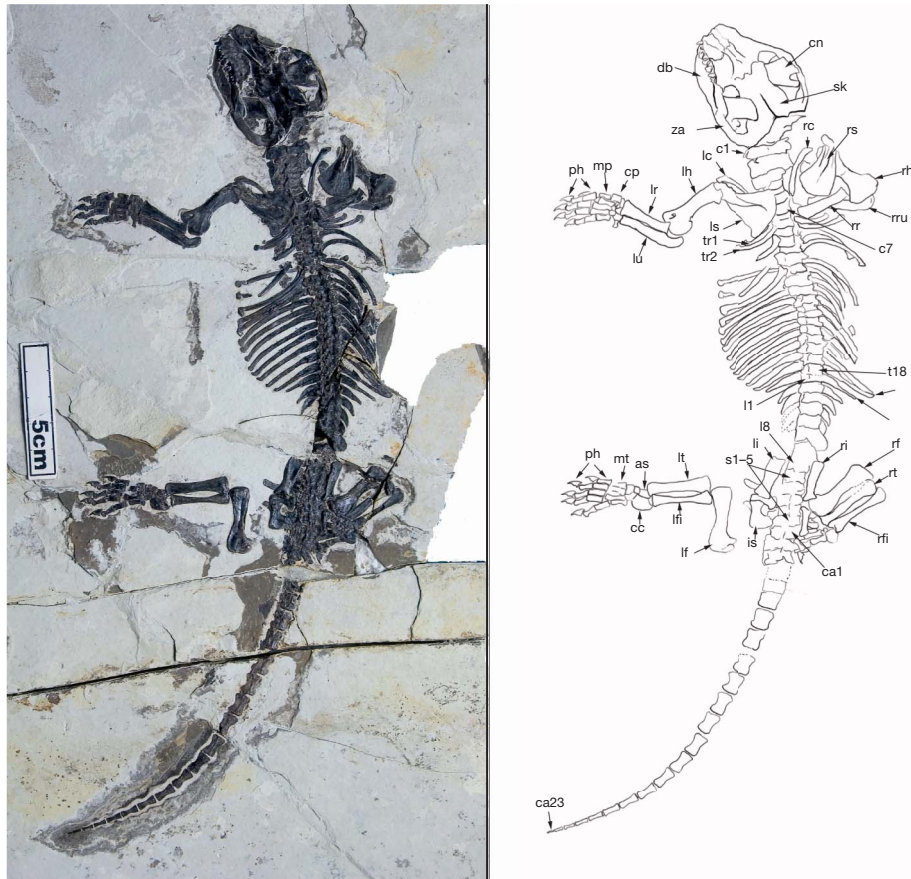
Figure 1 | The skeleton of the new mammal *Liaoconodon hui* (dorsal view of the holotype, IVPP V16051, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing). Abbreviations: as, astragalus; c1–7, first to seventh cervical vertebrae; ca1–23, first to twenty-third caudal vertebrae; cc, calcaneum; cn, coronoid; cp, carpals; db, dentary bone; l1–8, first to eighth lumbar vertebrae (the posterior ones are damaged); lc, left clavicle; lh, left humerus; li, left ilium; lr, left radius; ls, left scapula; lu, left ulna; mp, metacarpals; mt, metatarsals; ph, phalanges; rc, right clavicle; rf, right femurs; rfi, right fibular; rh, right humerus; ri, right ilium; rr, right radius; rs, right scapula; rt, right tibia; ru, right ulna; s1–5, first to fifth sacral vertebrae; sk, skull; tr, thoracic ribs; za, zygomatic arch.

Immediately medial to the glenoid fossa is the epitympanic recess. The squamosal sulcus[24] is a short and narrow valley between the postglenoid process and the paroccipital process (Fig. 2). The medial surface of the dentary has the Meckelian groove that bifurcates posteriorly, similar to that of *Amphitherium*[4]. The OMC[16,17] is splint-like anteriorly and thickened posteriorly with the posterior portion bending medially as in other species[16–18,27]. The three-pronged ectotympanic (=angular) abuts the malleus laterally and is similar to that of extant mammals in embryonic stage[9,20,28–31]. Its anterior limb contacts the prearticular and the posterior limb ends lateral to the malleo-incudal articulation. The ventral limb of the ectotympanic (=the reflected lamina of the angular) is crescent shaped and is less developed (shorter) than that in extant mammals (Fig. 2), indicating that the ectotympanic can hold only the anterior portion of the tympanic membrane (Figs 2 and 3). As in multituberculates[32] and extant mammals[33–35], the inner surface of the curved bone bears the tympanic sulcus for attachment of the tympanic membrane.

The malleus consists of a long anterior process and a hook-shaped body, homologous with the prearticular and the articular, respectively[2,4,7–9]. In the medial view of the bone, a zigzag suture exists between the two elements (Fig. 2). A longitudinal groove is present in the anterior portion of the anterior process, perhaps for the passage of the chorda tympani nerve; there is no foramen for the latter. The body of the malleus is probably equivalent to the pars transversalis in extant mammals[14,33,34]; it has the neck and the manubrial base but lacks the manubrium. We consider the ventral portion of the malleus body homologous with the retroarticular process of mammaliaforms[2,10,11]. The ventromedial edge of the body is rugose, indicating attachment of soft tissue in life, probably for a sizeable tensor tympani homologous

with the posterior pterygoid muscle[36]. On the posterodorsal corner of the bone is a process that is absent on the malleus of extant mammals[33,35]. The morphology and bone relationships show this process to be most probably homologous with the surangular boss in advanced cynodonts[2,37]. The lateral (ventral) surface of the malleus is flat and smooth, suggesting contact with the tympanic membrane in life. The incus is posterior to the malleus and free from the skull; it has a convex articular facet for the malleus and a process presumably for articulation with the stapes. The malleo-incudal articulation is hinge-like. The lateral surface of the incus is smooth and even with the lateral surface of the malleus if the bones are in articulation. Bone fragments at the fenestra ovalis (vestibuli) may represent parts of the stapes, and, if true, the stapes must be relatively massive.

The OMC as an ossicle stabilizer

The OMC in *Yanoconodon*, another eutriconodont from the Jehol Biota, was interpreted as having a paedomorphic resemblance to the embryonic pattern of modern mammals[18]. The middle ear of *Liaoconodon*, however, differs from that of *Yanoconodon* (Supplementary Information). The bone relationships (Fig. 2) show that during the early development of *Liaoconodon* the posterior end of the Meckel's cartilage must be separated from the rest of the cartilage, take the shape of the malleus body and join the dermal goniale (prearticular) to form the malleus; the rest of the cartilage became ossified at a later time but did not fuse with ear ossicles. In extant mammals the goniale usually ossifies earlier than other portions of the ossicles[30,31] and has a profound local influence upon endochondral ossification of the malleus[29]. Moreover, the Meckel's cartilage never fuses with the ectotympanic. These features
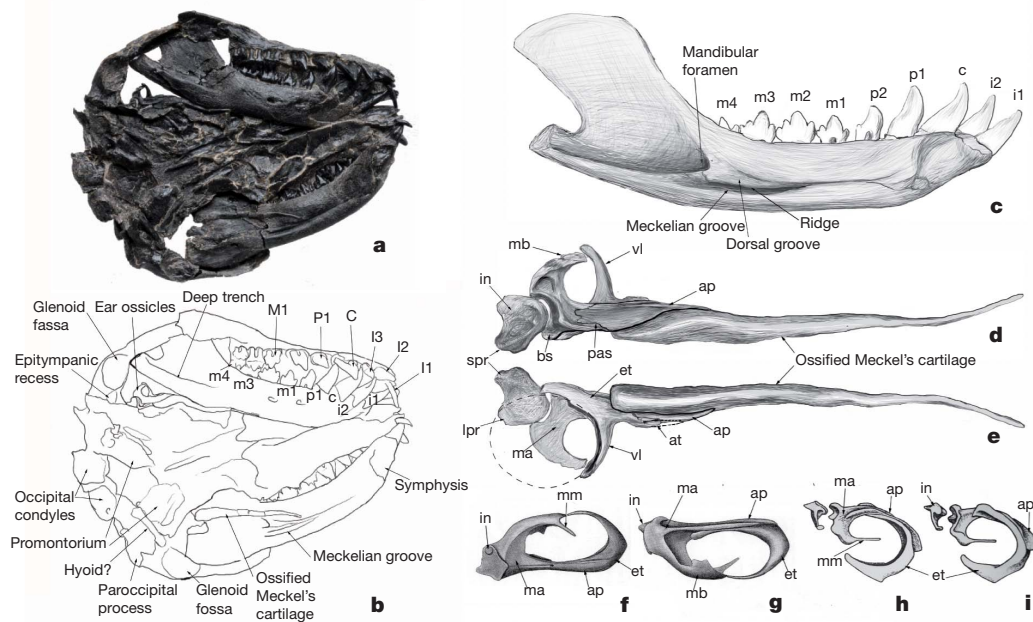
Figure 2 | Skull and ear ossicles of *Liaoconodon hui* (IVPP V16051).
a, **b**, Ventral view of the skull. **c**, Medial view of the dentary. **d**, **e**, Medial (dorsal) and lateral (ventral) views of the ossicles of *Liaoconodon*. Dashed oval indicates the estimated size of the tympanic membrane (actual shape could be more complicated). **f**, **g**, Dorsal and ventral views of the ossicles of *Ornithorhynchus anatinus* (modified after ref. 14). **h**, **i**, Medial and lateral views of the ossicles of *Didelphis* (modified after ref. 2). Ossicles are not on the same scale. The ear ossicles of *Liaoconodon* differ from those of extant mammals in having at least the following features: a long anterior process of the malleus wrapping around the OMC, ossicles proportionally larger, a hinge-like malleo-incudal joint, presence of the posterodorsal process of the malleus (boss of the surangular), lack of the manubrium, the ectotympanic partly developed. Abbreviations: ap, anterior process of malleus (prearticular); at, anterior process of the tympanic; bs, boss of surangular; et, ectotympanic (angular); in, incus (quadrate); lpr, long process of the incus; ma, body of malleus (articular); mb, manubrial base of malleus (retroarticular process); mm, manubrium of malleus; pas, prearticular–articular suture; spr, short process of the incus; vl, ventral limb of ectotympanic (reflected lamina of angular).

indicate that presence of the OMC in mammals[16–18,23,27] may not be interpreted as a simple paedomorphic feature.

It has been postulated that the Meckelian cartilage probably existed during a transitional stage in the evolution of extant mammals, later being replaced by the sphenomandibular ligament[1,4,5], and that such a ligament functions as a stabilizer for the detached ossicles[4]. Developmental studies also predict a persisting or ossified Meckel's cartilage in the common ancestor of recent mammals[14]. Along the same line of reasoning, we further hypothesize that during the evolution of mammals, the OMC or a persistent Meckel's cartilage functions as a stabilizing mechanism for the ear ossicles departed from the dentary but not yet supported by any cranial structure, as in the case of *Liaoconodon* (Fig. 3). Because the ossicles hold the tympanic membrane, it is necessary for them to be supported anteriorly so that the apparatus can function properly for hearing. This stabilizing mechanism becomes unnecessary when the ectotympanic fully suspends the tympanic membrane and the ossicles are moored on the cranium in more advanced mammals. In view of the new specimen, we think it inevitable to reinterpret the prearticular in the post-dentary unit of *Morganucodon*[11,12] as primarily the OMC (Fig. 3 and Supplementary Information part C).

Although known only in a few eutriconodonts[16–18,23] and symmetrodonts[17,27], the OMC or a persistent Meckel's cartilage in adults can be inferred from the Meckelian groove present in many early mammals (Fig. 4 and Supplementary Fig. 8). A Meckel's cartilage persisting in adult individuals of mammals has been observed or inferred elsewhere[14,38–40]. The sparse fossil record of the OMC is very probably because of its loose attachment to the dentary[16–18,23] so that preservation of the OMC is rare, similar to the record of ear ossicles[18,32,40]. It is also probable that the cartilage is not ossified; thus it left a contact groove on the dentary but is not fossilized.

Instead of being a paedomorphic resemblance, an alternative hypothesis is that the persistent Meckel's cartilage in Mesozoic mammals, along with features such as lack of the manubrium and a partial ectotympanic, represents a phylogenetic stage in mammalian evolution, and that the embryonic pattern of modern mammals recapitulates the phylogenetic changes.
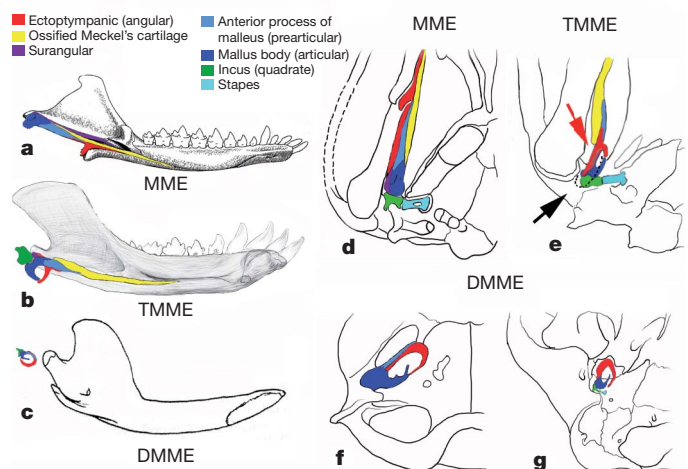

Figure 3 | Morphological transference of mammalian middle ear.
a–c, Medial views of the mandibles of *Morganucodon*, *Liaoconodon* and a generalized therian, showing the relationship with the OMC and ear ossicles. **d–g**, Ventral views of the basicranial and ear regions in *Morganucodon*, *Liaoconodon*, *Ornithorhynchus* and *Didelphis*, illustrating the relationship of the OMC, ear ossicles, the dentary and the basicranium. The black arrow in **e** points to the external auditory meatus, the red arrow to the gap between the ossicles and the dentary. The transference from the mandibular middle ear (MME) to the TMME and then to the DMME represents two distinct evolutionary stages, each involving several morphological changes (Supplementary Information part C). Source of drawings: **a** and **d** modified after refs 10 and 12, with the composition of bones reinterpreted; **c** from ref. 12; **f** from ref. 14; **g** from ref. 4.
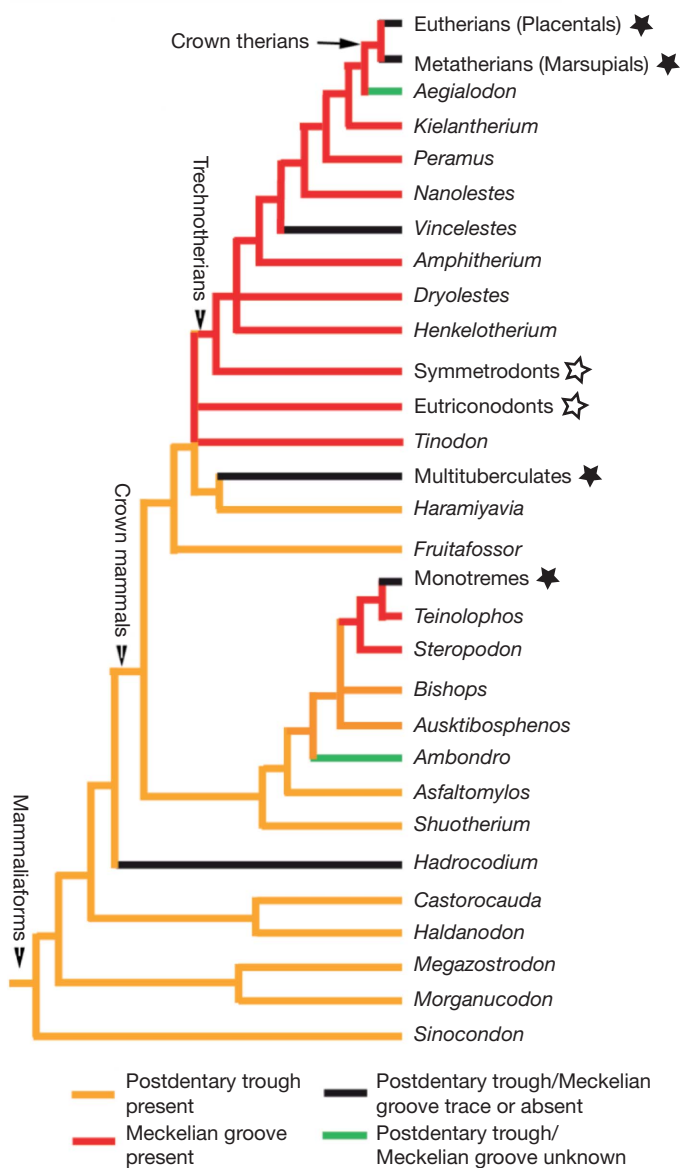
Figure 4 | Phylogeny of mammaliaforms (simplified after ref. 18) mapping distributions of the post-dentary trough and the Meckelian groove. A solid star denotes a group where the DMME is known in at least some members. An empty star indicates presence of the OMC is known in at least some members of the group. Given the phylogeny, the DMME evolved several times independently, and the transitional mammalian middle ear with a persistent Meckelian cartilage as a stabilizing mechanism, as inferred from presence of the groove, is consistent with the phylogeny (see also Supplementary Fig. 7).

The mammalian tympanic membrane

The origin of the mammalian tympanic membrane has been under extensive discussion[1,2,4,5,11,19,41–46] but still remains to be explained[5]. Four hypotheses have been outlined for the possible location and composition of the membrane in pre-mammalian synapsids, from which the mammalian condition is derived: (1) in a postquadrate location[1]; (2) in a post-dentary location[2]; (3) in both positions separately[44]; or (4) 1 and 2 coexisting as a continuous tympanic membrane[4]. The evidence from *Liaoconodon* supports hypothesis 4 (Fig. 4).

In *Liaoconodon* the crescent ectotympanic is insufficient to suspend the tympanic membrane fully; the latter must be in contact with the malleus and attached posteriorly to a cranial structure. The most feasible

cranial structure for attachment of the membrane is the posterior rim of the epitympanic recess where the tympanohyal is situated[17]. There are at least three reasons for this. First, such an attachment makes phylogenetic sense when compared with the condition in non-mammalian therapsids that have a squamosal sulcus[4]. Second, it is consistent with the condition of extant mammals in which the epitympanic recess is immediately dorsal or dorsomedial to the tympanic membrane[33–35]. Finally, developmental evidence shows that the membrane is supported by the tympanohyal and the element of Spence before full development of the ectotympanic[43]. This attachment is also consistent with the possibility that the posterior portion of the tympanic membrane is in contact with the malleus and incus, as evidenced by the fact that the lateral surfaces of the two ossicles are smooth and aligned even when the ossicles are in articulation.

The partly developed ectotympanic, absence of the manubrium of the malleus and lack of a fully suspended tympanic membrane in *Liaoconodon* echo the observations from developmental studies that phylogenetically older portions of the ossicles develop earlier than those that represent more recent evolutionary inventions[31,33]. Moreover, molecular–developmental studies also show that the manubrium, the processus brevis, the ectotympanic and tympanic membrane exhibit an interdependent relationship in the mammalian developmental programme[15,19]. Full development of the ectotympanic and the manubrium implies that they are probably neomorphs of mammals as co-members of an advanced complex adaptation late in therapsid evolution towards mammals[4,43].

The TMME

As the first unambiguous paleontological evidence, the middle ear of *Liaoconodon* corroborates the Reichert–Gaupp theory on the homology of the mammalian ear ossicles[7,8] as well as the hypothesis on the evolution of the mammalian middle ear[2,4]. The ear morphology of *Liaoconodon* represents a transitional stage in the evolution of mammalian middle ears regardless of how many times the DMME evolved[4,18,41]. The TMME can be characterized by several features: the articular, prearticular and angular lose their direct contact with the dentary (thus called as the malleus and ectotympanic) and are supported anteriorly by a persistent Meckel's cartilage, but not by cranial structures, in adult; the malleo-incudal articulation is hinge-like and lost its primary function for jaw suspension; all ear ossicles are primarily auditory structures but are not completely free from the feeding effect; the tympanic membrane is not fully suspended by the ectotympanic, and the manubrium of the malleus has not developed (Figs 2 and 3).

A key issue in the study of the evolution of the mammalian middle ear focuses on the detachment of the post-dentary bones[3,4,17,18,20], which primarily involves two events: separation of the ossicles from the dentary and degeneration of the Meckel's cartilage in adults[18]. The ear of *Liaoconodon* demonstrates that the transference from the mandibular middle ear to the TMME and then to the DMME involves complex morphological changes (Fig. 3 and Supplementary Information part C). Because of these changes, the TMME must be more efficient in airborne sound hearing than the mandibular middle ear, because the ossicles are proportionally smaller, the incus has more freedom and the other ossicles are separated from the dentary. In addition, the loose attachment of the OMC in the dentary, the sutured relationship of the OMC with the ossicles and the possible flexibility of the persistent Meckel's cartilage further enhance hearing by decoupling hearing from feeding. On the other hand, the hinged malleo-incudal joint, lack of the manubrium as a level arm in the ossicle chain and incomplete suspension of the tympanic membrane indicate that the middle ear of *Liaoconodon* is not so efficient as in extant mammals.

METHODS SUMMARY

Supplementary Information part F provides a full description of the methods.

1. Hopson, J. A. The origin of the mammalian middle ear. *Am. Zool.* **6,** 437–450 (1966).
2. Allin, E. F. Evolution of the mammalian middle ear. *J. Morphol.* **147,** 403–438 (1975).
3. Maier, W. Phylogeny and ontogeny of mammalian middle ear structures. *Neth. J. Zool.* **40,** 55–75 (1990).
4. Allin, E. F. & Hopson, J. A. in *The Evolutionary Biology of Hearing* (eds Webster, D. B., Fay, R. R. & Popper, A. N.) 587–614 (Springer, 1992).
5. Clack, J. A. & Allin, E. F. in *Evolution of the Vertebrate Auditory System* (eds Manley, G. A., Popper, A. N. & Fay, R. R.) 128–163 (Springer, 2004).
6. Lillegraven, J. A. & Krusat, G. Cranio-mandibular anatomy of *Haldanodon expectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implications to the evolution of mammalian characters. *Contrib. Geol.* **28,** 39–138 (1991).
7. Reichert, C. Über die Visceralbogen der Wirbeltiere im Allgemeinen und deren Metamorphosen bei den Vögeln und Säugetieren. *Arch. Anat. Physiol. Medizin* **1837,** 120–222 (1837).
8. Gaupp, E. Die Reichertsche Theorie (Hammer-, Amboss- und Kieferfrage). *Arch. Anat. Entwick.* **1912,** 1–416 (1913).
9. Goodrich, E. S. *Studies on the Structure and Development of Vertebrates* (Macmillan, 1930).
10. Kermack, K. A., Mussett, F. & Rigney, H. W. The lower jaw of *Morganucodon. Zool. J. Linn. Soc.* **53,** 87–175 (1973).
11. Kermack, K. A., Mussett, F. & Rigney, H. W. The skull of *Morganucodon. Zool. J. Linn. Soc.* **71,** 1–158 (1981).
12. Kielan-Jaworowska, Z., Cifelli, R. L. & Luo, Z.-X. *Mammals from the Age of Dinosaurs—Origins, Evolution, and Structure* (Columbia Univ. Press, 2004).
13. Zeller, U. Die Entwicklung und Morphologie des Schädels von *Ornithorhynchus anatinus* (Mammalia: Prototheria: Monotremata). *Abhandl. Senckenberg. Natur. Gesell.* **545,** 1–188 (1989).
14. Zeller, U. in *Mammal Phylogeny* Vol. 1 (eds Szalay, F. S., Novacek, M. J. & McKenna, M. C.) 95–107 (Springer, 1993).
15. Mallo, M. Formation of the middle ear: recent progress on the developmental and molecular mechanisms. *Dev. Biol.* **231,** 410–419 (2001).
16. Wang, Y.-Q., Hu, Y.-M., Meng, J. & Li, C.-K. An ossified Meckel's cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science* **294,** 357–361 (2001).
17. Meng, J. Hu, Y.-M., Wang, Y.-Q. & Li, C.-K. The ossified Meckel's cartilage and internal groove in Mesozoic mammaliaforms: implications to origin of the definitive mammalian middle ear. *Zool. J. Linn. Soc.* **138,** 431–448 (2003).
18. Luo, Z.-X., Chen, P.-J., Li, G. & Chen, M. A new eutriconodont mammal and evolutionary development in early mammals. *Nature* **446,** 288–293 (2007).
19. Takechi, M. & Kuratani, S. History of studies on mammalian middle ear evolution: a comparative morphological and developmental biology perspective. *J. Exp. Zool. B* **314,** 1–17 (2010).
20. Rowe, T. B. Coevolution of the mammalian middle ear and neocortex. *Science* **273,** 651–654 (1996).
21. He, H.-Y. *et al.* Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China, and its implications. *Geophys. Res. Lett.* **31,** L12605 (2004).
22. Ji, Q., Luo, Z.-X. & Ji, S.-A. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* **398,** 326–330 (1999).
23. Li Li, C.-K., Hu, Y.-M., Wang, Y.-Q. & Meng, J. A new species of *Gobiconodon* (Triconodonta, Mammalia) and its implication for the age of Jehol Biota. *Chin. Sci. Bull.* **48,** 1129–1134 (2003).
24. Meng, J., Hu, Y.-M., Wang, Y.-Q. & Li, C.-K. A new gobiconodont species (Mammalia) from the Early Cretaceous Yixian Formation of Liaoning, China. *Vert. PalAsiatica* **43,** 1–10 (2005).
25. Li, J.-L., Wang, Y., Wang, Y.-Q. & Li, C. K. A new family of primitive mammal from the Mesozoic of western Liaoning, China. *Chin. Sci. Bull.* **45,** 2545–2549 (2000).
26. Hu, Y.-M., Meng, J., Li, C.-K. & Wang, Y.-Q. Large Mesozoic mammals fed on young dinosaurs. *Nature* **433,** 149–153 (2005).
27. Ji, Q., Luo, Z.-X., Zhang, X., Yuan, C.-X. & Xu, L. Evolutionary development of the middle ear in Mesozoic therian mammals. *Science* **326,** 278–281 (2009).
28. McClain, J. A. The development of the auditory ossicles of the opossum (*Didelphys virginiana*). *J. Morphol.* **64,** 211–265 (1939).
29. Filan, S. L. Development of the middle ear region in *Monodelphis domestica* (Marsupialia, Didelphidae): marsupial solutions to an early birth. *J. Zool.* **225,** 577–588 (1991).
30. Clark, C. T. & Smith, K. K. Cranial osteogenesis in *Monodelphis domestica* (Didelphidae) and *Macropus eugenii* (Macropodidae). *J. Morphol.* **215,** 119–145 (1993).
31. Sánchez-Villagra, M. R., Gemballa, S., Nummela, S., Smith, K. K. & Maier, W. Ontogenetic and phylogenetic transformations of the ear ossicles in marsupial mammals. *J. Morphol.* **251,** 219–238 (2002).
32. Meng, J. & Wyss, A. R. Monotreme affinities and low-frequency hearing suggested by multituberculate ear. *Nature* **377,** 141–144 (1995).
33. Fleischer, G. Studien am Skelett des Gehörorgans der Säugetiere, einschliesslich des Menschen. *Säugetierk. Mitt.* **21,** 131–239 (1973).
34. Fleischer, G. Evolutionary principles of the mammalian middle ear. *Adv. Anat. Embryol. Cell Biol.* **55,** 1–70 (1978).
35. Henson, O. W. Comparative anatomy of the middle ear. *Handbook of Sensory Physiology: The Auditory System* Vol. 5, Pt 1 (eds Keidel, W. D. & Neff, W. D.) 39–110 (Springer, 1974).
36. Barghusen, H. R. in *The Ecology and Biology of Mammalian-like Reptiles* (eds Hotton III N., MacLean P. D., Roth, J. J. & Roth, E. C.) 253–262 (Smithsonian Institution Press, 1986).
37. Crompton, A. W. in *Studies in Vertebrate Evolution* (eds Joysey, K. A. & Kemp, T. S.) 231–251 (Oliver & Boyd, 1972).
38. Bensley, B. A. On the identification of Meckelian and mylohyoid grooves in the jaws of Mesozoic and Recent Mammalia. *Univ. Toronto Stud. Biol. Ser.* **3,** 75–81 (1902).
39. Krebs, B. Evolution of the mandible and lower dentition in dryolestids (Pantotheria, Mammalia). *Zool. J. Linn. Soc.* **50** (Suppl. 1), 89–102 (1971).
40. Rougier, G. W., Wible, J. R. & Novacek, M. J. Middle-ear ossicles of the multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: implications for mammaliamorph relationships and the evolution of the auditory apparatus. *Am. Mus. Novit.* **3187,** 1–43 (1996).
41. Allin, E. F. in *The Ecology and Biology of Mammal-like Reptiles* (eds Hotton, N., MacLean P. D., Roth, J. J. & Roth, E. C.) 283–294 (Smithsonian Institution Press, 1986).
42. Kermack, K. A. & Mussett, F. The ear in mammal-like reptiles and early mammals. *Acta Palaeontol. Pol.* **28,** 147–158 (1983).
43. Presley, R. Lizards, mammals and the primitive tetrapod tympanic membrane. *Symp. Zool. Soc. Lond.* **52,** 127–152 (1984).
44. Westoll, T. S. The mammalian middle ear. *Nature* **155,** 114–115 (1945).
45. Watson, D. M. S. Evolution of the mammalian ear. *Evolution* **7,** 159–177 (1953).
46. Shute, C. C. The evolution of the mammalian eardrum and tympanic cavity. *J. Anat.* **90,** 261–281 (1956).