Zoology 140 (2020) 125767

Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

# Making a mammalian ear. Modular decoupling of the mammalian middle ear and jaw discovered in a new species of Cretaceous stem therian mammals

Fangyuan Mao[a,b,c], Jin Meng[c,d,*]

[a] Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing, 100044, China
[b] CAS Center for Excellence in Life and Paleoenvironment, Beijing, 100044, China
[c] Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024, USA
[d] Earth and Environmental Sciences, Graduate Center, City University of New York, New York, NY, 10016, USA

ARTICLE INFO

*Keywords:*
Mammalian middle ear
jaw joint
Mesozoic
stem therians
modular evolution

ABSTRACT

Evolution of the definitive mammalian middle ear (DMME) as a textbook example in vertebrate evolution has been extensively studied during the last 200 years. Fossils provide the direct evidence on evolutionary stages of the DMME, but because of delicacy of the miniscule ossicles, unequivocal evidence about them has always been rare. Recent work on a stem therian mammal (124 million years old) shows presence of the surangular bone in the basal mammals as a primitive feature and potentially retained in the embryonic stage of some extant mammals. The work also proposed that the DMME and mammalian jaw evolved in a modular fashion. It started as a highly integrated complex in structures and functions, the two modules were regulated by similar developmental genetic mechanisms and eventually decoupled under natural selection so that the physical constraint the two modules imposed on each other was removed, allowing future improvement of each module for better function.

Non-mammalian reptiles (NMRs) have one bone, the columella auris (stapes), in the middle ear, but mammals have three: the stapes, incus, and malleus, which form a lever system that receives sound vibrations at the tympanic membrane and transmits them to the inner ear (Fig. 1A-B). The lower jaw of NMRs consists of several bones in which the articular bone articulates the skull bone, the quadrate, to form the primary jaw joint, contrasting the single-boned lower jaw (dentary) that articulates the squamosal, as the secondary jaw joint, in mammals (Fig. 1B). Since Darwin's time it had become known that the reptilian articular, prearticular, angular, and quadrate were homologous to the malleus, gonial, ectotympanic, and incus of mammals, respectively, a view recognized as the Reichert-Gaupp theory (Maier and Ruf, 2016). Incorporation of the ectotympanic and the malleus-incus complex into the middle ear as exclusive hearing structures are the most critical events in the evolution of DMME and jaw joint (Allin, 1975; Allin and Hopson, 1992 ; Fleischer, 2013).

Fossils show that the postdentary bones (articular, prearticular, angular, surangular) and the quadrate of NMRs gradually reduced size during the evolution of synapsids toward mammals. In basal mammaliaforms, the reduced postdentary bones served for dual functions: chewing (mastication) and hearing (sound transfer from outer to inner ear). In the transitional mammalian middle ear (TMME) of some Mesozoic mammals (Meng et al., 2011; Fig. 1C), the postdentary bones had detached from the dentary and functioned exclusively for hearing, while the secondary jaw joint was in full function. However, because the auditory bones were connected to the ossified Meckel's cartilage (OMC) that was anteriorly lodged in the medial side of the dentary bone in TMME, hearing and chewing must still have interfered with each other.

We recently characterized a novel stem therian mammal, *Origolestes lii*, from the Early Cretaceous Jehol Biota, China, which shed new light on the evolution of the DMME (Mao et al., 2020; Fig. 1D). High-resolution CT-scan revealed 3D morphologies of the auditory bones and OMC that were preserved in nearly anatomical positions. Of the auditory bones, the surangular bone was identified; this was a prominent postdentary bone in basal mammaliaforms but disappeared in extant mammals. Although the accessory malleus, present in embryonic stage of some mammals, was thought to be homologous to the surangular (McClain, 1939), there seems no convincing evidence for it. With the discovery of *Origolestes* and other evidence, we postulated that the

* Corresponding author at: Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024, USA.
*E-mail addresses:* maofangyuan@ivpp.ac.cn (F. Mao), jmeng@amnh.org (J. Meng).

https://doi.org/10.1016/j.zool.2020.125767
Received 5 March 2020; Received in revised form 12 March 2020; Accepted 16 March 2020
Available online 05 May 2020
0944-2006/ 

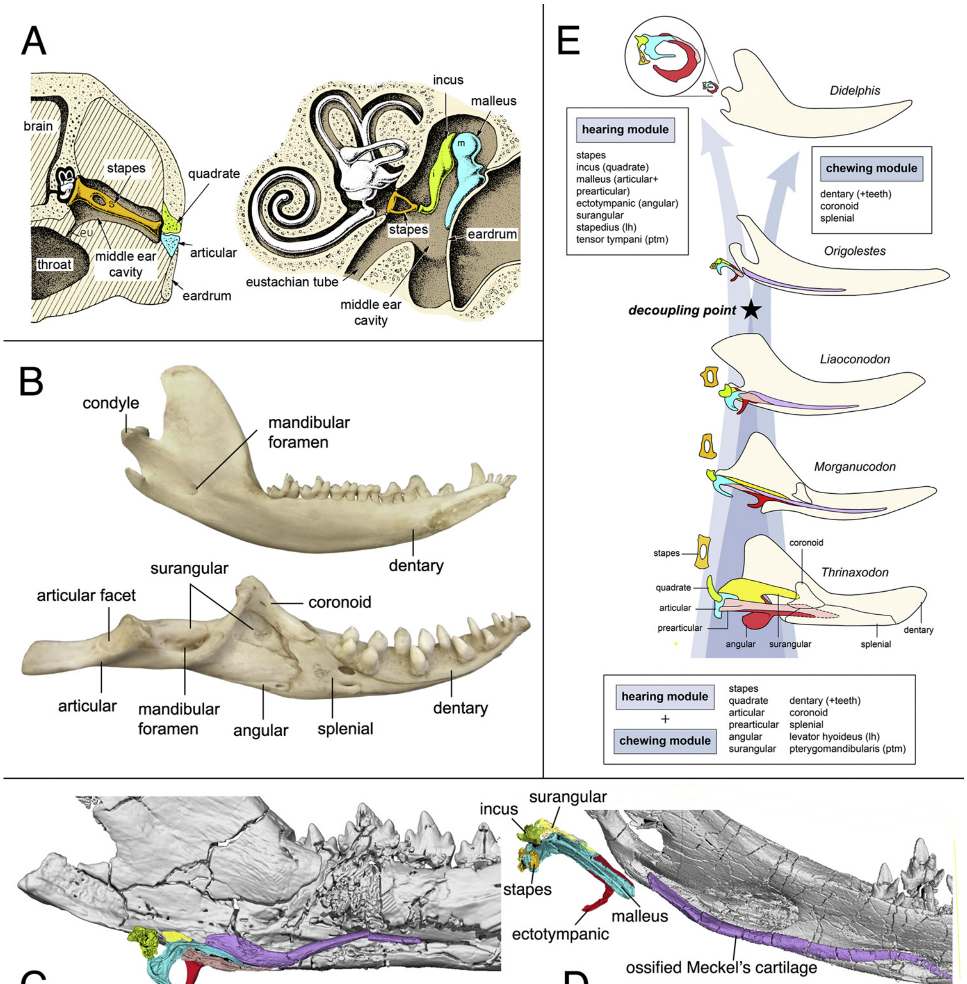


**Fig. 1.** A, Comparison of the middle ears of non-mammalian reptiles (left) and mammals (right) (modified from Romer and Parsons, 1977). B, Comparison of the single-boned mammalian lower jaw (*Didelphis*) and the multi-boned reptilian jaw (*Varanus*). C, TMME in which the auditory bones were still connected to the OMC (*Liaoconodon*). D, Decoupling phenotype in which the bony contact between the auditory bones and OMC disappeared (*Origolestes*). E, Outlined stages of the modular decoupling process during evolution of synapids toward mammals.

surangular had persisted in basal mammals as a primitive feature and probably exists as a remnant in embryonic stage of some extant mammals, a hypothesis that invites tests from paleontological and developmental studies. More importantly, the specimens of *Origolestes* preserved a critical configuration that shows separation of the hearing and chewing apparatuses. Compared to the TMME, the auditory bones had lost the bony connection with the OMC; a gap between the two units was likely connected by soft tissue, such as a ligament, in life (Fig. 1D). This phenotype probably marked the beginning stage of the DMME. Developmental genetic studies have shown that the reptilian jaw joint and the malleus-incus complex were regulated by similar genetic mechanisms and that the gene-controlled process is responsible for the developmental breakdown of the Meckel's cartilage in embryonic stage of mammals (Tucker et al., 2004; Anthwal et al., 2017; Urban et al., 2017). With the discovery of auditory bones and OMC in *Origolestes*, it becomes more evident that the embryonic developments of the mammalian middle ear and jaw recapitulate their evolutionary stages.

Evidence shows that the hearing and chewing elements have been phenotypically and genetically constrained as two modules during the evolution of synapsids; *Origolestes* visualized the snapshot of the evolutionary decoupling moment of the two modules (Fig. 1E). Modular evolution in biology, such as vertebrate limbs (Shubin and Davis, 2004) and mammal skulls (Koyabu et al., 2014) has been commonly discussed. However, the modularity of the DMME and mammalian jaw is intriguing, perhaps unique, in that they started as a highly integrated complex with mixed hearing and chewing functions in basal mammaliaforms. The stapes, for instance, is generally considered as a hearing bone but contributed to chewing, whereas the articular, a jawbone for chewing, participated hearing for transmitting sound vibrations. However complex, the phenotype and underlying genotype for each module must have been coupled and the natural selection has been working on both modules until their decoupling during the evolution of mammals. The decoupled modules removed the physical constraints they imposed on each other, allowing each module to evolve without bothering the other. Many questions can be asked in light of this new study. Did a similar process take place in other lineages, such as monotremes and multituberculates? The Meckel's cartilage arises from the first pharyngeal arch and the phenotypic boundary between the two modules is within it; then, how did the genetic mechanisms responsible for the two parts of the cartilage work during the evolutionary development in jawed vertebrates? Mammals, particularly therians, can hear high-frequent sounds and possess enormous tooth morphologies for processing diverse foods; could this biodiversity be partly attributable to the modular decoupling, as we see in *Origolestes*?

## Acknowledgements

We thank our colleagues who have helped us in various ways during the course of our studies on Mesozoic mammals. We are grateful to Thomas Bosch for inviting us to write this perspective on our work. We thank Nicole Wong for making the figure. The related researches have been supported by the National Natural Science Foundation of China (41688103, 41404022); the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB26000000); the Youth Innovation Promotion Association CAS (2019076); and the Kalbfleisch Fellowship, Richard Gilder Graduate School, American Museum of Natural History.

## References

Allin, E.F., 1975. Evolution of the mammalian middle ear. Journal of Morphology 147 (4), 403–437.

Allin, E.F., Hopson, J.A., 1992. Evolution of the auditory system in Synapsida ("mammal-like reptiles" and primitive mammals) as seen in the fossil record. The Evolutionary Biology of Hearing. Springer, New York, NY, pp. 587–614.

Anthwal, N., Urban, D.J., Luo, Z.X., Sears, K.E., Tucker, A.S., 2017. Meckel's cartilage breakdown offers clues to mammalian middle ear evolution. Nature ecology & evolution 1 (4), 1–6.

Fleischer, G., 2013. Evolutionary Principles of the Mammalian Middle Ear Vol. 55 Springer-Verlag, Berlin, Heidelberg, New York.

Koyabu, D., Werneburg, I., Morimoto, N., Zollikofer, C.P., Forasiepi, A.M., Endo, H., Kimura, J., Ohdachi, S.D., Son, N.T., Sánchez-Villagra, M.R., 2014. Mammalian skull heterochrony reveals modular evolution and a link between cranial development and brain size. Nature communications 5 (1), 1–9.

Maier, W., Ruf, I., 2016. Evolution of the mammalian middle ear: a historical review. Journal of anatomy 228 (2), 270–283.

Mao, F., Hu, Y., Li, C., Wang, Y., Chase, M.H., Smith, A.K., Meng, J., 2020. Integrated hearing and chewing modules decoupled in a Cretaceous stem therian mammal. Science 367 (6475), 305–308.

McClain, J.A., 1939. The development of the auditory ossicles of the opossum (*Didelphys virginiana*). Journal of Morphology 64 (2), 211–265.

Meng, J., Wang, Y., Li, C., 2011. Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodont. Nature 472 (7342), 181–185.

Romer, A.S., Parsons, T.S., 1977. The Vertebrate Body, Fifth ed. W.B. Saunders Co., Philadelphia.

Shubin, N.H., Davis, M.C., 2004. Modularity in the evolution of vertebrate appendages. Modularity in Development and Evolution. The University of Chicago Press, Chicago, pp. 429–440.

Tucker, A.S., Watson, R.P., Lettice, L.A., Yamada, G., Hill, R.E., 2004. Bapx1 regulates patterning in the middle ear: altered regulatory role in the transition from the proximal jaw during vertebrate evolution. Development 131 (6), 1235–1245.

Urban, D.J., Anthwal, N., Luo, Z.X., Maier, J.A., Sadier, A., Tucker, A.S., Sears, K.E., 2017. A new developmental mechanism for the separation of the mammalian middle ear ossicles from the jaw. Proceedings of the Royal Society B: Biological Sciences 284 (1848), 20162416.