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Integrated hearing and chewing modules decoupled in a Cretaceous stem therian mammal

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Based on multiple 3D skeletal specimens we report a new Cretaceous stem therian mammal that displays decoupling of hearing and chewing apparatuses and functions. The auditory bones, including the surangular, have no bone contact with the ossified Meckel's cartilage; the latter is loosely lodged on the medial rear of the dentary. This configuration probably represents the initial morphological stage of the definitive mammalian middle ear. Evidence shows that hearing and chewing apparatuses have evolved in a modular fashion. Starting as an integrated complex in non-mammaliaform cynodonts, the two modules, regulated by similar developmental and genetic mechanisms, eventually decoupled during the evolution of mammals, allowing further improvement for more efficient hearing and mastication.

In non-mammaliaform cynodonts, the primary jaw joint served for both chewing (mastication) and hearing (sound transfer) functions. In mammals, the two functions and related structures are separated, characterized by a single-boned lower jaw and a tri-ossicular middle ear. Although the primary jaw joint and postdentary bones differ from the mammalian auditory bones in morphology, their homologies have been demonstrated by developmental, genetic, and paleontological evidence (1–7). Here we report a new genus and species of symmetrodont mammal from the Early Cretaceous Jehol Biota, China. The unprecedented preservation of the specimens displays key structures related to hearing and chewing morphologies, such as tooth crown structures, ossified Meckel's cartilage and its lodging groove on the dentary, and the auditory bones (the stapes, malleus, incus, ectotympanic, and surangular) (Figs. 1 to 3). The configuration of the auditory bones most probably represents the beginning stage of the definitive mammalian middle ear (1) and narrows the morphological gap between the former and the transitional mammalian middle ear (8). Given their homologies and similar developmental generic patterning mechanisms (2–6, 9), the hearing and chewing apparatuses are hypothesized as two integrated modules that were decoupled during mammalian evolution. The final disassociation of the two modules could have increased capacity to generate heritable phenotypic variations (10) and thus pro-

vided the potential for improvement of hearing and chewing functions in future therians.

Origolestes lii, gen. et sp. nov. (11) has the acute-angled molars, typical for spalacotheriid 'symmetrodontans' (11–17), an extinct group of stem therian mammals (18) (Figs. 1 and 2). The embrasure between upper molars is a narrow but transversely deep wedge-shaped space, corresponding to a narrow cusp a of the lower molar. In contrast, the lower molar is transversely narrower but mesiodistally long so that the embrasure between lower molars are open and shallow, being able to accommodate a broad cusp A of the upper molar. Palatal fossae on the palate exist lingual to upper molars (fig. S3) and must have received tall cusps of lower molars while the lower jaws were at rest position in life. During the evolution of the tribosphenic tooth pattern, the upper molar was lingually extended by addition of the protocone and the lower molar developed the talonid; these changes let the protocone bite in the talonid for grinding. Additionally, the lower molar cusps no longer rested by biting in the palatal fossae, which could help to protect the palate and gum as well as increase the space of the mouth cavity that may assist in food holding and processing.

Because the lower teeth positioned lingual to the uppers at rest position, during mastication the opened lower jaw would close dorsolabially with a degree of eversion so that cusp a of the lower molar can fit in the narrow embrasure

between upper molars (Fig. 2). Then, the lower molar would move dorsolingually in a curved path during power stroke because the functional surfaces of the wedge-shaped tooth cusps are convex. Thus, in addition to the transverse component of the jaw movement, the tooth shape and occlusal relation dictate that the mandible had to invert by rolling inward relative to its long axis during jaw closing, and the unfused symphysis (Fig. 3) allows such eversion and inversion of the lower jaw, similar to other mammaliaforms (19). These features imply that components of both jaw yaw (20) and rolling (19) existed during mastication of *Origolestes*. The acute-angled molars of *Origolestes* are relatively wider than the triconodont molars but narrower than the tribosphenic ones, the degree of the two movements would be intermediate between those with triconodont and tribosphenic molars. While jaw yaw and rolling may be primitive mammaliaform features (19, 20), they probably played a role in the decoupling of the auditory bones from the dentary and eventually from the Meckel's cartilage during mammalian evolution.

The long ossified Meckel's cartilage is rod-like, broad posteriorly but tapering anteriorly, with its posterior end bending medially (Fig. 3 and fig. S6). The stapes has a large process for insertion of the stapedius muscle (Fig. 3 and figs. S6 and S7). The incus articulates with the malleus and possibly the surangular and anchors in the epitympanic recess by a dorsal plate; its stapedia process curves medially to articulate the stapes. The malleus has a short anterior process and a blunt manubrium, a neomorphic structure in mammals (2, 3, 21). The surangular is present as a distinct bone dorsolateral to the malleus body. In some non-mammaliaform cynodonts, a surangular boss is dorsolateral to the primary jaw joint and may have functioned to reduce the compressive load borne by the quadrate in life (1); a similar structure was interpreted in the same position in *Liaococonodon* (8) (Fig. 3). The surangular has been reported in the euharamiyidan *Arboroharamiya* but remains poorly known, or unknown, in other Mesozoic mammaliaforms; it may exist in some extant mammals as the accessory malleus (22). The ectotympanic is therian-like but has a slim and short ventral limb (= reflected lamina). The malleus, surangular, and ectotympanic are tightly connected, with the thin ectotympanic partly wrapping around the other two elements, so that they likely have functioned as one unit to transmit sound vibrations. A gap is between the auditory bones and the distal end of the Meckel's cartilage, probably left by a ligament in life. The lack of bone contact between the two units contrasts with the bone-contact condition of the transitional mammalian middle ear in *Liaococonodon* (Fig. 3).

A sizable stapedius muscle may be inferred from the distinct process for insertion of the stapedius muscle of *Ori-*

golestes, contrasting to the miniscule process on the stapes of extant therians. Moreover, we further postulated that the tensor tympani had inserted to the concavity on the medial side of the malleus body, near the base of the manubrium; a similar condition is present in the malleus of *Liaococonodon* (Fig. 3). The homologies of the two middle ear muscles have been treated in many studies (23–25). The tensor tympani was a derivative of the first arch and innervated by the trigeminal nerve, whereas the stapedius is a second arch derivative innervated by the facial nerve (2). Although different interpretations have existed, it is generally accepted that the tensor tympani (and tensor veli palatini) is derived from the pterygomandibularis (23, 25) and that the stapedius was derived from the levator hyoideus/depressor mandibulae (24). These muscles were associated with mastication in non-mammalian tetrapods but transformed into the middle ear of mammals for hearing. Contractions of the muscles dampen sound-induced oscillations of tympanum and middle ear bones and reduce sound amplitude, thus protecting the inner ear from intense sound signals (9, 26).

In non-mammaliaform cynodonts, such as *Thrinaxodon*, the postdentary bones had functioned for jaw articulation and sound transfer to the inner ear (1); even the stapes had played a role in mastication to resist medial displacement of the quadrate during chewing (27). Thus, the hearing and chewing apparatuses formed a structurally and functionally integrated complex. In the mandibular middle ear of *Morganucodon*, the postdentary bones greatly reduced and the secondary jaw articulation was formed. In the transitional mammalian middle ear of *Liaococonodon*, the auditory bones were detached from the dentary but retained substantial bone contact with the Meckel's cartilage so that hearing and chewing functions still interfere with each other. In *Origolestes*, such a bone contact is lost, showing the decoupling configuration of the hearing and chewing apparatuses that had been predicted in previous studies (1, 21). Finally, in the definitive mammalian middle ear, the auditory bones continue to reduce sizes and the Meckel's cartilage no longer exists in adults.

Although the postdentary bones in non-mammalian cynodonts are morphologically different from the auditory bones in mammals (Fig. 4), their homologies have been demonstrated by developmental, genetic, and paleontological evidence (1–4, 6, 9) and can be traced back through amniotes (28). In particular, it has been shown that genes working in concert in regulating the middle ear bones of mammals also regulate patterning of the jaw joint in non-mammalian vertebrates (5). Moreover, developmental studies in extant mammals support the findings of the persisting Meckel's cartilage and its groove in Mesozoic mammals (6, 9, 29). Thus, it is rational to assume that similar genetic regulating mechanisms and developmental pathways exist-

ed through the transition from the jaw joint bones to auditory bones during synapsid evolution. Phylogenetically, the definitive mammalian middle ear may have evolved multiple times (fig. S9) (8, 21), and the composition of the ear ossicles in different lineages remain the same. Based on fossil and developmental genetic evidence we hypothesize that in synapsids the hearing and chewing apparatuses have evolved as two modules that were regulated by similar genetic and developmental mechanisms, respectively. Starting as a highly integrated structural and functional complex in non-mammaliaform cynodonts, the hearing and chewing modules eventually decoupled, as evidenced in *Origolestes* (Fig. 4), which removed the physical constraint imposed on each other. Such modularity and dissociation would enhance the capacity to generate variation (or evolvability), which may confer a selective advantage on modular clades that possess it (10, 30). The Early Cretaceous *Origolestes* sets a phenotypic and temporal reference that supports the view that during the mammalian evolution the burden-free chewing module could allow modification of jaws, teeth and their functions for more efficient processing on diverse foods, whereas the hearing module could be further improved for sensitive hearing of high-frequency airborne sounds without being disturbed by mastication (1, 8, 12, 28).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Systematic Paleontology
Supplementary Text
Figs. S1 to S9
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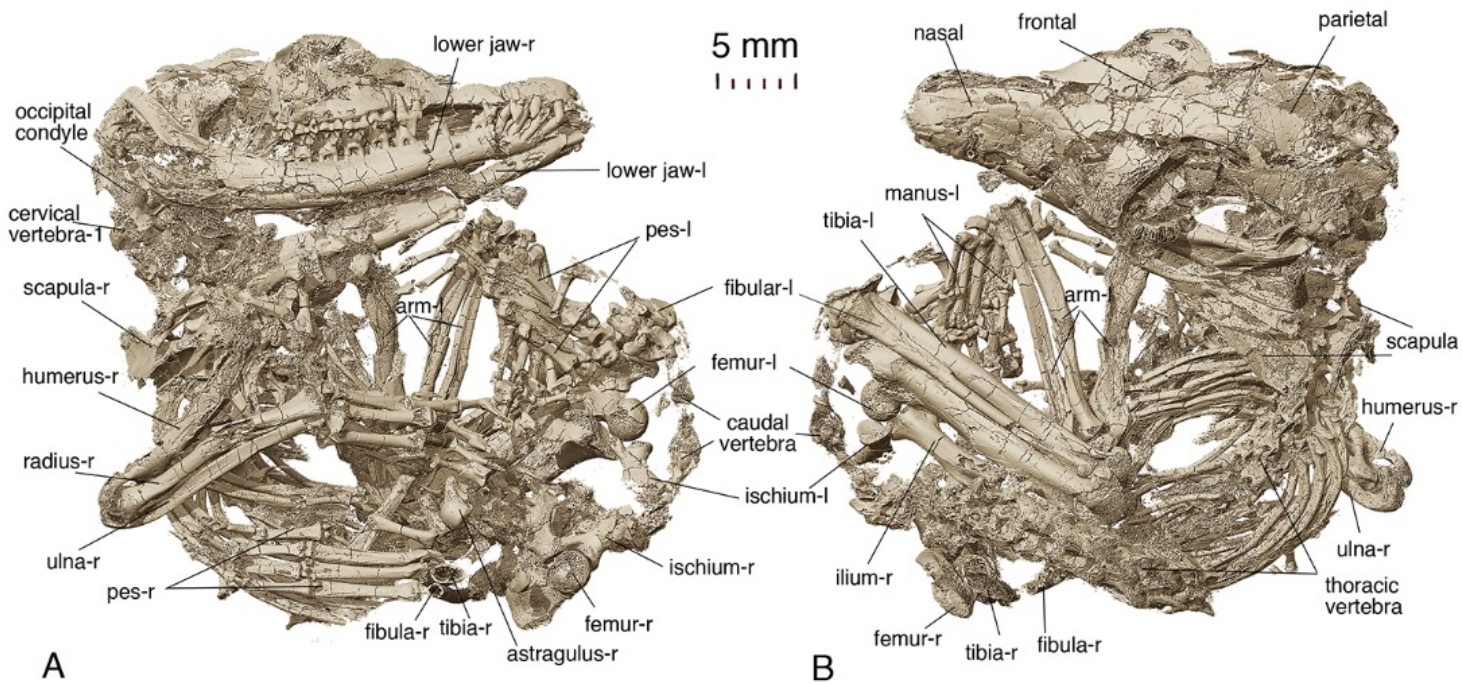


Fig. 1. Skeleton of V14383-1, the holotype specimen of *Origolestes*. (A and B) The skeleton in roughly ventral and dorsal views. See also figs. S1 and S2.

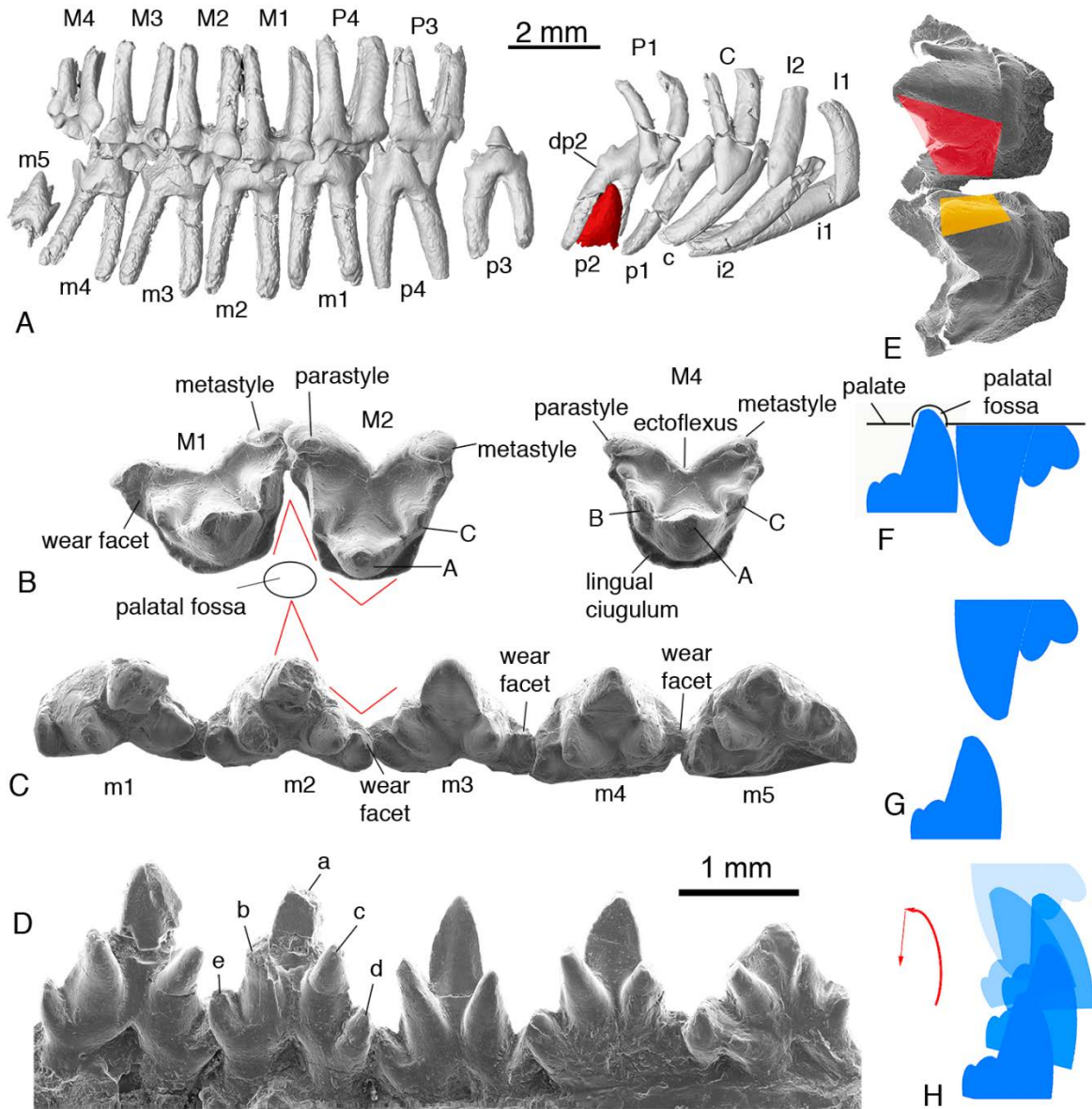


Fig. 2. Dental morphology of *Origolestes*. (A) Labial view of right dentitions (V14383-1, holotype). (B) Occlusal views of M1-2 and M4 (V13604); (C and D) Crown and labial views of left lower molars (V13604). (E) Lingual view of M1-2 (V13604) showing the wedge-shaped embrasure (shearing facets marked by yellow and red); (F to H) Diagram showing tooth occlusal relationships (at rest, open, and power stroke with red arrow indicating the path). See also figs. S3 to S5.

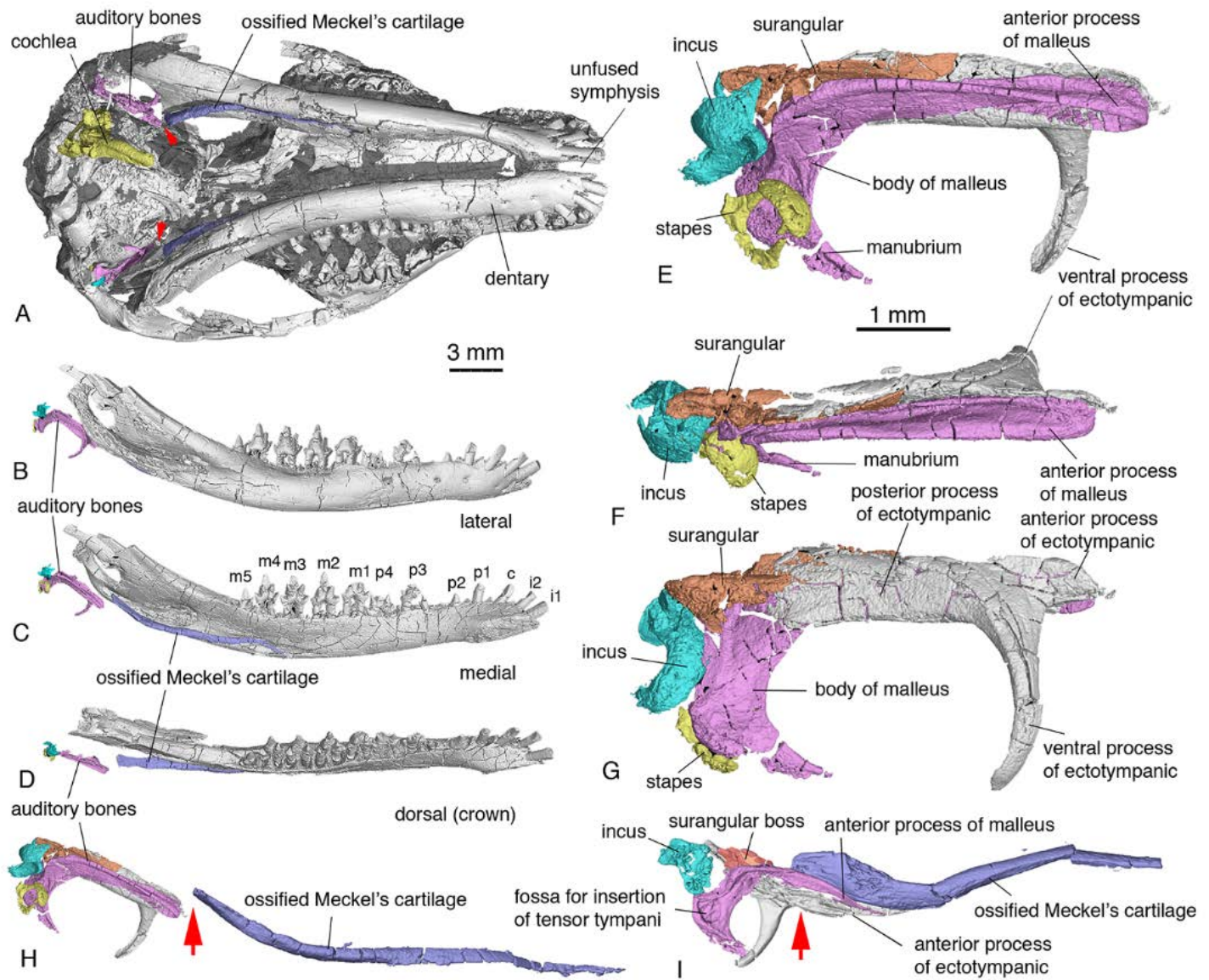


Fig. 3. Skull, lower jaws, and auditory bones of *Origolestes*. (A) Ventral view of the skull (JZD-DB0064), showing the relationship of the lower jaws, ossified Meckel's cartilage, auditory bones and the right inner ear with the petrosal bone digitally removed (see fig. S8). (B to D) Lateral, medial and dorsal views of the left mandible, Meckel's cartilage, and auditory bones. (E to G) Close-up medial, dorsal, and lateral views of left auditory bones. (H and I) Medial views of auditory bones and Meckel's cartilage of *Origolestes* and *Liaconodon*. (B) and (G) are horizontally flipped. Red arrows point to the gap between auditory bones and Meckel's cartilage in *Origolestes* and bone contact in *Liaconodon*. See also figs. S6 and S7.

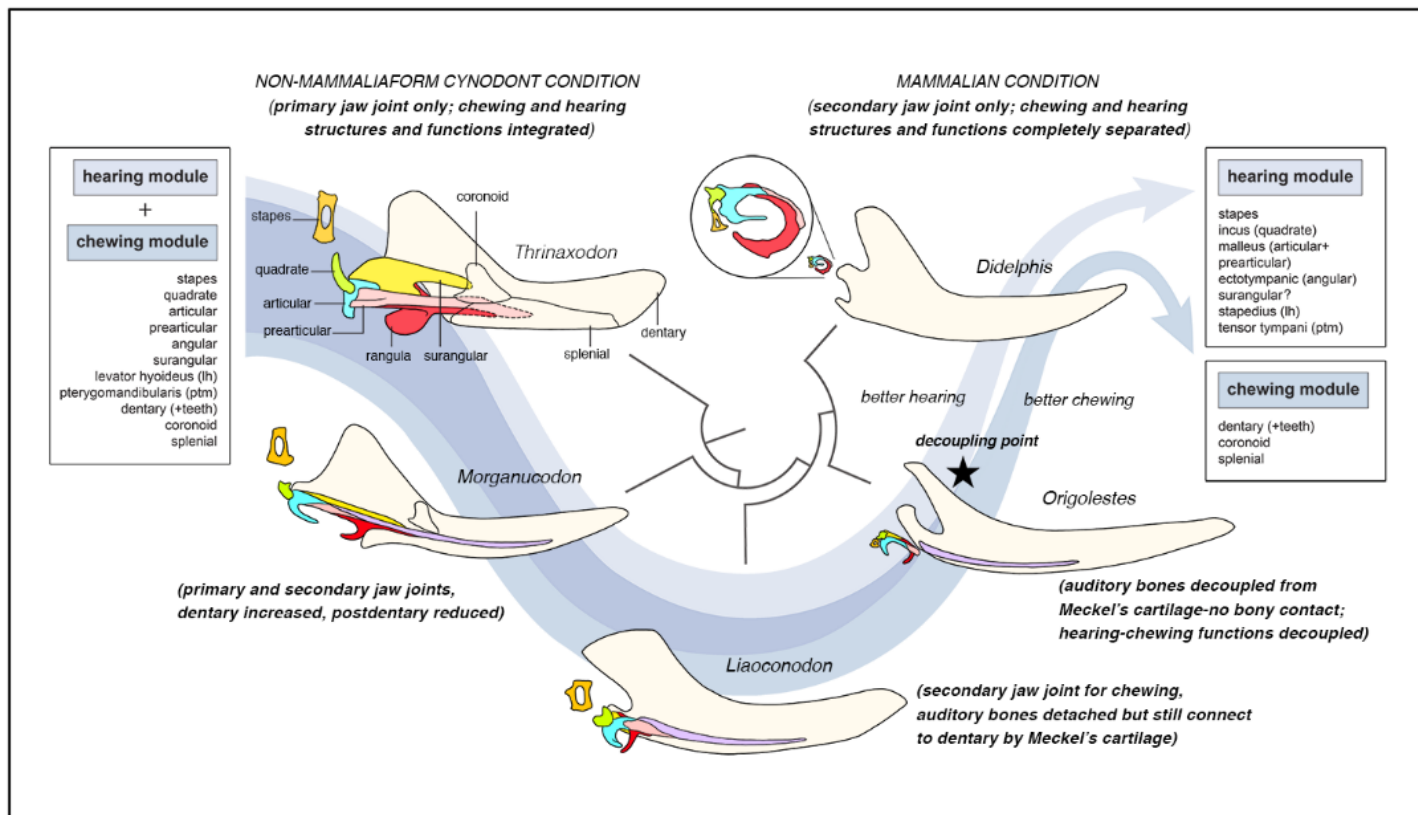


Fig. 4. Diagram illustrating evolutionary stages from the condition in non-mammaliaform cynodonts to that of mammals. See text for discussion. The simplified phylogeny is based on our phylogenetic analysis (fig. S9) and most figures were modified from Meng *et al.* (8).

Integrated hearing and chewing modules decoupled in a Cretaceous stem therian mammal

Fangyuan Mao, Yaoming Hu, Chuankui Li, Yuanqing Wang, Morgan Hill Chase, Andrew K. Smith and Jin Meng

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