

## PALEONTOLOGY

# New Jurassic mammaliaform sheds light on early evolution of mammal-like hyoid bones

Chang-Fu Zhou<sup>1,2\*</sup>, Bhart-Anjan S. Bhullar<sup>3,\*</sup>, April I. Neander<sup>4</sup>, Thomas Martin<sup>5,†</sup>, Zhe-Xi Luo<sup>4,†</sup>

We report a new Jurassic docodontan mammaliaform found in China that is preserved with the hyoid bones. Its basihyal, ceratohyal, epihyal, and thyrohyal bones have mobile joints and are arranged in a saddle-shaped configuration, as in the mobile linkage of the hyoid apparatus of extant mammals. These are fundamentally different from the simple hyoid rods of nonmammaliaform cynodonts, which were likely associated with a wide, nonmuscularized throat, as seen in extant reptiles. The hyoid apparatus provides a framework for the larynx and for the constricted, muscularized esophagus, crucial for transport and powered swallowing of the masticated food and liquid in extant mammals. These derived structural components of hyoids evolved among early diverging mammaliaforms, before the disconnection of the middle ear from the mandible in crown mammals.

Early diverging mammaliaforms of the Mesozoic are the nearest predecessors to modern Mammalia (1) and provide direct fossil evidence of how the mammalian structures have evolved (2–4). One early mammaliaform group is the docodontans, with a wide distribution on Laurasian continents in the Jurassic and Cretaceous (5–13). We report here a newly discovered, exquisitely preserved docodontan skeleton that offers fresh insight on the transformation of hyoid bones and the earliest evolution of hyolingual function in mammals (14–18).

*Microdocodon gracilis*, gen. et sp. nov. (16) is from the Middle Jurassic and was found in the Daohugou localities; it is preserved in part and counterpart (holotype PMOL-AM00025A and B, respectively; Fig. 1, fig. S1, and movie S1). The fully erupted teeth (I<sup>1</sup>/i4<sup>2</sup>-C1/c1-P6/p6-M4/m4) indicate that it was an adult. Among docodontans, *Microdocodon* is phylogenetically nested in the Tegotheeriidae (16), but differs from other tegotheeriids by several dental characteristics (fig. S2) (9–12). Geologically, it is the oldest of the tegotheeriid taxa (16).

This animal has a diminutive size with a body mass ranging from 5 g (as estimated from limb bone lengths) to 9 g (as estimated from skull length) (tables S1 and S2) (16). It is much smaller than other docodontans from the paleoecological

community of Daohugou (7, 11, 12, 16). Its skeleton shows a “T”-shaped interclavicle, curved clavicles, and strap-shaped scapulae, which are similar to those of other mammaliaforms (16). The girdle and limb bones are very slender, and the radius and ulna are elongate relative to the humerus. It has an exceptionally long tail: the postpelvic length of the caudal vertebrae is ~120% of the head–body length. On the basis of these characteristics, we interpret this to mean that it was a scansorial animal (figs. S1 and S10 to S12) (for details, see the supplementary materials) (16).

The middle ear and hyoids are preserved with the skull (Figs. 2 and 3, figs. S2 to S5, and movie S2). The middle ear is preserved in the postdentary trough of the mandible, as in other mammaliaforms (Figs. 2 and 3 and figs. S1 to S4) (5–7, 11, 16). The basihyal, thyrohyal, ceratohyal, and epihyal bones (distal part incomplete and possibly cartilaginous) are preserved near the base of the skull (figs. S3 and S4). The basihyal is a rod-like bone with two slightly enlarged ends that bear articulating facets for the paired thyrohyals and ceratohyals. These facets are similar to the articular facets of the basihyal–thyrohyal and basihyal–ceratohyal joints in the monotreme *Tachyglossus* (Fig. 3 and figs. S4 and S5). As in monotremes, the thyrohyals in *Microdocodon* have proximal ends wider than the shaft, whereas the distal ends are incomplete or unossified in the fossil. The right thyrohyal (best seen on the main part) overlaps the well-preserved manubrium of the right malleus (best seen on the counterpart). The ceratohyals are slender rods. The ceratohyal–epihyal joint was mobile and forms a sharp angle. We interpret this to mean that the basihyal, thyrohyals, and ceratohyals formed a “—(” configuration, in which the basihyal was the transverse strut (Figs. 2 and 3 and movie S2). This configuration, herein called the saddle-shaped configuration, is typical of the basal parts (basihyal, ceratohyals, thyrohyals) of

the hyoid apparatus in monotremes and placentals, and in a modified condition in marsupials (for details, see the supplementary materials) (16–18).

Based on the distinctly mammal-like morphology of the hyoid elements of *Microdocodon*, we can now identify hyoid elements of several other mammaliaforms (16) (figs. S4 to S9). The Jurassic haramiyidan *Vilevolodon* has preserved basihyal and ceratohyal bones (fig. S6 and movie S2) (19). The Cretaceous eutriconodontan *Yanoconodon* also has preserved hyoid elements (fig. S6) (20). Computed tomography (CT) scanning has revealed the basihyal, thyrohyals, ceratohyals, and epihyals of the trechnotherian *Maothierium* and the multituberculate *Sinobaatar* of the Cretaceous (figs. S7 and S8 and movie S2) (16). Additionally, *Sinobaatar* has preserved stylohyal bones (fig. S7), which is similar to the Cretaceous multituberculate *Kryptobaatar* (21). We interpret this to mean that multituberculates have an integrocoronate anterior hyoid cornu, characterized by the complete series of ceratohyal–epihyal–stylohyal connected to the basicranium (movie S2) (16). Moreover, we now can identify the hyoid elements in the early eutherian *Eomaia* (fig. S9) (16), which are similar to those of the recently discovered eutherian *Ambolestes* (22).

The newly identified hyoids in the early mammaliaform *Microdocodon* (fig. S4 and movie S2) show the rodlike basihyal, thyrohyals, ceratohyals, and epihyals, which are similar to those of *Yanoconodon*, *Sinobaatar*, *Maothierium*, and *Eomaia* (figs. S6 to S9), in an extant mammal-like configuration. Therefore, the hyoids of *Microdocodon* represent the ancestral characters of hyoid apparatus for the clade of *Microdocodon* and crown mammals. Phylogenetically, *Microdocodon* and *Vilevolodon* are the earliest-known mammaliaform fossils with mammal-like hyoids (Fig. 3, fig. S5, and movie S2).

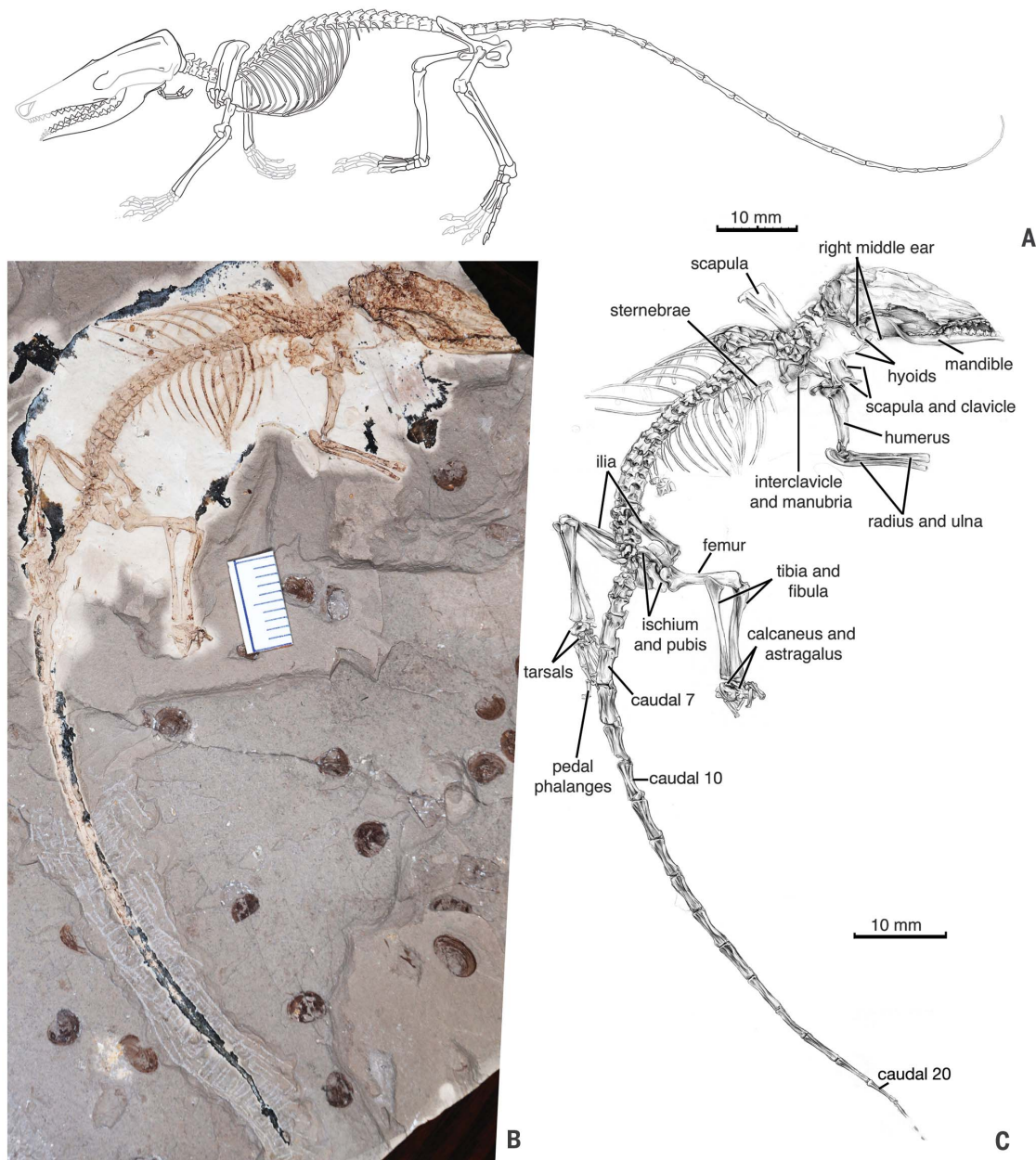
Although the hyoids are mammal like, the middle ear in docodontans is fully attached in the postdentary trough of the mandible (Fig. 3B), which is also present in haramiyidans, albeit in a modified condition (Fig. 3C) (19). The hyoids are also mammal like in eutriconodontans and spalacotherioids, whereas the middle ears in these animals are still connected by an ossified Meckel's element to the mandible (Fig. 3, fig. S6, and movie S2). The mammal-like, jointed anterior hyoid cornu and the saddle-like basal hyoid structure (Fig. 3) evolved before the separation of the middle ear from the mandible by resorption of Meckel's cartilage, which occurred convergently in separate clades of crown Mammalia. The development of a mobile linkage of the mammal-like hyoids is decoupled from transformation of the ear bones in articulation with the mandible into the separated middle ear during mammaliaform evolution (Fig. 3).

Mammaliaform hyoids show neomorphic characters not developed in nonmammaliaform therapsids (Fig. 2). (i) The basihyal is ossified and forms a transverse strut in a saddle configuration with the ceratohyals, and with the thyrohyals that connect the hyoids to the thyroid cartilage

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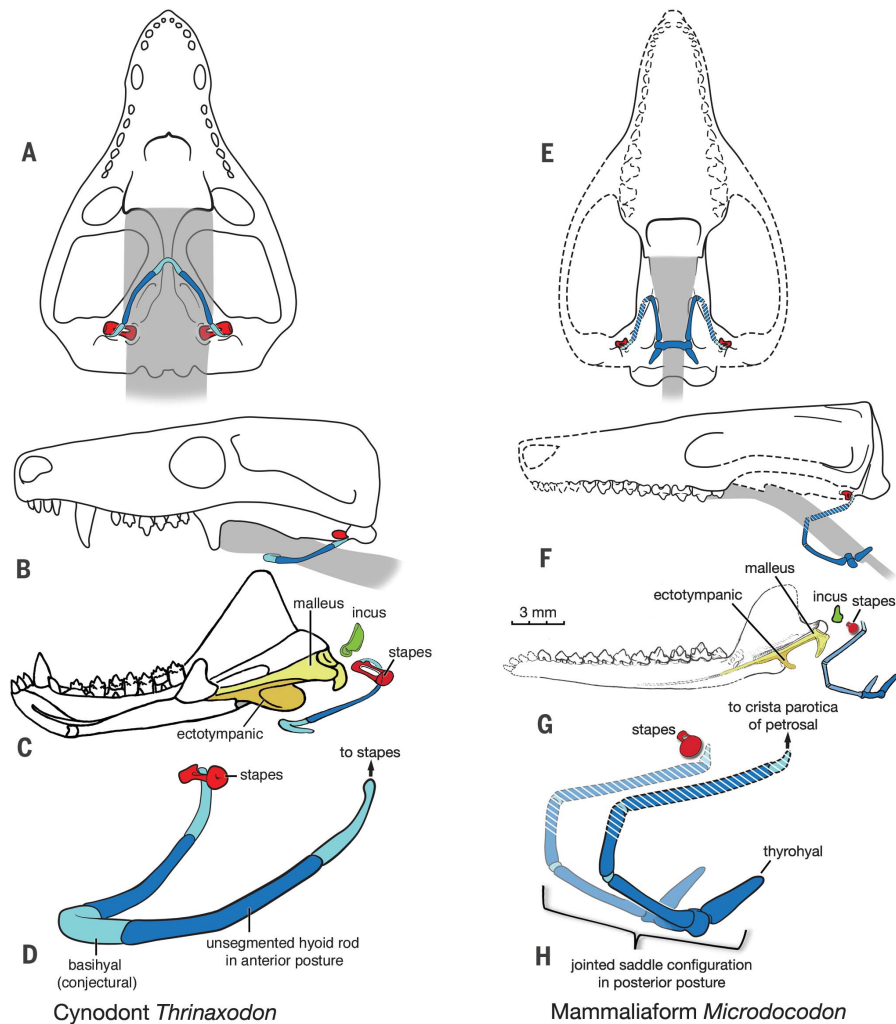
**Fig. 1. Mammaliaform *Microdocodon gracilis*.** (A) Skeletal reconstruction, (B) photo, and (C) illustration of holotype main part PMOL-AM00025A. PMOL-AM00025B is shown in fig. S1 and movie S1, mandible and dentition in fig. S2, and middle ear and hyoids in the details in figs. S3 and S4 and movie S2.

(14, 16). By contrast, the basihyal and thyrohyals are not ossified (unknown as fossils) in non-mammaliaform therapsids (2, 24–26) (for details, see the supplementary materials (16)). (ii) The basihyal, ceratohyal, and epihyal in the anterior hyoid cornu (which hypothetically also includes the stylohyal) form a jointed linkage to the crista parotica of the petrosal of mammaliaforms (Fig. 3 and fig. S5) (16, 23). However, in nonmammaliaform therapsids, the hyoids are a pair of long

and unsegmented rods that lack the flexibility of the anterior hyoid cornu of mammals (24–26). (iii) The jointed anterior hyoid cornu swings into a posterior posture in mammaliaforms, enabled by the angled joints of the basihyal–ceratohyal and the ceratohyal–epihyal (Figs. 2 and 3 and fig. S5). This posterior posture is necessary for the basihyal–thyrohyal to cradle the thyroid cartilage and the larynx for a narrow and muscularized pharynx, creating an oropharyngeal space

in which to swallow the masticated food, as seen in modern mammals (3, 14, 27). By contrast, in nonmammaliaform therapsids, the long hyoid rods are situated anteriorly in an “A-shaped” configuration, as seen in early synapsids (28) and in extant nonmammalian amniotes (15, 27).

In extant mammals, under the control of the suprahyoid and infrahyoid musculature, the mobile linkage of the jointed anterior hyoid cornu plays a crucial role in cyclic movement of the



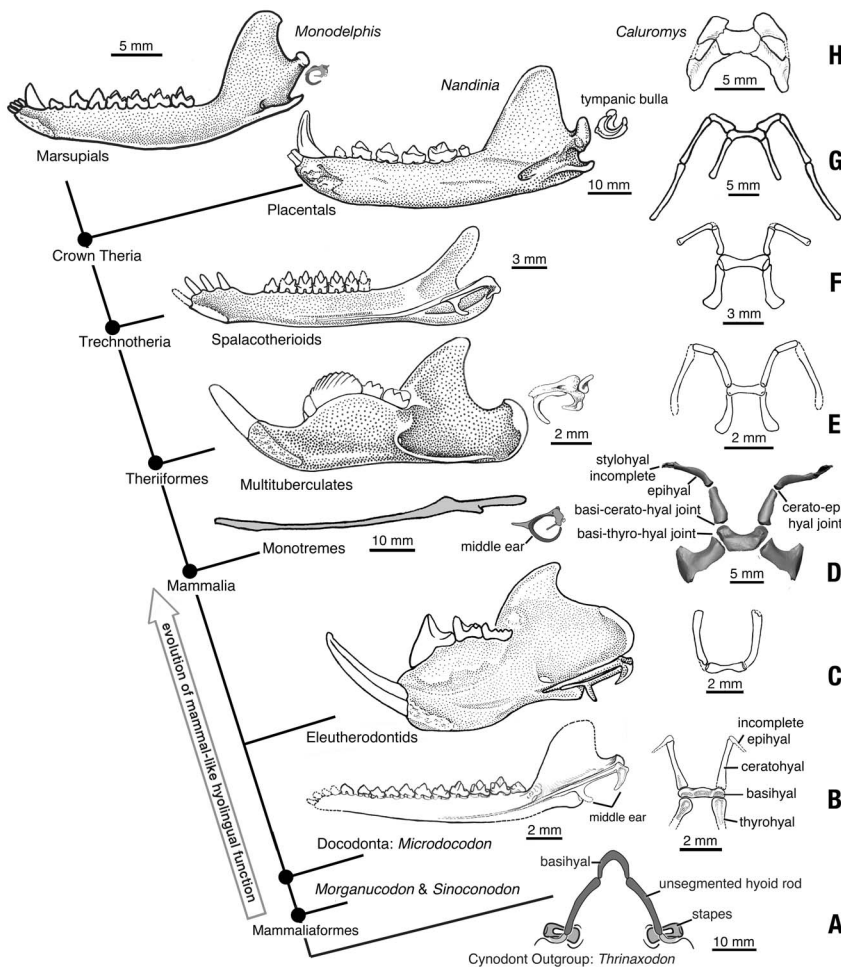
**Fig. 2. Apomorphic hyoid characteristics of mammaliaforms compared with nonmammaliaform cynodonts.** (A to D) Cynodont plesiomorphies of *Thrinaxodon*: “A”-shaped configuration of unsegmented hyoid rods in anterior hyoid posture; basihyal and thyrohyals unossified, as in therapsids. The hyoid–stapes connection in *Thrinaxodon* is based on comparison with the hyoid–stapes connection in other synapsids (2, 24). [(A) and (B)] Skull with hyoid–stapes in ventral and lateral views (for details, see movie S2). Gray shading indicates a wide pharyngeal passage conforming to hyoid rods, as in extant reptiles (27). (C) Reconstructed hyoids and middle ear bones of cynodonts; the incus and hyoids are separated to show their relationships. (D) Reconstructed hyoid and stapes: hypothetical cartilaginous connection (light blue) to stapes (red) [following (2)]; the cartilaginous basihyal is conjectural (16). (E to H) Mammaliaform apomorphies of *Microdocodon*: the hyoids form a rectangular and saddle-shaped configuration with a transverse

basihyal. The hyoid anterior cornu forms a mobile linkage of the jointed basihyal, ceratohyal, and epihyal (incomplete). The hyoid apparatus in a posterior hyoid posture, all like the crown Mammalia (Fig. 3, figs. S3 and S4, and movie S2). The lack of full ossification of epi-stylohyals (dashed lines) in *Microdocodon* is consistent with the condition of their homologs in monotremes, all marsupials, eutriconodontans, and spalacotherioids, but not multituberculates and the early eutherians (16). [(E) and (F)] Skull in ventral and lateral views. Gray shading indicates a muscularized pharyngeal passage, constrained by rectangle-shaped hyoids, as in extant mammals (14, 27). (G) Mandible and hyoids in medial view. (H) Reconstructed hyoid and stapes: the soft tissues in hyoid joints are conjectural. Missing parts of the epihyals, stylohyals, and tympanohyals are conjectural (hatched pattern). Separation of the stapes from the hyoid contact to the crista parotica of petrosal is based on *Haldanodon* (23).

tongue and the larynx simultaneously during mastication. After mastication, this apparatus is also responsible for transport and swallowing of the masticated food (3, 14, 29, 30) and for stabilizing the hyolingual structure by maintaining a dynamic hyoid posture (31). The mobile linkage and the saddle-shaped basal hyoid con-

figuration of the hyoid apparatus can now be traced to *Microdocodon* (also *Vilevolodon*) in synapsid phylogeny (Figs. 2 and 3 and figs. S5 and S6). Docodontans and haramiyidans have more complex teeth for mastication than does *Morganucodon* and most of nonmammaliaform therapsids; they also have the hyoid appara-

tus and related hyolingual function of transport and swallowing of the masticated food and liquid. It is likely that the mammal-like hyoid structure evolved with the first appearance of complex mastication in early divergent mammaliaforms. We hypothesize that this system evolved no later than the common



**Fig. 3. Mosaic evolution of the hyoid structure and the middle ear in mammaliaform phylogeny.**

The jointed anterior hyoid cornu from embryonic pharyngeal arch 2 had evolved into mammal-like structures before the separation of the middle ear bones from the mandible, both derived from (or in association with) pharyngeal arch 1. The mammaliaform *Microdocodon* has mammal-like hyoids with a saddle-shaped formation in posterior posture, with apomorphies of a transverse basihyal, and mobile joints between basi-thyrohyals, basi-ceratohyals, and cerato-epihyals. This indicates that the transformation to mammal-like hyoids and hyolingual function occurred no later than the common ancestor of crown mammals and docodontans. The hyoids, as exemplified by *Microdocodon*, are also partly preserved in other early mammaliaforms. The first appearance of mammal-like hyoids preceded, phylogenetically, the separation of middle ear bones from the dentary, which occurred later and convergently in monotremes, multituberculates, and crown therians. (A) Cynodont *Thrinaxodon* (based on UCMP40446, see also movie S2); basihyal is conjectural. (B) Mandible, middle ear, and preserved hyoid parts of *Microdocodon* (details in figs. S1 to S4 and movie S2). (C) Mammaliaform *Vilevolodon* (an eleutherodontid from the Late Jurassic) (fig. S6) (20). (D) Monotreme *Tachyglossus*, hyoids digitally disarticulated, with thyroid arches omitted to facilitate comparison (details in figs. S3 and S4). (E) Multituberculate *Sinobaatar* with reconstruction of hyoids (fig. S7 and movie S2) [for more details, see (16)]. (F) Cretaceous trechnotherian *Maotherium*, also shown in a CT rendering of hyoids and middle ear (JZT-B0064; fig. S8 and movie S2). (G) Extant carnivoran *Nandinia* [redrawn from (18)]. (H) Marsupials *Monodelphis* (mandible and middle ear) and *Caluromys* (hyoids, FMNH60697). Mandibles (left on cladogram) and middle ears are shown in medial view. Hyoids (right column) are shown in splayed ventral view or digitally disarticulated in ventral view.

ancestor of docodontans and crown Mammalia (Fig. 3).

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#### SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/365/6450/276/suppl/DC1  
Materials and Methods  
Supplementary Text  
Figs. S1 to S12  
Tables S1 to S3  
References (32–151)  
Movies S1 and S2

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### Early suckler?

One trait that is unique to mammals is milk suckling. Suckling requires the presence of stability and motion in the throat, both of which require a complex hyoid apparatus. Zhou *et al.* describe a mammaliform docodontan fossil from the Jurassic that was preserved with a nearly intact hyoid (see the Perspective by Hoffmann and Krause). The structure is complex and saddle shaped, like that seen in modern mammals, suggesting that a muscularized throat was present before the development of mammals.

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