Coevolution of the Mammalian Middle Ear and Neocortex

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The mammalian middle ear contains a chain of tiny ossicles whose parallel histories in ontogeny and phylogeny are among the most famous in comparative biology (1–5). The middle ear arose in mammalian history (1–6) as an integrated component of the mandible, where it participated in a continuous arcade of bones extending from the mandibular symphysis to the fenestra vestibuli (FV) of the inner ear (Fig. 1). The craniomandibular joint (CMJ) was formed by the quadrate and articular, which served the dual functions of hearing and feeding. Over a 100-million-year span of pre-mammalian history, the middle ear ossicles were gradually reduced, reflecting specialization for increasingly high-frequency hearing (3), while the dentary correspondingly enlarged to undertake a greater role in feeding (4). Hearing and feeding were structurally linked in pre-mammalian history, but in mammals (5) these functions became decoupled as the auditory chain detached from the mandible and repositioned behind it. The dentary remains as the only bone in the mammalian lower jaw, articulating with the squamosal to form a new CMJ. Anatomical relations of the ear ossicles to one another and auditory function were little affected in this transformation (3). Separation of the ossicles from the mandible is common to all adult mammals and was widely regarded as the definitive mammalian character under Linnean taxonomy (6).

In modern didelphid (marsupial) development (7), as in mammals generally (1, 2, 5), the auditory chain differentiates and begins growth attached to the mandible, forming an arcade of cartilages from the FV to the mandibular symphysis (Fig. 2A). Three cartilages are present at birth. The stapes extends from the FV to the incus (quadrate), which is braced against the ventral edge of the otic capsule and articulates with the rear extremity of Meckel's cartilage. In the second development week, Meckel's cartilage cleaves to form the malleus (articular). The two pieces

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**Fig. 1.** (A) Coevolution of the mammalian mandible and middle ear (right lateral view) and the brain (illustrated by dorsal views of endocasts), plotted on a phylogeny of selected mammals and their closest extinct relatives (5, 19). (B) Dorsal view of the brain of Didelphis (opossum). (C) Right lateral view of auditory chain of Didelphis; the stapes is rotated and offset from between the incus and fenestra vestibuli. Abbreviations: CMJ, craniomandibular joint; FV, fenestra vestibuli of the inner ear. Crosses signify extinct species.
then separate as Meckel's cartilage degenerates during ossification of the dentary. The dentary and ectotympanic bone (angular) begin to ossify in a common membrane and soon grow into contact with one another. Connective tissues joining them are torn at the end of the third week after birth as the entire auditory chain (stapes, incus, malleus, and ectotympanic bone) is carried backward during the next 9 weeks to its adult position behind the CMJ. Ontogeny thus recapitulates phylogeny in detachment and relocation of the auditory chain.

Two hypotheses attempt to explain the detachment of the auditory chain from the jaw. An evolutionary hypothesis (3) views premammalian history as shaped by selection for high-frequency hearing, with detachment of the chain from the mandible an extension of this trend. A developmental hypothesis (8) argues that the onset of jaw muscle functionality tears the auditory chain from the jaw. Neither hypothesis addresses both the developmental and phylogenetic transformations nor explains repositioning of the auditory chain to its new location behind the CMJ.

Using three-dimensional endocranial imaging (Fig. 3) with high-resolution x-ray computed tomographic scanning (9) for phylogenetic analysis of mammals and their extinct relatives, I have identified additional bony mammalian synapomorphies that arose concurrently with the repositioned auditory chain (2). Their common location about the endocranial cavity implicates the brain as a dominant morphogenetic influence in mammalian cranial evolution (2, 5). Late Permian synodonts are the first members of the mammalian “stem” lineage in which the brain filled the endocranial cavity. They have a simple tubular forebrain, with broad midbrain exposure dorsally and a pineal eye. Successive episodes of evolutionary forebrain enlargement are recorded in endocasts of Probanomylatus (Middle Triassic) and Sinodelphys and Morganucodon (Early Jurassic). A still greater relative increase in forebrain volume occurred in the last common ancestor of extant mammals (5).

This additional brain volume marks an episode of heterochrony (peramorphism) (10) in which the mammalian brain began to grow for a greater portion of ontogeny, and probably also more rapidly, than in Morganucodon and more distant outgroups. Details of endocast morphology indicate that this period also marks the origin of the mammalian neocortex (2). The developing mammalian forebrain hypertrophies into inflated hemispherical cortical lobes that swell backward over the midbrain and forward around the bases of the olfactory bulbs, which are themselves inflated. The circular fissure develops between the olfactory bulb and neocortex and is visible for the first time in a Late Jurassic endocast of Triadocyon meadori (11). The cortical hemispheres differentiate into separate neocortex (isocortex) and pyriform cortex. Each hemisphere has a columnar organization of six radial layers that are generated in ontogeny by waves of migrating cells that originate from the ventricular zone and move radially outward to achieve their adult positions (12). This inside-out pattern of neural growth is unique to mammals and produces a huge cortical volume (13). The cerebellum is also inflated and deeply folded.

The key to understanding the developmental transformation of the auditory chain is its differential growth with respect to the brain and the skull in general. Using the mandible of didelphids as an illustration, the tympanic ring or ectotympanic bone (reflected lamina of the angular) has begun to ossify at birth and at first grows more rapidly (positive allometry) than the dentary (Fig. 4). However, growth slows (negative allometry) as adult size is reached late in the third week after birth, and shortly thereafter the entire auditory chain is pulled free of the dentary. The brain continues to grow at a linear rate through a
Fig. 3. High-resolution x-ray computed tomographic imagery comparing Monodelphis (A through D) (100-μm slice) and Thrinaxodon (E through H) (200-μm slice). Sections (A) and (E) transect the floor of the branacase; sections (B) and (F) transect the FV; sections (C) and (G) transect the middle of the foramen magnum; and sections (D) and (H) transect the roof of the foramen magnum. Abbreviations: a, articular; co, cochlea; oc, occipital condyle; ec, endocranial cavity; f.v., fenestra vestibuli; mx/ec, matrix in endocranial cavity; q, quadrato; qj, quadratojugal; sq, squamosal; st, stapes; tr, tympanic recess.

Fig. 4. Differential growth of the didelphic eotympanic bone and forebrain. In the lower three graphs, relative growth of the forebrain is plotted as a series of ratios defined by the dimensions depicted on the mature forebrain [after (15)]. AH, anterior height; CL, cortical length; OL, occipital length; PH, posterior height.

REFERENCES


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