of actinopterygian fins as homologous to branching sarcopterygian limbs is poorly founded, owing to the paucity of information about early limb development in basal actinopt and sarcopt taxa and reliance on adult skeletal morphologies. Observations of early pectoral fin development in teleost and more basal actinopterygian fishes suggest alternative hypotheses for the patterning of different fin forms in teleosts, basal neopterygians, and basal bony fishes. In teleost pectoral fins the proximal endoskeleton (radials) develops by subdivision of a uniform cartilage plate, whereas in basal actinopts the proximal radials develop from separate condensations. The basal modes of development and the developmental changes leading to the derived teleost mode are examined and alternative hypotheses for homologies of metapterygia are considered.

In Vivo Loading Patterns in the Alligator Mandible

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Loading patterns in the mammalian mandible, especially the primate mandible, are well studied, but in vivo function of the mandible in sauropsids is unstudied. This study presents in vivo bone strain data from the mandible of the American alligator, *Alligator mississippiensis*. Bone strain data from various gauge locations were collected during unilateral bites on a bite force transducer. During biting, the ventral border of the working side mandible is tensed, likely due to the ventrally directed bite force and the dorsally directed bilateral muscle forces. The working side mandible is also loaded in torsion with the dorsal border everted. In contrast, the balancing side mandible is compressed on the ventral border, and the dorsal border is inverted. By placing three strain gauges around a cross-section, normal strain distributions and the neutral axis of bending during biting were determined. This analysis indicates that, on the working side, the orientation of the neutral axis is variable: dorsoventral at anterior bite points and mediolateral at posterior bite points. Principal strains are highest on the dorsomedial cortex of the mandible, ranging from 5,500 $\mu\epsilon$ tension during contralateral middle bites to –5,000 $\mu\epsilon$ compression during ipsilateral posterior bites. High mandibular strain magnitudes during biting in *Alligator* versus mammals indicate that the alligator mandible may be optimized following different criteria, namely, high-impact and relatively infrequent loadings.

Central Role of Gene Cooption During Neural Crest Evolution

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The appearance of neural crest cells was a defining event in vertebrate evolution. We have begun to examine the developmental genetic changes that may have driven the evolution of these embryonic cells in the ancestral vertebrate. Using amphioxus and lamprey as living representatives of the prevertebrate and primitive vertebrate conditions, we demonstrated that the novel deployment of three transcriptional regulators to the neural plate border coincides with the origins of the neural crest. AP-2 genes, critical regulators of neural crest induction and differentiation, are expressed at the neural plate border and dorsal neural tube of vertebrate embryos, but are absent from these cells in amphioxus. Id genes, potent inhibitors of bHLH-mediated differentiation, are robust neural crest markers but are not expressed in the amphioxus nervous system. SoxE genes, which are essential for neural crest induction and differentiation, are similarly absent from the amphioxus neural plate border. Furthermore, the expression patterns of Id and SoxE genes in amphioxus embryos suggest that cooption of these genes conferred novel mesodermal and neural properties upon the evolving neural crest. Taken together, our data support the idea that genetic cooption of high-order transcription factors was a major driving force in neural crest evolution.

Connexin Distribution in Mammalian Esophagus Epithelium, With Reference to Feeding Habits

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The mammalian esophagus epithelium tolerates chemical and mechanical strain exerted by the predominant nutrition type, whereby the carrying capacity needed may be influenced by epithelial responses. Considering the role of gap junctions and their connexin (Cx) proteins in regulating cell proliferation and differentiation, our study presents first information on Cx distribution within the stratified esophageal epithelial lining, as related to feeding habits of different mammalian groups. Cxs 26, 30, 43 were demonstrated immunohistochemically in the esophagus of six species, using paraffin sections and very sensitive dextran-polymer visualization. Positive reactions were confined to cell membranes in vital epithelial layers and to the cytoplasm of corneal (superficial) cells. Omnivorous species (mouse, dog, pig) showed homogeneously strong membrane reactions in basal and spinous layers, whereas the carnivorous cat exhibited such reactions only in the basal layer; the plantivorous species (sheep, horse) had a strong to very strong positive membrane staining in all of their numerous vital layers, including the str. granulosum. Cx 26 seemed particularly obvious in vital epithelial layers of the cat, Cx 30 appeared weakly in the cat and the horse, and the important epithelial Cx 43 was especially conspicuous in the sheep as well as the horse. The results emphasize a specific need of intraepithelial communication for epithelial differentiation in plantivorous animals with a high mechanical load of the esophagus epithelium.

Reconstructing Leg Function From Osteology in Mesozoic Birds

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The reversed or opposable hallux (digit I) of extant birds is critical for behaviors such as perching and grasping. Although a reversed hallux has been assumed present in Mesozoic birds since the discovery of *Archaeopteryx*, little work has focused on the leg morphology or functional implications associated with this important novelty. In extant birds, the degree of torsion of metatarsal I has been shown to correlate with the orientation of the hallux. Applying this anatomically based method to fossil theropods allows foot structure and function to be reconstructed from flattened or disarticulated specimens. Among all nonavian theropods, the morphology of digit I and thus hallucal orientation varies little. Digit I in *Archaeopteryx* and other Mesozoic birds has traditionally been interpreted as fully reversed and similar to extant birds in form and function. Here we reinterpret hallucal orientation in *Archaeopteryx* as more similar to the ancestral condition. This anteromedial or, at most, medial orientation is shared with *Confuciusornis*. Some enantiornithines exhibit metatarsal I morphology consistent with a medially directed hallux, as in living gannets. Due to missing or apomorphic halluces in more derived Mesozoic birds, reconstructing the origin of the "modern" avian foot remains problematic. However, the previously accepted reversed/unreversed dichotomy ignores informative diversity of hallucal morphology among Mesozoic birds.

Anatomy and Evolution of the Bizarre "Battering Ram" of the Brontothere, Embolotherium (Mammalia, Perissodactyla)

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Brontotheres, large Eocene perissodactyls, evolved paired hornlike protuberances situated between the orbits and naso-maxillary notch. Each "horn" is formed by an anterior process of the frontal overlapping the nasal. *Embolotherium*, a late-Eocene Asian brontothere, possesses a single massive battering-ram-like process, two-thirds the length of the skull, that projects upward almost vertically. This process was thought to have been formed by the nasal and to have originated independently of brontothere "horns." However, the sutural patterns of taxa (*Metatitan, Protembolotherium*) that, cladistically, are close relatives of *Embolotherium* form a series of transformations that suggest it is formed by the frontal bone overlying the nasal bone and is homologous to brontothere "horns." These transformations also indicate that the portion of the nasal anterior to the naso-maxillary notch was lost in *Embolotherium*. Earlier reconstructions portrayed a simple rhino-like nose and upper lip; however, *Embolotherium* lacks osteological support for this morphology. A deep channel containing an ossified remnant of the nasal septum runs up the anterior margin of the fronto-nasal process and bifurcates at the apex. This implies that the nasal cavity extended to its peak. The nostrils were probably elevated far above the orbits and the upper lip may have been extremely deep. The soft-tissue morphology of the nose and upper lip, although difficult to fully reconstruct, differed radically from other mammals.