How to Measure Ontogeny?

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When studying evolution and adaptations, it is crucial that the early life history of vertebrates is considered as well. Selective forces act upon each stage during development, thus constraining developmental processes. When studying ontogeny, developmental age is expressed in different ways: in relation to body size or to (chronological) age. Many discussions have tackled this. Deductive models have suggested that size is not a good measure, because it is linked to shape, which is frequently used as a descriptor of ontogenetic changes. This study is an empirical approach to the problem, using geometric morphometrics. Shape changes in the neurocranium of the African catfish *Clarias gariepinus* (Clariidae) are used as a measure of developmental age, and are dissociated from size (using generalized procrustes analysis). The obtained shape variables were regressed to size (log-transformed standard length) and age (days posthatching), indicating that size is a better measure for ontogeny. Supporting evidence is obtained from an experimental setup of two growth series of *C. gariepinus* larvae, in which the ossification pattern of the skull is in correspondence with body size and not age.

Promise of Basic Mechanics in Functional and Ecological Vertebrate Morphology

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Despite the many prosaic examples of the "perfect fit" between form and function, the underlying causes and adaptive nature (if present) of covariation between design, performance, and ecology are often far from obvious or straightforward. Constraints can make form–function relations much more complex than expected at first, or the causal links can just be too subtle, even hidden. In order to allow direct focus on the relevant design-traits, proper deductive assessment of form–function relationships needs an understanding of the demands imposed by the ecology and behavior of the organism. Next, insights into the mechanistic coupling between these traits and performance can be gained. In the case of musculo-skeletal systems, biomechanical reasoning and analyses (both through experiments and models) are especially suited to realize these aims: i.e., grasping the logical sequence from design-traits to differential performance and, finally, to ecological niche. Applied in this way, biomechanical modeling may reveal, for example, why long limbs are helpful, but not sufficient for the conspicuous jumping behavior of bush babies; why snake-necked turtles can do without long, forceful neck extensors in their fast and precise strike behavior during feeding; why forelimbs are "almost" redundant for fast intermittently running lizards, or why frogs seem to be lazy when swimming.

Air Sac Diverticula as Passive Support Devices in Birds and Saurischian Dinosaurs: An Overlooked Biomechanical System

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Just as impermeable and inelastic low-pressure air bladders used in shipping can support up to four tons at 2.0 psi, similar structures in organisms could provide substantial passive support. While portions of the minimally elastic and nearly impermeable diverticula of the air sac complex in birds function to pneumatize bones, other parts play no obvious role in this function. However, their morphologies and placement strongly suggest that, upon pressurization, they would provide passive support to much of the vertebral column, the femora, and the outstretched wings of soaring birds. We observed these effects at inflation pressures of 0.6 ± 0.2 psi. We focus here on the cervical vertebrae, especially in birds that fly with long extended necks. Avian cervical diverticula consist of anteroposterior passages through the transverse foramina and neural canal, connecting a series of intervertebral sacs that become progressively smaller craniad. Accessory diverticula may also be present. Experimentally pressurizing cervical diverticula demonstrates their role in neck support. Gravitational forces act on the extended necks of flying birds and would similarly affect the necks of saurischians, especially sauropods that held their necks relatively horizontally. Because many parallels exist between the pneumatic features of bird and saurischian cervicals, and because major nuchal ligaments are absent in both, we infer that saurischian dinosaurs also used pneumatic pressure to passively support their necks

Expression of beta-Keratin and Its mRNA in Differentiating Lizard Epidermis

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The hard form of keratin of lizard scales, beta-keratin, was isolated by electrophoresis after labeling with tritiated proline. The molecular weight and biosynthesis of beta-keratin was determined by autoradiography and immunoblotting showing that the components at 8–10 and 16–18 kDa form most beta-keratins. The primary sequence of beta-keratin was partially characterized after extraction and selection of a beta-keratin mRNA using RT-PCR. The derived cDNA probe was used to analyze by in situ hybridization the expression of beta-keratin mRNA during epidermal differentiation of lizard epidermis. The probe localizes specifically in cells of the differentiating beta-layer. Initially, the oberhautchen cells have no mRNA signal that increases after merging with cells of the beta-layer. This suggests that only beta-cells synthesize beta-keratin mRNA that can be exported into oberhautchen cells during maturation of the beta-layer. Suprabasal cells with presumptive beta-keratin differentiation show beta-keratin mRNA expression only at stage 3–4 of the shedding cycle, when they assume a fusiform shape. This suggests that beta-keratin synthesis is rapidly switched on when presumptive beta-cells reach 2–3 layers above the germinative. This result confirms and details previous morphological and immunocytochemical studies and opens the possibility to completely sequence the expressed beta-keratin mRNA. This will allow deriving the primary sequence of lizard beta-keratin for further analysis on the molecular evolution of beta-keratins in reptiles.

Evolution of Flight Morphology in Hummingbirds

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Hummingbirds are obligate nectarivores and are the only birds capable of sustained hovering flight. Despite this high degree of ecological and locomotor specialization, hummingbirds are remarkably diverse, with over 325 species in the New World, and are also highly variable in body morphology, ranging over an order of magnitude difference in body mass. Here we analyze the phylogenetic patterns in flight morphology using a new phylogeny that contains over 100 taxa based on sequences of one mitochondrial and two nuclear genes.

Biorhythmical Organization of Spermatogenesis

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We studied the daily dynamics of the mitotic index (MI) of type B spermatogonia and the frequency of spermatogenic cycle stages for intact and pinealectomized rats that consequently received an injection of epithalamin (or the complex of pineal gland neuropeptides). Biorhythms were detected through spectral and least-squares (OLS) analyses. The daily MI spermatogonia dynamics of intact animals were characterized by a circadian rhythm. This rhythm disappeared after pinealectomy but was restored after the injection of epithalamin between the 26th and 40th day postpinealectomy. The spermatogenic cycle of rats comprises 14 stages characterized by different combinations of spermatogenic cells. In intact animals, only 3 of 14 stages that include mitosis of spermatogonia and meiosis of spermatocytes had a circadian rhythm. If a given spermatogenic period included several stages, the daily frequency dynamics for this group were also characterized by a circadian rhythm. Pinealectomy led to the disappearance of all circadian rhythms and the injection of epithalamin to their restoration. Our study demonstrates the role pineal gland neuropeptides play in the formation of the spermatogenesis circadian rhythm. Stages of the spermatogenic cycle previously described in the literature seem to

DOI: 10.1002/jmor.10223
Published online in
Wiley InterScience (www.interscience.wiley.com)

reflect the topographic structure of the spermatogenic tissue cells, rather than the sequence of spermatogenesis.

Surface EMGs

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Physiological studies with surface-EMGs were undertaken to better understand the operating mode of muscles. The technique was established on the triceps brachii muscle of rats and will be used in future to investigate the activation pattern of back muscles during locomotion. The aim of this study was to investigate the activation pattern of the segmental paravertebral muscles and to compare their activation pattern to that of limb muscles in order to gain a better understanding of the physiology of muscles and their functional role during locomotion. The grid electrodes for the triceps muscle consisted of 16 spherical silver electrodes half-embedded in a thin silicon rubber. The spheres were in direct contact with muscle surfaces because the grid electrode was surgically implanted under the skin. The EMG was simultaneously recorded monopolar and bipolar with the locomotion of the rats using a high-speed camera system. Topographical surface EMGs of the lateral and long head of the triceps muscle demonstrated a distinct spatiotemporal pattern of muscle activity (Scholle, 2001, Exp Brain Res 138:2636; Schumann, 2002, Clin Neurophysiol 113:1142–1151). By high-pass filtered cross-covariance function, it is possible to localize the depth of the signals within belly muscles (Grassme, 2001, Pflügers Arch 441:R160).

Neuromuscular Compartments in Locomotory Relevant Muscles

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English et al. (1982, Am J Anat 164:67–77) hypothesized that muscles may be organized into neuromuscular compartments. These compartments are innervated by primary nerves and can therefore be activated separately. Microscopic dissections were used to investigate the intramuscular innervation pattern of the triceps brachii muscle in rats because of its important role in stabilization of the limb posture against gravitational forces. The heads consisted of five (caput longum), four (caput laterale), and three (caput mediale) neuromuscular compartments. These results are supported by topographical surface EMG studies to demonstrate the muscle activation pattern (Scholle et al., 2001, Exp Brain Res 138:26–36) and by enzyme histochemistry to investigate the fiber type composition (Fischer, 1999, Zool Anz 238:41–54). Further, it is interesting to compare the results from limb muscles to those of back muscles. The longissimus muscle is the largest back muscle and extends from the wing of the ilium up to the wing of the atlas. Microscopic dissections showed a segmental intramuscular innervation pattern. Fiber type distribution, muscular activation pattern, and intramuscular innervation together allow a more detailed interpretation of the physiology and morphology of muscles.

Kinematics of the Transition Between Walking and Swimming in the California Newt *(Taricha torosa)*

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Newts are capable of locomotion in both aquatic and terrestrial environments. The movements of swimming involve the axial musculature, which generates traveling waves of lateral undulation. In contrast, walking uses the paired limbs to generate force against the ground and propel the body forward. The transition between swimming and terrestrial walking was examined by videotaping newts walking both up and down a ramp (inclined at 15° to the horizontal) that had its lower end immersed in water and its upper end out of the water. When ascending the ramp, newts first approached it by swimming, then used the limbs to walk while still in water, and finally left the water using a normal terrestrial walking gait. The reverse of this sequence was observed when newts descended the ramp. In both directions, newts used a lateral sequence walk with a duty factor of ~76% when out of the water. Timing of footfalls was more variable in water and featured shorter duty factors, leading to periods of suspension. Limbs were held in a more extended position in water. Newts began generating traveling waves of lateral undulation after the entire body was immersed in water.

Design Principles of Gecko Adhesive Nanostructures

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Geckos have evolved setal nanostructures on the surface of their toes that function as a remarkable and novel adhesive. Each gecko seta splits into hundreds of tips only 200 nm in diameter, permitting intimate contact with rough and smooth surfaces alike. The gecko adhesive requires minimal attachment force, leaves no residue, is directional, detaches without measurable forces, is self-cleaning, and works underwater, in a vacuum, and on nearly every surface material and profile. A single seta can withstand large forces (20 mg). The 6.5 million foot-hairs of a single gecko attached maximally could generate 130 kg of force. Recently, we provided direct support for the van der Waals hypothesis of gecko adhesion, and rejected surface polarity as a predictor of adhesion force. New results support the hypothesis that setae are self-cleaning. We have identified six key design principles necessary to yield these properties: 1) van der Waals adhesion, 2) nanostructure, 3) hydrophobicity, 4) angled shaft, 5) spacing to satisfy an antimatting condition, and 6) shaft length to satisfy a roughness condition. We applied these principles in the fabrication of the first generation of synthetic adhesive nanostructures. While we have discovered many of the secrets underlying gecko adhesion, evolutionary nanotechnology continues to produce new questions and valuable answers.

Startle Response Motor Patterns and Mauthner Cell Morphology in Three Elongate Fish Species: *Anguilla Rostrata, Mastacembelus Armatus*, and *Protopterus Annectens*

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Numerous fish species respond to an abrupt stimulus with a startle response whose initial phase is a unilateral C bend (C-start). However, recent evidence indicates that startle responses that involve a withdrawal of the head (head retraction) have evolved independently in several elongate taxa. Head retractions are characterized by a posterior retraction of the head resulting from bilateral activation of axial musculature. Both C-starts and head retraction are thought to be initiated by a pair of large reticulospinal neurons called Mauthner cells (M-cells). In goldfish, activation of one M-cell results in crossed inhibition of the other M-cell, unilateral muscle activation on the opposite side of the body, and a resultant C-start away from the stimulus. This crossed inhibition is thought to be associated with an axon cap, a glial barrier surrounding the initial segment of the axon. Since head retractions are mediated by bilateral contraction of axial musculature, we hypothesize that both M-cells would be activated and the axon cap might be reduced or absent (no crossed inhibition). To test this hypothesis, we used electromyography to quantify the motor patterns during head retractions in *Anguilla rostrata* and *Mastacembelus armatus,* and during C-starts in *Protopterus annectens*. We also describe the M-cell morphology of all three species in order to assess the structure–function relationship between axon cap morphology and bilateral muscle activity.

Integration and Inheritance of Adaptive Environmental Effects: An Example With Foraging Apparatus of Shrews

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Deviations from normal development induced by environmental stress are often assumed to be random, yet their accumulation and expression can be influenced by preexisting patterns of morphological integration within an organism. Patterns of developmental variation were studied within and among individuals, between generations, and among species of four shrew species raised under normal and extreme environments. Patterns of among-individual variation and fluctuating asymmetry in a mandible were strongly concordant in traits that were involved in the attachment of the same muscles (i.e., functionally integrated traits), and stress-induced variation was largely confined to the directions delimited by functionally integrated groups of traits. A strong effect of preexisting functional complexes was found on directing and accommodating stress-induced variation during development and evolution, and suggest that this might explain the historical persistence of functionally integrated sets of traits in shrew foraging apparatus despite their high sensitivity to environmental variation.

Archosaur Shoulder Mechanics: Implications for Mesozoic Birds

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The archosaur shoulder is composed of a saddle-shaped glenoid socket, formed from the coracoid and scapula, and a rounded humeral head. Living crocodylians retain the primitive organization in which the relatively vertical saddle has open anterior and posterior margins. My mechanical model of an alligator predicts that the upward ground reaction force on the forelimb is opposed by the downward and inward pull of the pectoralis, loading the humeral head into the ventral lip of the glenoid socket. Similarly, in flying birds, the pectoralis counters the upward aerodynamic force on the wing. However, the avian glenoid is rotated about 90° from the primitive condition, leaving the humerus prone to ventral dislocation. My 3D force balance model demonstrates that the substantial acrocoracohumeral ligament (AHL) spanning from the acrocoracoid process to the humerus is well positioned to counter the pectoralis. Mechanical testing shows that pigeon AHLs can withstand forces up 53 times body weight and are strong enough to stabilize the shoulder during flight. The avian acrocoracoid process is thought to be homologous with the "biceps tubercle" of nonavian theropod dinosaurs. Tracing the evolution of the AHL on the line to birds should help to reveal patterns of forelimb loading and to evaluate competing hypotheses on the origin of the avian flight stroke.

Cenozoic Giants of South America

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The diversity and peculiarity of the South American fauna developed throughout the Tertiary (65–3 MY) as a result of the isolation of the continent. Some remarkable gigantic forms appeared in the Oligocene among mammals (Astrapotheria and Pyrotheria), and in the Miocene among terror birds (phororhacoids). But the spectacular climax, especially regarding body size, was reached during the Quaternary (the last 2 MY). Among the more than 120 genera, the estimated adult masses of about 40 genera exceeded 100 kg. About 20 of them were megaherbivores (their masses reached metric tons). No other fossil mammalian fauna is known to have contained such a diversity of megaherbivores. The greatest interest in the Pleistocene giant mammals is in ground sloths and glyptodonts (Xenarthra), macrauchenians (Litopterna), toxodonts (Notoungulata), and mastodonts (Proboscidea). Some of these forms are characterized by peculiar adaptations of the masticatory and locomotory systems, which lack clear ecological equivalents among living mammals. Furthermore, at least in xenarthrans, the absence of many dental specializations characteristic of advanced epitherians is most probably due to biomechanical and phylogenetic constraints. Ecomorphology, morphogeometry, and biomechanics have been applied recently to interpret their form–function relationships. They have provided new insights on the design of these giants (consequently allowing interpretations of their ways of life) and on long-accepted hypotheses that were based mainly on analyses of comparative morphology.

Evidence for Predominance of Orthal Masticatory Movements in Early Sloths

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The Miocene sloths from the Santa Cruz Formation (southernmost Argentina) occupy a basal position in the most recent phylogenetic schemes. The genera considered in this work are *Hapalops, Eucholoeops*, and *Pelecyodon*. Despite a wide range of morphological variability, they are characterized by an elongated and tubular skull, curiously small in proportion to body size. The jugal, formed by an ascendant and descendent rami, is not fused to the squamosal. The dental formula is 5/4, and all teeth are separated by variable diastemata. The first tooth is caniniform. The molariforms are transversely oval to rectangular, with two transverse crests of hard dentine separated by a deep valley formed on the soft dentine. The morphology of the craniomandibular joint, and some lingual and labial molariform wear facets, indicate anteriomedially directed masticatory movements, as in generalized therians. However, features of the masticatory muscular attachment areas and tooth–tooth contact facets on the distal surfaces of lower molariform cross-lophs and matching mesial wear surfaces on upper molariform cross-lophs indicate strong vertical (orthal) masticatory movement. Because of this, their primary method of food reduction must have been by simple crushing; grinding would have been accomplished through a slight mortar-and-pestle effect. In *Eucholoeops,* orthal movements must have been emphasized due to the vertical orientation of the wear facets on the caniniforms.

Wet Adhesion in Tree Frogs: Mechanisms and Biomimetic Implications

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The toe pads of tree frogs are remarkable structures that allow the frogs to adhere to smooth surfaces and thus prevent falling, yet detach easily so as not to impair the frogs' jumping ability. The area in contact with the substratum is covered in a specialized epithelium consisting of hexagonal columnar epithelial cells, clearly separated from each other at their apices. At intervals, pores of mucous glands open into the gaps between the epithelial cells. Possibly, the separation of the cell tips allows the toe pad to conform closely to surface irregularities, while the channels that surround each cell function to spread the mucus evenly over the surface and, under wet conditions, remove excess water. Such hypotheses are being tested using microscopical techniques that allow visualization of the toe pads of living, adhering frogs. Our work on tree frog adhesive mechanisms also involves biomechanical studies. They demonstrate that the main attachment force (force normal to surface that allows frog to adhere to smooth surfaces beyond the vertical) is generated by surface tension, while detachment occurs by peeling, achieved with minimal detachment forces. Shear forces are larger than normal forces and scale with mass, while coefficients of friction are high. Such properties could have important uses in attachment and nonskid devices, which we will examine through the manufacture of toe pad replicas.

Anatomical Features of Neotropical Glanapterygine Catfishes From the Interstitial Sand Environment of the Amazon–Orinoco System

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Among the poorly known glanapterygine catfishes in the "parasitic" Trichomycteridae of the Neotropics are seven species of the sister taxa *Pygidianops* and *Typhlobelus* that are nearly the smallest vertebrates known. They apparently all inhabit the interstitial space of sand bottoms of major rivers of the Orinoco–Amazon system draining the Guiana and Brazilian shields. Preliminary analysis of their sand substrate hyporheic environment indicates that the predominate particle size (1–4 mm, 64%) is approximately equal to the maximum width of these fishes (2 mm), making them the first vertebrates that could be considered part of the meiofauna community. Characteristic anatomy of mainly marine meiofauna is documented by Giere (1993) and others based on invertebrates only. Among these anatomical features, most *Pygidianops* and *Typhlobelus*, and in some cases their poorly known sister-group *Glanapteryx*, are synapomorphic for the following: 1) extreme pigment reduction / transparent integument; 2) increased length to width ratio (to 22) and number of body segments (vertebrae, to 84); 3) extreme eye reduction (no external manifestation in some); 4) increased surface area; and 5) possible copulatory organ. They also exhibit extreme reduction of appendages, with one species having only the caudal fin, and all with paired "metapleural keels." These latter structures are formed by the anterior and medial infracarinalis muscle, and are analogous to the metapleural folds of cephalochordates, animals that also inhabit a sand/gravel substrate.

Evidence for Suction Feeding in the Desmostylidae (Desmostylia, Mammalia)

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The extinct mammalian Order Desmostylia is a group traditionally interpreted as semiaquatic and hippo-like because of their resemblances to *Hippopotamus* and to their close tethytherian cousins, *Moeritherium* (a basal Proboscidean) and *Pezosiren portelli* (a basal Sirenian). A feature of the family Desmostylidae (*Cornwallius* and *Desmostylus*) is a deeply concave "vaulted" hard palate and narrow oral opening. This vaulted palate is associated with expanding the volume of the oral cavity and allowing for an enlarged tongue to be used as a piston for suction feeding in *Odobenus* (walrus) and other aquatic taxa. This leaves a characteristic wear pattern on the lingual surface of the molars that is similar to that seen in the comparably large molars of the Desmostylidae. The wear pattern observed on the lingual aspect of the molars of *Cornwallius* and *Desmostylus* could indicate abrasion from sand or food items between the tongue and molars. Despite the thickened enamel, no evidence as yet has clarified whether the group's increase in hypsodonty or the thickness of their enamel is related to durophagy (the crushing of hard food items such as mollusks). Along with taphonomic associations, we can at least say that the Desmostylidae were likely suction-feeders in shallow water environments.

Three-Dimensional Kinematic Analysis of Powerstroking by Hatchling and Pelagic Stage Loggerhead Sea Turtles *Caretta caretta* L.

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The understanding of thrust production during the powerstroke of sea turtles was previously limited to 2D studies combined with force measures. In this study, a 3D forelimb kinematic analysis of powerstroking by hatchling and juvenile loggerhead sea turtles, *Caretta caretta,* was made with direct measurements of the thrust generated. We addressed the questions: 1) When in the powerstroke is thrust produced and by what mechanisms? 2) How does the stroke vary between juveniles under normal and stressed (fasted) conditions? 3) Do the different life-stages execute the powerstroke differently? The stroke cycle was divided into five different phases: i) posteroventral downsweep, ii) posteroventral scoop, iii) posterodorsal sweep with bent elbow (recovery phase 1), iv) anterior sweep (recovery phase 2), and v) dorsal medial arch. A peak forward force was produced during phase 2 of the downstroke. From the qualitative observations and quantitative kinematic data, it was deduced that this was a drag-based thrust generation. The juveniles (but not hatchlings) generated a second, smaller force peak during phase 5 in the upstroke, probably lift-based thrust. The stroke of hatchlings was simpler, of shorter duration, and less variable than that of juveniles. Fasted juveniles (common in the pelagic environment) and normal juveniles did not differ in powerstroke kinematic parameters, showing that acute periods without food do not adversely affect swimming kinematics. The differences between hatchlings and juveniles probably reflect contextual function as well as the physical differences in neonate vs. juvenile morphology and motor skills.

Distinct Patterns of Neurogenesis in the Neurogenic Placodes

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Neurogenic placodes are specialized regions of the embryonic ectoderm that give rise to the majority of the neurons of the cranial sensory ganglia. The stereotypical location of these placodes within the head appears to reflect the localized inductive interactions that underlie their formation. Our previous studies in the chick have shown that the epibranchial placodes are induced by the pharyngeal endoderm through the action of the signaling molecule BMP7. Other studies have shown that the ophthalmic lobe of the trigeminal placode is induced by signals from the CNS. We compared neurogenesis in these neurogenic placodes and found major differences between the epibranchial and the trigeminal placodes, which is likely to be indicative of the different type of sensory neuron produced. We are currently examining differences between the individual epibranchial placodes. Interestingly, we find differences within the trigeminal, demonstrating that this placode consists of two separate placodes: maxillomandibular and ophthalmic placodes, which may reflect a distinct evolutionary history.

Development of the Lateral Line System of the Paddlefish *Polyodon spathula* (Actinopterygii: Acipenseriformes)

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Development from fertilization to hatching occurs in ~10 days in *Polyodon*; feeding starts ~10 days after hatching (Bemis and Grande, 1992, J Morphol 213:47–83). We collected and fixed embryos and yolk-sac larvae of *Polyodon* at hatcheries in Missouri and prepared specimens for scanning electron microscopy, ectodermal flat mounts, or plastic-embedded transverse serial sections. Three preotic and three postotic lateral line placodes are present by day 5 (stage 27); these begin to elongate to form sensory ridges by day 6 (stage 29). The first neuromast primordia form within the sensory ridges on day 7 (stage 31), and the first neuromasts erupt from the otic lateral line placode on day 8 (stage 33). Only the preotic lateral line placodes form electroreceptive ampullary organs, which arise from lateral zones flanking their more centrally located neuromast-generating zones. The first primordia of ampullary organs can be recognized by day 9 (stage 35), with ampullae open to the surface on day 12 (stage 38). Ampullary organs rapidly erupt during the larval period. Paddlefish thus retain the primitive number of lateral line placodes, which generate both ampullary organs and neuromasts, as well as the lateral line nerves that innervate these receptors. Generation of both receptor types by only preotic placodes may be a derived feature of polyodontids.

Locomotion of Extinct Giant Kangaroos: Inferences From Their Modern Relatives

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Modern kangaroos use a bipedal hopping gait at all but low speeds of travel that confers significant energetic benefits to the animal, related to temporary elastic strain energy storage in collagenous tissues during foot–ground contact. Such energetic savings are related to body size, with the largest kangaroos maximally exploiting the material properties of tendons. The extinct giant macropods were about twice the mass of the largest modern kangaroo, and this study explores how the hindlimb skeleton, muscles, and tendons permit inferences to be made about their locomotor performance. Tight relationships exist between limb segment lengths (femur, tibia, and pes) and body mass for extant Macropodoidea, with the exception of tree kangaroos. Tibial lengths scale with positive allometry, which is matched with a similar exponent for tendon length. Muscle fiber lengths for the gastrocnemius and plantaris show negative allometry. This relative elongation of the tibia and its major locomotor tendons allows larger animals to save more energy than small ones via tendon stretch and recoil during locomotion. Ternary plots of hindlimb proportions in modern species demonstrate clear relationships between limb segment lengths and gait, and the importance of elastic strain energy in locomotion. This combination of ternary plot analysis and scaling relationships permit inferences to be made about the locomotor performance of extinct giant kangaroos from the Miocene.

Role of Historical Constraint in Observing Patterns of Morphological Character Evolution Consistent With Rensch's Rule: An Example From the Family Mustelidae

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An allometric trend known as Rensch's Rule, the tendency of sexual dimorphism to increase with body size in species where males are larger than females, has been documented in various animal clades. Studies looking for selective and nonselective causes leading to the observed pattern employ comparative analyses of extant taxa at the tips of phylogeny, frequently basing their conclusions on evidence from a small number of species. However, a historical approach to this problem offers a better opportunity to study evolutionary patterns consistent with Rensch's Rule directly as clade-wide phenomena. I focused on historical constraint as channeling character evolution under the action of selection and expressed differently in the two sexes, therefore resulting in certain dimorphic patterns within extant clades. Specifically, a degree of historical constraint in the evolution of body size of males and females was estimated by degree of retention of ancestral character states (measured by strength of phylogenetic signal using randomization tests) and rates of character evolution (based on ancestral character state reconstructions) within the family Mustelidae. Results of this study showed that, historically, evolution of male body size in mustelids was less constrained than the evolution of female body size. Moreover, evolution of male body size was even more relaxed compared to females in subclades with species showing rapid increases in body size, thus corresponding to the dimorphic tendencies described by Rensch.

Use of Principal Component Analysis in Modeling Growth of Segmental Structures

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A segmental body plan characterizes animals as diverse as annelids, arthropods, echinoderms, and chordates. Despite such a prevalence of a metameric pattern of development and organization in these animals, including the vertebrates, the study of their growth from a segmental perspective has been largely ignored. We explore principal component analysis as a concise and effective way of modeling the growth of segmental structures using cross-sectional data. Specifically, when an ontogenetic series is used, the first principal component represents a proxy for growth, much like the slope of a regression equation. Such an approach can be used to compare rates of growth of many serial structures to one another simultaneously. This is applicable to a variety of biological questions and is directly comparable to molecular developmental patterns and ontogenetic shifts in performance and behavior. Despite the broad applicability of this approach, it is constrained by the occurrence of differing numbers of serially repeating structures between individuals in a cross-sectional growth series. An understanding of serial homology in the system of study is important in resolving this problem. The strengths and limitations of this approach are illustrated with examples.

Pelvic Shape in Reproductive, But Growing, Female Rats: Implications for Pregnancy in Adolescence

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One-third of the world's children have slowed skeletal growth as a result of insufficient dietary protein. Factors associated with protein malnutrition and adolescent pregnancy co-occur. Thus, many pregnant adolescents may have underdeveloped-for-age skeletal systems. Growth of pelvic bones would present special problems for compromised females. In an animal model of life-long protein malnutrition, undernourished female rats can successfully reproduce, although their axial skeletons are significantly smaller than those of adults, but are still growing. We used this model and geometric morphometric analyses to address two questions: 1) What are the differences in the scaled size and shape of the pelvis between adult and reproductive, but growing, female rats? 2) What are the differences in the pattern of pelvic size and shape change over time? To test our hypothesis that protein-malnourished females are reproductive before their pelves are of adult shape, we randomly assigned 16 females to a control or isocaloric low-protein diet at weaning. Rats were radiographed in the dorsoventral plane three times per week until reproductive maturity. We digitized 24 homologous landmarks on the bony pelvis. We applied thin plate spline analysis analyses to these data. We found significant differences both in absolute shape and ontogenetic shape change between control and chronically malnourished females. These data are useful for understanding the ramifications of protein malnutrition in human populations.

Patterns of Mechanical Energy Change in Tetrapod Gait: Pendula, Springs, and Work

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Terrestrial locomotion involves fluctuations in potential (PE) and kinetic (KE) energy of an animal's center of mass (COM). Following Fenn (1924), Cavagna and colleagues (1977) identified two basic mechanisms to reduce net mechanical work and the energy cost of locomotion: an "inverted pendulum" during walking that exchanges PE and KE and use of elastic energy storage in spring elements during running/trotting when PE and KE fluctuate in phase. Although these mechanisms likely reduce energy cost, they do not necessarily reduce the force or muscle work done to support the body and move over ground. As traditionally done, separation of limb work relative to the COM (Winternal) versus COM work (Wexternal) has some difficulties and does not explain well the energy cost of locomotion. Instead, the rate and magnitude of force required to support an animal's weight is important, and better explains patterns of energy cost with size and speed. The paradigm of pendula and springs works well for cursorial mammals and birds, but other tetrapods show intermediate patterns of mechanical energy exchange. Whether or not these reflect less effective mechanisms for reducing energy cost is unclear. Pendular and spring-like functions therefore represent idealized mechanical extremes on the spectrum of mechanical energy management, with many tetrapods exhibiting intermediate features of these two basic strategies.

Tetrapod Symmetrical Gaits and Their Relationship to Energy-Saving Mechanics

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Gaits describe limb footfall patterns, which are initiated and regulated by the neuromuscular system. Locomotor efficiency of terrestrial gaits may be measured by the degree to which animals utilize inverted pendulum and spring-mass (bouncing) mechanisms to conserve external mechanical energy. Although single-foot walks have been described for most quadrupeds, small quadrupeds rarely employ these gaits for steady-speed, linear locomotion. Rather, these animals frequently rely on trots (a diagonal couplet gait with either inverted pendulum or bouncing mechanics) to move with moderate speeds. Bouncing mechanics without an aerial phase, dubbed "Groucho running" in humans and birds, have been recorded in trotting and lateral-sequence singlefoot gaits within quadrupeds. An aerial phase may be obtained at the highest speeds in symmetrical gaits. A mechanical significance of an aerial phase is its potential for more fully loading spring elements in the limbs. While this should, in theory, improve the recovery of elastic potential energy with each running step, effective anatomical springs have been demonstrated only in larger, more cursorially adapted animals.

Is the Weberian Apparatus a Key Innovation?

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Key innovations such as novelties in jaw structure open new resources for exploitation, thus facilitating the rapid radiation of the included phylogenetic group. To determine if a novel structure is a key innovation, research into the evolution of the character is necessary to understand the impact of the novelty on the clade. One such novelty in fishes is a connection between the inner ear and swim bladder. While many fishes, such as mormyrids and clupeomorphs, have developed this connection, only the otophysan Weberian apparatus has led to a major radiation (~27% of all fish species), suggesting that the Weberian apparatus is a key innovation. We are testing this hypothesis by reconstructing the evolutionary history of the Weberian apparatus using both larval and adult morphology from various species. These data, when compared to those of Gonorynchiformes, sister group to Otophysi, and Clupeomorpha, sister group to Ostariophysi, will be used to map the evolution of this novelty. While Gonorynchiformes and Clupeomorpha possess otophysic connections, both lack the complexity of the Weberian apparatus. By tracking the evolution of the Weberian apparatus with precise morphological, developmental, and genetic data analyzed within an appropriate phylogenetic context, we may be able to identify the intermediate evolutionary states leading to the full Weberian apparatus, and hence the precise role the Weberian apparatus has played in otophysan diversification.

Effect of Shape on the Aerodynamic Forces Generated by Flexible Wings

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Little is understood about the evolutionary transition from gliding to flapping flight in bats. It has been assumed that glider wings would suffer aerodynamic failure if flapped, and that bats, which rarely glide, have wings that glide poorly. If both assumptions are true, any change in morphology or flapping behavior in a gliding form would result in poorer aerodynamic performance. To test the assumption that bat wings have poorer aerodynamic performance while gliding than glider wings, we employed physical models to study the effect of wing shape on the aerodynamic forces generated by flexible membrane wings. We measured lift and drag on the models in a wind tunnel at a biologically relevant range of speeds and angles of attack. We used the models to investigate two parameters of shape: aspect ratio and the ratio of the length of the leading edge to the length of the trailing edge. The highest lift-to-drag ratios at a given Reynolds number were measured in wings that were the most glider-like, i.e., rectangular wings with a low aspect ratio. The more bat-like wings, however, stalled at much higher angles of attack than glider wings. This suggests that glider wings may have better gliding performance than bat wings at moderate angles of attack.

Preliminary Analysis of Cranial Skeletal Development in *Nectophrynoides vivipara*

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Modification of ancestral ontogenies that are characterized by larval stages is often associated with ontogenetic repatterning. One such modification is direct development, or the loss of the ancestral free-living larval stage, which occurs within all three orders of extant amphibians. A review of skeletal development in direct-developing amphibians reveals similarities between many unrelated lineages. One example is embryonic jaw ossification. In direct-developing, viviparous caecilians, early jaw ossification has been attributed to the functional demands of intra-oviductal feeding. Similarly, there is also early jaw ossification in anurans in which all of development takes place within a terrestrial egg. In these anurans the larval jaw cartilages are often significantly reduced or absent. Here, I present a preliminary analysis of cranial development in an ovoviviparous frog, *Nectophrynoides vivipara*. Cranial skeletal development in *N. vivipara* differs from that of terrestrial direct-developing frogs by having distinct larval jaw cartilages. It is similar to both viviparous caecilians and terrestrial direct-developing anurans by having embryonic jaw ossification (i.e., before birth). However, as intra-oviductal feeding is unknown in *N. vivipara*, this "precocious" ossification is probably merely the result of metamorphosis taking place before birth. Comparison between these different lineages demonstrates that similar ontogenetic patterns may be the result of adaptation (intra-oviductal feeding), repatterning, and/or recapitulation.

Limb Muscle Activation Patterns During Locomotion in Loggerhead Sea Turtles

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The anatomy of sea turtles is highly derived relative to other turtles (and tetrapods), with the forelimbs modified as flippers and the hindlimbs modified to form paddles. Previous kinematic analyses have indicated that the larger forelimbs are primarily responsible for thrust production during aquatic locomotion. Although several muscles are in anatomical positions to power these movements, no data are available to evaluate which muscles power particular behaviors, or how motor patterns of sea turtles might be derived relative to those of other taxa. As an initial step in examining these questions, we used electromyography (EMG) to measure activation patterns of major fore and hindlimb muscles in juvenile loggerhead sea turtles (*Caretta caretta*) during swimming and terrestrial crawling. EMGs were recorded from pectoral muscles including pectoralis, deltoideus, coracobrachialis, triceps, latissimus, and the teres complex. Data were also recorded from the femorotibialis in the hindlimb. Among forelimb muscles, the extensive pectoralis is recruited during vigorous swimming and terrestrial crawling, but shows limited activity during slow swimming. In the hindlimb, the femorotibialis shows little activity during powerstroking (swimming) but is recruited during terrestrial crawling. These data provide a baseline for comparisons with other taxa and facilitate evaluations of motor pattern conservation during the evolution of derived locomotor morphology.

Patterning of Embryonic Development in Birds

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A large body of data has been accumulated in support of the hypothesis that the rate at which avian postnatal growth proceeds is in part determined by the distribution of growth between different organs. Individuals with higher than average growth rates (e.g., altricial avian species) are those that allocate a large share of the early growth to rapid development of "supply" organs, such as the gastrointestinal tract and liver. Such a large early investment in these organs may have been at the expense of growth directed to "demand" organs such as brain, muscle, and feathers. These findings illustrate that competition among organs during development is part of the mechanism that regulates the relative size of body parts. As a consequence, it would appear that such a mechanism also acts as a guiding signal for shaping patterns of development in the embryo. We tested this prediction by comparing patterns of embryonic development in birds that exhibit very different patterns of postnatal growth. We found that a high rate of growth generates changes at early embryonic stages in patterns of brain and intestinal development, consequently affecting "supply/demand" organ relationships. These findings are in close agreement with the postembryonic data and, moreover, conflict with the perceived wisdom that all vertebrate embryos share a common and highly conserved developmental program.

African Ecology and the Evolution of Large Terrestrial Vertebrates During the Cenozoic

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Africa is characterized by an impressive array of large vertebrates with roots in the continent's deep past. The earliest epochs of the African Cenozoic are poorly known, but from the early Miocene to the Recent the record is more complete. Although this study presents a review of the African record of Cenozoic large terrestrial vertebrates, the raw data derive from museum collections of fossil mammals from the Neogene and Quaternary of Kenya and Ethiopia. In these countries there is a rapidly expanding network of paleontological databases that presently include more than 65,000 fossil specimens. Ecomorphological analysis and body size estimates of mammalian species show that Africa's large mammal ($>$350 kg) communities evolved in stepwise mode during two episodes of environmental change. The first occurred toward the end of the Miocene with the first occurrences of Elephantidae, Bovini (*Simatherium*), Diceros, large equids (*Eurygnathohippus*), and diversification of Hippopotamidae. The second significant increase in the diversity of large mammals occurred at the beginning of the Pleistocene. The onset of drier and more unstable ecological conditions in Africa during the early Pleistocene led to an expansion of grasslands and to the emergence of dynamic ecosystems with complex mosaics of woodlands and grasslands capable of supporting a highly diverse vertebrate fauna with dental and postcranial adaptations to this new setting.

Coordination of Locomotion and Breathing in Flying Birds

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We explored several questions about the interaction of locomotion and breathing in birds: 1) Is there an impact of the locomotor cycle upon air sac pressures in birds? 2) Do birds coordinate the ventilatory and locomotor cycles phasically in a way that might minimize mechanical conflicts and maximize assistance? 3) Is there any evidence of an energetic advantage to coordinating the locomotor and ventilatory cycles? 4) Is there any evidence for an impact of locomotion-induced pressure oscillations on gas exchange? To address these questions we measured air sac pressures (interclavicular and posterior thoracic) as well as some respiratory (costosternalis and abdominal) and locomotor (pectoralis) muscle EMGs in pigeons and magpies flying in a wind tunnel with, in some instances, high speed X-ray cinematography to allow kinematic analysis. The last question was ultimately addressed through data from breathhold diving in ducks and penguins and blood gas analysis of an anesthetized duck model of the diving locomoting bird. All questions were essentially answered in the affirmative, although there is, of course, more work to do to understand the neuromuscular interactions of the locomotor and ventilatory systems more specifically in active birds, as will be discussed.

Inherit the Limbs: Did Near-Isometric Growth in Sauropod Dinosaur Humeri and Femora Exapt Them for Gigantism?

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Sauropod dinosaurs were the most successful terrestrial vertebrate giants, but understanding this success has been challenging. However, the functional morphology and growth of the appendicular skeleton may reveal more about sauropod gigantism than previously appreciated. It has long been recognized that the basic shape of adult sauropod limbs is virtually identical to those of juveniles. Morphometric analyses of several neosauropod humeri and femora substantiate this observation: linear regression of limb dimensions against maximum length revealed an underlying isometric or near-isometric pattern of humeral and femoral growth. These results contrast with allometric patterns in prosauropods, theropods, and living dinosaur outgroups (crocodylians, birds). By comparison with previous histological studies, it is suggested that isometric or near-isometric sauropod limb growth is explained by predominantly appositional, periosteal growth and reduced endosteal and metaphyseal remodeling. As a result, sauropods maintained simplified limb morphologies into adulthood characterized by greatly expanded proximal and distal articular surfaces and a relatively solid interior. These features may have distributed compressive stresses more effectively through the sauropod humerus and femur and across their respective joints and girdles. Moreover, limited remodeling of sauropod humeri and femora suggests axial rotation of these elements was restricted, whereas parasagittal limb movements were predominant. Therefore, a simplified locomotor repertoire and the retention of juvenilized limbs may have exapted sauropods for gigantism.

Some Questions About Locomotion in Living Aquatic Giants With Different Metabolic Rates

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The large size of some living aquatic vertebrates is the consequence of the choice of a specific (normally trophic) strategy rather than a strategy in itself, and size is limited only by functional features. The choice of a specific trophic strategy is associated with specific locomotion habits; hence, feeding, size, and locomotion are closely connected. The "giants" have to optimize the relationship between metabolic cost and the energy input. The metabolic cost is an exponential function of the speed (metabolic rate = a speed b), and the maximum speed is a linear function of the size (especially in fish). In conclusion, for different body sizes there are critical speeds. If that speed is exceeded, the locomotion would have a disproportionate metabolic cost. Under these assumptions, we analyze the locomotion patterns and speed of the principal groups of living aquatic giants: Chondrichthyans (for instance. the whale shark [*Rhiniodon typus*], the basking shark [*Cetorhinus maximus*], the white shark [*Carcharodon carcharias*]…) and Cetaceans (for instance. the blue whale [*Balaenoptera musculus*], the gray whale [*Eschrichtius robustus*], the humpback whale [*Megaptera novaeangliae*]…) with different metabolic rates. Aspects concerned with the locomotion at high Reynolds number and differences between a horizontal tail stroke in cetaceans and a lateral tail stroke in fish are also noted.

Yawning, Breathing, and Stretching in Humans and Other Vertebrates

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We collected video of yawn-like behaviors in cartilaginous and ray-finned fishes, a lungfish, salamanders, caecilians, mammals, turtles, lizards, an alligator, and birds. All share a similar jaw movement pattern during yawning: a slow opening phase, followed by a slower opening phase or plateau, followed by rapid closure. This similarity leads us to conclude that all of these behaviors may reasonably be called yawning. A common belief holds that the function of yawning in humans is to provide more oxygen to the brain. This is probably not the function of yawning in fishes, amphibians and nonavian reptiles, as yawning appears to interrupt rather than augment their breathing. We measured tidal and minute volume during normal breathing and yawning in five human subjects. We found that tidal volume is larger during yawns than during normal breathing (ANOVA, $P = 0.05$). Based on these results, we reject the hypothesis that the function of yawning is to increase oxygen delivery. Instead, our results lend support to an existing hypothesis that yawning and stretching serve a similar function, but the detailed nature of this function remains unclear.

Mechanics of the "Visceral Piston" in Galloping Dogs

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High-speed cineradiography and synchronized pneumotachography were used to test previous models concerning the importance and mechanical behavior of the hypothesized "visceral piston" and its relationship to locomotor-respiratory coupling (LRC) in galloping mammals. Specifically, we analyzed the internal movements of the liver, diaphragm, and chest-walls of dogs galloping on a treadmill and during which exercise the breathing and stride cycles were synchronized on a 1:1 basis. The kinematic patterns of the liver indicate that its rhythmic fore-aft displacements do not conform to those of a passively driven inertial mass, although much of its movement is consistent with gait-induced inertial forces. Instead, the timing of caudal and cranial inertial displacements of the visceral mass appears to be regulated by the abdominal and diaphragmatic musculature, respectively. Active modulation of the visceral piston is apparently required because its natural frequency is substantially higher than stride frequency in the gallop. Moreover, active control of visceral displacement permits inertial forces generated by the liver to contribute synergistically to lung ventilation. The high resonant frequency of the visceral piston in dogs may be related to lung ventilation in certain nonlocomotory contexts (e.g., panting). Control of the mechanical behavior of the visceral mass during asymmetrical gaits may also help to explain the morphological organization of the mammalian diaphragm, especially its separation into distinct costal and crural components.

Functional Microanatomy of Fossil Hominin Bone by Confocal Circularly Polarized Light Microscopy

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A new method is advanced for the study of early hominin skeletal functional adaptation and morphology. Typically, such investigations focus on bone at the organ level, although an appreciation of the influence of mechanical loading on bone tissue microstructure may also contribute to an understanding of skeletal function. Useful microanatomical features are those that influence mechanical properties and that can be modified by physiological processes in response to mechanical loading. Preferred collagen fiber orientation is one such feature, which relates to the biomechanical competence of bone and offers evidence for the manner in which a bone was used in life. Collagen fiber orientation is aptly investigated by circularly polarized light microscopy of histological thin sections. However, unique hominin skeletal remains are not readily available for histological sectioning and so a nondestructive method was developed for this purpose, employing a portable confocal microscope to "optically section" fossil hominin bone with circularly polarized light. Examples are provided from African Pliocene representatives of *Australopithecus, Paranthropus*, and early *Homo*. Such research holds the promise of complementing existing paleoanthropological research on hominin skeletal function.

Sperm Ultrastructure in *Pseudocorynopoma doriae* (Pisces: Ostariophysi: Characiformes: Characidae: Glandulocaudinae)

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Pseudocorynopoma doriae is a member of the Glandulocaudinae, a characid subfamily whose members are all inseminating. With the exception of the genus *Planaltina*, whose sperm nuclei are spherical, resembling those of externally fertilizing species, the sperm nuclei of all other glandulocaudine species range from slightly elongate (e.g., *Diapoma terofali*, 3.6 μm in length) to extremely elongate (e.g., *Pseudocorynopoma doriae*, 31.6 μm in length). We carried out an analysis of sperm ultrastructure on two male specimens of *P. doriae* collected in Brazil in 1996 (SL 60.5 mm, MCP18470; SL 56.0 mm, MCP 18471). Preliminary results show that the chromatin of the mature spermatozoon is not as condensed as seen in other glandulocaudines. The proximal and distal centrioles are perpendicular to one another. The greatly elongate cytoplasmic collar, which contains the flagellum, remains attached to the nuclear portion of the cell along its entire length as well as beyond. Small mitochondria are located along one side of the elongate nucleus and also extend beyond. Accessory microtubules are present in the late spermatids, but are not found in the mature spermatozoon. Nuclear elongation and other sperm modifications seen in these fishes appear to be adaptations for the habit of insemination. Cladistic characters obtained from sperm ultrastructure are proving to be useful in hypothesizing phylogenetic relationships among these fishes.

Teaching Comparative Anatomy: A Place for Pedagogical Theory and Practice

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Some pedagogical theories suggest a progression of learning skills with integration skills developing late. Another theory suggests that learning is accomplished through a balance of experience and its transformation, with these attributes differing among academic disciplines and changing over time. Common to many theories is their parallel to the scientific method, which suggests an advantage for the sciences (an inherent link to how students learn). Current texts provide data on anatomy, integrated with information on the dynamics of whole organisms (e.g., function, phylogeny, development, or physiology). However, the lecturer must facilitate learning and recognize the potential lack of student skills to integrate this vast amount of material. Instructors often choose either a strict "parts-are-parts" method or more integrative approaches. A consideration for the latter is whether to emphasize the approach (developing integration skills) or the many details of the subject (content). Simple integrative tools can be used to help students lacking learning skills or as reinforcement. In the scientific method, observation is followed by questioning, as in the comparative method (where pattern is followed by questions of process). Simple structures can be given "onion skin" definitions that include important integrative information. Laboratories can include practical experience using the comparative method and integration of organ systems (e.g., providing mounted skeletons to map attachments and estimate function–discovery versus rote memorization).

Integration of Ontogenetic and Phylogenetic Data in *Tyrannosaurus rex* and Its Kin

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In neontology, sequence heterochrony infers intrinsic evolutionary processes through phylogenetically constrained comparative analysis of the order of growth events that is unique to each species. The methods of sequence heterochrony can be applied to fossil species, although often growth series are incomplete. In this study, fossil species represented by the extremes of growth were used to infer the processes that underlie evolutionary transformations by pairwise comparison of the growth changes of phylogenetic characters. If the ontogeny of a derived species reflects the evolutionary change of a synapomorphy, then the general heterochronic process can be inferred. Species represented by segments of growth series were compared using the neontological method "event pair cracking," which identifies the magnitude and direction of shifts in events between plesiomorphic and derived ontogenies. For the first approach, among the six characters shared between four tyrannosaurids the evolution of two characters show evidence of peramorphosis, three show pedomorphosis, and one displays isomorphosis. The second approach was used to compare the growth series of *Albertosaurus libratus* and *Tyrannosaurus rex*. Relative to *A. libratus*, the growth series of *T. rex* shows evidence of four events shifted early and two events shifted late. This study illustrates the value of employing neontological approaches to formulate hypotheses of how evolutionary novelties in fossil taxa were produced developmentally, when such data are available.

How Do Aquatic Frogs Generate Negative Buccal Pressure during Feeding?

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Unlike most frogs, pipids are fully aquatic and capture prey underwater. For these aglossal frogs, the typical anuran mode of lingual prey capture is not possible. In an aquatic medium, suction feeding is a highly efficient mode of prey capture. Most teleost fish feed using suction. To create suction, pressure in the buccal cavity drops below ambient pressure by a rapid increase in volume. Water is then drawn into the mouth, as is the prey item. We examined aquatic feeding in pipid frogs using high-speed image analysis, pressure recordings, sonomicrometry, and anatomical measurements. Pipids were found to generate negative pressure in their buccal cavity during feeding. The magnitude of the pressure drop was greatest during prey capture (mean –1.8 kPa; max. –8.7 kPa) and decreased subsequently during prey manipulation and transport. The mean rate of pressure change was ~60 kPa s^{-1}. This is comparable to values seen in teleost fish. The buccal cavity of pipid frogs is greatly enlarged and was found to expand to ~30% of body volume, about 10 times greater than in other frogs. The sternum of pipids is greatly expanded; this area may provide additional attachment sites for muscles used during buccal expansion. The use of the forelimbs during feeding may have obscured the importance of suction in aquatic anurans.

Thermal Physiology and the Origin of Terrestriality in Vertebrates

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One of the most important transitions in the history of vertebrates was their emergence onto land. Despite an informative fossil record, the selective advantage for the origin of a terrestrial way of life remains contentious. Evidence from a diversity of footprints from the basal Carboniferous of the Horton Bluff Formation and from the anatomy of the pectoral and pelvic girdles of Upper Devonian amphibians shows the early achievement of the capacity to support their bodies against the force of gravity. Physical laws controlling the rate of gain and loss of heat through radiation and convection on land and in the water indicate that there would have been a strong selective advantage for the immediate ancestors of land vertebrates (whose anatomy indicates they lived in very shallow water) to have taken advantage of the radiant heat of the sun in raising their body temperature. Modeling of animals the size of juveniles and adults of Paleozoic amphibians and their aquatic antecedents shows that even short periods of exposure on land (as at low tide) would have enabled adults to raise their metabolic rate significantly and so be more effective predators in the water, as well as increasing their rate of digestion, respiration, and reproduction. This hypothesis is strongly supported by the importance of thermoregulation in the lives of modern, ectothermic lizards and crocodiles.

Scaling and Mechanics in the Long Bones of Caribbean Hutias (Rodentia Capromyidae)

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A maximum sample of 143 specimens from 13 species of fossil and extant capromyids was studied. On long bones (humerus, ulna, radius, femur, and tibia) of these specimens total length and sagittal and transverse diameters at midshaft were measured. Using these measurements, second moments of area and strength indicators were calculated, both in axial compression and bending. The quotient between both sagittal and transverse second moment of area was also calculated to estimate for each bone the relative magnitude of bending strength in sagittal and transverse directions. Correlations using these different geometrical and biomechanical parameters and body mass (when known) were carried out. Regarding geometrical parameters, capromyids show in general a tendency to have relatively short appendicular bones (length scales lower than predicted in geometrically similar animals), while diameters fit the geometrical predictions. This particular long bone morphology has not been previously described in rodents and it could be related to the arboreal activity of the group. Biomechanical parameters also scale in a strict geometrical way. In general, results show that the mechanical parameters were more efficient for discerning locomotor adaptations than the geometrical parameters. Adaptations to life on mangrove trees seem particular to this group and they can explain some of the shape particularities found in long bones of hutias.

Early Bone Growth in King Penguin Chicks (*Aptenodytes patagonicus*)

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King Penguin chicks have a peculiar growth that is interrupted 3 months after hatching by austral winter. Before this interruption, chicks undergo extremely rapid statural and ponderal growth. To understand the form and function in bone tissues, we experimentally recorded (by means of fluorescent labeling of bone tissue) the growth rates in four long bones (humerus, radius, femur, tibiotarsus) of four King Penguin chicks during their first month after hatching. We also assessed the associated bone microstructure in order to test for a relationship between growth rate and bone tissue type. We found the highest bone tissue growth rate known to date: up to 171 microns/day. Moreover, there was a significant effect of bone tissue type on growth rate ($0.0001 < P < 0.02$, depending on the long bone). Most notably, highest rates were obtained with a special microarchitecture of fibro-lamellar bone, in which cavities in the woven network are aligned radially. We discuss the heuristic value of the relationship between bone tissue type and growth rate, and the biomechanical counterparts of accelerated bone growth.

Getting a Bite on the Developmental Origin of Jaws: New Interpretation of "Maxillary" and "Mandibular"

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Cartilage of the vertebrate jaw is entirely derived from cranial neural crest cells that migrate to the first branchial arch and form a dorsal "maxillary" and a ventral "mandibular" condensation. Dogma states the former gives rise to palatoquadrate and the latter to Meckel's cartilage, forming the framework for the bones of the adult jaw. We tested this hypothesis using molecular and morphological markers of late-migrating cranial neural crest cells in axolotl and chick embryos. Surprisingly, we find that both palatoquadrate and Meckel's cartilage derive from the ventral condensation, whereas the dorsal condensation forms trabecular cartilage of the neurocranium. Therefore, the common textbook terms "maxillary" and "mandibular" condensations are based on false assumptions. These studies are the first to reveal the morphogenetic processes by which facial condensations build the jaw primordia of gnathostomes. Using comparisons with agnathans, we propose that these mechanisms may be a basal feature of vertebrates.

Deployment of Dorsal Fins Is an Integral Part of the Escape Response in Largemouth Bass (*Micropterus salmoides*)

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Although the fast-start escape response in fish is powered primarily by the axial musculature, the median fins are in a position to increase the body depth and thus enhance lateral thrust during the behavior. We quantified kinematics and electromyographic (EMG) activity in axial and dorsal fin muscles during the escape response in largemouth bass. High-speed videos from synchronous lateral and dorsal views were recorded at 500 fps and simultaneous EMG activity was collected at 5,000 Hz. Recordings were made from six fish; all exhibited the stereotypical C-start. Movement began an average of 9.1 ms following the startle stimulus; stage 1 lasted an average of 40.6 ms. In undisturbed bass, the spiny dorsal fin is depressed against the body, while the soft dorsal fin is semi-elevated. Both fins are erected during stage 1 and have reached full elevation by the beginning of stage 2, supporting the hypothesis that dorsal fins are deployed to increase lateral thrust at the start of stage 2. EMG recordings revealed that axial and dorsal fin muscles became active nearly simultaneously. Dorsal fin muscles on both sides of the body are activated synchronously, presumably to erect the fins while minimizing lateral deflection. Most muscles showed multiple discrete bursts of activity during the escape response.

Carnivore Spine: Does it Support Some Long-Held Assumptions?

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In a seminal article on the subject, E.J. Slijper established correlations between vertebral morphology and locomotion or habits in mammals. Many workers since have used his models in predicting behaviors of other taxa. However, Slijper's work lacked statistical rigor and examined unrelated taxa that display only extremes of mammalian locomotion. We explore relationships between vertebral morphology, phylogenetic relationships, and locomotion and habitat in the extant Carnivora. This clade contains almost 300 species, with numerous instances illustrating independently derived strategies for locomotion and habits. We categorized species by locomotion (digitigrade or plantigrade cursors, forelimb or hindlimb swimmers) and habitat (arboreal, scansorial, terrestrial, fossorial, or semiaquatic) from the literature and collected measurements from all presacral vertebrae representing 120 carnivore species. Using principal components and discriminant function analyses, we demonstrate that although hindlimb swimming can be reliably predicted, other types of locomotion cannot. Vertebral morphology is extremely poor for predicting habitat. Measures of spinous process and total vertebral height proved to be the most reliable predictors of locomotion (85–95% correct), followed by centrum length, width, and height (75–90%), and transverse process width (50–65%). In some cases, similarity in vertebral morphology appears to follow trends predicted by Slijper, while in others phylogenetic constraints appear to extract a greater influence on vertebral morphology than do environmental factors.

Genetic Analysis of the Canid Skeleton: Quantitative Genetics of Skeletal Size and Shape

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Evolution of mammalian skeletal structure can be rapid and the changes profound, as illustrated by the morphological diversity of the domestic dog. We are using the Portuguese Water Dog and the Silver Fox to analyze the quantitative genetics of the canid skeleton. Genetic loci (QTLs) are described that affect individual bones, systems of bones, or musculoskeletal systems. These can be simple, (e.g., affecting limb bone length), complex (e.g., affecting laxity in only the right coxofemoral joint), or they may regulate entire skeletal systems. We use principal component analysis of skeletal variation to reveal systems of traits defining skeletal structures. This analysis classifies phenotypic variation into independent components that can be used to dissect genetic networks regulating complex biological systems. We show that unlinked QTLs associated with these principal components individually promote both correlations within structures (e.g., within the skull, or among the limb bones) and inverse correlations between structures (e.g., skull vs. limb bones). These QTLs are consistent with regulatory genes that inhibit growth of some bones while enhancing growth of others. Detailed molecular genetic analysis of Portuguese Water Dog skeletal structure are described as well as preliminary experiments on Silver Fox populations that demonstrate the existence in these animals of similar regulatory systems.

Growth Patterns of Mesozoic Birds

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A host of studies have shown that the nature and texture of fossil bone tissues provides an assessment of the growth of the bone when the animal was alive. Thus, studies of bone microstructure of Mesozoic birds provide a host of information that enables the reconstruction of their growth dynamics. Evidence from bone tissues of several Mesozoic nonornithurine birds (e.g., enantiornithines, *Patagopteryx, Rahonavis, Vorona*) suggests that the growth patterns of basal birds was typically interrupted, and that they grew at slower rates than their modern relatives. Mesozoic ornithurine birds (e.g., *Hesperornis, Ichthyornis, Cimolopteryx, Polarornis*) appear to have grown in an uninterrupted, rapid manner, as is the case in modern birds. These findings suggest that the flexible, periodically interrupted growth strategy of basal birds was inherited from their dinosaurian ancestors, while the later inflexible, rapid growth that typifies the Ornithurae, was probably related to a shortened developmental time, and evolved later in the evolutionary history of birds.

Eurasian Giant Mammals of the Cenozoic

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The extant fauna is impoverished of giant mammals compared to most of the Cenozoic. The largest extant terrestrial mammals, the Proboscidea, are represented today by a mere one species of *Elephas* and *Loxodonta,* although some studies indicate the possibility of two species of the latter taxon, but their taxonomic status is phylogenetically irrelevant. This is probably the lowest diversity of the group since the Paleocene. Also, the Rhinocerotidae have also dwindled markedly in both species and morphological diversity since the last Ice Age. Past ecosystems appear to have supported a considerably greater faunal diversity of giant mammals. It is often claimed that elephant-sized terrestrial animals need columnar limbs and a nonrunning gait to support their large mass, but this is contradicted by the morphology of several extinct mammals within groups such as the Rhinocerotidae, where *Coelodonta* and *Elasmotherium* approached extant elephants in size despite having nearly identical physical proportions to *Ceratotherium. Indricotheres* appear morphologically to have been capable of at least slow trotting at body sizes far exceeding those of extant elephants. Faster terrestrial locomotion than ambling is possible at body sizes of 5–6 tons. New, multivariate analyses of body masses in proboscideans indicate that some significantly exceeded extant elephants in size, and others had different physical proportions corroborating the paucity of the extant fauna.

Hindlimb Morphology and Function at the Nonavian–Avian Transition

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Traditionally, the question of the origin of birds and flight have been synonymized, and a dichotomy has been invented for the origin of flight, claiming that from-the-tree-down was a biophysically well-supported model, whereas from-the-ground-up was supported by the phylogenetic relationship of birds to nonavian theropods, which were claimed to have been strictly terrestrial. Such a dichotomy is inherently false and misunderstood. Despite the plethora of synapomorphies of advanced coelurosaurs (sensu lato) and avialeans, there are still differences, particularly in forelimb, chest, and air-sac function, but also in hindlimb kinematics, where avialeans predominately move by knee flexion-extension, with a more stationary, near horizontal femur, although not during fast locomotion, and nonavian theropods appear to have included a much more pronounced femoral action. This is also reflected in differences in limb postures and bone proportions. Thus, models have been erected, based on available evidence, outlining the transition from terrestrial, nonvolant animals with femoral-based locomotion to animals specialized for flight, where alterations in body proportions brought about different limb postures and kinematics. Such scenarios can no longer be supported. They are contradicted by recent fossil finds, and it will be shown that phylogenetic and morphological analyses have long contradicted them as well.

***Ichthyostega*: Innovative But Not Intermediate**

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The Devonian tetrapod genus *Ichthyostega* has stood as an icon for the “fish-tetrapod transition” for almost 70 years. Recent study has shown that not only is *Ichthyostega* different from the image presented by Jarvik and more general texts, but that it possesses some extreme and bizarre specializations unexpected in so early a tetrapod. While retaining gill bars, it had a uniquely modified and apparently aquatically adapted ear region unlike that of any other known fish or tetrapod. It is the earliest tetrapod to show specialized dentition. The vertebral column shows the earliest evidence of regionalization along its length, and some of its modifications resemble those of mammals rather than any early tetrapod. The 7-digited pes with its unprecedented arrangement of digits is incompatible with a walking gait, but resembles a paddle. The digits of the manus are still unknown, but new forearm specimens suggest that the forelimb likewise did not perform a conventional walking gait: *Ichthyostega* did not “walk” on land. We present a summary of recent work and a radical new reconstruction of this exceptional animal. *Ichthyostega* illustrates the presence of considerable and previously unappreciated disparity among Devonian tetrapods, although its specializations were not perpetuated. Although its phylogenetic placement is still unclear, it should not be considered a primitive or intermediate form in tetrapod evolution.

Kinematics of Crocodylian and Avian Lung Ventilation: Investigating the Evolution of Breathing in Extant and Extinct Archosauria

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The morphology and function of the crocodylian and avian respiratory systems provide important information with which to interpret the respiratory anatomy and function of extinct archosaurs. However, detailed knowledge about the kinematics of lung ventilation in crocodiles and birds, the only living archosaur groups, has not been available previously. We examined the skeletal and soft tissue kinematics of breathing in *Alligator* and birds including *Dromaius* and *Numida* by cineradiography, and compared the novel information obtained with fossil archosauromorph anatomy. Crocodiles and birds possess two distinct and highly derived respiratory mechanisms. Crocodiles have the most complex lungs of any living reptile, and ventilate their lungs through (hepato)visceral movement coupled with pubic and sternocostal movement. Birds have fixed parabronchial lungs with unidirectional airflow in the paleopulmo, due to the interaction of bellows-like airsacs and fine-tuned valving of the respiratory tract. Inspiration in birds is accomplished through a whole chest aspiration pump involving the sternocostal apparatus. Movements of the pelvis have also been suggested to contribute to lung ventilation in birds. Differences in thoracic structure and joint anatomy between crocodiles and birds contribute to regional differences in trunk contraction or expansion and likely put constraints on the respiratory system ventilated. Primitive archosauromorph thoracic anatomy shows similarity to extant crocodylian anatomy. Changes to more avian-like breathing appear to have occurred in some theropod dinosaurs.

Rules of Construction in Proboscis Building in Mammals

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Fossil mammals with retracted nasal bones are commonly reconstructed with fleshy, tapir-like probosces. Extant mammals, however, show a variety of proboscis structures and not all have retracted nasals. We studied a diversity of extant probosces to determine causal relationships between soft-tissue specializations and underlying bony changes. Study specimens and outgroups were examined through CT, dissection, sectioning, and skeletonization, or were studied from the literature. Mammals show two large-scale anatomical conformations or styles of probosces. Maxillolabial probosces result from elongation of the rostral end of the nose, without retracted nasals, relying largely on maxillolabial musculature. Vestibular probosces show variable specializations in soft tissues, yet the nasal vestibule is always enlarged, causing retraction of the bony nostril. Vestibular probosces do not show increased capacities for more primitive functions such as olfaction or respiratory countercurrent exchange. Phylogenetic constraint and exaptation underscore the importance of outgroup anatomy and the anatomical substrates involved. Maxillolabial probosces leave few osteological correlates, and retracted nasals in vestibular probosces serve only as starting points in reconstructing a proboscis. Correlates for major soft-tissue structures (e.g., cartilages, muscles) provide rules of construction for proboscis building and for discriminating among functionally divergent conformations in vestibular probosces. These data permit proboscis inference to more adequately characterize narial specializations seen in fossil mammals and to clarify their behavioral and ecological roles.

Origin of Tetrapods

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Body-plans and bauplans are hypotheses of general and specialized shared conditions, usually abstracted from crown group memberships. Thus, body-plans and last common ancestors of living groups have tended to blur one into the other, and stem groups have emerged as a unique means of investigating the evolutionary sequence (and possible significance) of body-plan assembly. However, fossils are incomplete, thus raising issues

about conditions of unknown parts (ACCTRAN/DELTRAN decisions in phylogenetic reconstruction) and how much of any particular body-plan was, in fact, present. This problem usually increases away from the crown node and towards the stem group base, where membership is less diverse, fewer characters unite taxa with the crown group, fossils are rare and fragmentary, and hypotheses of stem-membership are more controversial. This is particularly true of the fragmentary fish at the very base of the tetrapod total-group. Moreover, although often treated as such, stem groups should neither be interpreted as ancestor-descendent sequences nor should their body-parts, or "character-states." Therefore, while stem groups are often used to explore the origin of classic evolutionary innovations, such as "the tetrapod limb," a phylogenetic series of fins and limbs does not constitute a legitimate transformation sequence. The implied evolutionary hypothesis is of sequential developmental change, which, in the case of tetrapods, is unexpectedly complex.

Fins, Limbs, and Genitalia: From Evolutionary Origins to Congenital Malformations

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The origin of fins and the transition of fins to limbs were pivotal events in the evolution of vertebrates. Considerable progress has been made in understanding the molecular genetics of vertebrate limb development, but the developmental mechanisms underpinning the evolutionary origin of paired appendages are not understood. The evolution of external genitalia contributed further to the success of terrestrial vertebrates by facilitating internal fertilization. From a developmental perspective, the embryo must solve many of the same problems in building limbs and genitalia. Despite obvious differences in adult morphology, limb buds and genital tubercles of vertebrate embryos undergo similar developmental processes, such as induction of proximodistal outgrowth, establishment of specialized signaling regions, and coordinated patterning along three axes. Comparative analyses of development in basal vertebrates are now shedding light onto the sequence of events that led to the origin of fins. Studies of the mouse embryo are elucidating the pathway that regulates external genital development. We are extending these studies to a range of organisms in order to identify developmental mechanisms of anatomical diversification. Comparative developmental studies are also beginning to uncover a relationship between congenital malformations in humans and the evolution of developmental processes. This work will cover recent progress in the genetics of vertebrate appendage development, and the implications of this work for our understanding of vertebrate evolution.

Is the "Stem-Gecko" Body Plan Really Plesiomorphic for Squamata?

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Little or no consensus exists among systematists regarding the basal interrelationships of Squamata (lizards and snakes), despite two decades of cladistic investigation. Nearly all possible combinations for the major groups (Iguania, Gekkota, Scincoidea, Lacertoidea, Anguimorpha, Amphisbaenia, and Serpentes) have been forwarded as phylogenetic hypotheses. Gekkota have been particularly problematic because of their combination of plesiomorphic and apomorphic character states. Indeed, both identification of the sister-group to Gekkota and constitution of its ingroup remain contentious. "Bavarisauridae," "Ardeosauridae," and Xantusiidae are often considered stem-geckoes because of their large eyes, insectivorous dentition, and blunt snouts, although retention of a pineal foramen (and some other plesiomorphic character states) eliminates them from Gekkota sensu stricto. Based on a morphological phylogenetic analysis (including a new Cretaceous Mongolian fossil), I suggest "bavarisaurids" and "ardeosaurids" are polyphyletic assemblages interspersed throughout basal squamate radiations. Importantly, the phenetically similar Xantusiidae, *Carusia*, and the Mongolian fossil, are basal Lacertoidea, Anguimorpha, and Nyctisauria (geckoes, amphisbaenians, snakes), respectively. I suggest that the previous conception of the basal gekkotan morphotype actually represents the plesiomorphic body plan for Squamata, Scleroglossa, Nyctisauria, Scincomorpha, and Anguimorpha. Conservation of this basic body plan along the "trunk" of the squamate tree represents an important confounding factor in determining squamate interrelationships.

Morphological Approach of Aquatic Locomotion in Birds (Penguins, Spheniscidae)

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Penguins (Spheniscidae) are flightless, pelagic seabirds restricted to the Southern Hemisphere (Antarctic and sub-Antarctic regions) and to different regions of South Africa and South America (western coasts and Galapagos archipelago). They are highly specialized marine divers (aquatic locomotion), spending much of their life at sea, but returning to islands and coasts to breed; they are therefore terrestrial in juvenile stages and aquatic in adult. Penguins have evolved an amazing array of morphological, physiological, behavioral, and ecological adaptations allowing them to exploit extreme, often very cold, habitats ranging from the snow and ice of Antarctica to the hot desert-like islands of the equatorial Galapagos. Skeletal anatomy is very particular in these birds. Geometrical morphometry methods (procrustes, phenetic trees) use some landmarks to depict taxa and allow quantification and visualization of morphological differences between organisms, independent of size. These methods have been applied to the study of the skull shape of penguins using two approaches (ontogenetic and comparative). The results of the analyses show clearly the very important influence of the locomotor pole on the modifications in cranial morphology during ontogenesis in relation to a significant change in the locomotion (terrestrial in juveniles and aquatic in adults). Skull shape in penguins is therefore highly constrained by environmental factors and in particular by the locomotor pole.

Cladistic and Functional Comparative Analysis of the Orbital Region of Mammalian Skulls

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The orbit, or eye-socket, is a region of the skull that varies greatly in its composition among the different mammalian orders. It is made up of seven to nine different bones, each of which varies in its contribution to the orbit in each mammalian group. However, despite its plasticity, little comparative anatomical work has been done in this area in any depth. Previous studies have concentrated on the insectivoran groups and the primates, to the exclusion of other taxa. Similarly, there is a shortage of research that has focused on the functional reasons underlying the different bone patterns. This study examines orbital region in most, if not all, eutherian families, with a view to determining the functionality of the orbital mosaic. Approximately 100 taxa have been examined and scored for each of 23 characters. These characters include the presence or absence of bone contacts and the presence and position of cranial foramina. When complete, the dataset will be subjected to cladistic analysis, as a whole and in sections. The resulting cladograms will be used to reconstruct character changes in the orbit, and to explore possible functionalities acting as selection pressures on orbital structure. It is hoped that the results will also contribute to current debates regarding the phylogeny of placental mammals.

Structure and Function of the Sperm Whale Nose: Science, Art, and Folklore

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The enormous nasal apparatus of the sperm whale has perplexed scientists, philosophers, and whalemongers for centuries. The sperm whale nose is extraordinarily asymmetric and hypertrophied. As a consequence, it is not surprising that curiosity has often spurred the imagination to speculate about its functional significance. Whalers nicknamed the sperm whale for the valuable milky lipids they harvested from the nose, the bulk of it from the spermaceti organ. One proposal described how the whale might actively cool the spermaceti organ to congeal the waxy lipids and adjust buoyancy during diving (Clarke, 1970). Another proposal conceived that the sperm whales nose evolved as a battering ram (Carrier et al., 2002), but this notion is difficult to evaluate because it is rooted in folklore and based on art rather than science. Norris and Harvey (1971) first proposed an acoustic function for the sperm whale nose. Since then a rising tide of evidence suggests that all odontocete foreheads contain a complex sound generation apparatus. In addition, the unique lipid components are important for acoustic beam formation and impedance matching. The sperm whales nose is the worlds largest bioacoustical machine, apparently with the capacity to produce sounds loud enough to debilitate prey (Norris and Møhl, 1983) and to attract mates or repel rivals (Cranford, 1999).

Industrial CT-Images of Large Whales as a Foundation for Sound Propagation Models

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The largest mammals on earth are also the least known. Almost nothing is known about the anatomic geometry of large whales of either suborder (odontocetes and mysticetes). The aquatic existence of cetaceans often puts them beyond our reach, but it is primarily the size of the large whales that makes them intractable subjects of investigation. A revolution in anatomy and physiology has been catalyzed by remote imaging technology over the past few decades. The development of industrial X-ray computed tomography (CT) scanners make it possible to collect information about the intact anatomy of large whales. I have pioneered two techniques that, when combined, provide anatomic images from whales. I have collected CT information from the head of a sperm whale and an entire Cuvier's beaked whale. These serial 2D datasets can be reassembled into volumetric structures that can be measured, adjusted, or output (in part or in whole) for scientific visualization, morphometric analysis, rapid prototyping, finite element modeling, and an array of other applications. Recent beaked whale stranding events associated with sonar operations catalyzed an effort to build a finite element (FE) model to simulate acoustic propagation within the body of a Cuvier's beaked whale. This FE model bears directly upon our understanding of the sound propagation pathways and the potential deleterious effects from seismic exploration and other acoustic sources.

Phylogenetic and Functional Effects of Bone Vascularization in Sauropsids

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Bone histological architecture can be preserved for hundreds of million years and, therefore, is an important potential source of information for reconstructing the life history traits of fossil species. To carry out this paleobiological investigation, it is necessary to understand the determinism of bone histological traits in extant species. Both small lepidosaurians and small birds have avascular bone tissue. However, while this character state is present throughout the ontogeny in small lepidosaurians, juvenile small birds have highly vascularized, lacunar bone. This fact suggests that the variation in the vascularization density of bone is clade-specific in Sauropsids and contains phylogenetic information. The importance of the influence of phylogeny on the variation in bone histology has been discussed for over 150 years. However, until now few studies have quantified these effects. We carried out a quantification of the influence of phylogeny on the variation in vascularization density of bone in Sauropsids, using phylogenetic permutational regressions. Although phylogenetic effects are significant, they are weak and only explain a small part of the variation of this character. In contrast, functional factors such as bone size and basal metabolic rate explain high percentages of the variation of bone density of vascularization.

Influence of Envenomation on Ingestion Mechanics in Snakes

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We compared ingestive performance among a sample of venomous species from four families (two atractaspidids, nine elapids, two colubrids, 42 viperids) with ingestive performance in selected nonvenomous colubrid species (five species), most feeding on similar mammalian prey. The global effects of the evolution of envenomating structures suggest that ingestive performance is slightly decreased in atractaspidids, unmodified in most elapids and venomous colubrids, and improved or unmodified in vipers. Despite many problems in making direct comparisons and considerable variability within major clades, the effects seem attributable to obvious structural differences. Decreased performance in Atractaspis results from reduction and loss of teeth on the medial palatal elements and dentaries. Absence of notable performance differences among elapids, venomous colubrids, and nonvenomous colubrids results from the retention of joint and bone features common to members of all three clades. Potential enhancement of ingestive performance in vipers is suppressed in many species because palatopterygoid travel is reduced during ingestion to limit fang erection.

Burrowing in Snakes: Past Efforts and Future Directions

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Burrowing mechanics in snakes have been studied largely by inference inasmuch as most of the animal is invisible while burrowing. The most accomplished burrowers, uropeltid snakes, have been observed penetrating soils of known hardness. Anatomical and molecular studies of their anterior trunks and heads correlate with available behavioral data. Cine records of burrowing in *Cylindrophis* suggest that penetration is achieved entirely by compaction of soils accomplished by both the head and anterior trunk. Initiation of burrows by *Atractaspis* and *Loxocemus* confirm previous results from uropeltids that the caudal trunk is not used in generating penetrating forces. Direct measurements of forces generated at the anterior tip of the head in a variety of burrowing snakes suggest that species vary widely in maximum force produced but none approach some other more specialized head-first burrowers, such as amphisbaenians and caecilians. Correlations between tunnel form and force output suggest that burrowing forces are generated near the head. Due to the inherent difficulties associated with observing subterranean behaviors directly, future progress in this field will depend in large part on the adoption of nonconventional techniques to study burrowing mechanics (i.e., force-platform analyses, infrared imaging, 3D-reconstruction of particle displacements).

Giant Flying Vertebrates

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The physical requirements of flight, launch, and landing impose constraints on the morphology of all flying vertebrates. The physical requirements of giantism impose further constraints. Even so, there is considerable variability in the solutions to these problems in very large animals, and these variations can provide as much illumination of the processes involved, as can the convergent similarities. Herein, we illustrate some of these differences and further discuss the possible effect of various launch and landing techniques upon limits of size and mass.

Morphometrics and Function of the Bonobo *(Pan paniscus)* Hindlimb

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Bonobos ("pygmy chimpanzees") display a very wide range of locomotor behaviors, including terrestrial bipedalism, knuckle-walking, modified brachiation, and jumping. Most of these locomotor types are hindlimb-powered, and here we evaluate how this can be achieved anatomically. We compare flexion-extension angles of the hip, knee, and ankle during bipedal walking, quadrupedal walking, climbing, and jumping based on the analysis of video footage (50–250 fps). Additionally, we report gross dissection and morphometric data (i.e., muscle moment arms measured using the tendon travel method) from three specimens (one juvenile, one adult male, one adult female), and segment inertial properties measured in anesthetized subjects. Joint range of motion was greatest during climbing, where average joint angles ranged from 50° to 130° in both the hip and knee, and thus, during all gaits, these joints remained considerably flexed throughout the stride. Compared to humans, muscles spanning the hip and knee are relatively light and have relatively short moment arms and long fascicles; this anatomical arrangement favors maneuverability. This arrangement also results in rather low values for joint torques, but allows bonobos to produce torques over the full range of joint positions observed during the various locomotor modes.

Locomotion and Ventilation in Humans: Are They Really Mechanically Independent?

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The locomotor-respiratory coupling (LRC) patterns observed in humans are distinct from those found in other mammals. While quadrupedal mammals usually exhibit a 1:1 (strides/breath) coupling ratio, humans demonstrate more flexibility in breathing patterns. Humans frequently utilize LRC ratios of 2:1, 2.5:1, 3:1, or 4:1, and sometimes lack entrainment of running and breathing. Does this flexibility exist because running and breathing are mechanically independent in humans? We addressed this question by investigating the relationship between locomotor cycles and ventilatory flow in humans while they ran on a treadmill. Ensemble averaging was used to calculate the fraction of ventilatory volume attributable to locomotion. To test the hypothesis that movement of viscera contributes to locomotor–ventilatory interactions, we compared locomotor-driven ventilation before and after drinking 1 L of water. This added 1–2% of body mass exclusively to the guts. During normal, moderate speed running, locomotor forces drive 5–20% of inspiration and 9–16% of expiration. These values are an order of magnitude greater than previously measured in humans. Once the guts were loaded by drinking water, the locomotor-driven volume increased by ~140%. These results suggest that while locomotion and ventilation are less mechanically linked in humans than in other mammals, substantial mechanical interactions do exist. Thus, LRC in humans might function to tune these interactions and improve the economy of breathing and/or running.

The Evolution of Pectoral Fin Development in Gnathostomes: Insights From Embryos and Fossils

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Development of the pectoral appendage endoskeleton differs in teleosts and tetrapods. In tetrapods, secretion of extracellular matrix components (collagens and proteoglycans) begins concomitant with, or subsequent to, condensation of individual elements. In contrast, the pectoral fin endoskeleton of teleosts begins as a single, plate-like chondrogenic condensation. This endochondral disc then subdivides into individual radials by decomposition of extracellular matrix in the interradial mesenchyme. Comparisons between these divergent mechanisms of skeletal patterning are complicated by the fact that teleost radials are not considered homologous to the tetrapod limb skeleton. However, basal actinopterygians and chondrichthyans possess fin skeletons with elements homologous to both teleost radials and tetrapod limb bones. A study of pectoral fin development in several basal actinopterygian and chondrichthyan taxa reveals that aspects of both teleost and tetrapod endochondral patterning mechanisms are present in basal gnathostomes. For example, in the Acipenseriform *Polyodon*, those elements considered homologous to teleost radials form via subdivision of a chondrogenic disc while those elements considered homologous to the tetrapod limb (the metapterygium) condense prior to extracellular matrix secretion. Such observations suggest that the distinct ways that teleosts pectoral fins and tetrapod forelimbs develop may not involve the acquisition of novel patterning mechanisms. Instead, these differences may involve correlative loss of patterning mechanisms specific to portions of the primitive gnathostome pectoral bauplan.

Morphological Variations in a Tooth Family Through Ontogeny in *Pleurodeles waltl* (Amphibia, Caudata)

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Nonmammalian vertebrates replace their teeth several times during their life (polyphyodonty). An appropriate polyphyodont species would permit study of the mechanisms controlling tooth replacement and the changes occurring in tooth morphology (size, shape, orientation) and structure during ontogeny. In the amphibian *Pleurodeles waltl,* teeth develop early, and through successive replacements (generations) their morphology and structure are modified. A series was fixed, from 2 days before hatching to the adult stage, for light, scanning, and transmission electron microscopy, to determine whether the tooth modifications either occur progressively during ontogeny or appear during one step, for instance, at metamorphosis. To this end we followed a single tooth family, i.e., the first-generation tooth and all replacement teeth that succeeded until adult stages. In larval *P. waltl* the teeth differ from the adult by a conical and monocuspidate shape versus bicuspidate; a homogeneous basal region of the dentin cone versus a pedicellate organization; the presence of a thin enameloid layer (both mesenchymal and epithelial contribution) versus only enamel; and a minimal structure with reduced pulp cavity and absence of dentinal tubules in the dentin versus a large pulp cavity containing large blood vessels, nerves endings, and the presence of dentinal tubules within the dentin matrix. Remarkably, the monocuspid-bicuspid transition occurs at metamorphosis, while the other modifications occur progressively during ontogeny.

Cenozoic Giants of North America

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North America mammalian faunas over most of the Cenozoic (about 65 to 3 MYA) were shaped partly by repeated migration events from Eurasia. Numerous megamammals (i.e., exceeding 100 kg) from disparately related groups appeared throughout this period. For example, Perissodactyla was represented by rhinocerotids (*Teleoceras*), brontotheres (*Brontotherium*), and equids (*Equus*); Dinocerata by *Uintatherium*; Pantodonta by *Titanoides*; Proboscidea by elephantids (*Mammuthus*); and mammutids (*Mammut*). Also, several artiodactyls (e.g., entelodonts) and carnivores (e.g., *Smilodon*) reached large body sizes. North America was not connected to South America for most of the Cenozoic, which, with minor exceptions, excluded from northern faunas many of the earlier and peculiar South American megamammals. The character and composition of the North American fauna, however, changed markedly following the emergence of the Panamanian isthmus about 3 MYA, which led to an intermingling of North and South American faunas (i.e., the American Biotic Interchange). As a result, the North America Pleistocene fauna included many large and often spectacular megamammals of South American origin, particularly as represented by xenarthrans such as pilosan mylodontids (*Paramylodon*) and megatheriids (*Eremotherium*), and cingulate glyptodonts (*Glyptodon*), and pampatheres (*Holmesina*). These taxa are particularly noteworthy as they lack modern analogs and their modes of life, including dietary and locomotory behaviors, are incompletely understood. Recent approaches involving biomechanical and comparative methods have shed new light on their habits.

Burrowing Strategies in Fishes: From Head to Tail

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Burrowing is not a common feature in teleost fishes, not even in cryptic ones. Within fossorial species, however, different strategies have evolved. Three main types of burrowing are observed: 1) oral digging (e.g., Protopteridae); 2) head-first burrowing by forcing the head into the substrate (e.g., Moringuidae); and 3) the less common tail-first burrowing (e.g., Heterocongrinae). With the exception of the oral burrowers, and apart from some lineage-dependent adaptations, fossorial fishes seem to share a constrained overall body plan, i.e., anguilliform with the loss of paired appendages, which also is the case in most tetrapod burrowers. To study possible structural adaptations for different burrowing strategies in teleosts, the anatomy of both the skull and the tail of two closely related species (both Anguilliformes) is compared: *Heteroconger* (Heterocongrinae), a tail-first burrower, and *Moringua* (Moringuidae), a head-first burrower. Striking differences were found in both the skull and the caudal skeleton which could be linked to the burrowing strategy. *Moringua* showed reduced eyes, extensive strengthening of the rostral tip of the skull and the skull roof, and large jaw muscles. *Heteroconger* showed a reduced caudal fin, as well as a reduced caudal skeleton, consisting of only two hypural elements. Some of the observed structural specializations in the head-first burrowing *Moringua* are shared with most fossorial vertebrates, including some tetrapods.

Do Mustelid Carnivores Have Semi-Retractile Claws? A Comparative Morphometric Assessment

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The claws of the American marten (*Martes americana*) have been described as semiretractile, suggesting intermediacy between the nonretractile claws of canids and the hyperretractility of felids. Osteological correlates associated with claw retraction in the marten are evaluated through comparison of its middle and distal phalanges with those of the cat (*Felis catus*) and other felids, and the dog (*Canis familiaris*) and other canids. The middle phalanges of the marten exhibit greater shaft symmetry than those of either canids or felids. The angle of arc of the keratinous sheath of marten claws is intermediate between that of canids and felids for manual digits I–V, while pedal digits display a larger angle of arc than either of these. Values for radii of claw curvature for manual digits I–IV and pedal digits II–V are intermediate between those of canids and felids, with the exception of manual digit V, which presents a higher value. The angle of orientation of the plantar process of the distal phalanx displays considerable variation among and between species, but the comparative results are not definitive. The results indicate that the characterization of semiretractility is not based on morphological features of the skeleton, but may be an attribute associated with hunting behavior and the relation between claws and manual and pedal soft anatomy.

Constraints on Asymmetric Variation in the Human Skull

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Fluctuating asymmetry (FA) is commonly used as a bioindicator of developmental stress, but asymmetric variation does not occur uniformly across component parts of an organism. This study addresses localized constraints on asymmetric variation in the human skull. The effects of three separate variables on FA in the skull were tested: systemic stress, sex, and biomechanical alterations in growth trajectory. An extension of Euclidean Distance Matrix Analysis was used to quantify asymmetry from landmark coordinate data in paired samples from three distinct populations, each chosen to test one of the variables under consideration. As expected, in a comparison of related samples under different levels of nutritional/systemic stress the “high-stress” group displayed a greater magnitude of FA than the “low-stress” group. However, only minor differences were found in comparisons involving sex and biomechanical alteration. Contrary to expectations, females displayed a slightly elevated degree of craniofacial FA relative to males. Also, normal children displayed a slightly elevated degree of craniofacial FA relative to children with sagittal craniosynostosis. Interestingly, localized patterns of fluctuating asymmetry within the skull were similar across the populations under consideration. These results provide evidence for common biological mechanisms that maintain developmental stability and constrain asymmetric variation in certain regions of the skull.

Tooth Development in a Scincid Lizard, *Chalcides viridanus* (Squamata), With Particular Attention to Enamel Formation

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Tooth morphology and development were studied in a series of the scincid lizard, *Chalcides viridanus*, from late embryos to 6-year-old specimens using light, scanning, and transmission electron microscopy. Tooth shape changes during ontogeny. Through successive replacements, the simple, conical shape of the embryonic tooth modifies into bicuspid in the juveniles. The dental lamina of the first teeth branches off from the oral epithelium, while it spreads from the enamel organ of the previous tooth, where a replacement tooth is initiated. The cells of the dental lamina proliferate and differentiate into the three layers of the enamel organ: the outer and inner dental epithelium (IDE) separated by the stellate reticulum. Next, the IDE cells differentiate into ameloblasts. Facing them, mesenchymal cells differentiate into odontoblasts and deposit predentin matrix. Opposite, the enamel matrix is synthesized by the ameloblasts. Mineralization of the dental matrices starts at the top of the tooth, where the ameloblasts stop to deposit the enamel matrix. Maturation of the enamel matrix progresses from top to base, while dentin mineralization proceeds centripetally. Tooth attachment is pleurodont. Replacement occurs from the lingual side, where the dentin cone is resorbed. Although tooth morphology in *C. viridanus* and in mammals is different, morphogenesis and differentiation are roughly similar. However, Tomes’ processes and enamel prisms that characterize forming enamel in mammals are absent in this lizard.

Dlx Gene Regulation of Pattern and Polarity in the Murine Jaw

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The successful diversification and radiation of vertebrates was driven in part by developmental innovations, including the acquisition of branchial-arch (BA) derived jaws. As exemplified by the Dlx gene family, large-scale gene duplications have been tied to these innovations. The correlation of an expanded gnathostome Dlx gene family with jaw development is the focus of the work presented here. Dlx genes can be placed into paralogous groups: Dlx1, 6, and 7 and Dlx2, 5, and 3. Importantly, genomically linked Dlx genes are expressed in similar patterns within the developing BA mesenchyme: Dlx1 and 2 are expressed throughout most of the proximodistal (PD) axis of the BA, while Dlx5 and 6 and Dlx3 and 7 share progressively restricted domains distally. The correlation of this PD nested pattern of mesenchymal expression with a PD BA skeletal series suggests the hypothesis that a combinatorial Dlx code sets skeletal identity within a particular gnathostome BA unit. Using a genetic approach, this code has been variously modified in mice to assess the nature of the subsequent changes in jaw development and morphology. These studies suggest that nested Dlx expression in the arches patterns their PD axes, and that the evolutionary acquisition and subsequent refinement of jaws may have been dependent on modification of Dlx expression.

Functional Plasticity of the Venom Injection System in Snakes

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We examined the behavior and morphology of the envenomation system in representatives of four snake families (Viperidae, Elapidae, Atractaspididae, Colubridae). Front-fanged families (Viperidae, Elapidae) differ mainly in maxillary relationships, as well as aspects of the dorsal constrictor muscles, with viperids showing greater palatomaxillary mobility. Preferred habitat, degree of maxillary rotation, as well as length and curvature of fangs influence the snakes’ propensity to release prey after the strike. Arboreal and long, straight-fanged viperids as well as elapids tend to hold on to prey. Prey size is also a factor, with larger prey being more frequently released by all front-fanged species. In atractaspidids, maxillary rotation is limited and envenomation occurs by a unique, unilateral, closed-mouthed, backwards stab of a fang. Rear-fanged colubrids vary in maxillary rotation capabilities, but most have relatively unmodified palatal morphology. They envenomate prey by repeated unilateral or bilateral chewing motions, aspects of which are kinematically similar to envenomation in atractaspidids and some elapids. Envenomation systems demonstrate a range of mechanics, correlated to sometimes minor modifications of a common palatomaxillary structure. The diverse basal clade Viperidae exhibits the mechanically most advanced system while incorporating aspects of non-colubroid prey capture kinematics. Only the front-fanged Elapidae reach comparable diversity, with little overlap in distribution.

Morphological Traits and Molecules Involved in the Renal Concentrating Ability of South American Hystricognath Rodents

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Arid environments represent a challenge for animals to maintain water balance. One way to conserve body water in mammals is to excrete concentrated urine. Different renal indices based on the development of the renal medulla have been used to estimate urine concentration. Nevertheless, urine concentration is also determined by the arrangement of vascular bundles and development of pelvic extensions and by the expression of some molecules such as the antidiuretic hormone receptor and water channels. In this study we assess all these renal features (including organ, tissue, and molecular levels) in hystricognath rodent species of South America due to their wide range of ecological adaptations to aridity. Stemming from phylogenetic analyses, it appears that the adaptive response of the different renal traits to osmoregulation has evolved independently. The tetraploid octodontids specialized in halophytic chenopods possess most of the renal traits associated with an increased urine-concentrating ability. The comprehensive approach used in this study and the particular cases reported here may contribute to understand the kind and degree of osmoregulatory strategies in rodents.

Vascular Immaturity Enables Plasticity of Adult Adipose Tissue

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Most organs of adult mammals are mass-stable and supported by a mature, quiescent vasculature. Adipose tissue, in contrast, can undergo large, bidirectional, rapid shifts in mass in response to metabolic need throughout the life of the animal. This rapid remodeling of adipose tissue similarly requires a vascular bed capable of extensive remodeling. We used immunostaining and confocal microscopy, as well as vascular casting and scanning electron microscopy, to examine the vasculature and pericyte distribution in epididymal fat pads of normal adult and obese mice. Based on the response of these vessels to angiogenesis inhibitors and their morphology, we propose that adipose tissue preserves the capacity to remodel into adulthood by maintaining a chronically immature vasculature.

Speculations on the Origin of Vertebrates From the Perspective of the Excretory System

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The beginning of vertebrate evolution is rather enigmatic, due to the deficit of fossils and the divergent and often highly derived anatomy of recent species that are considered to be phylogenetically "basal." Still, comparisons of the excretory systems of such species, mainly of the Agnatha, lead to considerations about vertebrate ancestry in the early literature. While many authors propose a marine origin of vertebrates, others assume vertebrates first evolved in a freshwater environment. These theories are largely based on the development of excretory structures, specifically the glomeruli (renal vascular tufts). The latter can be regarded as "water glands," a mechanism that is of obvious benefit in fresh water, while being disadvantageous in marine dwellers. Several inconsistencies remain between the "freshwater origin theory" and the limited paleontological data, which are presumably derived from marine species. Considering newer developmental, physiological, anatomical, and ecological data, however, a compromise may be sought. Accordingly, a hypothetical "protovertebrate" would be an osmoconformer, dwelling in a (portion of a) sea with a salinity approximately one-third that of today's oceans. Consequently, from the three major kidney functions—nitrogenous waste excretion, osmoregulation, and ionic exchange—only the latter would be relevant, with strong implications for structure and function. While this hypothesis is not fully established, many indications support (or at least do not contradict) such an approach.

Assembly of the Gnathostome Bodyplan: "Jawed Vertebrates" Without Jaws

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The interrelationships of the living jawed and jawless vertebrates have long been the subject of controversy. But no matter how this is resolved, the anatomical distinctiveness of the two living grades has confounded attempts to identify homology between perceived "key innovations" and representative precursor structures. Indeed, the vast inventory of characters that distinguish sharks from lampreys, or hagfishes, imply that structural homologies may not exist to be found. Perhaps this anatomical overhaul belies an explosive rush of characters, including jaws, paired fins, all skeletal systems, and much of what is considered the "vertebrate" brain, all in a single, essentially instantaneous, event. Of course, events did not proceed in this way, but we only know this from the vast array of extinct jawless vertebrate clades that belong to the same grade of organization as lampreys and hagfishes, but exhibit degrees of greater similarity and, therefore, closer relationship to living jawed vertebrates. These taxa exhibit only subsets of the full inventory of characters that diagnose the clade circumscribing living gnathostomes and, thus, they constitute the gnathostome stem-lineage. This stem-lineage reveals that, rather than acquired in concert, the characters that distinguish living jawed vertebrates were acquired consecutively over a protracted period of time, revealing, not least of all, that jaws were acquired prior to the origin of the clade.

Behavior and Kinematics of Burrowing in *Ambystoma* Salamanders

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Salamanders of the genus *Ambystoma*, the mole salamanders, spend much of their adult lives beneath the ground, yet little is known about their burrowing behavior. Previous studies of these salamanders have shown considerable interspecific variation in body shape and the ability to dig burrows. We began an examination of the ecology and evolution of structures and behaviors associated with burrowing in this genus. We observed burrowing behavior of eight species (*A. cingulatum, A. gracile, A. jeffersonianum* complex, *A. maculatum, A. opacum, A. talpoideum, A. texanum,* and *A. tigrinum*) in different substrates in laboratory chambers to determine the gross kinematics of burrowing movements and the properties of the tunnels created. We measured head, trunk, and limb dimensions for samples of adults from each species. Interspecific comparisons were examined pairwise and within a historical context by mapping traits on available phylogenetic hypotheses. Digging behavior varied interspecifically and intraspecifically with substrate type. We found differences among species in burrowing abilities and kinematics (head movements and use of forelimbs), and in the dimensions of tunnels created. Some of the behavioral and ecological differences corresponded with interspecific variation in head shape and relative forelimb size. From an evolutionary perspective, the behaviors and morphology associated with burrowing in *Ambystoma* appear to represent a combination of adaptation and phylogenetic signal.

Bite Force and Bone Strain in the Facial Skeletons of Bats

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Flight is energetically expensive and the postcranial skeletons of bats are lightly built to minimize weight and maximize aerodynamic efficiency. It follows that the skulls of bats are more likely to be optimized for structural integrity with minimum material than the skulls of other mammals. This feature, coupled with their extreme morphological diversity in cranial shape and well-documented feeding behavior and feeding performance, makes bats optimal subjects for analyzing the relationships between feeding and craniofacial form in mammals. Because analysis of in vivo bone strain is limited in most bats by their absolutely small size, we have turned to the finite element method for a comparative analysis of routine strain in the facial skeletons of Old and New World fruit bats (families Pteropodidae and Phyllostomidae). We constructed finite element models from serial micro-CT scans using a combination of commercially available software. Voluntary maximum bite force values measured at different locations along the tooth row were applied to models of Old and New World fruit bat species. Here we compare differences in both the magnitudes and distributions of resulting strain. Differences among species are interpreted in light of routine differences in feeding behavior and the primary sensory modalities that the bats use during foraging (vision in Old World fruit bats and echolocation in New World fruit bats).

In Utero and Lactational effects of TCDD and PCDF on Sprague-Dawley Rats: A Histological Analysis of the Liver

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Numerous sources of dioxin exist. Therefore, it was felt necessary to ascertain the histopathological effects of TCDD and PCDF through in utero and lactational exposure on liver of Sprague-Dawley rat pups. Exposure of pregnant Sprague-Dawley rats to one oral dose of TCDD and PCDF were conducted using both low and high concentrations (1 and 10 μg/kg for PCDF; 1 and 2.5 μg/kg for TCDD). Light microscopy was used to observe changes of the cellular structure of the liver from 5, 10, and 20 days relative to the control. The findings of this research revealed that the effects of dioxin exposure to the liver were severe. The hepatocytes were severely damaged throughout the liver from the beginning of dioxin exposure in both the PCDF and TCDD groups. The nuclei within the hepatocytes disintegrated in the majority of cells. Cell demarcations were broken up. The area around the central and portal veins and arteries demonstrated even more pronounced damage. Increasing distance from the veins and arteries revealed a decreasing effect on the hepatocytes. One of the most important functions of the liver is the degradation and excretion of hormones and toxins, which pass through the system. Therefore, any damage to this important organ will affect the aforementioned functions and eventually the health of an individual.

Sharks Exhibit All Skeletal Features Driven by the Genetic System Underlying Bone Formation

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Chondrichthyes, fish whose internal skeleton is entirely cartilaginous, evolved from an ancestral vertebrate population that possessed bone. What happened to the ability to make bone during chondrichthyan evolution? Perhaps there were alterations to the genetic system underlying bone formation in these fish. Recent studies in mice have identified a transcription factor, Runx2, which plays multiple roles during skeletal tissue formation. Using genetic techniques, mice were created that lacked the function of Runx2, and they did not develop bone anywhere in their bodies. Interestingly, these mice also had several other skeletal defects, including absence of tooth formation and lack of chondrocyte hypertrophy and mineralization. If sharks were defective in this gene or in the same genetic pathway, then their skeletons would appear similar to Runx2(-/-) mice. We tested the hypothesis that members of the chondrichthyan lineage phenocopy mice lacking functional Runx2. A histological and histochemical analysis of the entire embryonic skeleton of the swell shark, *Cephaloscyllium ventriosum,* revealed the presence of all skeletal attributes known to be under the control of Runx2 in mice. Most strikingly, we found abundant bone formation in the shark vertebrae. In addition, teeth formed and most of the cartilage displayed evidence of chondrocyte hypertrophy and mineralization. A direct characterization of the genetic system underlying bone formation in shark may reveal molecular mechanisms of vertebrate skeletal evolution.

Magnetic Resonance Elastography

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Valid estimates of the elastic properties of tissues are essential in studies of the biomechanical function of living structures, yet such data are scarce in the literature. Conventional mechanical testing methods have limited capability for evaluating semisolid tissues. The goal of this research is to develop noninvasive imaging technology for quantitatively mapping the viscoelastic properties of biological tissue in vivo. A critical component is a method for directly observing propagating acoustic waves in tissue, using an NMR sequence with synchronous motion-sensitizing gradients. This approach can image acoustic shear waves with displacement amplitudes as small as 100 nm. The wave images are processed to yield quantitative maps of viscoelastic properties. The technique, called magnetic resonance elastography (MRE), has been developed to the point where it is now being used to image the elastic properties of muscles, breast, and brain in humans. While much of the current development effort is focusing on evaluating the technology for detecting breast cancer and other malignancies, MRE appears to have broad potential as a general tool for studies of tissue biomechanics. The technique allows in vivo measurement of shear modulus, shear viscosity, and the anisotropy of these properties. In addition, the capability to directly visualize propagating mechanical transients in structures, such as the head, offers new opportunities to study the mechanisms of traumatic injury.

Biological Roles of Locomotor Modes in Basal Birds

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The identification of an unknown function involves establishing the range of mechanistically possible actions of the structure and matching their possible effects to the needs of vacant biological roles. As a result, the potential range is narrowed down to the functional effects. By this logic, the pre-enantiornithine basal birds (PEBB) must have used their wings, as well as legs, for a climbing escape and/or takeoff. With a partial exception for fragmentary *Rahonavis*, all PEBB including *Archaeopteryx, Sapeornis, Jeholoronis*, and Confuciusornithidae have both manual and pedal claws curved and suitable for climbing by all biomechanical and comparative criteria (as applied to *Archaeopteryx* and *Confuciusornis*). At the same time, all of them show consistent evidence of their inability to take off from the ground without special circumstances. The constraints on wing maneuverability, takeoff, as well as wing folding, limited the foraging of predatory PEBB to either ground or air pursuits (without landing). Only the earliest avian herbivores (*Jeholornis*) may have foraged in tree crowns. While the PEBB mastered cruising flight, the following adaptive radiation of the Enantiornithes was probably triggered by their enhanced wing maneuverability and the ensuing abilities to take off from the ground and to fold their wings completely. In addition, the capability for a ground-up takeoff placed enormous advantage on the precociality of flight.

Diversity and Evolution of Terrestrial Loading Patterns in Tetrapod Limb Bones

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A major demand placed on limb bone design is the accommodation of loads placed on the skeleton. However, among terrestrial tetrapods bone loading has been evaluated in species with only a limited variety of locomotory styles, primarily mammals and birds that walk or run using parasagittal limb posture. To evaluate evolutionary patterns in tetrapod limb bone loading and design, limb bone loading data are required from taxa with diverse phylogenetic affinities and locomotor habits. To initiate such evaluations, we performed in vivo strain recordings in nonmammalian and nonavian species with distinctive locomotor styles expected to produce limb bone loading patterns distinct from those previously observed in other taxa. Our results show distinctive patterns of terrestrial limb bone loading among previously unsampled tetrapod lineages. For example, reptiles generally show lower bone strains than other amniotes. Among reptiles, slowly moving turtles show particularly low strains, well under 1,000 microstrain for the femur and tibia even during nonstandard terrestrial locomotion (e.g., climbing). However, as in other reptiles, torsion is significant in the limb bones of turtles, suggesting that prominent torsion may represent an ancestral condition for tetrapods. Broad scale phylogenetic comparisons of limb bone loading patterns such as these will greatly facilitate evaluations of the influence of limb bone loading on the evolution of limb bone design.

Cranial Crests of Lambeosaurine Hadrosaurids: Function and Evolution of Nasal Passages

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The function and evolution of the hypertrophied nasal passages within the cranial crests of lambeosaurine dinosaurs is still actively debated. Determination of homologies between the nasal cavity of lambeosaurines and that of extant archosaurs is critical for making functional inferences about the crest. Reconstruction of the neural olfactory system and other anatomical aspects of the nasal capsule in lambeosaurines were used to test hypotheses of homology within a phylogenetic framework. New paleoneurological data derived from lambeosaurine presphenoid bone osteology and forebrain endocast morphology suggest that the olfactory bulbs were housed within the ossified braincase, not within the cranial crest cavity. Robust afferent olfactory nerve bundles joined the bulb in a diffuse manner from the rostrolateral and rostroventral directions. This, combined with the position of the choana, orientation of the nasolacrimal duct, and the inferred path of the ramus medialis nasi (V1) indicate that the nasal cavity proper was not confined to the common median crest chamber, as previously thought, but extended ventrally to the level of the palate. The nasopharyngeal duct was short. All available data suggest that the olfactory nerve did not proliferate within the crest cavities. Therefore, the hypothesis that the crest evolved to increase olfactory capability can be definitively rejected.

Spatial and Functional Modeling of Carnivore and Insectivore Molariform Teeth

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The interaction between the two main competing geometric determinants of teeth (the geometry of function and the geometry of occlusion) was investigated through the construction of 3D spatial models of several mammalian tooth forms (carnassial, insectivore premolar, zalambdodont, dilambdodont, and tribosphenic). These models aim to emulate the shape and function of mammalian teeth. The geometric principles of occlusion relating to single- and double-crested teeth are reviewed. Function was considered using engineering principles that relate tooth shape to function. Substantial similarity between the models and mammalian teeth were achieved. Differences between the two indicate the influence of tooth strength, geometric relations between upper and lower teeth (including the presence of the protocone), and wear on tooth morphology. The concept of "autocclusion" is expanded to include any morphological features that ensure proper alignment of teeth on the same tooth and other teeth in the tooth row. It is concluded that the tooth forms examined are auto-aligning and do not require additional morphological guides for correct alignment. The model of therian molars constructed by Crompton and Sita-Lumsden (1970, Nature 227:197–199) is reconstructed in 3D space to show that their hypothesis of crest geometry is erroneous and that their model is a special case for a more general class of models.

Fish Teeth Wet Lab

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Cyprinid fish (carps, minnows, and barbs) lack teeth on their jaws but have enamel-covered pharyngeal teeth on the fifth gill arch (ceratobranchial). These teeth, which are constantly being replaced in a regular sequence, bite against a horny pad on the ventral surface of the basioccipital bone. By observing the developmental stage of replacement teeth, it is possible to determine the sequence of replacement. Each participant will be given a cleared and stained cyprinid fish in glycerin or propylene glycol to dissect under a microscope with fine-pointed forceps. Microscopes, lamps, dishes, forceps, and specimens will be provided. A brief discussion and a printed handout will illustrate the features to be observed. The unstained otoliths of the inner ear and the sound transmitting Weberian apparatus formed by vertebral elements will also be observed. Demonstration specimens of several species will be available for examination.

How to Be a Giant and Not Die-Out at Trying

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There have always been vertebrate giants, at least from the mid-Paleozoic onwards. Huge vertebrates are found as living animals or fossil remains in every drifting continent and all the changing seas. This subject has often been an important aim of scientific endeavor. This symposium intends to update and summarize the many approaches that give us a hint about the problems posed by being very large, although such a definition is variable according to the group referred to, from the relatively small flying giants to the massive sauropods and cetaceans. As usually stated, all life history features (ecological, physiological, biomechanical, among many others) are influenced by body size and this is especially true at the upper extreme of the range. Here, those approaches are exposed by biologists, paleontologists, and an engineer, who try to express the diversity of giant vertebrates according to a chronological-geographical criterion, with an emphasis on their morphological characteristics, such as allometry, and particular solutions to the problems posed by being huge (and especially those found only in fossils). We also hope to discuss future directions of research, including other aspects, the proneness of extinction of huge giant vertebrates, which may become an important issue both in understanding evolution and in helping decision-makers about large-scale conservation policies.

Engineering Meets Paleontology: Finite Element Analysis of Extinct Light-Weight Vertebrates

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Explaining organismic operation is a major problem in vertebrate morphology and paleontology. Rather than yielding definite answers, biomechanical analyses, especially of extinct vertebrates, often can only constrain optional operational ranges of a given structure. Lately, finite element analysis (FEA) has become a major tool for testing biomechanical hypotheses. In a case study for extinct vertebrates, FEA was used to investigate the constructional morphology of pterosaur skulls and their biomechanical behavior during bite. Pterosaurs are characterized by a great range of skull morphologies and dentition types. Furthermore, pterosaurs possessed bone walls even thinner than those in birds. The mechanical consequences of the different skull constructions were analyzed, beginning from the level of the individual tooth to complete skulls. By reconstructing force vectors of the jaw-closing muscles, different model complexities and simplifications can be compared with each other. Based on these results, various skull constructions were analyzed by using FEA and lever mechanics. It can be demonstrated that formation of crests is negligible for the overall mechanical behavior of pterosaur skulls. The analyses allowed the assignment of different skull constructions to certain mechanically founded ecomorphotypes, characterized by special optional operational ranges. An evolutionary pathway diagram was reconstructed by determining constraints and possible transformations. Finally, the use and limitation of FEA for extinct vertebrates in general is discussed.

Surface Adhesion in Insects and Vertebrates: Functional Similarities and Convergent Design

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Adhesive pads of arthropods and vertebrates feature surprisingly similar designs. In both taxa they occur in two distinct forms: "hairy" pads in lizards, spiders, and several insect orders, and "smooth" pads in frogs and insects. The striking morphological convergence suggests that both designs are optimized solutions to common functional constraints. Several performance requirements for adhesive pads may have exerted selective pressure and shaped their design in the course of evolution: Pads must 1) generate sufficient adhesion and friction to counteract gravity in climbing animals, 2) be flexible to adapt to surfaces of varying roughness, and 3) have highly dynamic surface contact for rapid attachment and detachment during locomotion. Contact-mechanics theory predicts that adhesion can be increased by splitting the contact zone into many microscopic subunits, which provides a functional explanation for "hairy" design. Only lizards and spiders with minute adhesive hairs use "dry adhesion." In the larger insect adhesive setae, and in all "smooth" systems, liquids are involved that help to maximize contact area. However, liquid films can lubricate and strongly reduce friction. The considerable friction forces of frogs and insects can only be explained by direct pad-surface interaction. To achieve intimate contact, secretion must drain away, which is facilitated by the convergent hexagonal structures and microfolds on the surface of frog and insect pads.

Evolution in a Hominin Lineage: The Appearance of the "Classic" Neanderthal Morphology

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The search for hominin origins has produced a wealth of material from Africa, Eastern Asia, Australasia, and Europe. Europe preserves the largest sample of a distinct hominin species, the Neanderthals and their antecedents, because of historical factors, remarkable sites, and the preservation that results from potential burials. This ongoing investigation combines two notions into one continuous and comprehensive concept. There appears to have been a gradual shift toward the "classic" Neanderthal morphology in European *Homo heidelbergensis* resulting in the emergence of a novel species *Homo neanderthalensis*. This assertion is based on purported Neanderthal apomorphies and their distribution in the European paleoanthropological population. Through the union of G. Phillip Rightmire's hypothesis of *Homo heidelbergensis* as a viable species and Jean-Jacques Hublin's "Accretion Model" of Neanderthal evolution, the prehistory of Europe can be elucidated. The "Accretion Model" is of importance because it establishes a four-stage framework for defining the evolution of Neanderthal morphological features, while Rightmire's idea of a distinct Middle Pleistocene hominin provides a precursor for the Neanderthals. Utilizing the European sample from the Middle Pleistocene until the disappearance of Neanderthals 27,000 years ago, the accumulation of Neanderthal features can be witnessed. This suggests that a hypothesis for the evolution of Neanderthals lies within a composite of both Hublin's and Rightmire's ideas.

Joint Kinematics, EMG, and Inverse Dynamics of Quadrupedal Locomotion

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A comparative study of fore- and hindlimb kinematics of 14 mammalian species has revealed basic principles in the locomotion of therians. Kinematics were surprisingly independent of systematic position, specific anatomy, and even natural habitat in small mammals. Kinematics of the forelimbs were also independent of gaits or speed. Basic parameters of locomotion up to mid-sized mammals (e.g., goats) are: a three-segmented limb with zigzag configuration, pivots at the same height in fore- and hindlimbs, propulsion by the action of proximal segments, touch down position below the eyes (except in primates), and two segments operating in matched motion. Fundamental changes occur in hindlimb kinematics with the change from symmetrical to in-phase gaits. Advantages of in-phase gaits preferably used by small therians are discussed. Torque patterns are completely described for the forelimb (including the scapula!). Uniform kinematics result in very similar torque patterns, especially of the forelimbs. As the limbs are transmitting the ground reaction forces to the trunk, the displacement of the center of mass relative to the foot's anchor point on the ground is of interest. An extensive topographical EMG study shows a totally uniform pattern of successive activation of the long head of the triceps brachii muscle. Although called an extensor, the triceps brachii is completely silent during elbow extension, but only acts against load caused by gravity.

Evolution of Swimming Mechanics in Cetaceans

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Cetaceans function in the aquatic environment, which is denser and more viscous than the terrestrial environment in which their ancestors arose. Transition from terrestrial to semiaquatic and then fully aquatic species required changes in body design and propulsive mechanisms. These changes were correlated with selection for rapid swimming, maneuverability, and diving. Examination of modern species within a terrestrial–aquatic continuum as surrogates of ancestral transitional states has aided in the identification of potential selection pressures and mechanical constraints, which directed the evolution of cetaceans. As ancestral cetaceans became more aquatic, there would have been a shift from use of nonwettable fur to blubber, which provided insulation, streamlining, and better buoyancy control. Semiaquatic ancestors would have propelled themselves by use of the paired appendages in a low-efficiency, drag-based paddling mode. With fewer amphibious habits, appendicular paddling was replaced with axial propulsion by undulation of the tail. The elongate tail of ancestral cetaceans could be undulated to permit continuous thrust generation. Observation of modern species indicates that the shift in swimming mode would have occurred through an intermediate stage where feet, body, and tail were all involved in swimming motions similar to terrestrial motor patterns. Ultimately, cetaceans have reduced or modified the appendages to reduce drag and shifted to lift-based hydrofoil propulsion using the caudal flukes for increased propulsive performance and efficiency.

Ontogenetic Changes in the Cranial Kinematics of a Larval Pleuronectiform Fish, *Paralichthys lethostigma*

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Cranial kinematics of premetamorphic and metamorphic *Paralichthys lethostigma* larvae were recorded using high-speed digital video to determine the consequences of increasing morphological complexity, morphological asymmetry, and behavior for performance. Both paired (left and right sides of the head) and unpaired kinematic variables reflecting excursions, angles, and timings of cranial structures were recorded for behaviors associated with feeding and respiration. While recordings of aquatic prey capture were limited, gulping, respiration, and expulsion or coughing behaviors were successfully filmed. Primarily based on measurements of lower jaw depression, principal component analysis grouped feeding attempts with gulping and respiration with expulsion. Additional parametric differences in kinematics between premetamorphic and metamorphic larvae appeared to be primarily due to differences in size. Bilateral kinematics of metamorphic larvae were not significantly different between left and right sides of the head ($P > 0.234$, $\alpha = 0.05$). However, angular measurements of premaxillary protrusion and lower jaw depression were not completely symmetrical. In *P. lethostigma*, ontogenetic changes in lower jaw depression and elevation corresponded with changes in the contribution of hyoid and opercular movements. Morphological asymmetry between left and right sides of the head did not produce significant lateral jaw protrusion, as has been observed for some pleuronectiform fishes. Finally, kinematic differences between behaviors demonstrated greater functional complexity than previous studies of larval fish have suggested.

Craniofacial Development: Facing the Future

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The head is probably the most complex part of the body and its development is dependent on tissue interactions between the ectoderm, ectomesenchyme, endoderm, and mesoderm. Until recently, there was a relative paucity of, and contradictory, data about the tissue and molecular interactions that control the development of the head. However, classical embryological studies, the generation of mouse loss-of-function mutants, together with the identification of gene mutations that cause human craniofacial syndromes has now given us significant new insight into the mechanisms of head development. We know that development of each region of the head is dependent on a different set of tissue interactions reflecting the evolution of the distinct regions of the head. In addition, we now know some of the genes involved in these processes and, in some cases, the molecular hierarchy of signaling interactions. This article will give an overview of craniofacial development, discussing the current state of this field of research, focusing on recent advances and highlighting future challenges.

Evolution and Developmental Conservation of Vertebrate Dentition

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Studies investigating the genetic regulation of odontogenesis have principally used the murine model. The assumption that all vertebrate dentitions are homologous has recently been challenged for taxa at the base of jawed vertebrates. Therefore, the genetic mechanisms that pattern and regulate odontogenesis in other vertebrates, in particular fish, now need to be investigated. A number of genes identified as homologous to the murine genetic cascade responsible for tooth initiation have been isolated from the rainbow trout (*Oncorhynchus mykiss*) using RT-PCR. These comparative studies document the expression of key genetic regulators during the patterning and development of vertebrate dentition. The results suggest a level of developmental conservation between trout and mouse in initiation of dentition. In addition, in the trout model we can show that these genes are also involved in the mechanism for tooth replacement, and we can compare expression patterns for teeth located in both oral and pharyngeal regions. There is evidence for subfunctionalization of a number of genes involved in odontogenesis in fish, presumably as a result of the whole genome duplication believed to have occurred independently in the teleost lineage. Although genetic subfunctions are present in *O. mykiss*, the majority of key odontogenic regulator genes are conserved in comparable oral domains to the murine model. These data aim to test problems of homology and evolutionary significance.

Highly Specialized Larynx of the Mongolian Gazelle *(Procapra gutturosa* Pallas, 1777): Classical Morphological Methods and Computed Tomography Combined

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The entire heads and necks of two wild adult male Mongolian gazelles were dissected macroscopically and analyzed by CT with special reference to their evolutionarily enlarged larynges. CT scanning was done by means of a GE Lightspeed 4-Slice Spiral CT. Processing of data was carried out at a work station applying the General Electric's volume rendering software VolumeViewer. The half-kilogram larynx of the male Mongolian gazelle requires improved stabilization by adjacent musculature to diminish lateral swinging movements during locomotion. Its vocal tract has evolved several unique features, e.g., an unpaired palatinal pharyngeal pouch, a paired tympanic pharyngeal pouch, an exceptionally large epiglottis, a V-shaped cuneiform process, a paired two-chambered lateral laryngeal ventricle, and a massive vocal fold supported by a cymbal-like fibroelastic pad. The hyoid apparatus connects to the rostral horn of the thyroid cartilage via a thin and elongated rod-like cartilaginous element, indicating a high mobility of the synovial thyrohyoid articulation. The difference between vocal tract lengths obtained by anatomical dissection and by use of CT images also suggests a considerable laryngeal mobility. The achieved results were substantially improved by using both classical macroscopic dissection and computed 3D-mode reconstructions. Some characters would have been inadequately understood if only one method had been applied.

Sexual Dimorphism of the Larynx of the Mongolian Gazelle (*Procapra gutturosa* Pallas, 1777, Mammalia, Artiodactyla, Bovidae)

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The polygynous Mongolian gazelle is characterized by a pronounced sexual dimorphism of the larynx. Dimorphism with regard to the length of the entire larynx and of the thyroid cartilage is about 2:1, whereas the difference of mean body mass is about 1.3:1 between males and females. Unexpectedly, and in contrast to other bovids, the larynx of the male *Procapra gutturosa* has a paired lateral laryngeal ventricle. The "neck" of this two-chambered ventricle is embraced and kept in position by a V-shaped cuneiform process. The vocal process of the male arytenoid cartilage is relatively shorter than that of the female. The male thyroarytenoid muscle is separated into a rostral ventricularis and a caudal vocalis portion, whereas the female's, as in other bovids, is almost uniform. The bow-like vocal fold in the male is supported by a cymbal-like fibroelastic pad which is absent in the female. The peculiar shape, size, and tough consistency of the male vocal folds may, as in roaring felids, assist in producing high amplitude and low frequency vocalizations. The evolution of the enlarged larynx of the male *P. gutturosa* may have been favored by both intrasexual selection (more effective repelling of rival males) and by intersexual selection (females preferring "large-goitred and deep-voiced" males).

Highly Specialized Larynx of the Mongolian Gazelle (*Procapra gutturosa* Pallas, 1777): Classical Morphological Methods and Computed Tomography Combined

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The larynx of the male Mongolian gazelle (or Dzeren) is evolutionarily specialized and enlarged to an extent that it bulges the ventral neck region. In contrast, the size and structure of the female larynx corresponds to that of other bovids of comparable body size (Kleinschmidt, 1961, Stuttgarter Beitr Naturk 79:1–24). The half-kilogram larynx of the male requires improved muscular stabilization to diminish lateral swinging movements during locomotion. The hyoid apparatus connects to the horn of the thyroid cartilage via a thin and elongated cartilaginous element, indicating a high mobility of the synovial thyrohyoid articulation. The vocal tract of the male Mongolian gazelle has evolved several unique features, e.g., a palatinal pharyngeal pouch rostral to the epiglottis. Understanding of morphological structures was substantially improved by using both classical macroscopic dissection and computed 3D-mode reconstructions. The evolution of the pronounced sexual dimorphism of the larynx of the Mongolian gazelle has been related to its mating system and, ultimately, to sexual selection (Frey and Riede, 2003, Zool Anz 242:33–62).

Marsupial Placentation

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Marsupials first attracted scientific interest by the presence of a pouch in which the young are suckled, leading to the belief that the young would grow out of the teat instead of being born through the vagina. This might have contributed to the still-widespread view of marsupials as "nonplacental" mammals. However, there is now overwhelming evidence that the yolk-sac placenta of marsupials, which is the definitive placenta, serves in physiological exchange and synthesis in all marsupials, and did so in the marsupial stem species. Histotrophic nourishment during early pregnancy is replaced by hemotrophic nourishment after shell coat rupture in most marsupials, as it was in the marsupial stem species. Macropodids derived from that have continued histotrophic nourishment up to birth. The distribution of placental invasion among marsupials is inconsistent. However, factors known to be involved in placental invasion are present in marsupial yolk sac placentas. A uterine recognition of early pregnancy is restricted to macropodids and probably did not occur in the marsupial stem species. An endocrine role of the yolk sac placenta in the initiation of birth, as found for macropodids, has not been investigated in other marsupials. Although the yolk sac formed the definitive placenta in the marsupial stem species, it is possible that there was an allantochorion with an exchange or waste release function.

Ecomorphological Analysis of Small-Bodied Carnivorans

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Neontologists and paleontologists have done many studies distinguishing larger-bodied carnivorans according to their masticatory morphologies and related feeding ecologies. However, much less attention has been paid to smaller carnivorans, largely because of their supposedly more generalized diets and poorly studied habits. Modern members of the carnivoran families, Herpestidae, Viverridae, Procyonidae, and Mustelidae, are generally small-bodied (<25 kg) but display a range of dental morphologies and corresponding diets. By limiting dietary classification to broad groups, including those that are more insectivorous, more carnivorous, more herbivorous, and hard-object feeders, some trends in dietary/dental correlations can be found. Multivariate analyses, including principal components analysis and discriminant function analysis, performed on functionally meaningful ratios, help discern those variables that are important in the delineation of the dentition of these groups. Ratios such as relative grinding area, premolar size and shape, and carnassial blade length consistently distinguish the predefined dietary groups from each other. Although a phylogenetic effect was expected to group more closely related taxa in these analyses, results show that morphological groupings are spread across taxonomic classification, and show that these ecomorphological studies can be used for forms assumed to be intractable due to there generalized ecologies. These studies could be used to infer the ecologies of early Tertiary mammalian carnivores which are also small-bodied, and represent the earliest representatives of modern taxa.

Skeletal System of Neonatal Caribbean Manatee (*Trichechus manatus latirostris*) Imaged by Computed Tomography

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The Caribbean manatee is an endangered species. Only a few publications about basic anatomy exist in the literature. In an effort to correct the lack of data, we studied the complete osteology of two frozen bodies of stillborn manatees using computed tomography (CT). With the resulting datasets, 3D volume rendering models were created during postprocessing. The special anatomical features unique in the skeleton system of manatees were imaged. Aspects like the dense and relatively heavy skeleton were analyzed. The special arched ribs allow the lungs to be positioned much higher along the vertebral column than is found in most other mammals. The lifelong, continually horizontal replacement of teeth is otherwise only known in elephant species. During evolution, the hindlimbs regressed. The pectoral limbs were remodeled to flexible and paddle-shaped flippers. CT scans allow visualization of the whole skeleton system in situ, not influenced by postmortem preparations, with possible resulting artifacts. The radiological process is a reliable technique and allows a nondestructive approach for anatomical investigations. The 3D reconstructions gave a viable image of the complex structures of single bones and the whole skeleton in situ.

Imaging of Whale Fetuses: Computed Tomography of Preserved Specimens of Different Cetacean Species

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The collection of Willy Kuekenthal (1861–1922) is a very famous historical compilation of cetacean fetuses at the Museum of Natural History, Berlin. We had the opportunity to examine fetal specimens of several species of Odontoceti and Mysticeti, a representative selection out of the nearly 80 living species. The Cetacea are one of the most distinctive and highly specialized orders of mammals. We were able to visualize in situ some specialized adaptations for their aquatic life, like the highly compressed neck vertebrae, the inner ear with its heavily ossified structures, the skeleton of the flipper-shaped forelimbs, the greatly elongated anterior skull bones, and the nostrils, located on top of the head, forming the blowhole. For the first time, we were able to visualize the upper respiratory tract within the head, applying a special CT window and performing a "virtual endoscopy" along it. In some specimens of the baleen whales, the vestiges of the pelvis and the fetal teeth, lacking completely in the adult, could be imaged. CT has proved to be an excellent technique for imaging various structures and organs of the fetuses in situ nondestructively.

Evolution of Developmental Mechanisms of the Vertebrate Ear

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Ear evolution shows extreme conservation in the molecular governance of mechanoelectric transducer cell development across phyla (Wang et al., 2002), which contrasts with genes exclusively expressed in the vertebrate ear to guide development of vertebrate specific acellular covering structures of the ear (El-Amraoui et al., 2001). Between these two extremes are the genes for ear morphogenesis, mostly represented by developmental modules, coopted into the ear, and specifically modified to suit specific aspects of ear development. Keeping the mechanotransducer sensory element constant allows evolution to optimize aspects of ear morphogenesis to maximize acquisition of specific mechanical signals. Evolution of the vertebrate ear can thus be best understood as an iterative developmental transformation towards optimized signal transmission at conserved mechanoelectric transducer elements. Such aspects of ear evolution are particularly clear when comparing the morphocline of hagfish, lamprey, and jawed vertebrate ears. Hagfish have a single canal with two epithelia. Lampreys have evolved a two-canal system, and jawed vertebrates have evolved a three-canal system that allows them to extract selectively angular stimuli in three orthogonal planes. This evolutionary change is not a matter of optimizing the mechanoelectric transducer, but rather of optimizing morphogenesis of the ear. Molecular data on canal development show a diversity in morphogenetically important transcription factors that is equivalent to that of ear morphogenesis.

Nonmasticatory Functional Complexes and Their Effect on the Morphology of the Insectivoran Glenoid

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The mammalian glenoid displays a wide range of morphologies. It varies from the tight transverse hinge of some carnivorans, through the gently concave surface found in humans, to the longitudinal slot of hystricomorph rodents. These morphological variations are normally explained in terms of allowing particular styles of mastication to be performed. It is nevertheless probable that the position and form of the temporo-mandibular joint are influenced by other aspects of cranial morphology. Geometric morphometrics were used to examine the relationship of the braincase and pharyngeal region to the glenoid in insectivorans. It was found that: 1) The position of the glenoid moves posteromedially as basicranial flexure decreases (as indicated by the foramen magnum becoming more posteriorly directed and by pharyngeal narrowing), with this rotation seeming to conserve the length of the vector of the lateral pterygoid muscle; 2) The position of the lateral margin of the glenoid changes with braincase width and basicranial flexure; and 3) The shape of the glenoid varies with the anteroposterior length of the auditory region.

Conservation of Body Plans Through Internal Selection

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Body plans are those combinations of morphological characters of a taxon that have been unusually conserved during evolution. Yet, 1) even the highly conserved characters of body plans virtually always display minor intraspecific variation, and 2) new mutants with major effect on those characters are common. This suggests that evolutionary conservation of body plans is usually caused by strong stabilizing selection. Studies on fetal deaths in humans indeed show extremely strong ongoing internal selection against variations of body plan characters. The selection against variation appears to be caused by highly deleterious pleiotropic effects. Examples are the conservation of the number of cervical vertebrae and digits. Many conserved characters of the vertebrate (and insect) body plan, such as the number of eyes, limbs, rhombomeres, and kidneys, are determined during the early organogenesis stage. This is a stage of maximum similarity in vertebrates, and, in particular, amniotes. The cause for the relatively high degree of conservation appears to be that mutations with an effect during this stage almost invariably lead to deleterious pleiotropic effects in other parts of the body. I discuss the possibility that the cause for the relatively high conservation of this ontogenetic stage is also causally implicated in the conservation of adult traits of the body plan determined during this stage. The data show that applications of the concepts of evolutionary constraint and pleiotropy provide a novel and unexpected insight into medical risks associated with seemingly harmless anatomical variations. Finally, I discuss factors that can lead to the occasional breaking of long-term constraints on body plans and, thus, to morphological novelties.

Recent Developments in Phylogenetically Based Statistical Methods

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Increased phylogenetic information (often based on analyses of DNA sequences) has revolutionized comparative biology. Phylogenies are used to guide the choice of species for comparisons and to identify traits that are homologous versus analogous. They are also used to perform "phylogenetically correct" statistical analyses that attempt to account for the fact that related species tend to resemble each other (exhibit "phylogenetic signal"). The first fully phylogenetic method for continuous-valued traits was "independent contrasts" (Felsenstein, 1985), based on a simple Brownian motion model of character evolution. This algorithm is now viewed as a special case of (phylogenetic) generalized least-squares approaches (Grafen, 1989; Martins and Hansen, 1997; Garland and Ives, 2000; Rohlf, 2001). Recent methods to test for and quantify phylogenetic signal show that it is ubiquitous, but stronger in some types of traits (e.g., body size, other morphometric traits) than in others (especially behavior). All of the foregoing approaches may employ Monte Carlo simulations along specified phylogenies (Martins and Garland, 1991; Garland et al., 1993) or randomization tests for hypothesis testing. Current work aims to develop more realistic models of character evolution, sometimes by transformation of branch lengths, to avoid overcorrection for possible phylogenetic effects, and to incorporate within-species variation (e.g., measurement error) into phylogenetic comparative analyses. (Methods for categorical traits [e.g., see Ridley, Maddison, Grafen, Pagel] will not be covered.)

Small Mammal Burrowing: Multiple Evolutionary Pathways to Similar Results

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It is currently known that mammals underwent a long period of secretive life before their explosive radiation after the KT crisis. The boundary between secretive habits and true subterranean life is subtle for small-sized animals. However, the morphological features of fossils as well as extant species reveal that complete subterranean life appeared among several lines of the mammalian clade. A clear distinction between digging capability during foraging and life in the soil can be established only through field data, followed by experimental analysis of the function of the organs involved. Morphological homoplasy within and between rodents and former "insectivores" reveals that multiple pathways lead to similar levels of ecological efficiency.

Functions of Fish Myosepta: A Derived Design of Myosepta in Two Carangiform Swimmers

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Carangiform swimmers have been shown to differ from subcarangiform and anguilliform swimmers in several respects, such as body shape, undulatory wavelength, lateral displacement of the body, muscle activation patterns, and muscle distribution along the body. However, it remains unknown whether the musculotendinous system of carangiform swimmers differs from that of noncarangiform swimmers. Here, we investigate the myoseptal and muscular system of two carangiform swimmers (the Mackerel, *Scomber scombrus*, and the Atlantic Horse Mackerel, *Trachurus trachurus*) and compare their morphology to that of noncarangiform swimmers. Three conspicuous morphological specializations are identified in the two carangiform swimmers: 1) mediolateral tendons (the epineural and epipleural of other fishes) are absent in the posterior body half; 2) longitudinal tendons (the myorhabdoid and lateral tendons) are elongated (up to 20% of body length compared to a range of 5–9% of body length in other fishes); and 3) red muscles are associated with the elongated lateral tendons. Integration of these morphological results and experimental data may explain some of the unique characteristics of carangiform swimming and lead to an extended functional understanding of this swimming mode.

Targeted Growth and the Regulation of Mammalian Body Size

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Targeted growth, also known as “catch-up growth,” has deep historical roots (Tanner, 1986). Traditionally, targeted growth was the idea that growth is a self-stabilizing trajectory with a genetically or endocrine-determined endpoint. If interrupted by an environmental insult that is eventually relieved, growth will reach that endpoint. Our data measuring the impact of protein malnutrition on organ, skeletal, and body growth in an animal model both support and falsify this hypothesis. Individuals experiencing protein malnutrition, either with or without rehabilitation, can reach control adult body weight. However, adult weight of some visceral organs and linear dimensions of bones in the malnourished animals were absolutely or relatively larger than controls, suggesting that the concept of a “norm” may be inaccurate. Finally, there are some malnutrition insults from which animals do not recover: a second generation raised on the same diet never reached adult size. These results suggest that the concept of targeted growth as originally formulated is less than useful for understanding variation in size. However, an alternative hypothesis, using the concept of a multifactorial basis of variation, including environmental, genetic, and developmental factors, is consistent with our data.

Ontogeny of Escape Performance in Teleost Fishes

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Unlike most terrestrial vertebrates, teleost fishes typically first encounter the environment in a larval form. The larval form is morphologically distinct from the adult form, and major anatomical structures are incompletely formed. Thus, during posthatching development, larvae undergo a series of dramatic morphological changes until they reach a near-adult morphology and are considered juveniles. Previous research has shown that larval fish are able to perform an escape response (typically a C-start), which is used to evade predators. Interestingly, escape response performance improves during early posthatch development: as larvae grow they become faster (i.e., duration of behavior decreases, maximum velocity in total lengths/second increases). However, improvement ceases when they become juveniles. Here we examine the functional basis of the escape behavior to test the general hypothesis that developmental changes to the musculoskeletal system allow improved performance. To do this, we combine high-speed video studies of escape response performance with morphological studies of axial muscle and vertebral column development. We suggest that changes to the musculoskeletal system during the larval period produce increased axial stiffness, which in turn allows the production of a more effective escape response. This implies that any reproductive strategy where progeny enter the environment in an advanced stage of development will result in an improved ability to evade predators.

Working Hypothesis for the Origin of the Turtle Shell

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We present a working hypothesis to model the development of the turtle shell. First, the carapacial ridge (CR) induces the rib primordia to migrate dorsolaterally into the dermis. Second, the ribs and carapacial ridge interact through Fgf signaling to extend the CR to form the boundaries of the shell. Third, when the ribs undergo endochondral ossification, the Ihh and BMP molecules induce ossification of the surrounding dermal cells. These cells transmit the BMP signal as they ossify. Fourth, neural crest cells migrate late and form the plastron and nuchal bones. We believe that the turtle trunk neural crest cells, in migrating so late, have changed gene expression patterns and may be able to form skeletal elements. We present preliminary evidence for each component of this model.

Perching and Ground Dwelling Behavior in Extinct Bird Relatives: Inferences Made From Functional Morphology of Extant Bird Claws

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The hypothesis that *Archaeopteryx* was arboreal has previously been supported by comparative studies of the curvature of the keratinous claw sheath in modern birds. These studies have shown that greater claw curvatures are correlated with increased arboreal/climbing habits. A primary goal of this study was to explore whether claw morphology is subject to phylogenetic constraint or scaling effects, which could weaken such functional inferences made for extinct animals. Data were collected from at least 80–90% of the genera from Cuculiformes (cuckoos), Columbiformes (pigeons and doves), and a single family Picidae (woodpeckers). Additional comparative data were collected from a wide variety of ground-dwelling species from taxa such as Struthiornithiformes, Charadriiformes, Ciconiiformes, Galliformes, and Gruiformes. Claw radius of curvature was found to have little correlation with function and was found to have a strong scaling relationship with body mass. However, no significant scaling relationship was found for claw angle with respect to body mass; rather, this characteristic appears to be indicative of function. The arboreal/terrestrial habitat preferences of extinct bird relatives such as the flightless *Sinosauropteryx, Caudipteryx, Sinornithosaurus, Protoarchaeopteryx,* and the flight-capable genera Confuscisornis, Sinornis, and Changchengornis were then interpreted by comparing their claw angles with those of modern birds.

To Bleed or Not to Bleed: Functional Significance of Nasal Foramina in Head-Lift Diggers

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Modern head-lift digging rodents, such as the mole rat *Spalax* (Ukrainian mole rat), show a roughly linear arrangement of foramina along the edges of the nasal bones that may relate to protective nasal “armor.” In head-lift digging, the head and rostrum function like a spade, transporting or tamping loosened soil. The anterior portion of the rostrum, which is susceptible to injury from chafing against the substrate, is covered with an adaptive “shield” of thickened skin or keratin. Similar nasal armor occurs in chrysochlorids (golden moles), notoryctids (marsupial “moles”), and amphisbaenid reptiles, all of which burrow with the head. Foramina in *Spalax* and other rodents appear to outline the shape of the nasal shield, and may increase its blood supply and innervation. Alternatively, the foramina supply well-developed vibrissae, as in pinniped mammals. However, the absence of similarly positioned foramina in nonhead-lift diggers, such as the pocket gopher *Geomys*, and their occurrence in amphisbaenids lacking vibrissae indicate a separate association. The foramina may provide osteological evidence with which to identify head-lift diggers among extinct mammals. Extinct, fossorially adapted multituberculates and mylagaulid rodents have linear or clustered nasal foramina, suggesting convergent nasal armor and digging strategy. Paired bosses on the nasals of late-appearing mylagaulids may have evolved from calluses on the rostrum for head-lift digging.

Meckel’s Anatomical Collection: Imaging Techniques and Ancient DNA Analysis in Diagnosing Human and Animal Anomalous Collection Specimens

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One of the finest European private anatomical collections in the early 19th century was the Meckel Collection founded by Johann Friedrich Meckel the Elder (1724–1774), his son Philipp Meckel (1755–1803), and his grandson Johann Friedrich Meckel the Younger (1781–1833). The collection increased substantially during Meckel the Younger's activity as professor of anatomy at Halle University. Most of the specimens of the Meckel Collection were described in his comprehensive textbooks on human, pathologic, and comparative anatomy. These specimens are still an integral part of the Anatomical Collections of the Department of Anatomy and Cell Biology in Halle. During recent years we recataloged the original normal and anomalous samples used by Meckel the Younger as the bases for his research work. The reexamination and diagnosing of the specimens provided a unique opportunity to present the highlights of the Meckel Collection with up-to-date information on teratology. The collection contains many alcohol preparations that represent rare samples of human and animal congenital malformations. In order to diagnose these rare anomalies we developed a research project (FKZ-5/24) in which ancient DNA analysis and imaging techniques were employed. The history of the Meckel Collection as well as the value of the investigative methods in diagnosing syndromes of the collections' specimens are discussed.

Morphological Integration in the Mammalian Skull: The Influences of Ontogeny, Phylogeny, and Function

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Recent genetic and developmental studies have produced compelling hypotheses of the importance of trait correlations to morphological evolution. However, these hypotheses have never been tested with a broad, comparative dataset or with fossil material. This study uses the analysis of *morphological integration* to examine discrete sets of highly correlated cranial traits and their relationship to factors influencing mammalian skull evolution. Here, I present detailed analyses of patterns of cranial trait correlations across a broad range of taxa within the terrestrial Carnivora, Primates, and Marsupialia, addressing the relationship of these patterns to phylogeny, ontogeny, and function. A 3D digitizer was used to record 60 homologous skull landmarks from ~20 specimens of ~100 extant species and 15–20 fossil species. While previous studies generally exclude fossil taxa due to small sample sizes, several extinct carnivoran taxa (e.g., *Mesocyon, Dinictis,* and *Thalassictis*) have sufficient intact specimens for this study. The inclusion of fossil taxa expands the phylogenetic breadth and permits testing of temporal trends in skull modularity and the influence of increased brain size within lineages. *Matrix correlation analysis* and *random skewers analysis* support a loose relationship between phylogeny and patterns of trait correlation, although these patterns are not generally conserved across mammals. Brain size, convergence of diet, and cranial development are explored as alternative or additional influences on cranial integration.

Neural Crest Derivation of the Osteocranium in Recent Anurans

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The vertebrate skull is a composite organ derived from both the mesoderm and the cranial neural crest (CNC). Investigations in other vertebrate models (namely, chicken and mouse) have yielded detailed "fate maps" of the relative contributions of these two embryonic cell types to the adult skull. These fate maps have revealed some distinct differences. One example is the developmental origin of the skull vault. This region of dermal bones (comprised mainly of the frontal and parietal bones) overlies the majority of the central nervous system in vertebrates. In mice, the frontal bone is derived from the CNC, while the parietal is derived from the mesoderm. In avian models, both the frontal and parietal are derived from the CNC. A fate map of the CNC contributions to the skull in anurans could shed light on these differences. Using a chimeric grafting technique along with an indelible fluorescent marker, we made progress towards such a fate map of the osteogenic cranial neural crest in *Xenopus laevis*. We hope that this fate map will inform our understanding of the changes in cranial form that accompanied the evolutionary transition from "lower" to "higher" vertebrates.

Trials and Tribulations in Creating Finite Element Models of Vertebrate Morphology from CT Scans

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In the engineering world, finite element analysis is widely used to predict the behavior of engineered products or manufacturing processes, and the process of creating finite element models is relatively straightforward. Engineers use sophisticated computer-aided design tools to construct 3D solid or surface model representations of the product geometry. This model is then discretized into a contiguous set of finite elements, called a mesh, by software mesh generators with little or no human intervention. Often, these models are parameterized so that engineers can easily vary the values of design parameters, conduct finite element analysis, and find the optimal design solution. Unfortunately, nothing could be further from the truth in the biological world, and in vertebrate morphology specifically. The problem stems from complex and highly variable, but unparametrized, 3D-geometry of biological systems which must be digitally reconstructed from 2D CT-scan data. In this article we examine the process of transforming 2D CT-scan data into valid 3D finite element models and offer our insights into the best tools, techniques, and modeling guidelines for accomplishing this tedious task as efficiently as possible. Finally, we offer a vision as to what capabilities are needed in tools of the future that would address many of the current problems faced in the digital reconstruction process.

Evolutionary Relationships between Chordates, Hemichordates, and Echinoderms: New Implications From the Retro-Engineering Approach

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Different evolutionary relationships among chordates, hemichordates, and echinoderms have been inferred in the past, depending on whether morphological, developmental, molecular, or genetic approaches were used. More recent investigations, based on analyses of 18S rDNA, proposed that the deuterostomes comprise only the chordates, hemichordates, and echinoderms, and that the tentaculates, pogonophorans, chaetognaths, etc., belong to the Protostomia, which were reorganized into the Lophotrochozoa and Ecdysozoa. Furthermore, the chordates were placed at the base of the deuterostomes, while the hemichordates and echinoderms were considered derived. However, none of these previous approaches (including the 18S rDNA analyses) provide nomological deductive or historical narrative explanations for the evolutionary transitions between the groups. In contrast, the method of retro-engineering, which conceptualizes organisms as structural–functional entities, provides an evolutionary scenario in which early chordates evolved from a metameric ancestor by evolving a notochord within the tissues of a dorsal mesentery soon after the formation of the neural crest. This hypothetical early chordate gave rise to three main evolutionary lineages, the Acrania, Craniota, and Ambulacraria. From the Ambulacraria, first the enteropneusts, then the pterobranchs, and finally the echinoderms evolved. The latter differentiated into three main evolutionary pathways comprising the direct pentameric echinoderms, the indirect pentameric echinoderms, and the asymmetric echinoderms.

Retro-Engineering: A Morphological–Analytical Method for Inferring Function and Evolution of Extinct Organisms

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The technological approach of retro-engineering is particularly powerful for the biomechanical analysis of structurally complex apparatus of extant organisms. An initial analytical dissection phase identifies and describes the structural elements of an apparatus and analyzes their mechanical roles and their relationships between themselves, with the organism, and with the environment. A subsequent integrative phase uses these data to create a mechanically coherent model of the apparatus based on the mechanical and hydraulic properties of the various tissues. Such a model describes the functional, mechanical, and constructional roles of each structural element and, therefore, can predict the consequences of a modification or absence of particular elements for the entire apparatus. By comparing these predictions to the configuration of other organisms, the functional properties of their apparatus can be inferred by analogy and macroevolutionary transformations can be reconstructed. Two illustrative case studies are presented: 1) A review of the diversification of chordates within the basic deuterostome bauplan into the Craniota, Acrania, and Ambulacraria shows how fossil organisms and missing evolutionary links can be reconstructed. 2) The retro-engineering of the central feeding, respiratory, and circulatory apparatus of the head of the shark (*Squalus acanthias*) shows how it prompted a reinterpretation of the functional and evolutionary significance of the scapulocoracoid cartilage, jaw apparatus, and rectus cervicis muscle.

Evolutionary and Ontogenetic Transformations in Anuran Tadpoles

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Recent cladistic analyses (Haas, 2003) proposed a basal position of the Ascaphidae in the system of the Anura and positioned the Pipidae more basal (Púgener et al.) than in previous analyses. The question of how to reconstruct the character composition of the larval form for the most recent common ancestor of these families is not trivial, because tadpoles from both families are highly specialized, suctorial, and suspension-feeding larvae, respectively. They possess a mosaic of plesiomorphic and apomorphic features. Yet, from phylogenetic considerations and ontogenetic transformations, predictions can be made about the character state composition of the ancestor and about possible evolutionary scenarios concerning morphological transformations. Transformation processes of the jaw and jaw musculature in particular show that the increasing uncoupling of larval and postmetamorphic structure, recruiting from differently programmed cell populations, was essential for tadpole evolution and allowed for amazing modifications of the original body plan, often convergently in several groups. Certain aspects of metamorphosis may inspire ideas of gradual evolutionary changes, which necessarily require maintenance of integrity of structural parts and function during change.

Inner Ear of *Tachypteron franzeni*, the Earliest Emballonurid Bat From the Middle Eocene of Messel

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The cochlea of *Tachypteron franzeni*, a recently described new Eocene emballonurid species bat from Grube Messel, near Darmstadt (Germany), was studied. Morphological details are extraordinarily well-preserved. The external ear, the relative size of the inner ear, and internal features of the cochlea also appear identical with extant Taphozous species. Additionally, the flight apparatus of *Tachypteron franzeni* is highly specialized for a rapid and constant flight style and the proportions of the narrow foil and the outline of the flight membranes are almost identical with extant Taphozous species. This suggests that when the earliest radiation known from an extant bat family took place, acoustical specializations similar to those known from their extant representatives were already present. Various radiographic and tomographic methods were applied and compared in this study to manage the problem of very small regions of interest on a large fossil plate.

Influence of Head-Bobbing on the Dynamics of Locomotion in Quail

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During a small mammal's half-bound a large sagittal flexion of the spine takes place in the last thoracic and lumbar vertebra. It induces a horizontal displacement of the center of mass in the trunk (Hackert et al., 2001, in: Blickhan, editor, Motion systems, Aachen: Shaker, 137–141; Hackert, 2003), and therefore a change in the angle of attack at the forelimbs. The importance of this parameter for the dynamic stability of running has been recently underlined (Seyfarth et al., 2002, J Biomech 35:649–655; Hackert, 2003). With head-bobbing, birds experience an extraordinary large deformation of the cervical part of the spine that is synchronized with the motion of the legs and involved in their vision. Videoradiography (500 fps) and ground reaction forces (GRF) were recorded synchronously in five quails in order: 1) to quantify the influence of head bobbing on the position of the center of mass, 2) to determinate the relationships between the GRF and the distance between CoM and ground contact points, and 3) to understand whether the measured displacement of the center of mass affects the dynamic stability of birds' biped locomotion.

Activity Pattern and Morphology of the Visual System in Birds and Lizards

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Extremes of light availability impose the same constraints on all visually dependent animals. It has been demonstrated that the anatomy of the visual system reflects activity pattern, with photopic (diurnal) and scotopic (usually nocturnal) animals exhibiting significantly different gross morphology of the eye and orbit. Across vertebrates, photopic eyes have enlarged posterior chambers that allow a larger retinal area, potentially maximizing the number of photoreceptors and thereby increasing visual acuity. Scotopic eyes usually have enlarged anterior chambers to maximize photon collection, thereby increasing sensitivity. Importantly, analyses of the related bony anatomy, the orbit and scleral ossicles, show similar patterns to the eyeball data, indicating that activity pattern analysis may be possible for fossil specimens. However, it is unclear to what extent this pattern is dependent on phylogeny or on the objective conditions set by light in the environment. To test this, representative species of visually dependent diapsids were compared, including birds and lizards of all known activity patterns. Avian study groups include Strigiformes, Caprimulgiformes, Apodiformes, Psittaciformes, and Falconiformes. Lepidosaur groups include Agamidae, Chamaeleondiae, Iguanidae, Gekkonidae, Xantusidae, and Teiidae. Results indicate that transitions in activity pattern in birds and lizards lead to the independent evolution of similar patterns of eye and orbit size and shape, indicating that activity pattern may play a larger role than phylogenetic affinity in determining visual system morphology.

Ontogeny of Variance and Developmental Noise

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Phenotypic variability, or the tendency to exhibit variation, is an emergent property of complex developmental systems. Although the significance of variance at different levels of biological organization is of central concern to evolutionary biologists, variation has not been an important area of research for developmental biologists. The study of the developmental-genetic basis for the regulation of variance is a central topic that links together evolutionary and developmental biology. One approach to this question is to examine how different types of perturbations to growth affect components of variability such as fluctuating asymmetry, phenotypic variance, and morphological integration. We report results from studies of two perturbations involving mouse craniofacial development. One model, A/WySnJ mice, have reduced growth of a specific component of the face, the maxillary process. The other, growth hormone-releasing hormone receptor (Ghrhr) null mice, exhibit an overall reduction in the rate of postnatal craniofacial growth. We find that A/WySnJ mice exhibit an increase in FA and decrease in integration that is localized to the region affected by the mutation while phenotypic variances are not significantly different when compared to C/57BL6J mice. Preliminary results indicate that, by contrast, the effects of the Ghrhr null mutation produce more widespread effects on variability components. These results support the hypothesis that mutations that affect growth rates are important in the regulation of phenotypic variance.

Kinematics of Surface Descent and Horizontal Swimming of the Thick-Billed Murre (*Uria lomvia*)

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The thick-billed murre (*Uria lomvia*; Family Alcidae) is a wing-propelled diver capable of reaching depths of 200 meters. While swimming, it must produce both thrust to move forward and a downward-directed force to overcome its own buoyancy. I used high-speed video (250 Hz) to document the movements of the wings and feet during horizontal swimming (3D) and during the initial wingbeat of the dive (surface descent; 2D) of two murres swimming in a flume. Markers were fixed to the wrist, cranial and caudal ends of the sternum, wing tip, and the trailing edge of the wing for 2D analysis and the elbow, shoulder, and alula for 3D. In both surface descent and horizontal swimming, the wing is highly pronated and is depressed and retracted relative to the body during downstroke. The duration of the first wingbeat of surface descent is longer than wingbeats of horizontal swimming and has a larger amplitude and longer downstroke phase (53% vs. 44%, respectively). The feet are only used for propulsion during surface descent. Horizontal acceleration patterns of surface descent and swimming are similar; peak acceleration occurs at mid-downstroke. At mid-upstroke, a reduced deceleration or slight positive acceleration suggests the production of thrust. Vertical acceleration patterns also indicate that upstroke is important in countering buoyancy, both during surface descent and horizontal swimming.

"Groucho Running" in Tinamous

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Avian terrestrial locomotion was examined in a primitive bird, the tinamous (*Eudromia elegans*). Whole body mechanics of the tinamous were determined using ground force data from a force platform integrated into a terrestrial trackway. Video images (250 Hz) were simultaneously obtained in order to synchronize kinematics of the limbs and torso with the force data. Kinetic energy and gravitational potential energy fluctuate in phase across speeds ranging from 0.6–2.7 m/s, and external mechanical energy recovery by inverted pendulum mechanisms is poor (generally $<15\%$). These results are consistent with bouncing mechanics typical of runs, although video records illustrate a lack of an aerial phase. This suggests that tinamous are "Groucho running," a gait best described for humans in which high limb compliance limits the elevation of the center mass at midstance. To better characterize this gait in tinamous, speed-dependent change in limb kinematics and leg stiffness are assessed.

Cryptic Diversity and Evolution of Miniaturized Vertebrates: the Mexican Salamander Genus *Thorius*

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The plethodontid salamander genus *Thorius* comprises a clade of miniaturized salamanders endemic to southern Mexico; they are the smallest tailed tetrapods. The adult morphology of *Thorius* is highly derived in many respects, reflecting the fact that these animals are approaching the lower size limit for vertebrates. Although the genus was erected (by E.D. Cope) more than 130 years ago, for more than 70 years following its initial description *Thorius* was thought to include just a single species. Nine named forms were added by 1970, and subsequent morphological and molecular studies have continued to reveal additional species. At present, 23 valid species are recognized, yet at least 11 undescribed species await formal description. These species coexist with and replace one another in complex geographic and elevational patterns, which include numerous instances of sympatry involving two, three, and possibly four species. Phylogenetic analyses suggest surprising trends in morphological evolution associated with miniaturization, including frequent homoplasy involving character loss and gain. Thus, despite the functional and developmental features of vertebrate design that constrain the morphology of *Thorius* at small body size, the lineage remains evolutionarily dynamic and viable.

Development of the Pectoral Girdle in *Discoglossus* (Anura: Discoglossidae)

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The pectoral girdle connects the anterior pair of appendages to the axial skeleton. Primarily it consists of bones that arise by different types of ossification—endesmal (dermal or membrane bones) and endochondral (within the cartilage). The dermal part of the pectoral girdle (i.e., the clavicle and cleithrum) evolved in tetrapods from the most posterior series of bones of the skull of their piscine water-dwelling ancestors. The endochondral part of the girdle is present in fish and primitive tetrapods as a single scapulocoracoid. Anurans are the earliest group of amphibians in which the scapula and coracoid became separated. Among them, the Discoglossidae are convenient models because their earliest paleontological record is from the Middle Jurassic. We followed the development of the pectoral girdle in *Discoglossus pictus* on the basis of both cleared and stained whole-mounts and 3D reconstructions from serial histological sections. The development of the pectoral girdle begins as a single element located near the proximal end of the rudimentary humerus. Isolated scapula and coracoid may be recognized in subsequent stages. In spite of the fact that the pectoral girdle of the Anura is a very complicated structure, in which the identity of some components remains obscure, its development is quite uniform. We can infer from comparing anurans with temnospondyl amphibians the main evolutionary trends that affected this part of the amphibian skeleton.

Neural Correlates of Orbit Orientation and Binocular Visual Field Overlap in Mammals

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Primates are characterized both by convergent (forward-facing) orbits and relatively large brain sizes. Comparative analyses of mammalian orbit orientation suggest that primate orbit convergence first evolved in a context of nocturnal visual predation. Similar analyses of the relative sizes of brain components in mammals suggest that areas responsible for sensory processing are correlated with aspects of ecology, including foraging habits and diet. However, it is unknown whether mammalian orbit convergence is correlated with either the overall size of the brain or with individual brain components, such as the visual cortex and subcortical structures. This study examines the relationship between orbit convergence, binocular field overlap, and brain size in primates and other mammals. Data on orbit orientation are combined with those on overall brain size in primates, carnivorans, chiropterans, insectivorans, artiodactyls, marsupials, and rodents taken from the literature. In addition, data on brain component volumes were collated for a subset of these taxa. Primates differ from other mammals in that orbit convergence is correlated with brain size in anthropoids, and less strongly in strepsirrhines. In other taxa with relatively high orbit convergence, such as carnivorans and megachiropterans, orbit orientation is not correlated with overall brain size. These results suggest that there is a relationship between overall brain size as well as visual components and orbit convergence that is unique to primates.

Axial Stress as a Growth Constraint in the Vertebrae of Sauropod Dinosaurs

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With their long necks and tails, and very large body size, the sauropod dinosaurs represent an extreme example of biological engineering. It is hypothesized that the individual centra of the necks and tails of sauropods are responding as though they are axially loaded columns designed to resist buckling, and that the distinctive radius-to-length ratios are measures of the strength of a centrum as it functioned as a supporting element in the living animal. Additionally, it is proposed that the vertebrae grew in such a fashion that the cross-sectional areas of each centrum experienced a similar stress magnitude and maintained a constant safety factor.

Role of Endoderm in Pharyngeal Arch Development: Ugly Stepbrother to Neural Crest Has Its Day

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During craniofacial development, neural crest cells interact with mesoderm, ectoderm, and endoderm to bring about the ultimate structures of the head. The actions of the neural crest cells in the elaboration of the pharyngeal cartilages have classically been portrayed as playing a central role in the development and evolution of the head. Thus, until relatively recently the role of the endoderm has been deemphasized in studies of craniofacial development. However, a number of recent articles have shown that the endoderm plays a key role in the patterning and development of the pharyngeal arches. Hedgehog (Hh) has been shown to regulate important developmental processes including morphogenesis of teeth and chondrocyte proliferation. Hh proteins are expressed in the pharyngeal endoderm during pharyngeal cartilage development. Work in my laboratory shows that the Hh pathway is

important in differentiation and proliferation of pharyngeal cartilages. Using both mutant analyses with zebrafish mutants deficient in genes encoding members of this signaling pathway, as well as pharmacological treatment with cyclopamine, which inhibits Hh signaling, we have gained a better understanding of the role of this signaling pathway on branchial arch outgrowth. We conclude that while Hh is involved in cell proliferation within all pharyngeal cartilages, it plays a unique role in differentiation of branchial cartilages, since in the absence of Hh signaling these cartilages fail to develop.

Ontogeny of Bite Force and Diet in Lizards and Turtles

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Young animals often forage in the same environment as adults, and consequently must compete for the same resources. However, when competing for food or other resources, young animals are often at a competitive disadvantage because of their smaller size relative to adults. Thus, selection on juvenile performance is likely to be strong, and the adult phenotype may be affected by selection on juvenile performance. Yet in some mammals juveniles perform equally as well as adults by modifying the growth trajectories of muscles and bones. Here we examine the ontogeny of the cranial system and bite performance in several species of ectothermic vertebrates (lizards and turtles). Additionally, we examine the ontogeny of diet in these species based on both empirical and literature data. Our data suggest different growth trajectories for different species, with bite forces increasing to a higher degree than predicted in the lizards and one species of turtle. For *Trachemys scripta*, our data suggest rapid growth in juveniles up to a size where bite forces are large enough for the animals to switch to an herbivorous diet. In all other species examined, no patterns of altered growth in relation to diet are obvious. These data suggest that, whereas selection on juvenile performance might be strong, ectotherms generally do not show increased performance of the jaw system in juvenile life-history stages.

Feeding Underground: Consequences of Burrowing on the Design and Use of the Cranial System in Lizards

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Head-first burrowing likely places severe constraints on the design of the cranial system. To optimize soil penetration, pointed, cone-, or wedge-shaped heads are needed. However, these shapes may constrain the space available for the jaw adductors, which could affect an animal's bite performance. Additionally, as the absolute head diameter may also constrain an animal's burrowing performance, it is often reduced. Because of these demands, burrowing animals often have small heads and low bite forces, which may constrain the range of prey types and sizes eaten. Here we examine how these potential tradeoffs may have shaped the jaw system in amphisbaenians, by comparing head shape and bite force in species with different cranial morphologies. Unexpectedly, our data suggest that amphisbaenians are much better biters for a given head size than all other lizards tested. In part, this can be explained by their relatively wide and high postorbital regions and short lower jaws (decreasing the jaw outlever). Additionally, published data on the morphology of the jaw adductors suggest that amphisbaenians have optimized the jaw adductors for biting by having strongly pennate and short-fibered muscles. This allows them to bite as hard as nonburrowing lizards despite their much smaller heads and to consume a wide variety of prey similar in size and type to those consumed by other lizards.

Mechanical Loading and the Mammalian Skull

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Mechanical strain in the skull bones and sutures is remarkably complicated, as indicated by a series of in vivo studies in pigs, *Sus scrofa*. Regional effects are strong. Loads perpendicular to the bone surface arise from the contraction of adjacent muscles. In the plane of the bone surface, braincase and jaw joint strains respond to the pattern of jaw muscle contraction, whereas occlusion determines strain in the jaws. Both muscle coordination and tooth contact change rapidly during chewing, so strains are highly dynamic. Furthermore, during postnatal growth not only the magnitude, but also the orientation and even the polarity of strain change. Close examination of individual bones suggests ways in which loading may affect growth and therefore morphology. Periosteum is the key element. For example, when the predominant strain pattern in the interfrontal suture changes from compression to tension, the new (periosteal) part of the suture takes on a simpler morphology than the old (endocranial) part. Braincase suture fusion is also accomplished by the periosteum rather than the suture itself. In the zygomatic arch periosteal apposition is trabecular on the squamosal but laminar on the jugal. This difference is not explained by the distribution of replicating cells or vascular elements, but does correlate with the pattern of strain in the two bones.

Rhinoceros Horn Attachment: Anatomy and Histology of a Dermally Influenced Bone Rugosity

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Associations between rugosities on the skull and cutaneous appendages (e.g., horns) often seem obvious when examined in extant specimens in which the conformations of epidermal appendages remain intact. Inferences regarding the morphology of unpreserved cutaneous appendages from extinct animals, however, are not always so clear. Rhinoceros horn provides an example of an epidermal appendage in which the detailed morphology cannot be readily determined from its associated rugosity. The horn attachments of two adult white rhinoceros (*Ceratotherium simum*) were examined by dissection and histological sectioning. The horn proper is a keratinized epithelial structure affixed to the dense irregular connective tissue of the dermis. Rhinoceros dermis is 1.5–5 cm thick across the skin of the head, and retains much of its thickness beneath the horn, at 1–2 cm thick beneath the nasal horn and 2–3 cm thick beneath the frontal horn. The horn-dermis complex is affixed to bone by dense populations of extrinsic fibers derived from the reticular dermis. These fibers create an osteohistological structure similar to that of a fibrous tendon attachment. Irregular mineralization of the extrinsic fibers gives the cleaned bone surface its rugose appearance. A more thorough understanding of how this appendage affects the morphology of the underlying bone aids in differentiation between horn-induced rugosities and rugosities with other causal associations, such as tendon attachment or secondary dermal ossification.

Scent in a Sac: The Preorbital Apparatus of Deer

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A preorbital fossa occurs in several ungulate mammals, but is especially well developed in bovid and cervid artiodactyls. Although the fossa contains a single, well-developed, and encapsulated gland in some antelopes, in other bovids and deer it is lined by a sac of relatively unmodified skin, which contains only a few more glandular elements than the surrounding skin. These structures appear to play a role in chemical signaling in most, if not all, of these animals. At least in deer, the posterior lobe of the Harderian gland (PLHG) may be a significant source of secretant in the preorbital sac, which is connected to the orbital conjunctiva via a distinct, pigmented furrow. However, the degree of development of the Harderian gland and the preorbital apparatus varies among deer. These structures are the most highly developed in primitive cervids, such as *Muntiacus*, where the preorbital fossa and sac, as well as the PLHG, are relatively large and show considerable sexual dimorphism, and where the sac can be everted by specialized facial musculature. In *Cervus* these structures are proportionately smaller, and cannot be everted, but the PLHG is still present. In the more derived cervids *Odocoileus* and *Capreolus*, the preorbital structures are relatively the smallest and the PLHG is absent. These observations suggest an evolutionary trend toward reduction of the preorbital apparatus within Cervidae.

Developmental, Descriptive, and Comparative Osteology of Sturgeons (Actinopterygii, Acipenseriformes, Acipenseridae)

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Acipenseridae includes 25 extant species in four genera (*Scaphirhynchus, Pseudoscaphirhynchus, Huso, Acipenser*) and is the largest extant group of nonteleostean actinopterygian fishes. Members of this family are therefore interesting from both anatomical and phylogenetic standpoints. We assembled an extensive growth series of *A. brevirostrum* (1,000 mm TL) that serves as the basis for our developmental, descriptive, and comparative osteological studies. This presentation focuses on skull development, scute formation, and fin development. For example, dorsal and lateral scute rows develop in an anterior to posterior direction, whereas the ventral scutes develop bidirectionally from a posterior position within the series. Dorsal scutes develop within the elongate dorsal fin fold, whereas lateral scutes develop as ossifications surrounding the lateral line sensory canal; ventral scutes develop independent of any other structures. Our series includes many adult specimens, allowing us to comment on late-stage (e.g., post-maturational) ontogeny and individual skeletal variation of sturgeons. For instance, we discovered an ossified articular bone in the lower jaw of an exceptionally large individual (899 mm SL); this element previously had been reported as absent in sturgeons. We comment on the comparative osteology of sturgeons as a group, as well as in the broader context of lower actinopterygians.

Integrating CT-Scanning, 3D-Morphometrics, and Phylogenetics to Reconstruct Hypothetical Ancestral Morphologies of Horned Lizards

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Phrynosoma are unique lizards easily recognized by their wide, flat body shape and expanded skulls adorned with parietal and squamosal horns. This genus represents an ideal group for studying character evolution because substantial diversity in morphology and ecology is present, yet it remains a tractable group with 13 extant species. Using morphological and molecular data, Hodges and Zamudio (in press) presented two most parsimonious phylogenies, which I use in studies of character evolution. I first present analyses of reproductive mode and life history traits (Hodges, in revision). Viviparity, altitude, and latitude exhibit strong phylogenetic signal within *Phrynosoma*. Viviparous species occur at higher minimum and midpoint altitude, which partially supports the cold-climate hypothesis for the evolution of live-bearing in squamates (Shine, 1985). Then I show how to use phylogeny and mathematical techniques to reconstruct ancestral traits using the evolution of horns in *Phrynosoma* as an example. I apply these methods to 3D-reconstructions of morphological data generated from a high-resolution X-ray, computed tomography scanner. Changes occurring along a phylogeny will be shown via metamorphosis (morphing). Morphing is a dynamic process that allows visualization of transformational changes from one form to another in real time (DeCarlo and Gallier, 1996). All CT data from this project are made available through the NSF-supported, public digital library www.digimorph.org.

Amphioxus and the Evolution of Placodes and Neural Crest

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To investigate the evolutionary origins of placodes and neural crest, we are using amphioxus, the closest living invertebrate relative of the vertebrates, as a stand-in for the ancestral vertebrate. Amphioxus has neither definitive placodes nor neural crest, but has numerous ectodermal sensory cells, and the edges of the neural plate express homologs of several vertebrate neural crest markers. To investigate the commonalities of amphioxus ectodermal sensory cells and vertebrate placodes, we determined expression of several amphioxus homologs of placodal markers and used DiI labeling to trace the axonal trajectories of ectodermal sensory cells. This work suggests evolutionary antecedents of some placodes and supports previous ideas that placodes may have multiple origins. To investigate the evolutionary origin of neural crest, we asked what the cells at the edges of the amphioxus neural plate lack that prevents them from migrating as individuals. One thing missing is expression of FoxD. The single amphioxus FoxD is homologous to the five vertebrate FoxD genes, one of which, FoxD3, is expressed in neural crest and may function in initiation of migration. To determine how gene regulation and function changed to allow a role in neural crest, we are comparing the regulation and function of AmphiFoxD and vertebrate FoxD3. The results provide insight into the relationship between gene duplication and the evolution of new functions and structures.

Homology and Evolution of Jaw Muscles in Archosauria

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A paucity of integrative data from extant and extinct taxa has led to an incomplete understanding of jaw muscles in Archosauria, confounding interpretation of their homology and evolution, particularly among fossil groups. Adductor chamber, palate, and postdentary mandibular anatomy of birds, crocodilians, and outgroup taxa were investigated using dissection and imaging techniques. Pattern homologies of jaw muscles were identified using topologies of muscles, nerves, blood vessels, and bony structures in a similarity test. New phylogenetically informative, topological characters were identified that consistently discriminate different parts of adductor mandibulae. Galloanseromorphs have an apomorphic arrangement of adductor chamber tissues, precluding them as a model for basal avian musculature. Osteological correlates of jaw muscles and relevant tissues were identified in these extant taxa to serve as proxies for soft tissues in extinct taxa. These structures were tracked through particular clades of the archosaur fossil record (e.g., nonavian dinosaurs) in a phylogenetic congruence test. Comparisons of archosaur taxa must take into account major changes in the compartmentalization of the head such as the presence or loss of an epipterygoid, rotations of the laterosphenoidal cotylar crest, and modification of the rostral border of the middle ear. These hard- and soft-tissue structures are integral to interpreting adductor chamber anatomy and, hence, muscular anatomy in dinosaurs, and must be understood before evaluating feeding function in fossil taxa.

Possible Role for the Internal Vertebral Venous Plexus in Thermoregulation of the Spinal Cord

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Optimal functioning of the central nervous system depends on the temperature of the brain and spinal cord. It is known that brown, multilocular fat is specialized in the generation of heat. This heat can be transported by blood. We investigated the vascular connections of the brown fat areas with the internal vertebral venous plexus (IVVP) in various mammals, including man. It appeared that in most species studied veins can be found that connect the brown fat areas with the IVVP. Most of these veins contain valves that direct the bloodstream directly to the IVVP. Since pigs have no real brown fat pads, such connections are not found in these animals. In the dolphin, venous blood from the trunk muscles also is drained to the IVVP before it reaches the caval veins. These veins may transport heat generated in the muscles to the IVVP. In most animals studied, blood from subcutaneous veins can reach the IVVP through interspinal veins. These veins may subserve cooling of the spinal cord. The present study shows that the anatomical preconditions for a thermoregulatory role of the IVVP are present in all the mammalian species studied.

Gas Bladder Movement in Lionfishes: A Novel Mechanism for Control of Pitch

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Lionfish (*Pterois volitans*) possess bilaterally symmetrical muscles that originate on the skull and insert on the gas bladder. We hypothesize that these muscles induce changes in gas bladder position within the fish, thus changing the center of buoyancy and allowing for pitch changes with little use of fins. We examined gas bladder movement within *P. volitans* using a high-speed digital cineradiographic system. Lionfish were induced to pitch head-up or head-down in response to prey. Pitching behavior and gas bladder movement were recorded and three angles were calculated: 1) the angle between the main axis of the body and the horizontal, 2) between the main axis of the gas bladder and the horizontal, and 3) between the main body and gas bladder axes. As fish pitched head-up, the angle between the gas bladder and the body increased, whereas when fish pitched downward this angle decreased. This suggests that lionfish move their center of buoyancy forward of their center of mass by shifting the gas bladder within the body cavity, allowing for a change in body pitch and fine-tuning of position. Thus, it appears that these muscles may provide *P. volitans* with a novel mechanism for pitch control.

Powering Locomotion: Correlating Mechanics With Energetics

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Do energy requirements for work or force production determine the energy cost of terrestrial locomotion? Several observations suggest that there is very little correlation between work and energetics: 1) Mass-specific metabolic rate increases as a linear function of running speed and the slope of this relationship scales with body mass, but the mass-specific total mechanical energy output during running is independent of body mass. 2) The mechanics of trotting and galloping differ substantially, and the $\sim$10% increase in duty factor when a horse changes from trotting to galloping produces a decrease in peak force production, but the metabolic rate at the trot gallop transition is the same in both gaits. 3) In a variety of bipeds and quadrupeds of different sizes, metabolic rate as a function of speed correlates best with the inverse of the time of contact (a parameter assumed to be correlated with the rate of force application) and the ratio of weight-specific rate of oxygen consumption to the inverse of time of contact (cost coefficient) is similar in animals of different body mass. However, some data suggest work may explain part of the energy cost of locomotion: in some species the cost coefficient changes with speed and strain rate increases with speed in some locomotory muscles.

Amphibious Locomotion and Morphology of the Pacific Leaping Blenny, *Alticus arnoldorum*

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The amphibious Pacific leaping blennies, *Alticus arnoldorum*, are found primarily in violent surf zones along coastlines in the tropical Pacific Ocean and possess a remarkable locomotor repertoire characterized by extremely rapid movements. These blennies can climb smooth surfaces such as glass, leap up to five body lengths between rocks, and appear to skip across the water surface. During terrestrial locomotion, they routinely curl their tail towards the head, forming a U or O shape, and then straighten the body, pushing off with the lateral side of the tail. The ability to twist the tail along the longitudinal axis and thereby use it as a dorsoventral propulsor (rather than a lateral propulsor in other fishes) appears to be unique to this genus. I am interested in examining the amphibious locomotion of these fish, combining kinematics and kinetic results with morphology to gain a better understanding of how fins can be used for rapid terrestrial locomotion. Fifteen individuals of *A. arnoldorum* were filmed with two orthogonally oriented high-speed video cameras as they moved freely in a glass aquarium. Forces were then measured as these fishes jumped off a three-axis optical force plate while they were simultaneously filmed for positional information. I also present preliminary results comparing tail morphology in *A. arnoldorum* with that in aquatic blennies not exhibiting this tail-twisting behavior.

Cranial Biomechanics of Sharks Utilizing Durophagous and Piscivorous Feeding Mechanisms

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The feeding mechanisms of elasmobranchs span a wide array of morphological designs, each uniquely suited to exploit prey resources in the various ecological niches of these animals. Through mechanical analysis of the forces generated by the cranial musculature of the durophagous horn shark, *Heterodontus francisci,* and the piscivorous lemon shark, *Negaprion brevirostris*, and the manner in which these forces are utilized in the environment, the cranial loading regimes associated with these feeding mechanisms were investigated. Three-dimensional vector analysis of the forces generated during the expansive, compressive, and recovery phases of the gape cycle revealed the loadings on the jaws and their articulations with the chondrocranium, as well as provided theoretical estimates of the bite forces these species are capable of. Having determined these loadings, function can be ascribed to the various architectural attributes of the heads of *H. francisci* and *N. brevirostris* and the relationship between the designs of their feeding mechanisms and the diverse ecological niches they inhabit can be clarified, leading to a better understanding of the selective pressures associated with these mechanisms. Through the first-ever high-precision measurements of bite force in free-swimming sharks, the influence of behavior as a mediator between morphology and performance is discussed as well.

Digimorph.Org: A Digital Library of Morphology Based on High-Resolution X-Ray Computed Tomography

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Description of morphological diversity lies at the heart of our attempts to classify and explain the natural world. High-resolution X-ray CT scanning is one of the new technologies that can examine the internal and external 3D anatomy of vertebrates, invertebrates, and even plants. CT is now generating exquisitely detailed imagery of even very small objects, and a growing suite of software tools can process original CT imagery into extraordinary visualizations of external form and internal structure. With modern scanners, a detailed 3D dataset can be generated in a few hours for most specimens. Digimorph.org is currently a repository for over 200 datasets and over 2,000 movies (animations) of 3D digital imagery. This growing international archive of digital morphology provides a glimpse of how we can distribute and share digital representations of morphological data. Details of methods for processing CT data and visualizations and preparing these for web delivery are presented.

Glycosaminoglycans (GAG), Hyaluronan (HA), and Type-II and X Collagens in Rat Bone Repair After Perforation of the Tibia: Effects of Training and Immobilization

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We studied posttraumatic bone repair immunochemistry with computerized histomorphometry and microspectrometry after bicortical perforation of tibia in 72 young adult male Wistar rats. The repair was studied in normal and affected (training, immobilization) animals at 1–42 days after operation. The posttraumatic bone repair is a normal process of osteohisto- and organogenesis and depends on environmental factors. Training had no significant effect on routine histology, as reported previously (Hussar et al., 2001). Also, the bone extracellular matrix synthesis (GAG, HA, collagen II-type, and X-type) was not affected and therefore did not accelerate skeletal repairs. Immobilization of animals depressed these processes and bone repair was inhibited. After perforation, the repair processes were inverted (first endosteal desmal repair and then periosteal-chondral repair), which is contrary to the "classic" repair sequence (first periosteal-desmal and then endosteal chondrous). This periosteal-chondral ossification is similar to endochondral ossification of metaphyseal (growth) plate (similar HA distribution, similar collagen II-type, and collagen X-type express). The reparative postnatal histogenesis of the bone tissues is newly made clear by similarities and peculiarities of posttraumatic osteohistogenesis and embryohistogenesis of the metaphyseal plate (ECM matrix protein, GAG, collagen I and II type, and HA synthesis, different effects of trained and immobilized animals).

Vasculature of the Parotoid Glands of Four Species of Toads (Bufonidae: *Bufo*)

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The parotoid glands of toads are large aggregations of granular glands located near the shoulders. To determine the circulatory pattern of these glands, we perfused the vascular systems of *Bufo alvarius, B. marinus, B. terrestris,* and *B. valliceps* with either ink or latex. The perfused glands were studied by gross dissection, microscopic examination, and histology. The vasculature of the parotoid glands was compared to that of the dorsal skin of *Rana sphenocephala.* The parotoid glands receive blood from the lateral and dorsal cutaneous arteries and are drained by one or more branches of the internal jugular vein. The dorsal cutaneous artery supplies most of the blood to the parotoid glands in *B. terrestris* and *B. valliceps.* In *B. alvarius* and *B. marinus,* both the lateral and dorsal cutaneous arteries play major roles in supplying blood to the glands. This pattern of blood flow has not been described for parotoid glands and conflicts with previous accounts of *B. alvarius* and *B. marinus.* The arteries and veins associated with the parotoid glands of toads are present in *R. sphenocephala,* but are arranged differently. In the toads, these vessels ramify into capillaries that surround the individual lobules of the parotoid glands. Extensive vasculature is presumably important for delivering precursor molecules to the parotoid glands, where those compounds are converted into toxins.

Biomechanical Modeling of Musculoskeletal Function in Extinct Taxa: Methods, Assumptions, and Challenges

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Given that almost all animals that have ever lived are dead or extinct, those interested in animal locomotor diversity eventually must confront the problem of how to study this defunct majority. Experimental data from extant taxa are indispensable for rigorously linking form and function, but because experiments cannot be conducted with extinct animals, a theoretical approach is also crucial. My research on locomotor function in extinct dinosaurs and their living avian descendants shows how realistic 3D biomechanical models can be used to infer details of locomotor function in extinct animals. I emphasize the sequence of steps taken to construct such models, the explicit assumptions about unknown parameters that are required, and the difficulties of analyzing such complex models with so many unknowns. I show how sensitivity analysis of unknown parameters is vital for determining which unknown parameters matter the most, and how empirical studies of extant taxa can be synthesized with such theoretical models. With this procedure, I can investigate how individual animals might have functioned, and can reconstruct steps in the evolution of hindlimb muscle function in dinosaurs on the line to crown clade birds. In particular, I focus on how muscular contributions to providing vertical support have evolved and how those contributions reflect changes in limb orientation and joint function.

Patterns of Tooth Replacement in Osteichthyans: Variations on a Theme

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Nonmammalian tooth-bearing vertebrates usually replace their teeth throughout life. Much about how a replacement pattern is generated has been learned from zebrafish. However, to understand general mechanisms of tooth replacement, advantage can be taken from studying other, "non-model" species. We have mapped the patterns of tooth replacement in widely divergent aquatic osteichthyans using 2D charts, in which one axis is time, the other linear spacing along the tooth row. New teeth that are generated simultaneously are considered part of the same odontogenic wave. Using this approach, it appears that a similar, general pattern underlies very distinctive dentitions in distantly related species. A simple shift in spacing of odontogenic waves, or in distance between subsequent tooth positions along a row (or both), can produce dramatically different dentitions between life stages within a species, or between closely related species. Examples will be presented from salmonids, cyprinids, and cichlids. Our observations suggest that lines linking subsequent positions may have more biological significance than replacement waves (usually linking alternate positions), often used to explain the generation of patterns. The presence of a general pattern raises questions about common control mechanisms. There is now increasing evidence, at least for the zebrafish, to support a role for stem cells in continuous tooth renewal and control of replacement patterns.

From Lampreys to Salamanders: Neuromechanical Simulations of Gait Transition Between Swimming and Walking in Salamanders

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This work presents the results of several computational modeling efforts aimed at understanding the neuromechanical mechanisms underlying pattern generation and gait transition in salamanders. Salamanders are believed to be one of the modern tetrapods closest to the first vertebrate that made the transition from aquatic to terrestrial habitats during evolution. While the different oscillatory centers for limb and axial musculature have been identified in the salamander spinal cord, it is currently not known how these centers are interconnected for producing and switching between salamander typical swimming and walking gaits. Using a neuromechanical simulation, i.e., a simulation that combines a biomechanical model of the body and a neural network model of the locomotor central pattern generator (CPG), we investigate several organizations of neural networks capable of producing this bimodal locomotion. Results show that a system composed of a lamprey-like body CPG extended by limb CPGs is capable of producing swimming and walking gaits very similar to those observed in salamanders. Gait transition is then controlled by the modulation of simple tonic signals from supraspinal centers.

Experimental and Analytical Study About Schooling Motion of Fish Based on the Interorganism Relationships Among School Individuals

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The schooling motion of fish was studied, with a focus on two types of motion: approaching motion, in which an individual moves toward the position of its neighbors, and parallel-orienting motion, in which an individual adjusts its body direction to be parallel to the body directions of its neighbors. Correlation of measured motion parameters (position, body direction, and moving direction) among individuals was used to determine which motion each individual was executing. Conspicuous differences and similarities between the two motions were evident in several motion parameters, such as the direction of interacting neighbors from the body direction of an individual, and the time delay of an individual's motion from the motion of interacting neighbors. The results provide insight for analytical study of schooling motion. An analytical model that simulates individual motion in the school was designed based on the measured parameters of approaching and parallel-orienting motion, and it successfully mimicked the motion of a natural fish school. The analytical model was then used to study the relationship between local interactions among individuals and global properties of schooling motion. Thus, the study clarified the property of schooling motion both quantitatively and qualitatively by the experimental and analytical approach.

Whole-Organism Studies of Adhesion in Lizards

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Arboreal geckos and *Anolis* lizards are both remarkable climbers and possess specialized toe-pads for climbing. Previous studies have shown that these toe-pads provide remarkable adhesion for movement on smooth surfaces. Nevertheless, little is known about how much extra mass such toe-pads can support during locomotion. Further, how whole-organism clinging ability changes with ontogeny is poorly understood. I present the results of several whole-organism studies that examine the ability of animals both to climb with external loads and to cling to an external substrate. Loading studies with two gecko species show that geckos can climb uphill on smooth surfaces with extremely large loads (up to 200% body weight). Interestingly, simple calculations show that muscle power output, not the toe-pads themselves, limits geckos from carrying greater loads. Another study examines ontogenetic growth in both the toe-pad and in the clinging ability in two *Anolis carolinensis* populations that differ dramatically in their natural substrate use. This second study shows that there is a discernable shift in clinging ability prior to sexual maturation, resulting in very small juveniles being much worse clingers than larger juveniles and adults. However, contrary to predictions, anoles in the two habitats showed similar scaling of both toe-pad area and clinging ability. Consequently, I suggest that whole-organism adhesion studies provide a valuable window into investigating aspects of animal ecology and evolution.

Evolution of the Tubular Venom-Conducting Fang: What Can Development Tell Us?

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Recent work based on the integrative study of morphology and molecular phylogenies suggests that the front-fanged venom-delivery system of snakes has evolved independently in three colubroid groups: the viperids, elapids, and atractaspidids. Morphological study of the venom gland and of the main venom gland compressor muscle clearly indicates by structure, innervation, and vascularization that these structures are not homologous in the three front-fanged groups. The morphology and embryology of the tubular fang, however, suggest a different interpretation. Tubular fangs occur in no vertebrate group other than the colubroid snakes. In contrast to other morphological components of the venom-delivery system, there is nothing in the structure or development of the tubular fang to suggest that the tubular fangs of the elapids, viperids, and atractaspidids are not homologous. Four hypotheses are considered here to account for this anomaly: 1) elapids, viperids, and atractaspidids form a clade; 2) tubular fangs have evolved independently in the three lineages; 3) tubular fangs represent a latent homolog in colubroid snakes; and 4) tubular fangs represent the plesiomorphic condition for the Colubroidea. Each of these possibilities is discussed.

How Snakes Eat Snakes (and Why)

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We investigated the mechanisms by which snakes are able to ingest other snakes longer than themselves. Kingsnakes (*Lampropeltis getula*) were fed meals of corn snakes (*Elaphe guttata*). The kingsnakes readily accepted the prey snakes, killed them by constriction around the neck, and swallowed them head-first. Only two distinct phases of prey transport (oral and orocervical) were observed, in contrast to the four (oral, orocervical, cervical, and thoracic) typically exhibited by snakes feeding on rodents. The predator snake fit the prey snake into its body cavity by transporting the head of the prey snake almost to the level of the predator snake's cloaca and by bending the vertebral column of the prey snake into waves. Transport of the prey snake's head to the caudal end of the predator's body cavity was accomplished by stretching and displacing the stomach caudally. We propose that one possible advantage of feeding on snakes may be that it allows the predator to ingest a meal of large mass without requiring the morphological adaptations for a large gape that are necessary for feeding on massive mammalian prey.

In the Eye of the Beholder: A Geometric Morphometric Assessment of the Batagurine Process of Testudinoid Turtles

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The batagurine process and associated rearward extension of the pterygoid, putative diagnostic characters of the turtle taxon Bataguridae, were evaluated by comparing the results of visual inspection and standard morphological description with those gained from geometric morphometrics. Visual examination of skulls from each of the three clades within Testudinoidea revealed the presence of a possible batagurine process and rearward extension of the pterygoid in the majority of specimens, but identification of the batagurine process sensu stricto could not be objectively established. Landmarks on the palatal surface and sets of semilandmarks on the basioccipital and pterygoid were digitized on photographs of the ventral surface of each skull and subjected to geometric morphometric analysis. No significant differences in basioccipital, pterygoid, or palate shape were detected. A relative warps analysis was also unable to distinguish among the three taxa. The batagurine process and accompanying posterior extension of the pterygoid are therefore of questionable phylogenetic utility in the separation of the Bataguridae from other testudinoid turtles.

Virtual 3D Reconstruction of Embryonic Head Structures From Physical Sections

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Embryonic heads of the early to late developmental stages of *Alligator mississippiensis* and *Struthio camelus* were transversely sectioned at 8–15 μm and stained with standard procedures for differentiation of all types of head tissues. Sequences of variable periodicity of histological sections were digitized using the Leica Image Manager software in association with the Leica MZ-16 stereomicroscope and the Leica DC 300 digital camera. The images of adjacent sections were registered by translation and rotation either interactively or automatically, minimizing the correlation of intensity. Contours of structures to be reconstructed (neurocranium, muscles, nerves and associated ganglia, inner ear, arteries and venae, pharyngeal evaginations, and pneumatic recesses) were outlined in distinct colors in the image-editing Ellipse program. Volumetric models of the structures were created by plotting the contours in successive planes of the 3D datasets. To remove irregularities due to deformation of microscopic sections, the datasets were resampled and smoothed. Surface models of the structures were constructed as triangulated isosurfaces of the data. The final model was created by combining the colored surfaces. The images of models were obtained by rendering the resulting 3D scenes in a viewer.

Analogs, Near-Misses, Experimental Data, and the Problems of Using Finite Element Analysis as Applied to Fossil Vertebrates

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Finite element analysis (FEA) can examine the hypothetical stress and strains in fossil skulls during biting. But recent strain-gauge work on the orofacial regions of feeding primates has cast doubt on the validity of this methodology. However, comparison of stress-strain results from FE skull models simulating biting with strain-gauge (and other) data from extant skulls during feeding show a good correspondence. But this is only for primates and cats. Little or no such potentially supportive data exist for nonmammalian taxa which might be, and are frequently, used as analogs for extinct tetrapods. This situation is exacerbated if the size difference between the extinct animal and its potential modern "analog" is very large. This might be viewed as a "near-miss analog." External validation of FE results for a fossil instance is very important for a meaningful interpretation. The validity of FEA usage on fossils is strengthened each time an instance of good correspondence between experimental and FE model stress/strain data is demonstrated. Thus, FE models for many (but not all) mammalian taxa are more likely to be meaningful than for nonmammalian taxa (for which no such experimental data currently exists). Ultimately, there is the potentially misleading use of FE on fossils that have no modern analog whatsoever, examples being ceratopsians, stegosaurs, ankylosaurs, most sauropterygians (all reptiles), and archaeocetes (mammals).

Place and Role of Comparative Vertebrate Anatomy in the UK: A Perspective From a Veterinary Science School

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In UK academic institutions, the teaching and recognition of "nongenetic" comparative anatomy is dying—indeed, almost dead. As a subject that is almost totally unfunded by research councils it is in a critical situation. University comparative anatomists are often subsumed into departments where big-money winners exist (e.g., geneticists, developmental biologists, and neuroscientists in anatomy departments). As a result, they are seen even further as being anachronistic (at the politest!); this is a vicious circle. A little gets taught in one or two universities during the first and occasionally the second years, but usually in a paleontological context, not in terms of extant animals. Invariably, comparative anatomy receives only 1 hour per year exposure to students! In the second year of the Veterinary Science degree at Bristol University, students cover the anatomy of exotic pets (rodents, rabbits, birds, reptiles, amphibians, and fish) in a total of 23 hours of lectures and 20 hours of dissection classes. At least here there is a little scope for inserting comparative anatomy—a total of about 1.5 hours. One-third of the students show great enthusiasm, another third indifference, a final third loathing: by these students it is seen as irrelevant. There seems little indication that this situation will change; "Evo-Devo" is increasingly genetically orientated and classical morphology is in its death throes in the UK.

Denticles and Teeth at the Origin of Jaws

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At the base of the jawed vertebrate clade, the fossil taxon Placodermi lacks a dentition homologous with crown-group Gnathostomata. Crown-group gnathostome teeth are part of an ordered dentition, patterned by a dental lamina, function together with articulated upper and lower jaws, and are made of typical dentine. Although basal placoderm taxa, all with articulated jaws, adopted various strategies for feeding, none have teeth in a patterned dentition, of a type regulated by a dental lamina, with typical dentine. However, within the derived Arthrodira, regulated tooth addition is recognized with teeth made of typical dentine, identical to crown-group gnathostomes. Therefore, origin of a patterned dentition in placoderms occurs late in phylogeny and evolved convergently with other jawed vertebrates. A pre-pattern for regulated tooth addition may exist in oral denticle arrays in taxa close to the base of arthrodires, or in their sister group. Alternatively, the posterior wall of the pharyngeal cavity is covered in rows of patterned denticles, and these may be coopted into the oral cavity to become a dentition with regulated tooth addition. Denticle pattern control is inferred to be from endoderm, rather than ectoderm, as denticle morphology, orientation, and arrangement differ significantly from external tubercles of the dermal armor. These pharyngeal denticles are homologous to those of other gnathostomes (including *Loganellia*), with pattern similarities for ordering and positioning.

Scapulocoracoid Homology Among Bony Fishes Based on Morphology and Development of the Queensland Lungfish, *Neoceratodus forsteri* (Sarcopterygii)

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Among bony fishes, the ontogenetic sequence by which the actinopterygian scapulocoracoid develops is well described, but that of the sarcopterygian scapulocoracoid is poorly understood because most taxa are only known from fossils. Moreover, homology of the sarcopterygian scapulocoracoid is problematic. However, by examining a series of early ontogenetic stages of the extant lungfish, *Neoceratodus forsteri*, the different regions of the scapulocoracoid are identified and applied to fossil taxa. The first part of the *Neoceratodus* scapulocoracoid to develop, supporting the glenoid fossa, forms a simple ball and appears nearly contemporaneously with the proximal endochondral element (humerus) of the pectoral fin. Pectoral fin elements develop by segmentation from a continuous field of cartilaginous precursor cells extending distally from the scapulocoracoid. Subsequent scapulocoracoid development produces a ventromedial process, comparable to the zebrafish coracoid, which does not form from this particular field of cells. Thus, the scapulocoracoid of *Neoceratodus* may consist of at least two developmentally distinct regions, the ventromedial being homologous to the coracoid of actinopterygians, tetrapods, and other jawed vertebrates. A smaller dorsal process, homologous to the scapula, also develops, giving an overall triangular shape. The scapulocoracoids of fossil lungfish and other sarcopterygian fishes are also triangular and can be identified as scapular and coracoid regions, rather than the "buttresses" associated with scapulocoracoids of Actinopterygii and Tetrapoda.

Hydrodynamics of Swimming Frogs: Hindlimb-Generated Vortex Wake Patterns

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To test different hypotheses regarding the hydrodynamic mechanisms of frog swimming, we used digital particle image velocimetry (DPIV) to determine/quantify the flow structure of the vortex rings produced by the feet during propulsion. Previous studies of the kinematics of swimming frogs have suggested that interaction between the feet, resulting in a jet as the feet come together at the end of synchronized kicks, may augment force production. Our results show, however, that each foot produces its own distinct vortex ring in both alternating and synchronized kicking of the feet. There is no evidence of a jet being produced even during powerful synchronized kicks (maximum thrust calculated was 0.97 N per foot). The magnitude of the thrust (T) produced by the feet differs between alternate ($T = 0.13 \pm 0.021$ N/foot) and synchronized kicking ($T = 0.24 \pm 0.040$ N/foot), as do maximum swimming velocity with higher swimming velocity and forces produced during the synchronized kicks. The kinematics of our surface-swimming frogs (*Rana pipiens*) shows that the frogs follow a similar acceleration pattern as those reported in previous studies. The observed acceleration is therefore not explained by a single jet produced by the merging feet at the end of the power stroke, and alternative explanations are discussed.

How Labile Are Tooth Cusps?

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Molar morphology has played a central role in studies of mammalian evolution. A general theme emerging from evolutionary studies is the parallel evolution of new cusps. The development of all the cusps involves iterative activation of the same set of genetic pathways. Gene knockouts often lead to an early and total disruption of tooth development that makes them useless for the analysis of tooth crown formation. In order to compare developmental lability of tooth cusps, we investigated first a gene mutation with a weaker tooth phenotype. Ectodysplasin (Eda) is a cell signaling protein expressed during development of several ectodermal organs. In the Eda mutant most teeth still develop. We examined how dental characters change when Eda activity levels rise from zero to normal (wildtype controls), and much beyond normal. We found that with increasing Eda levels, the number and position of cusps increases and changes, respectively. Next we manipulated the relative growth of wildtype mouse tooth germs prior to cusp formations, which resulted in substantial reorganization of cusp configuration. Both the Eda and growth manipulations are concordant with models about tooth development in which a simple change in one variable is able to produce global alterations of the final morphology.

Tooth Structure in Snakes: Mechanical and Functional Significance

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The morphology of snake teeth is correlated with the physical properties of prey skin and the mechanical processes in which the teeth participate during prey capture and swallowing. Most prey skin is a feltwork of collagen and elastic fibers that act like a compliant elastomer, yielding when stressed. A comparison of tooth shapes indicates that sharp, slender shapes serve best to penetrate and enter such elastomers, not by use of frictional forces, but instead by concentration of forces. Similarly, blade-like edges take advantage of force concentrations, not friction, to produce damaging tensile and shear forces within the collagen feltwork when cutting skin. Unexpectedly, grooves in teeth actually weaken the bending strength of the tooth. The implications for the design of snake teeth are several. Piercing and entry of compliant prey integument is served by sharp, slender teeth oriented with tips coincident with the angle of approach to the skin. Raised enamel ridges on tooth tips facilitate entry. Extended ridges along snake teeth contribute to effective cutting, and such blade-like teeth are usually placed at the most advantageous geometric position (posterior maxillary bone) to be deployed during swallowing. Grooves do not increase bending strength but instead facilitate fluid flow to the surface of the prey and/or to change the frictional properties of the tooth surface.

Egg Shell Morphology and Calcium Logistics in Bird

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Egg shell composition and structure are widely analyzed in the literature. Few studies, however, consider them in the broader context of the breeding biology of birds. It has long been recognized that the shell of eggs contributes to successful embryogenesis in many ways, such as in protection, respiration, and water exchange. It is also now well established that egg shell is the major source of calcium for skeletal development in the embryo. Recent studies suggest, moreover, that growth rate may play a fundamental role in the pattern of skeletal development in birds: the faster the growth, the less the skeleton becomes ossified. We predicted, therefore, that fast- and slow-growing bird species should lay eggs with shells designed to support different rates of calcium removal to compensate. We tested this prediction by comparing the structural composition of egg shells from birds displaying a wide range of growth rates and modes of development (e.g., from Struthioniformes to Passeriformes). Using scanning electron microscopy, we examined the fine structure of the inner shell surface (mammillary layer) of both pre- and postincubated eggs, i.e., before and after embryonic development/calcium removal, and obtained results in agreement with the prediction. The number of mammillary tips per unit of surface area was inversely correlated with the growth rate and degree of precociality of the chick.

Candidate Gene Approach to the Evolution and Development of Bone Formation in Metamorphosing and Direct-Developing Frogs

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Key genes have recently been described that regulate cartilage and bone differentiation in several model organisms, such as the mouse and domestic chicken. Among these, the dramatic knockouts in mice of two transcription factors, Sox9 and Cbfa-1/Runx2, eliminate cartilage and bone formation, respectively. This indicates an essential role for both genes in the cascade of events that lead to skeletal formation. Surprisingly, the expression of these genes has not been examined during anuran metamorphosis. This developmental event is unique to tetrapods in its postembryonic formation of bone and adult cartilages, which replace the strictly cartilaginous tadpole skeleton. Our results show that both Sox9 and Cbfa1/Runx2 have been recruited into the metamorphic formation of the adult frog skeleton in *Xenopus laevis*. This indicates that the regulation of both genes is controlled during metamorphosis, possibly through the thyroid hormone cascade. We also examined the expression of several genes in the direct-developing frog *Eleutherodactylus coqui*, where the timing of bone formation has returned to an embryonic stage. Again, we find a conservation with the mouse and chick models. These results indicate a role for Cbfa1/Runx2 in controlling the timing of skeletal formation in species with dramatic differences in both life history and development.

How Is Morphology Encoded in the Genome?

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The vertebrate skeleton is one of the most highly patterned systems in higher animals. Although the unique sizes, shapes, and numbers of skeletal elements underlie many morphological adaptations in different organisms, we know relatively little about the detailed molecular mechanisms that determine the morphology of specific skeletal structures. We are using genetic approaches in mice and fish to study the molecular processes that control the size and shape of specific bones in the skeleton. Studies of classical mouse mutations have identified a family of secreted signaling molecules whose detailed expression patterns control the form of individual skeletal elements. Genetic crosses between divergent stickleback populations has made it possible to map the number and location of chromosome regions responsible for evolutionary change in natural populations. Further study of these chromosome regions should make it possible to determine the type of DNA changes responsible for morphological changes in the vertebrate skeleton, and to test whether evolution has found few or many ways to reach particular morphological endpoints in independent evolutionary experiments around the world.

Effect of Coelomic Septation on Lung Ventilation in Lizards

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In contrast to most lizards, whose viscera lie in a single pleuroperitoneal cavity, the body cavities of teiid and varanid lizards are partitioned into pleural and peritoneal compartments by intracoelomic septa, which physically separate the lungs from other viscera. Although invested with sparse smooth muscle fibers, these septa appear to play an important role in breathing. In the tegu (*Tupinambis merianae*), surgical removal of the posthepatic septum (PHS) results in disorganization and cranial displacement of the viscera. Without PHS, resting and maximum lung volumes, and static compliance of the entire respiratory system, are significantly reduced. During locomotion, tegus without PHS cannot increase tidal volume and, despite increasing breathing rate, cannot match the minute ventilation of tegus with intact PHS. In savanna monitors (*Varanus exanthematicus*), the respiratory effects of detaching the postpulmonary septum (PPS) from the caudal lung surface are seen only when the accessory gular pump is disabled. Loss of PPS constrains costal breathing during treadmill exercise, as both tidal volume and breathing rate are reduced. Inadequate lung ventilation limits the aerobic capacity and endurance of monitors with detached PPS. This suggests that PHS and PPS both assist costal inspiration by restricting cranial translation of the viscera. Understanding the respiratory role of intracoelomic septa in squamates may shed light on the evolution of the respiratory design in birds and mammals.

Structure of Parasphenoid of Reptiliomorph Tetrapods in Light of Fish–Tetrapod Transition

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In osteolepiform Eusthenopteron, the parasphenoid is represented by an element called the parasphenoid stem or corpus that underlies the sphenetmoid portion of the neural endocranium. Besides this, parotic, subotic, spiracular, and suboccipital dental plates are present that underlie the otoccipital portion of the endocranium. It is presumed by some authors that all these components fused together during the fish–tetrapod transition and formed a compound bone called the parasphenoid in tetrapods. An alternative hypothesis suggests that the posterior portion of the parasphenoid of Eusthenopteron (and also of stem tetrapods like Ichthyostega and Acanthostega) has migrated posteriorly through an ancestral preotic fissure and sheathes the otic region of the original otoccipital moiety of the endocranium. In such a way, the parasphenoid of early tetrapods, consisting of a long cultriform process and a large posterior parasphenoid plate, should originate. Indications of such a scenario have not been recorded in ontogenetic sequences of early tetrapods. In the ontogeny of Recent urodeles, the parasphenoid develops from several ossification centers underlying the sphenethmoidal and otoccipital moieties of the endocranium. This second hypothesis is also in contradiction with the ontogeny of the parasphenoid in Recent reptiles. In Lacerta, the parasphenoid arises from five ossification centers: one rostral underlying the trabecula communis and two paired ossifications underlying the otic region of the endocranium. The newest investigations of crocodylian cranial ontogeny and two basal taxa of the archosauromorph clade support the theory of the compound nature of the tetrapod parasphenoid and help to interpret several presumably fish structures incorporated in the archosaurian parabasisphenoid.

Feeding Apparatus Specialization and Ecological Diversification in Angelfishes (Pisces: Pomacanthidae): Implications of a Novel Feeding Mode?

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We examined functional morphology, linkage kinematics, and performance characteristics of feeding apparatuses in representative Indo-Pacific pomacanthids. Three linkages appear of major importance in pomacanthid feeding apparatus kinematics: An intramandibular (I-M) articulation, of modified construction and function to previous teleost examples, facilitates jaw closure with the mandible depressed. Hyomandibular rotation facilitates movement anteroposteriorly of the suspensorium (previously identified in cichlid and chaetodontid genera). The interopercular-articular linkage appears of importance in mandible depression (previously only suggested for larval teleosts). Kinematics of these linkages, and novel patterns of onset, duration, and magnitude of movement in cranial and sternohyoid linkages, characterize a pomacanthid grab-and-tearing feeding mode with performance characteristics distinct from previously described teleost feeding modes. A variety of manipulation feeding, grab-and-tearing involves a high degree of morphological and biomechanical complexity, yet appears most important in basal pomacanthids, enabling large, robustly built and omnivorous taxa to prey on attached and structurally resilient prey in confined microhabitats where large size would otherwise obstruct foraging. Contrary, in many derived and smaller pomacanthid taxa, feeding apparatus architecture remains largely unaltered, while reductions in linkage robustness and specimen size, combined with altered kinematic profiles, correspond with a radiation in diversification of feeding ecology. The implications of the grab-and-tearing feeding mode on patterns of ecological diversification in Indo-Pacific pomacanthids are discussed in an evolutionary context.

Thunniform Swimmers With Internalized Red Muscles: Derived Features in the Musculotendinous System of Mako Sharks

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The external body design of lamnid sharks is well optimized for high-performance thunniform swimming. In addition, lamnid sharks are endothermic fish with internalized red muscles. However, little is known about the internal mechanics of swimming in these specialized cruisers. We compare the musculotendinous system of one lamnid shark, the Mako (*Isurus oxyrhinchus*), to that of other sharks and the gnathostome ground-pattern using microdissection of cleared and stained specimens as well as standard histology. The goal was to identify derived features in the Mako that might lead to a functional understanding of thunniform swimming mechanics. Results show that the Mako is morphologically specialized in several respects: 1) Dorsal- and ventralmost cones of posterior myosepta are elongated (between 9% and 13% of body length) and consist of longitudinally arranged collagen fibers. These tendon-like structures are associated with white muscles. 2) The main anterior cone of posterior myosepta is highly elongated (up to 20% of body length). It mainly consists of longitudinal collagen fibers. These are condensed to a distinct tendon (the hypaxial lateral tendon), the anterior part of which is connected to the internalized red muscles. Results suggest that elongated tendons or tendon-like structures are involved in force transmission of both red and white muscles in the Mako shark.

Structure and Development of the Ethmoidal Part of the Skull in Anura, and Its Ancestral Pattern in Temnospondyli

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The ethmoidal part of the skull is uniform in adult anurans, whereas in their larvae two morphologically distinct types occur. In nonpipoid tadpoles it consists of a pair of the trabecular horns and a pair of the suprarostral cartilages that serve as larval upper jaws. In pipoid larvae it consists of a single internasal plate, the anterior edge of which serves as the larval upper jaw. Homologies of these structures in pipoid and nonpipoid tadpoles are still being discussed. We investigated development of these structures in representatives of nonpipoid and pipoid anurans (*Discoglossus pictus, Xenopus laevis*) by means of 3D computer-generated reconstructions from serial sections. In early stages, both trabecular horns of *Discoglossus pictus* are interconnected by an intertrabecular ligament, which may posteriorly chondrify in a continuous horizontal plate. This indicates that the ligaments or horizontal cartilaginous plate can be homologous with the medial part of the internasal plate of pipoid frogs. Given that the ethmoidal endocranium of temnospondyls (e.g., *Benthosuchus*) was a continuous horizontal plate, we suppose the trabecular horns in nonpipoid frogs evolved from the internasal plate by suppressed chondrification along the midline.

Two Morphotypes of the *Velociraptor* Neurocranium

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Two dromaeosaurid neurocrania with exposed endoneurocranial cavities were compared. The first specimen was diagnosed as *Velociraptor mongoliensis* [IGM 100/982], the other one [IGM 100/976] has been considered attributable to the same species. Both specimens, however, differ in morphologies valuable either ontogenetically or phylogenetically. In contrast to the IGM 100/982, the IGM 100/976 is characterized by: triangle-shaped auricular fossa; the utriculo-saccular and anterior semicircular canal prominence does not extrude too far medially; a hollowed area behind the posterior internal acoustic fossa is absent; cerebral impressions indicate a minor expansion of the medulla oblongata either rostrally between the roots of III–VI and VII, and ventrolaterally below the metotic fissure; the endoneurocranial base is not clearly corrugated longitudinally; transversal convexity of the endoneurocranial base at the anteriormost point of the metotic fissure is absent; the superior tympanic recess is less expanded anteriorly; absence of the crista intertuberalis; shallow parabasisphenoid recess is separated by a low median ridge; the basi-exoccipital recess encompassing passages for the jugular vein and the IX–XII nerves are projected ventrally; and the foramen magnum is considerably compressed dorsoventrally. IGM 100/976 reflects a complex of more primitive differences associated with development of the CNS and inner ear. In conclusion, IGM 100/982 represents a more advanced velociraptorine morphotype than does IGM 100/976, and indicates that the latter might be referable to a new velociraptorine taxon.

Skeletal and Dental Development of Therizinosauroid Embryos From China

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Dinosaur embryos from the Upper Cretaceous of China that were fossilized unusually well and exceptionally prepared in ovo are reported. The embryos, which died during the final third of their development, enable the first in-depth insight into morphogenetic processes of an extinct amniote. The specimens show advanced ossification patterns of both the axial and appendicular skeleton. Fused neural arches and vertebral centra, co-ossified tibia-fibula complexes, well-developed cristae and tuberosities, and small epiphyses of long bones argue for a higher level of precociality than that suggested for oviraptorid embryos from the Upper Cretaceous of Mongolia (IGM 100/971). Hyaline cartilage of the small epiphysis caps is fossilized and shows hypertrophied chondrocytes with a calcified interstitial matrix. Advanced development of bone elements increases their taxonomic value and allows comparisons with both poorly preserved members of Therizinosauroidea and the closely related sister group of Oviraptorosauria. Uniquely documented is an odontogenetic shift between the generations of erupted teeth, each with quite different crown morphologies. The crowns are transformed from a primitive archosaur pattern into an advanced pattern, indicating omnivorous dietary habits of the hatchlings. Rapid in ovo transformation of the teeth may indicate the appearance of the odontogenetic shift very early in the evolution of therizinosauroid dinosaurs.

Oviraptorid Neurocranium From Mongolia

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Several Late Cretaceous oviraptorid skulls have been described from Mongolia and China. However, as the neurocranial region in oviraptorids is overlapped laterally by expanded bones of the temporal region, little has been known about its detailed anatomy. Here we present characters of an exposed wall of neurocranium in an oviraptorid specimen (ZPAL MgD-I/95) from Mongolia. As with most other oviraptorid skull bones, these of the neurocranium are highly pneumatized except the orbitosphenoid. The epipterygoid encloses a passage for the ophthalmic branch of the trigeminal nerve laterally. Ventrally to the auricular fossa, two acoustic fossae are hollowed into the medial side of the neurocranium. The anterior one comprises rostrally the foramen for the facial nerve. The prominentia canalis semicircularis anterior et prominentia utriculo-saccullaris points to a sharp tip. Approximately 2 cm of long right columella is found between the otic region and quadrate, and indicates projection of the tympanic membrane at the distal end of the concave posteromedial edge of the quadrate. The metotic fissure is divided into the smaller upper part and larger lower part by a posterior process of the opisthotic. Anterior to the fissure opens the bilobically shaped external acoustic fossa. It communicates with the superior tympanic recess, which deepens anteriorly.

Developmental Regulation of Contractile Protein-Encoding Genes and Fates of Mesodermal Components in the Lamprey, With Special Reference to the Evolution of the Gnathostome Jaw

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Lampreys, the jawless vertebrates, are assumed to retain multiple ancestral traits including oral structures and undifferentiated myotomes. To investigate the changes in gene regulation associated with the evolution of vertebrate body plan, we isolated multiple contractile protein genes expressed specifically in muscles of the Japanese lamprey, *Lethenteron japonicum*. Lamprey myosin heavy chain genes, *LjMyHC1* and *LjMyHC2*, are both expressed only in the cells originated from myotomes, whereas the actin gene *LjMA2* is expressed in both myotomal and unsegmented head musculature. Interestingly, its paralog, *LjMA1*, is specifically expressed in the upper lip muscles in the posthatching larvae. By microinjection of the vital dye DiI into the embryonic mesoderm, these muscles were found to arise from the mandibular mesoderm. Simultaneously, the primordium of the cartilage, called trabecula in this animal, was strongly labeled, implying its homology with gnathostome parachordals. Retrograde labeling of the upper lip muscles revealed that these muscles are innervated by a posterior subpopulation of the trigeminal motoneurons. These results suggest that the lamprey upper lip is patterned through a secondarily migrating mandibular mesodermal component into the premandibular region, associated with specific regulation of an *MA* gene isoform, and the innervation by the caudal, lamprey-specific neurons in the hindbrain. None of these features exists in the gnathostome oral patterning, implying the partial deletion of the ancestral developmental program in jaw evolution.

Effects of Ontogenetic Changes in Performance on Behavior and Fitness (or, Why Size Matters)

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A central paradigm in evolutionary biology is that morphological variation should be intimately related to variation in performance capacity. While many studies have documented shifts (typically increases) in performance capacity with size within ectotherm species, less is known about the consequences of these performance changes on an organism's behavior and life history. For ectotherms, which exhibit indeterminate growth, ontogenetic performance changes may also result in consequent behavioral shifts. We describe an example of such a morphological and behavioral shift in adult male *Anolis carolinensis* lizards and discuss the evolutionary implications from this ontogenetic shift. As adult male *Anolis carolinensis* lizards change from subadult to very large adult males, they change dramatically in two kinds of performance (biting and jumping), and this performance shift results in differing behavioral strategies for winning male–male contests. This example shows how changes in size after sexual maturation can also result in important behavioral shifts. Besides this work, we also review a variety of studies from other nonreptile vertebrate taxa to determine whether such size-related behavioral changes are also present.

Biodynamics of Arboreal Versus Terrestrial Locomotion in Gray Short-Tailed Opossums (*Monodelphis domestica*)

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The effects of substrate diameter on limb function were studied in the gray short-tailed opossum (*Monodelphis domestica*). Two horizontal substrates with integrated force-transducers were constructed: a flat "terrestrial" trackway and a cylindrical "arboreal" trackway (20.3 mm diameter). On both terrestrial and arboreal substrates, forelimbs exhibited higher dorsoventral (DV) impulses and peak forces than hindlimbs. Furthermore, forelimbs were consistently net braking and hindlimbs net propulsive. A sharp contrast was found in the mediolateral (ML) forces: limbs exert net lateral forces on the terrestrial trackway (forelimbs $>$ hindlimbs), whereas medially directed limb forces were found on the arboreal trackway (no difference between limbs). A further distinction between trackways is that DV impulses were, on average, lower on the terrestrial substrate. These results bear significance for understanding the differential roles of limbs during terrestrial versus arboreal locomotion. Placement of paws obliquely around the arboreal substrate develops shear forces by components of DV, craniocaudal, and ML forces (not just craniocaudal and ML forces as in horizontal, terrestrial locomotion). Choosing slower speeds also allows these small, generalized mammals to safely move on narrow substrates.

Size, Shape, and Metamorphosis: Ontogeny of the Aquatic Escape Response of Spotted Salamanders, *Ambystoma maculatum*

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Spotted salamanders begin development inside a gelatinous egg mass and then hatch as larvae into ephemeral aquatic habitats where they grow and metamorphose into terrestrial adults that eventually return to water to breed. Throughout this complex life history, an individual will encounter many different aquatic predators while its locomotor morphology undergoes continuous changes in size and shape. We reared *Ambystoma maculatum* in the laboratory at 23 $\pm$ 1°C and sampled morphology and escape performance from late-stage embryonic ($n = 11$), larval ($n = 40$), metamorphosing ($n = 23$), and young adult ($n = 15$) salamanders to study how escape behavior changes over ontogeny. We predicted escape performance would peak early in ontogeny when locomotor morphology has matured and predation risk remains high. We also predicted that the process of metamorphosis would decrease locomotor performance. As salamanders grew, the tail became gradually more elongate, while tail area peaked during the larval period. Escape responses consisted of a high-curvature preparatory stroke and a propulsive stroke that propelled salamanders away from the stimulus. Escape response duration, angular velocity during stage 1, and swimming speed during stage 2 all peaked early in the larval period, indicating a compromise between developmental maturity and selection on locomotor performance early in ontogeny. Among similarly sized salamanders, larvae had higher performance than adults, but metamorphosing individuals did not exhibit the predicted decrease in performance.

Nasal Cartilages: Neomorphs in Theria

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In all therian mammals the skeleton of the anteriormost end of the nose is cartilaginous. Since this cartilaginous framework articulates with the ethmoid bone (a cartilage replacement bone) immediately to its rear, in contrast to the surrounding nasals and premaxillae, it is logical to assume that the nasal cartilages represent the unossified anterior end of the ethmoid bone. If this is so, what can be the phylogenetic history of this region? In most tetrapods the anteriormost end of the skull is formed by the premaxillae. In pelycosaurs and cynodonts, typically there is a narrow plate of bone between the two nostrils. Obviously, no cartilage replacement bone projected forward here. *Morganucodon* appears to have the same structure. In therians the anterior edge of the nasals has retreated from the front end of the skull, leaving a space occupied by the lateral nasal cartilages. The nasal cartilages project forward beyond the anterior edge of the premaxillae. This space is not found in monotremes, which have no nasal cartilages. Figures of multituberculates, and other nontherians showing this feature, result from hypothetical restorations based on modern mammals. The absence of this hiatus in the rostral wall of nontherian mammals indicates the absence of the nasal cartilages, which must be regarded as neomorphs in the Theria.

Morphology of the Digestive Tract of Cetaceans and Ungulates: Maternal Investment and Phylogenetic Implications

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From 20 discrete anatomical characters of the gastrointestinal tract, a phylogenetic tree was constructed for mammals belonging to the PSHM-group (sensu Fischer and Tassy, 1993), Cetacea and Artiodactyla. This tree was used to calculate relationships between body mass and other characters with the help of independent contrasts and to determine residuals of characters on body mass. This was also done in four "manipulated" trees. These were created by shifting the positions of taxa. Relationships between anatomical and life history data, as well as information on food quality (g crude fiber per kg dry matter) and energy contents (MJ per kg food) of food were determined. In the ungulates, including whales, differentiations of the postoral digestive tract are independent of life history characters, such as length of gestation and lactation, milk-only and mixed-feeding periods, all expressed as absolute values and as percentages of the length of the total maternal investment period. Relative mixed-feeding periods are not significantly different in the three groups considered here. This period, in which the young animal is weaned, requires about a third of the total time of maternal investment.

Ontogeny, Phylogeny, and Morphology in Anuran Larvae: A Morphometric Analysis of Cranial Development and Evolution in *Rana* Larvae (Anura: Ranidae)

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Comparative studies of chondrocranial morphology in larval anurans are typically qualitative in nature, and detailed data on chondrocranial allometry are currently limited to a single species, *Rana sylvatica*. This study uses geometric morphometric and multivariate statistical analyses to examine interspecific variation in both chondrocranial shape and patterns of ontogenetic allometry among six species of *Rana*. Variation is interpreted within the context of hypothesized phylogenetic relationships among these species. Canonical variates analyses of geometric morphometric datasets indicate that species can be clearly discriminated based on chondrocranial shape, even when whole ontogenies are included in the analysis. Ordinations of chondrocranial shape data indicate the presence of three primary groupings (*R. sylvatica; R. catesbeiana + R. clamitans; and R. palustris + R. pipiens + R. sphenocephala)*, and patterns of similarity closely reflect phylogenetic relationships. Analysis of chondrocranial allometry reveals that some patterns are conserved across all species (e.g., most measurements scale with negative allometry, those associated with the posterior palatoquadrate scale with isometry or positive allometry). Ontogenetic scaling along similar allometric trajectories, lateral transpositions of individual trajectories, and variable allometric relationships all contribute to shape differences among species. Overall patterns of similarity among ontogenetic trajectories also strongly reflect phylogenetic relationships. Thus, this study demonstrates a tight link between ontogeny, phylogeny, and morphology in larval anurans of the genus *Rana*.

Arboreal Quadrupedal Locomotion in Primates: Use of Forearm Rotators and Long Tails to Maintain Balance

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Animals that live and travel in the trees display a variety of morphological and behavioral adaptations to help them maintain balance on narrow, flexible supports. Among these adaptations are long tails that can be used as counterweights and freely mobile limbs used to reach discontinuous supports. Here we describe two additional ways in which these two features can contribute to balance during arboreal locomotion. Electromyographic (EMG) recordings of the forearm rotators, pronator quadratus and supinator, during quadrupedal locomotion in five species of Old World monkeys revealed their contribution to shifting body weight to help maintain balance on a branch. In addition, we observed a coordinated balancing mechanism consisting of a sweeping tail rotation toward the direction of imbalance to impart counter-angular momentum to the body. While all five primate species utilized their forearm rotators to shift weight toward one side or the other during arboreal quadrupedal walking, the tail whip mechanism was most frequently used by the largest and most terrestrial species. We suggest that their large size and/or terrestrial habits have made them less adept at arboreal locomotion and are therefore most likely to utilize auxiliary balancing mechanisms. The usefulness of a long tail as a balancing aid during arboreal locomotion highlights the puzzling nature of the evolutionary loss of a tail in the ape and human lineage.

Experimental Hydrodynamics of Median and Paired Fins in Fishes

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Median and paired fins serve as control surfaces allowing fishes to swim and maneuver in the three-dimensional aquatic medium. Although there have been numerous hypotheses in the literature concerning fin function and theoretical models of how fish fins exert force on the water, recent experimental analyses of fin hydrodynamics have shed new light on the diversity of fin function and have demonstrated novel hydrodynamic interactions among fins. New hydrodynamic features associated with fish fin function include: 1) a previously undescribed ring-within-a-ring vortex structure in the wake of sharks; 2) considerable conformational flexibility and reorientation of the direction of shed vortices in fish pectoral fins; 3) high-magnitude lateral forces generated by fish fins often exceeding thrust force; 4) dorsal fins able to generate a thrust wake that contributes significant thrust during swimming. In addition, dorsal fin wake patterns can change markedly with speed, and may be oriented to produce primarily lateral forces. Hence, even during steady rectilinear locomotion, dorsal and anal fins may play a critical role in the maintenance of stability and in thrust generation. As a result of new techniques in experimental hydrodynamics, many well-described evolutionary trends in fish fin design and placement are now amenable to study in freely swimming fishes, and such studies may reveal some of the mechanistic underpinnings of classical morphological patterns.

Adaptations for Digging in Living and Fossil Octodontidae (Rodentia: Caviomorpha)

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The Echimyidae (spiny rats) and its sister family Octodontidae (taken here to include the degu and allies of the subfamily Octodontinae, and tuco-tucos of the subfamily Ctenomyinae) are the most diverse clades of South American octodontoids. In order to examine the evolution of burrowing specializations in octodontid rodents, we produced a synthetic phylogeny, combining both molecular and morphological phylogenies, and including both fossil and extant genera. We surveyed numerous morphological specializations and mapped them onto our phylogenetic hypothesis. Finally, we attempted to match morphological diversity with information on the ecology and behavior of octodontid taxa. Burrowing for sheltering and rearing is the rule within octodontids. Digging adaptations developed since the Late Miocene, presumably in association with the climatic deterioration and development of open habitats characteristic of that period. However, only a few taxa evolved fully subterranean habits. Scratch-digging is widespread among both semifossorial and fully subterranean lineages. Consequently, morphological changes associated with scratch-digging, including elongated olecranon processes, distally placed and expanded deltoid processes, and enlarged teres major processes, are not restricted to subterranean lineages. Adaptations related to chisel-tooth digging involve changes in incisor procumbency and cross-sectional area and expansions of the masseteric crest and angular process in the lower jaw. These features have evolved independently in the coruro (*Spalacopus*), the fossil ctenomyine *Eucelophorus,* and some tuco-tucos (*Ctenomys*).

Arboreal Locomotion of the Chameleon *Chamaeleo calyptratus*, Sauria

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Chameleons are highly adapted to arboreal life, with a flattened body, tong-like feet, and a grasping tail. They also have nearly parasagittal limb trajectories. We used X-ray-videography and the marker-based system Qualisys to study metric and kinematic parameters of locomotion in *Chamaeleo calyptratus*. X-ray-videography reveals that the scapulacoracoid moves in a sternal ridge with an amplitude of ~45°, and thus increases step length by nearly 30%. The Qualisys analysis indicates that the angle of abduction of the humerus during stance phase is ~40°. The difference between the angle of abduction at liftoff and foot down is 20°. At foot down, the humerus has an abduction of 30°. The fiber type distribution of selected muscles, which are important for locomotion in the chameleon, like the M. scapulo- and humerotriceps, will also be presented. The aim of the study is to compare the locomotion of *C. calyptratus* with the locomotion of arboreal primates (*Loris tardigradus* and *Nycticebus coucang*). With this comparison, we hope to identify constraints on locomotion that are related to an arboreal habit. We define arboreal locomotion as movement on a substrate that has a diameter smaller than the body.

Simulation-Based Biological Fluid Dynamics

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Conventional theories for understanding of power and energetics in swimming rely exclusively on consistent potential theories to analyze physics qualitatively as well as observations and measurements to visualize flow so as to support theories. Recently, a new paradigm of simulation-based biological mechanics has been proposed as a third method in modeling and analyses of fish swimming. This paradigm is designed to digitize and visualize swimming by using computational mechanical modeling of biological mechanics through reconstruction of complex morphologic geometry and representation of the realistic kinematics of an individual object. This new methodology shows great potential and provides us not only with an efficient method in deepening our understanding of fish swimming, but also a useful tool for designing man-made vehicles such as the UAV/UMV (unmanned air or marine vehicle). In this article we describe the methodology of simulation-based biological fluid dynamics in detail as well as its applications in fish swimming and give a review of the state-of-the art in modeling of multibody, complex geometry and realistic kinematics as well as in computation of highly unsteady fluid dynamics in fish swimming.

Ontogeny of Prey Capture Kinematics and Cranial Morphology in the Leopard Shark, *Triakis semifasciata*

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Research concerning ontogenetic changes in the feeding behavior of elasmobranchs suggests that substantial changes occur during the neonatal period. To establish whether ontogenetic changes in feeding kinematics occur in the leopard shark, *Triakis semifasciata,* and to investigate potential morphological bases for these changes, four individuals were filmed weekly for 1 year. Numerous external morphological characters associated with the jaws and chondrocranium were also measured weekly throughout the year. Timing variables increased significantly over time when sharks fed on various dead prey types but decreased over time when they fed on live prey. Excursion variables generally decreased in magnitude within individuals over time, with the exception of hyoid depression. The result of this discrepancy in hyoid chronology is that individuals employed a functionally smaller oral aperture and depressed their hyoid relatively more as they aged. Although suction feeding was primarily used when feeding on dead prey, individuals adopted a ram-dominated modality when consuming live prey as time progressed, indicating behavioral modulation. These changes in kinematics and feeding modality were accompanied by a negatively allometric increase in mouth width and a positive allometric change in mouth length, causing the mouth to become narrowed anteriorly and elongated. The results of this study indicate that ontogenetic changes in feeding kinematics occur in leopard sharks and that these changes are both behaviorally and morphologically rooted.

Evolution of Diphyodont Dental Replacement and Determinate Skull Growth Through Cynodont–Mammal Transition

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The origin of mammals is characterized by evolution of apomorphic patterns in dental replacement and in skull growth, two developmental features that can be studied using fossils of stem mammals, known also as mammaliaforms. As in extant diapsids, most premammaliaform cynodonts have multiple replacements for all teeth, accompanied by prolonged skull growth through the individual lifetime. By comparison, placental mammals have diphyodont dental replacement, with a single replacement for antemolars, and no replacement for molars. Eruption of the last molar and termination of antemolar replacement usually coincides with the termination of skull growth. The primitive mammaliaform *Sinoconodon* lacks the typical diphyodont dental replacement, and has some primitive, cynodont-like features in postcanine replacement. *Sinoconodon* does not show determinate skull growth. It is more similar to cynodonts than to extant mammals in having a prolonged skull growth and sustained dental replacement in older individuals. Derived mammaliaforms, such as *Morganucodon, Haldanodon,* and *Hadrocodium,* have developed a diphyodont dental replacement that ends with the termination of skull growth, as in crown mammals. Optimization of these features among mammaliaforms by phylogenetic analysis suggests that dental replacement and skull growth patterns in *Sinoconodon* may represent an intermediate stage in the transformation series toward the evolution of the diphyodont dental replacement and determinate skull growth through the cynodont–mammal transition that occurred in the Late Triassic and Early Jurassic.

Finite Element of Approach to Studying the Functional Adaptations of Extinct Primate Enamel Microstructure

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We recently developed a computer program that allows interactive recreation of prism decussation from broken enamel surfaces (Jiang et al., 2003; Macho et al., 2003). All primates studied thus far exhibit a distinct pattern of prism arrangement, although the functional consequences of these different designs are poorly understood. To this end, we converted the graphical models to finite element (FE) models for biomechanical testing. First, models of straight enamel prisms were validated against published data (Spears, 1997). Subsequently, the FE models of decussating enamels were tested under compression. The enamel blocks differ in both maximum principal stresses obtained and the distribution of stress concentration. For example, the enamels of the African apes, although stiffer and stronger than those of modern humans, are apparently poorly designed to dissipate high loads. Conversely, *Pongo* not only shows a high degree of prism decussation but also exhibits low levels of stress concentration. This is in accord with what is known about the species' dietary adaptations. The concordance between diet, morphology of the masticatory apparatus, and dental microstructure in extant primates with known behavior makes it reasonable to suggest that the study of dental microstructure in extinct primates may provide insights into these species' dietary niches. This was attempted for a number of extinct Plio-Pleistocene hominins.

Bioweapons Synthesis and Storage: The Venom Gland of Front-Fanged Snakes

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An enigmatic quality of the venom gland of snakes is the simultaneous need for an immediately available arsenal of toxin proteins and for protection of the snake against its own venom components. Further, particularly among viperid venoms, which are typically rich in lytic enzymatic components, autolysis of constituents due to the action of venom metalloproteases is an additional problem. To address questions of venom stability and protection of rattlesnakes from their own toxins, gland ultrastructure was investigated using SEM and TEM. Venom stability under varying storage conditions was evaluated using enzyme, electrophoretic, and toxicity assays, and mechanisms of simultaneous stabilization and inhibition of venom components were evaluated biochemically and using immunohistochemical techniques. Results from several species demonstrate that the gland is structurally complex, particularly a small anterior portion (accessory gland) which could be a site of venom component activation. Expressed venom is stable to extremes of temperature and dilution and several proximate mechanisms (including pH and endogenous inhibitors) exist that regulate enzymatic activity of the venom during storage but allow for spontaneous activation upon injection. Currently we are utilizing immunohistochemical methods to define specific roles of nonsecretory cells of the gland epithelium. We demonstrate that the venom glands of snakes represent an excellent model for study of protein stability and maintenance of toxic proteins.

Feather Development and Evolution: Only the Whole Story Will Suffice

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Evolutionary biologists have long been intrigued by the unique epidermal appendages of birds. Recent reports of putative "protofeathers" have thus engendered much excitement. However, their interpretation, and critical assessment of hypothetical models for feather evolution, demand a knowledge of developmental anatomy not readily available from the literature. The most recent comprehensive survey (Lucas and Stettenheim, 1972) lacked allusion to Rudall's (1947) seminal X-ray diffraction study documenting two different types of keratin in feathers. Reevaluation of classical studies in light of advances in our understanding of sauropsid epidermal biology since 1972, especially the distinct cytodifferentiative patterns seen in α- and β-keratogenic tissues (Alibardi and Maderson, 2003), permits presentation of a more precise account applicable to all feathers, in all species. Lack of consideration of many relevant data on keratin biology severely weakens the factual underpinnings of recent summaries of feather development (e.g., Prum and Brush, 2002). Such summaries form the basis for an allegedly "function-phylogenetically independent" "developmental" model for feather evolution widely cited by paleontologists accepting Chinese protofeathers. In contrast, a model that accommodates all available morphological, developmental, molecular, and physiological data concerning the skin of avian and nonavian sauropsids readily supports a homology of the integumentary appendages of the Triassic fossil *Longisquama* with avian feathers.

***MorphologyNet:* A Web-Based, Interactive Library of 3D-Visualizations of Animal Anatomy**

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We describe the development of a Web-based, interactive digital library of 3D visualizations of animal anatomy called *MorphologyNet*. Contrary to many anatomical libraries (based on CT or MRI technology), the visualizations in *MorphologyNet* are reconstructed from serial sections. Thus, images represent all tissue types (including soft tissues) and include minute structures that usually are not available in digital anatomical libraries. Furthermore, this project differs from most Web-based anatomy libraries in that each visualization consists of layers representing different anatomical structures (e.g., muscles, nerves, etc.). By showing and hiding layers, visualizations can be "dissected" as would real biological objects. Users can customize images by modifying the color, texture, opacity, and lighting of each layer. Images can be resized and rotated about the x-, y-, and z-axes simultaneously (via mouse clicks/drags). The functionality of the *MorphologyNet* user-interface was developed as a Java applet that imports DXF images (i.e., simple wire frame models with layers) and applies surfaces to them. Therefore, the *MorphologyNet* project is capable of incorporating visualizations that are generated from a variety of reconstruction or drawing applications (e.g., *WinSURF, CAD,* etc.). Finally, because the user-interface is simple to use, all images are available online, and the manipulation tools are included as an applet, *MorphologyNet* visualizations are easily accessible by research scientists, students, and the public.

In Vivo Bone Strain Through Ontogeny: A Comparison of Two Vertebrate Taxa

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Juvenile and adult vertebrates place different physical demands on their musculoskeletal systems. Juveniles of pack species must not only keep up with the group, but also avoid predation by animals the adults need not worry about. Consequently, a juvenile's skeleton will inevitably experience a greater frequency of relatively higher mechanical loads than an adult's skeleton. How are these differing physical demands reflected in the growth of the skeleton? To answer this question we collected limb-loading data and in vivo bone strains throughout ontogeny from two species of terrestrial vertebrates, goats and emu. The goat radius experienced equivalent relative limb-loading throughout ontogeny. However, within each gait strains in the radius were greater in adults than in juveniles. This increase in strain despite similar limb loads resulted from negative allometric growth patterns in cross-sectional area and second moments of area. Relative limb-loading also showed no increase with age in emu. However, as in the goat radius strains in the femur, and to a lesser extent in the tibiotarsus, increased throughout ontogeny. Initial analysis of the emu bones indicates that bone diameters scale with positive allometry as emu grow. Interestingly, these two phylogenetically disparate species show similar ontogenetic patterns of uniform limb-loading but increased strain, despite different bone growth patterns.

Teratogenic Effects of 4-Nonylphenol on Early Development of *Xenopus laevis*

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Environmental estrogens are synthetic compounds that interfere with normal hormone functioning. Research has shown that many environmental estrogens, such as nonylphenol, have teratogenic effects on organisms exposed to them during development. This study investigated the effects of the environmental estrogen, nonylphenol, on *Xenopus laevis* tadpoles. Previous studies have shown that neurula-stage tadpoles exposed to nonylphenol through 96 h postfertilization exhibit abnormalities such as retarded growth, kinked tails, edema, and underdeveloped guts and heads. By exposing different embryonic stages to different concentrations of nonylphenol, and allowing tadpoles to develop through 12 days postfertilization, this study established more accurate environmental conditions for assessing the effects of nonylphenol on tadpole development. Abnormalities were observed in nonylphenol concentrations as low as 0.1 μmol l^{-1}. Concentrations of 5 μmol l^{-1} resulted in 100% mortality, while exposure to all other concentrations resulted in at least 40% mortality by the completion of the experiment. Exposing preneurula tadpoles to refreshed solutions of nonylphenol at subsequent 4-day intervals inhibited growth and induced developmental abnormalities in all nonylphenol concentrations. These conditions resulted in more severe abnormalities than have been previously documented. Further research is needed to investigate the relation between the endocrine system and cell populations, such as neural crest, that might be affected early in development by exposure to nonylphenol and other environmental estrogens.

Transformations of Aortic Arches During Metamorphosis of the Spade-Foot Toad, *Pelobates fuscus*

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Changes in breathing during transition of vertebrates to dry land also affected their circulatory system. Metamorphosing *Pelobates* may better reflect the anatomical condition of primitive amphibians than do more advanced anurans. We injected its vascular system through the heart ventricle with methylmetacrylate (Mercox). Soft tissue was diluted and the corrosion cast was observed in SEM. In tadpoles, four aortic arches (III–VI) emerge from the heart. All are divided into two branches from which gill arteries emerge. Gills are present on the ventral side of the aortic arches. On their dorsal side the filter apparatus is developed, supplied by arteries from IV and V. The external carotid artery arises from the ventral part of III and the internal carotid artery emerges from its dorsal part. The pulmonary artery splits off from the VI arch just before its entry into the lateral dorsal aorta. All aortic arches in tadpoles are connected with the lateral dorsal aorta. During metamorphosis, gills and filter apparatus disappear and the aortic arches become shorter. On aortic arch III, the carotidal labyrinth begins to develop. Aortic arches III and VI lose their connection with the lateral dorsal aorta, IV being the main trunk into the body; V is reduced completely. For the first time we described a. palatonasalis, circulus Willisi, and branches of the internal carotid artery in frogs.

Cambrian Fossil Animal, *Haikouella*, and the Origin of the Vertebrates

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The 530-million year fossil animal *Haikouella*, from the Chengjiang fauna of the Maotianshan Shale of Southern China, has generated much controversy since its discovery in 1999 (Nature 402:518). Some have argued it is a vertebrate-like chordate, whereas others say it is not a chordate but a basal deuterostome (Science 300:1372c, 1372d). Here, the case for the vertebrate-like nature of *Haikouella* is reiterated. Color photos of multiple specimens are presented, showing branchial bars and gills, muscle fibers in trunk myomeres, a three-dimensionally rod-shaped notochord, postanal tail, paired eyes, a large brain, and a head region resembling that of ammocoete lampreys. The contribution of *Haikouella*, and of the closely related fossil animal *Yunnanozoan*, to the understanding of the origin of the vertebrates is discussed. It is argued that such an animal was predicted by past hypotheses of vertebrate evolution, and therefore corroborates those hypotheses, essentially solving the longstanding problem of the origin of the vertebrates. However, *Haikouella* has no hagfish characters, so it, along with recent molecular studies, refutes the formerly widespread idea that hagfishes represent the basal-vertebrate line.

Placodes in Ascidians

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Late differentiation of the ectodermal layer in *Ciona intestinalis* and *Botryllus schlosseri* (Ascidiacea, Tunicata) embryos was analyzed by means of light and electron microscopy in order to verify the possible presence of placodal structures. These are transitory ectodermal regions giving rise to nonepidermal cell types, and are classically considered exclusive to vertebrates. A number of transitory ectodermal thickenings were recognized, some of which were identified as neurogenic placodes. These may be considered homologs of vertebrate placodes: the neurohypophysial placode may include a homolog of the vertebrate olfactory placode; part of the stomodeal placode contains one portion differentiating hair cells, homologous to the acustico-lateralis placode, and another portion gives rise to the ciliated duct of the neural gland, homologous to the adenohypophysial placode; the rostral placode, producing sensory papillae, may be homologous to the placode of the vertebrate adhesive gland. Notably, the atrial and stomodeal placodes possess the ability to differentiate, in time, subgroups of other placodes. Available data on the lineage in the ascidian nervous system show that some of these placodes derive from blastomeres located at the border of the neural plate / future epidermis, suggesting that the presence of a preplacodal field is a common feature in chordate early embryos.

Finite Element Modeling of the Anthropoid Mandible: The Effects of Altered Boundary Conditions

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Finite element modeling provides a full-field method for describing the stress environment of the skull that cannot be achieved through conventional experimental approaches (e.g., strain gauges). The utility of finite element models for improving our understanding of the functional morphology of the skull, however, remains somewhat uncertain given our ignorance of whether such models accurately portray states of stress and strain. For example, the effects of boundary conditions that are chosen to represent the mechanical environment in vivo are largely unknown. Employing a simplified loading regime under various conditions of isotropy/anisotropy and homogeneity/heterogeneity, we use a finite element model of a *Macaca fascicularis* mandible (13,616 quadratic tetrahedral elements) to measure the effects of changing boundary conditions (force orientation and nodal constraints) on strain values at two locations remotely situated from the applied constraints and points of load application. Reduction of nodal constraints bilaterally below the condyles and at gonion (n = 25, 12, 6, 3, and 1 at each location for each iteration) has predictably large effects (>50% increase in principal strain magnitudes), and altering occlusal point load directions by as little as 5° alters principal strains from 5–15%.

Cranial Sutures in Fish: Using Suture Morphology to Infer Function in Fossil Taxa

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The goal of this project is to understand what mechanical role sutures play in fishes, and identify whether a relationship between suture form and function exists that can be applied to patterns of suture change observed in the fossil record. For example, changing suture morphology may indicate a shift from aquatic to terrestrial environments across the fish–amphibian transition. Several paleontologists have suggested that skull roof sutures of fossil fish and amphibians may capture information about function. However, functional interpretations of fish sutures have been confined to descriptions of unusual suture morphologies and speculation about their roles in skull function; no experiments on extant fish have been conducted. (The majority of experiments on cranial sutures have been conducted on mammals). This study begins to address the question of how specific suture morphologies relate to function in living fish, with the aim of applying this knowledge to the fossil record. In this study strain gauges were surgically implanted across skull roof sutures of *Amia calva* and *Polypterus senegalus*. In addition, electromyography (EMG) was used to record muscle activity during feeding and resting. Finally, the 3D morphology of the sutures is described and compared to the strain data and muscle activity patterns to establish correlations between suture shape and function that can now be applied to fossil taxa.

Morphometric Exploration of the Macroevolutionary Disparity in the Skull of Archosaurs

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Archosauria is one of the most diverse groups of vertebrates. Perhaps this is why the morphology of this clade has been a subject of interest for centuries, and it is often the focus of contemporary morphological studies. However, there is a need for studies that address morphological variation in regard to disparity. These types of studies imply the quantification of form in morpho space, which becomes operatively useful within a theoretical context, serving to uncover possible hidden variables related to processes that underlie the pattern of disparity (e.g., structural constraints). Because archosaurs display a high degree of structural variation and have a well-established phylogeny, they allow us to explore these ideas within a macroevolutionary scenario. The skull is one of the anatomical complexes with a high degree of disparity. We describe an example of the quantification of the morphological features that characterize the skull in archosaurs that helps describe disparity in terms of the geometrical relationships that occur within the whole. Quantitative variables were obtained using both geometric and classic morphometrics. Natural occurrences of shape variation are statistically explored and contrasted to theoretical possible variation that will help elucidate the underlying processes that have lead to this distribution pattern.

Common Patterns of Morphological Variation in the Skull of Vertebrates: Invariant Processes?

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During the middle of the last century, European morphologists were concerned with the analysis of the structural patterns of amniote skull variation. They investigated whether similar processes underlie the observed patterns of skull variation, even though the organisms under study were systematically quite distant, i.e., diapsids and synapsids. They introduced a categorical system of skull typology within a framework of heterochrony and developmental biology, based on the relationships of the facial orientation with respect to the basicranium. Their studies were based mostly on descriptive morphology, although some morphometric approaches were also attempted. In the present study, large-scale patterns of skull variation were studied by geometric morphometrics in primates and modern birds as a reappraisal of the former studies. We found that in both groups large portions of morphological variance in adults follow two main principles: 1) upward and downward orientation of the face, and 2) allometric independence of these variation patterns. In primates, facial orientation was independent from allometric growth, and in a phylogenetic context, comparative analyses yielded similar observations in which craniofacial patterns of flexion were independent from evolutionary allometry. We propose this study as a preliminary example for the comparison of the macroevolutionary patterns of variation for each group. We address the operative difficulties, the relevance of these approaches, their morphological meaning, and their evolutionary implications.

Phylogeny of the Branching Pattern of the Nerve Bundles in the Shoulder Region of Tetrapods

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The disposition of the limb nerves and muscles in ventral (flexor) and dorsal (extensor) bundles has been accepted as a fundamental arrangement in tetrapods. On the other hand, we have reported that in reptiles and amphibians this separation was incomplete and that the extensor nerve for the forearm muscles took the pathway in the flexor side. Furthermore, the formation pattern of each nerve fiber bundle in the brachial plexus shows interesting phylogenetic characteristics. In this study we observe the precise branching pattern of the nerve fiber bundles in the brachial plexus and the arrangement of the target muscles in mammals (man and dogs), monotremes (platypus and echidnas), reptiles (monitor lizards and green iguanas), and amphibians (giant salamanders and tiger salamanders). In the lower tetrapods the nerve branches to the upper limb girdle muscles have a tendency to form an independent bundle of the other nerves to the upper limb at the proximal region of the brachial plexus. This fact suggested that the limb girdle muscles supplied by this independent nerve bundle had little interaction with other limb muscles. This nerve fiber arrangement in the brachial plexus is thought to have a close relationship with the change of the locomotion pattern in tetrapods.

New Training Box for an Assessment of the Upright Posture in Operant Bipedal Rats

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The bipedal rat is known as an animal model for investigating the relationship of the mode of human bipedal locomotion and muscular-skeletal morphology. Since bipedalism experiments with rats with removed forelimbs were carried out by Colton in 1929, many researchers have examined the influence of bipedal behavior on the hindlimb bones, hindlimb muscles, and the morphology of vertebrae. However, the hindlimbs and trunk cannot be fully extended in rats with removed forelimbs (Moravec and Cleall, 1987; Matsumura, 1991), and maintenance time of taking an upright posture does not differ from the quadrupedal rats (Bailey et al., 2001). Since the forelimbs of the animal are damaged, there is a problem also from a viewpoint of animal welfare. On the other hand, in the experimental animal model, which takes a bipedal posture using operant conditioning (operant bipedal rat, Matsumura and Okada, 1990), a rat can take an upright bipedal posture in which the hip and knee joints are extended nearly to the maximum. An improved bipedal training box was developed in order to examine the upright posture of a rat and its maintenance time in detail for video, cineradiography, and EMG studies.

Adaptation of the Rat Femoral Neck to Bipedal Standing Exercise

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Effects of bipedal standing exercise on the femoral neck cross-sectional geometric properties and bone density were simultaneously investigated in 17 growing male rats, divided into a control group and exercise group. For this a bipedal training box was used, in which the rat achieved a fully upright stance through positively reinforced operant conditioning. The exercise group was burdened with a bipedal standing exercise from 64–140 days of age, totaling 136–138 sessions. At the age of 140 days the left femur was removed. Bone density and cross-sectional geometric properties were measured using pQCT (peripheral quantitative computed tomography). Four serial cross sections of the femoral neck were scanned 4 mm apart from each other, just below the femoral head. The bipedal standing exercise had the following effects on the femoral neck: Cortical and trabecular bone density per unit volume significantly increased near the base of femoral neck. The results suggest that adaptation of the mechanical strength of a rat femoral neck to bipedal standing exercise depends mainly on the changes in bone density, rather than on the changes in the cross-sectional geometric properties of the bone, in contrast to the femoral shaft.

Homologs of Vertebrate Placodes in *Ciona intestinalis*

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Ectodermal sensory placodes are often considered a vertebrate character; however, recent studies suggest that two ascidian embryonic structures, the primordial pharynx and the atrial invaginations, could be considered homologous to placodes. We examined a range of *Ciona intestinalis* genes, orthologs of markers of vertebrate placode development and differentiation, including members of the *Pax, Six, Eya, Dach, Fox, Sox* families, and several markers of neurogenesis. Our results show that both atria and pharynx express marker genes in agreement with their status as proposed placode homologs. They also suggest a complex coordination of their expression as well as the subdivision of the tunicate primordia in discrete units. We examine how expression of specific genes is restricted to these cells and compare this to the patterns and pathways observed in vertebrates. We also discuss what mechanisms might have led to the evolution of elaborated sensory organs and ganglia in vertebrates.

Mesozoic Terrestrial Giants

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Dinosaurs were the truly terrestrial giants of all times. Although the largest complete skeleton belongs to *Brachiosaurus*, there is a growing body of evidence indicating that some other species must have been even larger. According to rigorous estimates after regression analyses on limb bone and vertebra measurements, the titanosaurian sauropod *Argentinosaurus huinculiensis* must have been the largest ever found, at 73 tons. Another titanosaur, *Antarctosaurus giganteus*, was the second, at 68 tons. Among carnivores, the holotype of the carcharodontosaurid theropod *Giganotosaurus carolinii* rivaled the average-sized *Tyrannosaurus rex*, and was only marginally smaller than "Sue," the largest specimen. However, a new dentary of *Giganotosaurus* is 8% longer than that of the holotype. Assuming geometric similarity, that individual must have had a body mass above 8 tons and hence must have been the largest theropod ever found. The body mass of the Cretaceous African crocodile *Sarcosuchus imperator* has also been estimated as about as much, and hence cannot be excluded as the largest continental flesh-eater ever described.

Microevolutionary Variation of the Chondrocranium in Three Inbred Mouse Strains

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This study examines morphological variation in the chondrocranium of three inbred mouse strains: A/J, C57BL/6J, and DBA/2J. These strains have previously been shown to have variation in mature cranial base morphology. However, when this morphological divergence first occurs during development is not known. In this study we compare chondrocranium morphology among these strains in order to test if the variation seen in adults is present at or prior to chondrogenesis. Euclidean distance matrix analysis (EDMA) was used to quantify and compare the form and shape patterns of 2D linear distances measured between landmarks from whole mounts and sections of cartilage-stained E15.5 fetuses. We hypothesize that if the variation seen in adult bony morphology is already present by E15.5, then the size, shape, and orientation of cartilages should be similar to the adult results. Thus, we expect the widths of the posterior portion of the trabecular cartilage and hypophyseal cartilage to be significantly smaller in A/J mice and significantly larger in C57BL/6J mice. We also expect the orbitosphenoid cartilages to be rostrocaudally narrower and more lateromedially angled in DBA/2J mice. This study is aimed at understanding the cellular and molecular mechanisms responsible for developmental differences that lead to morphological divergence of the cranial base in these inbred mouse strains.

Mechanics of Locomotion in Lizards

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Lizards (one skink and one gecko) have been shown to exhibit both "pendular" and "spring"-like patterns of energy fluctuation during terrestrial locomotion. Lizards have also been shown to use a wide variety of quadrupedal gaits. The relationship between gait and patterns of whole-body mechanics has not been well quantified in these sprawling animals. We examined gaits and mechanical energy patterns and associated posture and segmental dynamics in several lizard species locomoting over a force plate. In lizards, certain gaits (trots) are clearly associated with the performance of uniform sustained locomotion (and both pendular and spring-like mechanics), while others are not. Thus it appears that lizards can employ known energy-saving mechanisms while trotting. The results of studies of the mechanics of other gaits are presented

Bone Histology in Catarrhine Primates Relates to Aspects of Life History

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The microscopic organization of primary bone tissues records variations in bone growth rate during ontogeny, including periods of growth disturbance. As such, it constitutes an important source of information about aspects of individual life history, including growth patterns and environmental conditions. This study examines relationships between life history and bone microstructural development in primates by focusing on ontogenetic series of catarrhine taxa selected for their body size, life history, and known geographic origins: wild-caught vervet monkeys (n = 32), white-handed gibbons (n = 28), and chimpanzees (n = 13). Conventional and polarized light images of 100-μm-thick midshaft femur and humerus cross-sections were acquired and processed for the quantification of aspects of primary bone tissue design (tissue type proportions, vascularization, growth arrest lines) and secondary remodeling. Individual body weights, bone lengths, and dental eruption were also obtained to examine the correspondence of microstructure with traditional measures of somatic growth. Results show marked age-specific variability in primary bone microstructure, consistent with predictions based on somatic growth in other body measures. Species differences, such as the marked vascularity of primary bone in chimpanzees, are interpreted within the context of life history. Growth arrest lines are found in all taxa, although remodeling complicates their interpretation in chimpanzees. These and other results form a foundation for extending life history investigations to paleontological contexts.

Differential Design for Hopping in Two Species of Wallabies

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This study explores differences in the distal musculoskeletal anatomy and hopping mechanics in two species of wallabies, *Macropus eugenii* (tammar wallabies) and *Petrogale xanthopus* (yellow-footed rock wallabies). These species were selected because of the differences in their preferred habitats, with tammar wallabies inhabiting open, relatively flat areas, and rock wallabies living on rocky outcrops. These environments place very different demands on the musculoskeletal systems of these animals, and the aim of this study was to explore any differences in their muscle–tendon morphology and how these influence hopping mechanics. Musculoskeletal anatomy of the hindlimbs was determined from dissections (n = 5 each species). Hopping mechanics were evaluated with combined high-speed video and ground reaction force measurements during level, steady hopping, as this is an activity commonly observed in both species. Morphological analysis shows that both species are very similar in hindlimb proportions and mechanical advantage at the ankle, but the ankle extensor tendons (gastrocnemius and plantaris) are 25% thicker in rock wallabies. Preliminary results of hopping mechanics show that for similar velocities rock wallabies have higher peak ground reaction forces (7 vs. 5 times body weight) associated with shorter contact times (105 vs. 135 ms). These data suggest that rock wallabies operate with stiffer legs that store more elastic energy, allowing them to travel higher or further with each hop.

How Do Ontogenetic Changes in Morphology and Behavior Affect the Swimming Performance of Zebrafish?

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As fish grow from larvae to adults, changes in their morphology and behavior cause unpredictable variation in swimming performance. In order to understand the hydrodynamic consequences of ontogenetic change, the present work used a combination of mathematical modeling, flow visualization, and experimental manipulation to study the routine swimming of zebrafish (*Danio rerio*). Like many fish, zebrafish swim with an intermittent beat-and-glide pattern. Adults swim disproportionately faster during the beat phase and glide disproportionately further than larvae during the glide phase. Our results suggest that these allometric changes in performance may largely be attributable to an increase in the relative importance of inertial forces to the hydrodynamics of swimming, an increase in the behavioral control of paired and median fins, and an enhanced ability to generate propulsive power in the later stages of the life history.

Developing a Biomechanical Model of the Feeding Apparatus in Aquatic Tetrapods, Part 1: An Investigation of the Crocodilian Skull Using Finite Element Analysis

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Although the aquatic environment seems to produce convergences in many aspects of tetrapod morphology, particularly in body shape and locomotory style, the biomechanical implications of convergences in head shape and tooth form have proved difficult to understand. Attempts to reconstruct the feeding ecology of extinct marine reptiles by using comparisons with modern aquatic tetrapods have enjoyed limited success. There is a complex interplay between the structural requirements of the skull and teeth and the hydrodynamic properties of the head. We present the early results of our own attempts to introduce a mechanistic basis to the traditional comparative approach. A finite element model (FEM) of an alligator skull was constructed and preliminary investigations gave encouraging results. Further models encompassing the range of skull shape and tooth morphology in modern crocodiles will be developed and tested against in vivo data. These models will, along with standard comparative techniques, enable us to develop a general model of the crocodilian skull, which will in turn lead to a set of models of the feeding apparatus in aquatic tetrapods. As FEM tools have only recently become available to biomechanists, an important part of the study is to ensure that appropriate questions and methodologies are developed as work progresses. This conference will enable researchers to compare approaches and develop more robust methodologies.

CT Scans and 3D-Reconstructions: Tools Investigating Evolution and Function of Soft Tissue Structures

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This study used CT scans and 3D reconstructions to obtain landmark data, linear measurements, angles, volumes, and densities of soft tissue structures. Of primary interest is the melon, a large component of toothed whale foreheads used in the formation of biosonar beams, and composed of unique lipids and collagen fibers. Previous studies have failed to preserve anatomic geometry and led to ambiguous characterizations and confusion in evolutionary and functional interpretations. Our primary objectives are to arrive at a rigorous definition of the melon based on shape variation, position, and orientation. This foundation should shed light on the evolution and functional morphology of the melon. Preliminary results suggest that the melon has a conserved shape across a diverse taxonomic range; however, there are other key areas of significant differences. Based on osteological correlates of the soft tissues we can infer melon size and position in extinct odontocetes. A distinct pattern of gradation in density in the melon and subsequent separation of the structures provided an informative morphological character, supporting the theory that the melon functions to focus the sound beam generated inside the dolphin head.

Forelimb Homologies Among Archosaurs: Reconstructing Anatomy Using the Extant Phylogenetic Bracket

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Since the Triassic the archosaurian forelimb has undergone profound transformations, ranging from its primitive use in terrestrial locomotion to its use in powered flight in two different major clades. Despite this functional diversity within a single lineage, little work has gone into elucidating the evolution of musculoskeletal forelimb anatomy within Archosauria. Drawing on recent advances in the study of musculoskeletal anatomy of the forelimb in extant crocodylians, this work establishes the muscular homologies among the living members of Archosauria (birds and crocodylians), as well as their immediate outgroups. Muscular homologies were determined following classical techniques, including similarity of attachment sites and pattern of innervation, as well as phylogenetic congruence. The result is a phylogenetically rigorous assessment of the musculoskeletal anatomy of the common ancestor of crocodylians and birds, or the Bracket Ancestor for the clade Archosauria. The results of this research can subsequently be used to more rigorously infer the soft-tissue anatomy and functional morphology of extinct archosaurs.

Evolutionary Transformations of Yolk Sac Placentation in Rodentia With Special Respect to Hystricognathi

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Exchange processes during pregnancy are often assigned to the chorioallantoic placenta, which shows remarkable differentiation within the Rodentia and its subgroups such as Hystricognathi (Mess, 2003, J Exp Zool 299A:78–98). However, other fetal membranes seem to also be involved in such feto-maternal exchange. Here, the morphological organization of the yolk sac is presented for hystricognaths. Particular emphasis is given to the dassie rat, *Petromus typicus*, a species that is suspected to have retained plesiomorphic features of that group. Data from other rodents are included, and the stem species pattern of Hystricognathi is reconstructed using MacClade. Initial results confirm that Hystricognathi possesses a complete and very early inverted yolk sac that includes a peculiar arterial ring system, the fibrovascular ring, in their stem species pattern. Adjacent to the fibrovascular ring system, the yolk sac becomes highly folded in late ontogenetic stages and establishes an intimate contact to the chorioallantoic placenta, suggesting transfer of substances between both placental types. These characteristics seem to be the outcome of evolutionary transformations along the stem lineage of Hystricognathi. Moreover, in early ontogenetic stages a yolk sac placenta appears to have been established for the uptake of histiotrophe as a plesiomorphic character state of hystricognaths. The significance of these characteristics for evolutionary scenarios of Hystricognathi is discussed.

Pectoral Fin Evolution: Developing New Branches

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The prevailing view of the posterior branched portion (the metapterygium) 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.

Early Development of Cranial Neural Crest Streams in Anurans

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Different aspects of neural crest development have traditionally been studied in birds and amphibians. Main study objects among the latter were the anurans *Bombina bombina, B. variegata, Rana pipiens, R. temporaria*, and *Xenopus laevis*. When comparing early embryogenesis among a variety of anurans, including bufonids, discoglossids, ranids, hylids, scaphiopodids, pelobatids, microhylids, and pipiids, we found that the embryogenesis of no anuran species can be considered to be representative for anurans. Early cranial neural crest cell migration has a variable relative timing among anuran species when compared to the formation of other embryonic anlagen. Within discoglossids, for example, we found the formation of the mandibular stream to start earlier relative to the closure of the neural tube in *Discoglossus hispanicus* than in the *Bombina* species investigated. The branchial streams divide from the hyoid stream before the formation of somites in *D. hispanicus*. In *Bombina* species this event only happens after somites have been formed, the neural tube is almost closed, and the embryo has elongated. Somites form later relative to neural tube closure in *D. hispanicus* than in *B. orientalis* and *B. variegata*. Early timing of embryonic events is plastic in anurans, and certain heterochronies were not confined to certain phylogenetic clades in our sample.

Isolation of Skate Elastin-Like Genes From the Skate and Their Developmental Role in the Skeleton

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The recent explosion in genomics has changed the landscape of biological inference. The bacterial artificial chromosome (BAC) library is a powerful genomic resource that has been utilized for positional cloning, large-scale genomic sequencing, as well as functional studies (e.g., as substrates for transgenesis, for identification of *cis*-regulatory elements). We have been constructing BAC libraries from numerous chordates and are beginning to use these reagents for functional studies of development and evolution of vertebrate morphology. We recently constructed a BAC library from the clearnose skate, *Raja eglanteria*, a representative chondrichthyan fish in which developmental series can be readily obtained. This library has been used for isolation of various genes and gene families, including elastin-like genes. Previous analyses have identified putative elastin-like molecules in the skeleton of several species of fish, particularly in bones, cartilages, dentine, and scales. Using the reagents at hand, we wish to more fully characterize the elastin-like molecules from the skate and their roles in the developing skate skeleton. In addition, we will characterize the genomic organization of the elastin BAC clones and use a combination of comparative genomics and empirical methods to identify *cis*-regulatory elements that drive expression of elastin genes in the skate skeleton.

Is Sand Swimming in Reptiles True Swimming?

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Sand-swimming reptiles move in an environment that has properties of both fluids and solids. Sand is a continuous medium that flows downward, but it does not flow upward to fill cavities and it does not form vortices, which are important to propulsion in many aquatic swimmers. I studied sand swimming in the scincid lizards *Pygomeles braconnieri* and *Voeltzkowia fierinensis* and in the colubrid snake *Chionactis occipitalis* by measuring the animal movement into and within loose sand. For the snakes, I also measured sand displacement and axial bending during undulation through dry and wet sand from the animals' natural habitat. On the surface, both lizards and snakes anchored posterior parts of the body while pushing the head into the sand. The lizards used their reduced hind limbs as anchors, whereas the snakes used bends in the body. The animals, particularly the snakes, moved through sand using undulations that were kinematically and mechanically more similar to the irregular bends used on surfaces with fixed push-points than to the broad and highly regular undulations used when swimming in water. Thus, although loose sand is a fluid-like medium, sand swimming in reptiles is more similar to terrestrial locomotion than to aquatic swimming.

Ontogeny of Contractile Performance and Physiological Capacity in Rattlesnake Shaker Muscle

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The tailshaker muscles of western diamondback rattlesnakes (*Crotalus atrox*) can sustain contractions of up to 100 Hz for minutes to hours. Shaker muscles are high in both aerobic and anaerobic capacity and have high blood flow that removes lactate and thus helps prevent fatigue. These features are known from adult snakes. However, rattling frequency and shaker muscle mechanics are size-dependent. To assess how shaker muscle function changes with size, we measured shaker muscle contraction frequency in snakes of 17–911 g, and then removed the tail muscles and measured maximal activities of the enzymes citrate synthase (CS) and lactate dehydrogenase (LDH). Rattling frequency at 30°C increased from ~10–100 Hz from small to medium-sized snakes, but then declined gradually to a maximum of ~70 Hz in the largest snakes. The increase in contraction frequency with size paralleled an increase in aerobic (CS) capacity, which remained high in snakes of all sizes despite the gradually declining contractile frequency in large snakes. There was no clear relationship between contraction frequency and anaerobic (LDH) capacity. These results suggest that the initial increase in performance in small snakes results from increasing aerobic capacity, and that the gradual decline in performance at larger sizes results from a nonphysiological factor, perhaps the increasing ossification and mass of the rattle base throughout life.

Phenotypic Flexibility in Response to Feeding and Fasting in Green Iguana (*Iguana iguana*)

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We studied flexible changes of morphology and physiology of the gastrointestinal tract of green iguana in response to feeding and fasting. This frequently feeding herbivorous lizard easily tolerates fasting periods of 2 weeks under natural and under experimental conditions. We studied 10 juvenile iguanas during feeding and a 10-day fasting period. Small intestine and liver size were measured daily using transcutaneous ultrasonography. Open system respirometry was used to record resting metabolic rates. Light and transmission electron microscopy were used to study histological changes in six individuals. The length of intestinal villi, the thickness of the mucosa, and the length of the microvilli were measured from micrographs. During the fasting period the size of the liver and the small intestine declined to 65% of feeding size. When animals were refed, the intestine returned to normal size within 3 days; liver size was reestablished within 2 days. These changes were accommodated by a transitional mucosal epithelium of the gut. Resting metabolic rate declined significantly during the fasting period. Within 48 h after refeeding the animals resumed normal resting metabolic rates. A comparison of the herbivorous iguana with carnivorous reptiles and amphibians shows the same general morphological features. Thus, a transitional mucosal epithelium seems to be a phylogenetically old feature that may be traced down to the stem group of tetrapods.

Giant Marine Vertebrates of the Past

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Vertebrates originated in water, and the majority continued to inhabit aquatic environments; these are primary aquatic vertebrates. Some aquatic vertebrates, however, are tetrapods, representing reinvasions of water by various vertebrate clades that once adapted to terrestrial environments (secondary aquatic vertebrates). The former usually use gills for primary respiration, and the latter lungs. Giants appeared among both primary and secondary aquatic vertebrates. Those approaching/exceeding an arbitrary value of 15 m in total length are found only in the latter, although there are debatable cases for the former. Physiological constraints from the respiratory system may be involved in this observed taxonomic bias, but such has never been clearly established. It is difficult to determine the maximum body size of an extinct species, because complete fossil skeletons of large individuals are rarely found. Accordingly, the maximum size is usually estimated from partial skeletons, or sometimes even based on isolated body elements. Estimates involving a large degree of extrapolation should be disregarded, and when scrutinized, only four clades of secondary aquatic vertebrates, viz., cetaceans, ichthyosaurs, mosasaurs, and plesiosaurs, seem to have defendable cases for giants in the body size range of 15 m or greater. Species exceeding 20 m are restricted to cetaceans, although there is one scientifically unreported case among ichthyosaurs worthy of debate.

Functional Morphology, Suction Performance, and the Enigma of Protrusion in the Nurse Shark, *Ginglymostoma cirratum*

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The functionally specialized nurse shark ***Ginglymostoma cirratum*** is nested within a clade of suction and filter-feeding sharks. Food capture was analyzed by electromyography and high-speed video on captive sharks and pressure-recording on wild sharks. Food capture, which is invariably by suction, is relatively stereotyped, rapid, and explosive, generating subambient pressures as low as –98 kPA. The terminal mouth is small and laterally bounded by enlarged and reinforced labial cartilages that pivot forward during jaw opening to form a tubular orifice for effective suction feeding. Maximum gape occurs in 32–56 msec, with the prey being ingested in ~36 msec. Jaw opening and buccal expansion are mediated by a conservative group of muscles similar to that of other sharks, but unlike that of most sharks, the preorbitalis and levator palatoquadrati muscles appear to play no role in palatoquadrate protrusion. Upper jaw protrusion, which reaches peak anteroventral excursion during the compressive phase of the bite, and is confined within the buccal cavity, is effected by a mechanism unlike most other sharks. Upper jaw protrusion apparently has little functional utility during its suction prey capture, which appears at odds with its unique biomechanical design, perhaps reflecting its shared phylogenetic history with other orectolobid sharks.

Intraoviductal Feeding in Embryos of *Schistometopum thomense* (Amphibia: Gymnophiona: Caeciliidae)

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Several observations indicate that fetal caecilians are nourished via secretions from the oviductal lining of the female. We here report our findings on *Schistometopum thomense*. Several collected females were found to be gravid, all containing fetuses in their oviducts that turned out to be well developed. The fetuses found were between 52 and 126 mm long and showed neither signs of gills or gill attachment sites, nor any other obvious larval characters like neuromast organs or fins. In one female, only one of the oviducts contained fetuses. The other was found to be empty, but hypertrophied and its internal surface lined with a thick, folded epithelium, which formed comparatively large grooves and folds, running along the entire length of the oviduct. This suggests that hypertrophy of the oviducts does not occur in response to local stimulus by developing embryos or fetuses, respectively. The walls of the oviduct containing the fetuses were much thinner and lacked the conspicuous ridges, except some small patches of similar thick epithelial lining. Detached pieces of epithelium were found floating inside the lumen of the oviduct. One of the fetuses had its mouth full with epithelium, indicating that it was feeding on it. These findings corroborate and supplement earlier observations by Parker (1956). Data on the histology of the epithelium and its secretions are presented.

Cardiorespiratory Coupling During Terrestrial Locomotion in Reptiles: Consequences of Intra-Abdominal Pressure and Respiratory Mechanics

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Functional integration of the cardiovascular and respiratory systems becomes increasingly important during elevated metabolic demands such as locomotion. However, this integration may be lacking in some reptiles. Cardiorespiratory coupling during treadmill locomotion was investigated in the Savannah monitor lizard, *Varanus exanthematicus*, and the American alligator, *Alligator mississipiensis*. In varanids, costal ventilation was reduced at high speeds due to the conflicting demands of ventilation and locomotion on the hypaxial musculature (axial constraint). Axial constraint was the likely cause of an increased intra-abdominal pressure (IAP) during exercise in varanids, and has important consequences for hemodynamics. Venous return is a major determinant of cardiac output and is affected by alterations in both ventilation and IAP. Ventilation, specifically expiration, aids venous return. The reduction in costal ventilation during locomotion in varanids reduces the supplementary effect of the respiratory pump on venous return. Elevated IAP collapses the major veins in the abdomen and decreases venous return. Alligators differ from varanids in their respiratory mechanics (hepatic-piston pump) and cardiovascular anatomy, both having important consequences for cardiorespiratory coupling during exercise. The respiratory pump is not compromised during terrestrial locomotion in alligators, and the small increase in IAP has no significant effects on venous return. Thus, cardiorespiratory coupling is compromised during terrestrial locomotion in varanids due to increasing IAP and axial constraint, but not in alligators.

Phylogeography of Cave Hyena and Cave Bear: Morphology Versus Genetics

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The geographical occurrences of the cave hyenas are widespread; however, the morphological differences are small and accounted to a single, mainly Eurasian species, *Crocuta crocuta spelaea*. Specimens from Africa are assigned to be the fossil forms of the modern *Crocuta*. The cave hyena entered Europe during the Middle Pleistocene and displayed a size fluctuation following the Bergmann rule. Therefore, British and Alpine material included very large specimens. New DNA investigations on recent hyenas and fossil ones from Europe confirm the close relationship between the spotted and the cave hyena, but shed doubts on the separation on a subspecies level. The mitochondrial DNA sequence of the cave hyena falls into two clades. One is different from the modern hyena, the other one falls into the clade of the modern spotted hyena. The genetic investigation indicates a lack of phylogenetic differentiation. The cave bear, on the contrary, is known only from Europe and evolved rapidly into four subspecies, all occurring at the same latitudes. They can be distinguished by four different clades of mitochondrial DNA and morphology: two subspecies at 2,000 m above the sea level and two in lowland areas. These very complex results support the recent investigations that phylogeographic patterns can develop even in the absence of geographical boundaries.

Skeleto-Muscular System of the Tongue of the Common Moorhen, *Gallinula chloropus meridionalis* (Aves, Gruiformes, Rallidae)

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The lingual apparatus of the Common Moorhen is distinguished from that of previously studied birds by its unusual structure of the skeleto-muscular system of the free part of the tongue. The paraglossale is entirely cartilaginous. The diarthrosis connecting it to the bony basihyale is crossed on its ventral surface by unpaired, purely elastic ligament. The one-joint paired M. hypoglossus anterior crossing the paraglosso-basihyal joint is subdivided into medial and lateral parts. A collagenous ligament originates from each hyoid horn and extends to either side of the paraglossale, thereby crossing both the unpaired paraglosso-basihyal and paired cerato-basiurohyal joints. This ligament has developed on the lateral surface of the two-joint M. ceratoglossus, whose muscle fibers originate from the ceratobranchiale, but insert mainly on this ligament in the Common Moorhen. The Common Moorhen lives in marshlands of the Nile Delta of Egypt as a migrant from Europe from November to February. Its diet consists of small fishes, crustaceans, and aquatic vegetation. Future studies will elucidate the causal mechanistic relationship between the diet, feeding mechanism, and morphology of the lingual apparatus of this species.

Molecular Developmental Studies of the Mammalian Middle Ear and Its Evolution

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Mammals are characterized by possession of three auditory ossicles in the middle ear, unlike the other amniotes with only one element called the columella, the homolog of the mammalian stapes. Reichert (1837) was the first to assume origin of the jaw joint, malleus, and incus. Although the above homology is generally accepted, we still do not understand how this change has occurred and which molecular mechanisms were involved behind this change. We constructed 3D images of the middle ear in chick and mouse embryos on the bases of histological observations, especially focusing on the developmental patterns of the tympanic membrane. In the chick, the first pharyngeal cleft and pouch extend, surrounding the columella in the second arch, whereas in the mouse the first pharyngeal cleft invaginates ventromedially and the first pharyngeal pouch extends dorsally to surround the otic capsule. Also, molecular analysis revealed that the *goosecoid* gene that is expressed specifically in the external acoustic meatus (EAM) and malleus in mouse, is expressed in EAM and articular (lower jaw element) in chick. Considering mouse specific signaling may cause the morphological changes, we are analyzing the *endothelin* gene pathway that includes *goosecoid* and is important in pharyngeal arches development. We also grafted murine cranial neural crest cells into chick embryos to identify mammalian specific signaling pathway during epithelium–mesenchymal interactions.

Phylogenetic and Developmental Constraints on the Mammalian Vertebral Formula in Terms of *Hox* Code Evolution

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The mammalian vertebral column consists of morphologically well-differentiated groups of vertebrae such as cervical, thoracic, lumbar, sacral, and caudal groups. Such a morphological specification is known to be regulated by the nested expression of the *Hox* genes along the anterior–posterior axis. In mammals, the number of cervical vertebrae is almost fixed at 7, while the number of other vertebral groups differs significantly between species. Differences in the vertebral formula are thought to result from changes in *Hox* gene regulation. To understand how the mammalian vertebral formula evolved, it is necessary to identify the emergence and the loss of developmental constraints along the mammalian phylogenetic tree. We collected vertebral formula data from 155 species in 17 mammalian orders based on the catalog of the Hunterian Collection by Richard Owen (1853) and plotted them onto the phylogenetic tree reported recently based on molecular data. Through analyses of the distribution of the vertebral formulae, we could identify some developmental constraints that were consistent with the body plans of mammalian groups that define the taxa. As a first step toward clarifying the evolutionary changes of vertebral formulae in terms of *Hox* gene regulation, we also report the comparative analyses between the chick and mouse *HoxC8* enhancer.

Tuning the Natural Frequencies of Locomotion and Breathing in Mammals and Running Birds

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Despite differences in the anatomy of the avian and mammalian respiratory and locomotor systems, the underlying mechanics of these systems in both groups of animals appear to behave in a similar manner. It has been shown that the respiratory system of mammals and birds has a natural, or resonant, frequency at which the respiratory impedance to breathing is minimized and the flow rate is maximized. It has further been shown that exercising mammals and birds run at a preferred speed, suggesting that locomotion may operate at a natural frequency at which the metabolic cost of transport is minimized. The observation that a 1:1 coupling between stride rates and respiratory rates in treadmill-run guinea fowl occurs at the natural frequency of both systems demonstrates that locomotion and respiration can be tuned to the same frequency, with the arguable benefit of enhancing aerobic performance. This suggests that despite their evolutionary independence, a similar mechanism combining neurological and musculoskeletal interactions was present in the drive for increased locomotor stamina in both mammals and birds, although more studies on these types of interactions need to be performed to determine the scope of this theory.

Origin of Ruminant Cranial Appendages: Biochronological and Biogeographical Aspects

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Ever since Darwin, the origin and evolution of ruminant cranial appendages has been considered a classic example of evolution by means of sexual selection. In addition to the economic and ecological importance of ruminants, their cranial appendages are relevant to the study of evolutionary novelties. Cranial appendages of seven extinct and extant ruminant families present profound anatomical, histological, and developmental differences, indicating that these structures appeared independently in each group. Data concerning extinct bovids and giraffids from Namibia and Pakistan provide a more complete picture of the geographical and temporal distribution of the earliest horned ruminants. Cranial appendages originated during the Early Miocene over a wide geographic area encompassing the Old World and North America. Latitudinal segregation related to the Alpine Orogenic Belt is evident. Cervidae, Lagomerycidae, Palaeomerycidae, and Antilocapridae appeared in boreal realms, while Bovidae, Giraffidae, and Climacoceratidae appeared in tropical ones. Cranial appendages in all these families originated during a relatively short time span, 19–17 million years ago, a period of major climatic change on earth (expansion of the Antarctic Ice Cap to continental proportions, resulting in increased seasonality worldwide). These observations indicate a fundamental relationship between the origins of cranial appendages and global scale environmental changes. Having originated, cranial appendages then became important in sexual selection.

Modeling Ballistic Jaw Movements Using Equations of Motion for a Damped Mass-Spring System

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During ballistic tongue projection, the mm. depressor mandibulae (DM) of toads produce high mass specific power ($>$7 W/g) with little storage of strain energy in other structures. To account for this high-power output, we imaged feeding (1,000 Hz) with simultaneous EMG, performed force-lever experiments, and made anatomical measurements. Imaging and the in/out-lever ratio were used to calculate DM shortening during fast mouth opening. EMG provided DM activation duration and amplitude preceding fast mouth opening. Using the force-lever, muscles were allowed to shorten at a series of reduced loads after 200 ms of isometric preactivation. The fast phase shortening distance was measured at each load, and a logarithmic function was used to estimate the displacement from equilibrium that occurred during isometric preactivation. Stiffness was calculated as force divided by displacement at the in vivo load. Time-dependent behavior was modeled using the equation for an underdamped mass-spring system. Three parameters (mass, stiffness, displacement) were acquired from experimental results. The damping coefficient was assumed to increase linearly with time. A sensitivity analysis demonstrates that the model is highly sensitive to displacement, fairly sensitive to stiffness and damping coefficient, and least sensitive to mass. A major implication is that isometrically preactivated muscle behaves as though it has experienced a large strain, and the strain increases with the duration of preactivation.

Ornithopod Jaw Mechanisms

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Ornithopod dinosaurs were relatively abundant and diverse members of an extinct clade of herbivorous diapsid amniotes of the Mesozoic Era. Their skulls exhibit a generally contradictory set of features: teeth arranged so as to become worn down to form obliquely inclined abrasive "pavements," isognathy, evidence of fleshy cheeks to allow oral processing through repetitive chewing cycles, and a keratinous beak. This curious anatomy provoked the suggestion that ornithopods were pleurokinetic: this mechanism permitting a power-stroke to be combined with an isognathic jaw framework. The pleurokinetic mechanism has been accepted quite widely, but the more detailed implications of the mechanism have not been considered. This article reviews pleurokinesis in ornithopods and discusses the osteology of the skull as well as the implications concerning associated soft tissues and their characteristics. It also considers the dynamic interactions between opposing "magazines" of teeth during jaw closure, and the constraints this places on the design of the lower and upper jaws as an integrated functional unit. Pleurokinesis has become well established as a mechanism that operated within a range of ornithopods; however, its presence is not universal within the clade. Factors governing the origin of the pleurokinetic mechanism are considered with respect to basal members of the clade and consideration is given to those factors that might result in its loss/nonadoption in some more derived taxa of ornithopods.

New Head Hypothesis Revisited

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In 1983 Northcutt and Gans (Q Rev Biol 58:1–28) proposed that unique craniate cephalic features were linked to the phylogenetic origin of neural crest, neurogenic placodes, and muscularized hypomere and that the origin of craniates involved the use of these tissues to reorganize the pharynx and elaborate the circulatory, digestive, and nervous systems (see also Gans and Northcutt, 1983, Science 220:268–274). Thus, craniates were said to have evolved a new head. It was believed that these changes occurred during a shift from filter feeding to active predation, a shift also involving the evolution of new sense organs. Twenty years later, it still appears that neural crest is a unique craniate embryonic tissue, although there are genetic indicators that a precursor tissue does exist in amphioxus. The claim that neurogenic placodes arose with craniates has been contested on both anatomical and genetic grounds, but present data are not persuasive. New data on the genetic basis of the induction of these placodes, however, suggest that they did not have a single origin. In the original scenario, most craniate neural and sensory tissues were proposed to originate from elements of the protochordate epidermal neural plexus. Outgroup analysis of metazoan fate maps, however, suggests that many unique craniate tissues arose due to a shift in the topographical position of mesoderm within fate maps.

Evolution of Underwater Hearing in Whales

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Ear morphology changed radically during the early evolution of whales in order to enable underwater hearing. In modern toothed whales the lower jaw receives and guides sound through an internal fat body to the lateral wall of the tympano-periotic complex, the tympanic plate. The ear is acoustically isolated from the skull by air sinuses, the malleus is synostosed to the tympanic plate, and the ossicular chain transmits sound to the inner ear. The earliest whales, pakicetids, could hear both air- and waterborne sounds. In air, the sound path was no different from that in land mammals: sound passed through the external auditory meatus to the tympanic membrane and the ossicular chain. Underwater, pakicetids relied on bone conduction, as do modern pinnipeds, and lacked directional hearing. Remingtonocetid and protocetid whales postdate pakicetids. Their ear morphology resembled that of modern dolphins. Underwater, sound passed through the lower jaw and the tympanic plate, bypassing the external auditory meatus and tympanic membrane. Directional underwater hearing was developed to some degree. Taken together, the modern toothed whale sound path evolved within about 7 million years of the origin of cetaceans, well before the origin of echolocation.

Distal Limb Pneumaticity in Extant Birds: Anatomical and Functional Correlates

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Postcranial skeletal pneumaticity results from invasion of the skeleton by air sac diverticula. Among extant sauropsids, postcranial pneumaticity is restricted to birds, and is often considered an adaptation to reduce body mass in this extremely energy-constrained group. Commonly pneumatized elements include portions of the axial skeleton, limb girdles, and proximal limb bones, whereas distal limb elements are rarely pneumatized. Taxa exhibiting distal limb pneumaticity (DLP) include such varied groups as anhimids, bucerotids, cathartids, and certain pelecaniform and gruiform birds. The goals of this study are twofold: 1) to examine the anatomical basis of distal limb pneumaticity (i.e., how do pneumatic diverticula gain access to distal limb elements), and 2) to explore functional hypotheses regarding the distribution of distal limb pneumaticity in extant birds. Results from this study demonstrate that DLP is correlated with a subcutaneous diverticular network. This network is usually quite extensive, covering much of the dorsal and ventral surfaces of the thorax and forelimb. Subcutaneous diverticula associated with the hindlimb are less common. Although DLP is often associated with large body size, small-bodied bucerotids do exhibit pneumatic distal limb bones. Flying behavior also appears to correlate well with DLP, in that birds utilizing soaring (e.g., cathartids) and semisoaring behaviors often have pneumatic distal limb bones.

Molecular Evolution of the Endostyle

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The endostyle is a pharyngeal organ used in internal filter feeding in lower chordates, such as urochordates, cephalochordates, and larval lampreys. Despite the different histological organization of the endostyle among these species, this organ has an iodine-concentrating function and, therefore, it is generally thought to be related to the vertebrate follicular thyroid. Several lines of molecular evidence, such as the prominent expression of the thyroid transcription factor-1 (TTF-1) gene in the endostyle, and expression of the thyroid peroxidase (TPO) gene in the thyroid-equivalent region of the endostyle, support this scenario. However, overlapping expression of these genes in the follicular thyroid was not observed in the endostyles. To investigate the molecular mechanisms involved in the formation and function of the endostyle, with special reference to the evolution of the follicular thyroid, further analyses of several thyroid-related gene expressions were performed in lower chordates. The TTF-2 gene, which encodes a FoxE class winged helix/forkhead transcription factor for the regulator of *TPO*, was expressed exclusively in the thyroid-equivalent region of both ascidian and amphioxus endostyle. The expression pattern of *Pax258,* which is an ancestral gene for *Pax8,* was closely related to that of *TTF-1. FoxA* and *FoxQ* were also prominently expressed in the endostyle. These observations might provide insight into the evolutionary relationship between the endostyle and the follicular thyroid.

Development of the Parachordal Chondrocranium in *Pelobates* and *Scaphiopus* (Anura: Pelobatidae)

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The parachordal region of the chondrocranium was reconstructed from serial sections of larval and metamorphic stages (Nieuwkoop and Faber stages 46–66) of *Pelobates fuscus* and *Scaphiopus holbrooki*. The basic structural scheme develops similarly in both genera; however, some differences were also recognized. For instance, in *Pelobates* the septum separating the posterior semicircular canal from other parts of the otic capsule becomes reduced and ultimately disappears, whereas it persists even in metamorphosed *Scaphiopus*. The operculum of *Pelobates* can be recognized at the beginning of metamorphosis, whereas considerably later in *Scaphiopus*. In both genera the pars interna plectri and pars media plectri arise during metamorphosis from ligamentum suspensorio-columellare, from independent ossification centers. In contrast, the pars externa plectri is not present even in adult *Pelobates*, whereas it does develop after completion of metamorphosis in *Scaphiopus*. In general, the ear ossicle is completely developed in *Scaphiopus*, but only partly in *Pelobates*. Perichondral and endochondral ossification (manifested by remarkable thickening of the otic capsule walls) starts earlier in *Pelobates* than in *Scaphiopus*. A significant difference is that in *Scaphiopus* there is an accessory connection between the posterior margin of the palatoquadrate and anterolateral surface of the otic capsule, posterior to the basal articulation, whereas it is absent in *Pelobates*. With the exception of the latter, most of these differences may be ascribed to heterochrony.

Skull Asymmetry in Toothed Whales: Methods of Measurement, Interspecfic Comparisons, and Evolutionary Trends

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The odontocete skull is a bizarre and intriguingly complex structure due to dorsal migration of external nares (telescoping), but also because of directional skull asymmetry, a hallmark of the suborder. Within the group, variation in the degree of asymmetry is obvious to the naked eye. Surprisingly, only a single study (Ness, 1967, J Zool 153:209–221) has previously attempted to systematically quantify asymmetry to facilitate interspecific comparisons. This is due to problems involved with establishing a midsagittal axis from which to compare asymmetrical landmarks. Furthermore, indices used in Ness' study were calculated from only two landmarks, revealing little about the distribution of asymmetrical structures within the skull. We present preliminary results from a survey of skulls representing 35 odontocete species, for which we compare axis-based and axis-free methods of quantifying asymmetry. For the latter method, we employ a novel use of procrustes analysis to describe asymmetry using 15 bilaterally distributed landmarks. Previous suggestions that degree of asymmetry may correlate strongly with skull size or dorsal projection of the skull vertex into the soft tissues of the nasal complex are not supported. When interpreted within a phylogenetic framework, it is demonstrated that the most basal odontocete groups (Ziphiidae, Physeteridae, Monodontidae) possess the most asymmetrical skulls, suggesting a strong phylogenetic signal in the distribution of asymmetry.

Morphogenesis and Evolution of the Cranial Musculature and Skeleton in Lungfishes and Amphibians

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I report on a comparative project, the goal of which is to describe the order of acquisition of innovations in selected phases of amphibian evolution. Both skull and cranial muscle development are studied. I present selected parts of this ongoing project, including cranial muscle differentiation and morphogenesis in the Australian lungfish and in Mexican axolotl, cranial muscle and skeleton development in *Xenopus laevis* and its relative *Hymenochirus boettgeri*, as well as skull development and morphology in a caecilian, *Ichthyophis kohtaoensis*, a burrowing animal in which the head is used as a locomotory organ. To determine the onset of differentiation we use antibodies against desmin and optical sectioning using confocal laser scanning microscopy on whole-mount immunostained embryos. Antibodies against acetylated tubulin are used to clarify muscle innervation patterns, and collagen II staining gives an overview of developing cartilage. This technique makes it possible to document head development in three dimensions while keeping the specimens intact. To obtain an appreciation of complicated 3D structures in the head, we use reconstructions based on serial sections (two different methods are shown). The project provides a morphological foundation for further studies of the head skeleton as well as cranial muscle cell fate and early differentiation in a comparative context. The focus is on understanding the developmental origins of morphological innovations.

Asymmetries in Feeding and Respiration in the Hogchoker, *Trinectes maculatus*

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We investigate the purpose and function of extreme morphological asymmetry of the jaw apparatus in flatfishes. Flatfishes are specialized to reduce visibility to predators by burying in sediment while maintaining 360° vision to feed on benthic organisms. We used the hogchoker, the most asymmetrical flatfish studied to date, to test the general hypothesis that the eyed side of the mouth is specialized for respiration and the blind side of the mouth is specialized for feeding. During feeding, the upper jaw protrusion is minimal on the eyed side while, the blind side upper jaw elements swing towards the substrate. During respiration, water enters the buccal cavity through the opening and closing of a flap on the eyed side of the mouth; no water appears to enter through the blind side of the mouth. These results suggest that the mouth is divided into two functional units: the blind side is primarily used for feeding and the eyed side is primarily used for respiration. Although the two halves of the head must work together, anatomical modifications allow separate functions for each side of the head. In addition, the mechanism that produces feeding asymmetry in hogchokers is markedly different from that described for other flatfishes.

Development of the Dogfish Spiracular Organ and Chick Paratympanic Organ: Placodal Origins and Evolutionary Implications

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Cranial neurogenic placodes give rise to paired peripheral sensory organs in all vertebrate species. These regions of epidermal thickening are thought to have evolved from areas of mechanosensory hair cells on the heads of ancestral organisms. Not all placodes, however, are known to produce ciliated hair cells; the trigeminal and epibranchial placodes produce neurons exclusively. Here, we examined the development of two homologous organs in dogfish and chick that are thought to derive from the geniculate placode, yet contain ciliated hair cells. The dogfish spiracular organ (SO) is a small, pouch-like structure associated with the first gill cleft. Although its function is unclear, it is known to contain ciliated neuromasts and is believed to be a lateral line organ. The chick homolog of the SO is the paratympanic organ (PTO). Found in the middle ear, this structure may have a role in measuring barometric pressure. Although often referred to as a lateral line remnant, the chick has no known lateral line placodes. We aimed to determine whether the SO/PTO are derived from epibranchial placodes, or from a novel lateral line placode. Using in situ hybridization, we analyzed the expression of various molecular placodal markers. The results shed light on the true developmental origins of the SO/PTO and provide insight into the likely evolutionary history of the neurogenic placodes in vertebrates.

Is There an Evolutionary Tradeoff Between Force and Speed in Limbless Burrowing?

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In limbed locomotion, there is generally a tradeoff between high-speed movement on the one hand and strength on the other. The tradeoff between speed and force is unavoidable because reaction forces generated during limbed locomotion are transmitted via biomechanical levers and lever systems cannot be optimized for both force and speed. Similar performance tradeoffs in limbless locomotor systems have not been documented. However, preliminary observations indicated that species living in loose substrates (e.g., sand-swimming skinks) were capable of faster movements than species specialized for burrowing in more resistant substrates (e.g., burrowing amphisbaenians). A 20-fold range in maximum burrowing forces (scaled as a function of body cross-sectional area) appeared to be negatively correlated with dramatic differences in both maximum burrowing speed and sprint speed in artificial tunnels. To explore the hypothesis that the evolution of locomotor performance in limbless burrowers is subjected to force-speed tradeoffs, we performed kinematic and kinetic analyses on a variety of fossorial tetrapods that penetrate the substrate using only their heads and axial musculature. Maximum burrowing speed, maximum sprint speed, and maximum pushing force were then analyzed in the context of previously proposed phylogenetic hypotheses.

Terrestrial and Aquatic Locomotion in the Mudskipper *Periopthalmus argentilineatus*

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Amphibious fishes are superb organisms for studying biomechanical contrasts between aquatic and terrestrial locomotion. Perhaps the most well-studied amphibious fish is the mudskipper, which is known to use pectoral fins for terrestrial and aquatic locomotion. During terrestrial locomotion, the pectoral fins synchronously protract and then retract to generate thrust. While swimming, the pectoral fins are used for paddling (during slow locomotion) and steering. We hypothesized that the kinematics of terrestrial movements of the pectoral fins are significantly different than the kinematics of aquatic movements. Both lateral and ventral views of aquatic and terrestrial trials were filmed at 125 frames/sec using a high-speed digital camera system. Sequences were digitized in NIH image and 3D coordinates were calculated. Mudskippers have a unique pectoral fin, where the radials protrude from the body wall to form a fin that effectively has two joints. In terrestrial locomotion, the most proximal of these joints (the basal lobe formed by the radials) is anteriorly extended farther than in aquatic locomotion, and therefore increases the stride length of each pectoral fin during retraction. In contrast, aquatic pectoral fin use is characterized by extended rays, such that the fin surface area is much larger than that in terrestrial locomotion. As representatives of amphibious fishes, mudskippers demonstrate one method of balancing the demands of terrestrial and aquatic locomotion.

Characterization of Two Novel Genes Specifically Involved in Fin Development in Zebrafish

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In a screen for genes differentially expressed during fin regeneration in adult zebrafish, we identified two novel genes of the same family coding for secreted proteins with unknown function. Besides their expression during fin regeneration, we found that they are specifically expressed in the fin buds of zebrafish embryos. In pectoral fin buds, expression is first restricted to mesenchymal cells of the progress zone underneath the apical ectodermal ridge, suggesting a possible role in maintenance of bud outgrowth. Later, expression is also observed within the developing fin folds of both paired and unpaired fins. The paired fins are phylogenetically related to the limbs of higher vertebrate species and we and others demonstrated that many of the genes and developmental pathways involved in their development are similar. However, database searches revealed very limited similarity between 2-H06 or 2-F11 and proteins from the mouse and human. However, related sequences are present in the genome of *Takifugu rubripes*, another teleost fish. This raises the interesting possibility that the encoded proteins are specifically involved in fin development and would be good candidates to understand the evolutionary aspect of the transition from fin to limb. Functional investigations using a gene knockdown approach in zebrafish are currently under way.

Origin of the Avian Body Plan

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Neornithes (crown-group birds) differ substantially from the first birds of the Late Jurassic and Early Cretaceous. Basal Aves (*Archaeopteryx* and all more derived forms) were much like their small contemporaneous theropod dinosaur relatives, but their feathered wings and tail provided flight. Flight shaped much of bird evolution, but not all of it. The locomotor emphasis shifted: the tail module differentiated from the hindlimb module, and the forelimb module gradually dominated as flight evolved. Flight evolved as bird ancestors reduced their body size to the point that the feathered limbs were aerodynamically effective. They did this by truncating the normally rapid period of growth at juvenile stages. At this size, feathers became aerodynamically effective. Nonavian bird relatives already had a motion capable of producing the flight stroke, but it was used in the context of prey capture. The wishbone evolved in this functional context. Feathers evolved for insulation, color, and other behaviors, but flight evolved later. Many skeletal features associated with birds were already present in their nonavian relatives, sometimes with a different function. Basal stem-group birds fused some skeletal elements, reduced the tail, lost teeth, expanded the respiratory adaptations, and evolved the alula.

Variability and Morphogenesis of Mammalian Teeth

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A comparative approach to studying patterns of morphological variation and evolution is a powerful perspective from which to scrutinize morphogenetic processes and their evolutionary effects. The mammalian dentition provides an excellent model system for such studies because its development is now well understood, because it has an excellent fossil record, and because its morphology is easily quantifiable in a way that can be related to morphogenetic processes. I made a comparative study of molar shape variation and divergence among intra- and interspecific populations of shrews and marmots to determine the relationship between phenotypic covariance and divergence patterns and development. Major axes of shape variation, or phenotypic covariance matrices (P), within populations generally correspond with developmental expectations. Furthermore, cusp features, which are associated with molecular signaling centers during development, have higher heritabilities than do notch features, which are associated with interactive events that lie downstream of cusp tips in morphogenesis. Additive genetic covariances in shape are more precise predictors of evolutionary divergences than are the raw phenotypic covariances. P evolves rapidly, showing significant differences over tens of thousands of years, but the gross pattern of covariance does not change substantially, suggesting that significant constraints (developmental or functional) are operating.

Does the Nasal Septum Support the Cranioskeleton?

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The ability of the nasal septum to support the facial framework depends on its having comparable stiffness to the nearby facial structures. This study tested the hypothesis that the septum is stiffer than the nasofrontal suture in the pig, *Sus scrofa*. The nasofrontal suture and nasal septum were cut into rectangular test pieces and mounted in an MTS/Sintech materials testing machine for stress-relaxation testing. The loading rate of 0.03 mm/sec mimicked the physiological strains of sutures during chewing. The nasofrontal suture was tested in compression and tension ($n = 3$), whereas the septum was tested only in compression, but either in vertical or horizontal orientation ($n = 4$). For all locations and testing methods, peak stress and relaxed stress were linearly related to strain, and both sutures and septum were viscoelastic regardless of testing modality or orientation. Both peak and relaxation moduli for the nasofrontal suture were higher than for the nasal septum (16–54 MPa vs. 0.33–2.75 MPa, respectively). Furthermore, the nasal septum showed a greater reduction in modulus from peak stress to relaxed stress (39–62% for septum vs. 16–23% for suture). During chewing the septum would deform more than sutures under the same chewing loads, and would become increasingly more deformed during clenching. Thus, the septum is unlikely to be a significant support for the sutures during function.

Functional Shape of the Skull Under Consideration of Ancestral Synapsids and Primates

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Simple, unspecific models of the facial skeletons of higher primates (including fossil hominids) and the entire skull in ancestral primates were loaded by bite and chewing forces. The stress flows in these unspecific models are very similar to the arrangement of bone material in real skulls. Morphological differences between mammals and reptiles have been shown to depend on a priori given conditions: size of the braincase, length and position of the toothrow in relation to the braincase, arrangement of muscles, position and direction of the orbits, and position of the nasal channel. In long-snouted lower primates, and in ancestral synapsids, the application of external forces to the skulls seems to play a more prominent role than in higher primates, and their influence is therefore compared to that of masticatory forces. FES-analysis shows again the close similarity between stress flows and real skulls. A major difference between primates and mammal-like reptiles is the size of the brain. This difference accounts for most of the morphological divergence.

Hand Development and Sequence of Ossification in the Forelimb of the European Shrew *Crocidura russula* and Comparisons Across Therian Mammals

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Histological sections, cleared and stained specimens, and macerated skeletons of an ontogenetic series of the common European shrew *Crocidura russula* were used to document hand development. A prenatal specimen (about 20 days after conception) has three cell condensations that, because of their topological position, are homologized with a centrale, the lunatum, and the styloid process of the radius. These elements are at birth already lost, fused, or, in the case of the lunatum, just fusing. The adult carpal arrangement is found only after birth, which occurs 30 days after conception. As in other placental mammals, several changes in carpal number and arrangement occur during development. We compared the relative sequence of ossification of forelimb elements in *Crocidura russula* with that of 19 other therian mammals and one outgroup (*Alligator mississippiensis*) in a phylogenetic context, using data from the literature and the event-pairing method. There are no major deviations in the ossification sequences of shrews in comparison with other placentals. The bat is unique for several characters, mostly concerning acceleration in the onset of ossification of more proximal hand elements in relation to more distal ones.

Original Lujanian Megatherioidea From Peru: Implications Concerning the Locomotion of Sloths

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Lujanian localities from the coastal site Piedra Escrita and the Andean Cave Casa del Diablo have yielded three specimens of a new Tardigrada (Mammalia: Xenarthra). This original fossil sloth exhibits a peculiar mosaic of characters. Some of these are probably convergent (e.g., 5/4 quadrangular teeth, a formula characteristic of Megatheriidae), while others indicate arboreal capabilities, distinct from the suspensory locomotion of extant sloths. The arboreality of this sloth is suggested by poorly constrained elbow, hip, and ankle joints, a short olecranon and a convex posterior border of the ulna, good capacities of pronation-supination, a wide range of dorsiflexion at the wrist, and hook-shaped digits. This new taxon underscores the great diversity of locomotor modes that evolved in Tardigrada: an arboreal species is now added to the already known terrestrial, subarboreal, and aquatic sloths. A preliminary phylogenetic analysis suggests that the evolutionary history of Megatherioidea has been influenced by locomotor adaptations.

Recognizing Stem Group Vertebrates and Their Importance in Understanding the Evolution of the Body Plan

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Living jawless vertebrates and invertebrate chordates are few in number and potentially exhibit derived morphologies. Consequently, extant animals can tell us little about the origin and early evolution of vertebrates, and fossils hold the key to understanding how and when the vertebrate body plan was assembled. Recognition and interpretation of the vertebrate stem group, however, are fraught with difficulties. Exceptionally preserved fossils, such as *Yunnanozoon, Haikouella*, and *Haikouichthys* from the Chengjiang Lagerstätte provide clear illustrations of this. Although exquisitely detailed, these fossils can be misleading: they are not "preserved specimens" in the biological sense, but the products of capricious fossilization—carbonized residues and mineral replacements of partially, and variably, decomposed carcasses. Anatomy cannot simply be read directly from the fossil, and complications arise because interpretation is necessarily predicated on comparisons with extant organisms, which inevitably color subsequent anatomical determinations and hypotheses of affinity. Analysis of the origins and early evolution of vertebrates would benefit from more careful interpretation of the fossils, paying closer attention to their taphonomic history and with greater awareness of the unintentional consequences of anatomical comparison. More rigorous application of stem lineage concepts, with stem taxa identified from explicit hypotheses of relationship, not based on a checklist of key characters of the vertebrate body plan, would also help to illuminate the murky depths of the clade.

Tooth Microwear Determinations of Trophic Niche in Three-Spined Sticklebacks

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Understanding the ecological controls on the origin of new species is central to understanding evolution. Much recent work has focused on competition for food resources as the cause of speciation through ecological character displacement. Tracking feeding patterns over time is central to this research, but this is difficult for living animals and almost impossible for fossils. Yet it is fossils that hold the key to looking at speciation over evolutionary timescales. Tooth microwear may provide some answers. Sticklebacks (*Gasterosteus aculeatus* species complex) are important model organisms in investigations of ecology and evolution and we report here the results of an experimental investigation of tooth microwear in stickleback populations raised under controlled laboratory conditions. Our research indicates that stickleback teeth develop clear patterns of microwear that reflect tooth use and feeding strategy. Quantitative analysis demonstrates that tooth microwear provides an accurate guide to trophic type. The method will be of great use for unraveling the diets of fossil fish, but can also be used to determine the foraging niche of extant fish where information on diet is not available.

Using Finite Element Analysis to Investigate Intracranial Mobility: A Case Study Using Large, Carnivorous Dinosaurs

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Finite element analysis (FEA) can be used to investigate the mechanical significance of sutures and regions of intracranial flexibility in skulls. By modeling the stress response to feeding forces in an FE skull model (with appropriate boundary conditions), one can compare the axis of distortion and orientation of stress and strain in the model to the degree of movement at actual sutural contacts in the real skull. Hypotheses detailing the effect of introducing patency or flexibility on mechanical performance can be constructed and subsequently tested. In this study, the correlation between stress environment, cranial strength, and sutural morphology and mobility is investigated in the cranium of the large theropod dinosaur *Allosaurus fragilis*. Theropods are an especially interesting model system because their skulls were massive (over 100 cm in some cases), may have generated extremely large bite forces, yet patent sutures persisted between many of the facial bones. In this analysis it was discovered that *Allosaurus* cranial sutures appear generally capable of accommodating stress and strain patterns generated during biting, although a dual-feeding regime may have been present. This study highlights the potential of FEA in devising and testing hypotheses of form and function, and argues that useful information can be obtained from FE models of extinct animals, providing that adequate assumptions are made and appropriate questions asked.

Homology of the Harderian Gland

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The Harderian gland is an enigmatic glandular structure in the anteromedial part of the orbit of most tetrapods. However, the homology of the various ocular glands referred to as the "Harderian gland" has never been addressed. Using a series of three tests, we assess whether the previously described "Harderian glands" of the various tetrapod groups are in fact homologous structures, or whether these structures represent unrelated, independently derived orbital glands. The only contentions for the test for similarity are the incorrectly described posterior "Harderian gland" in turtles, and the obligatory association of the "Harderian gland" with the nictitating membrane. Absence of the nictitating membrane does not result in the loss of the "Harderian gland." The test for conjunction is only potentially violated in some mammals, in whom a "nictitans" gland could potentially be confused with the "Harderian gland." However, it appears that the "Harderian gland" in these species is a bilobed structure, in whom the "nictitans" gland is only the anterior, nonmucous secreting lobe. Finally, the presence of the Harderian gland appears to be plesiomorphic for Tetrapoda, whereas its absence is an apomorphic attribute of only certain tetrapod lineages. This satisfies the test for congruence. The numerous anterior ocular structures known as the "Harderian gland" thus pass all three tests of homology and thus can be considered homologous.

Integrating Locomotor Energetics, Mechanics, and Gaits: Insights and Key Directions

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In recent decades the study of terrestrial locomotion has seen a welcome and varied array of perspectives at the organismal level. Mechanical studies have used locomotor forces to reveal energy-saving mechanisms used by animals. Energetic studies have related patterns of center of mass fluctuation and oxygen consumption to the work, power, and cost of movement. Kinematic studies have quantified footfall patterns (gaits) which reveal similarities in the output of the complex neuromuscular control of limbs in quadrupeds. It is of great interest to know how patterns of limb movement, produced by neuromuscular mechanics of tetrapods, relate to patterns of mechanical energy fluctuations and energetics. Yet to date these seemingly complementary fields have seen little integration and, in fact, remain quite isolated. I attempt to synthesize and integrate the conceptual landscapes of the mechanical, energetic, and gait approaches to the study of locomotion (each reviewed in the previous presentations in this symposium), and attempt to overlay these landscapes to identify emerging patterns and connections between them, and to expose new insights and future directions to understand how the neuromuscular control of tetrapod axial and limb systems moves the center of mass to take advantage of energy savings to increase the efficiency of locomotion.

Life History, Morphology, and the Transition to Dry Land

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In basal members of the three living amphibian groups—frogs (Anura), salamanders (Caudata), and caecilians (Gymnophiona)—a more-or-less terrestrial adult phase is associated with an aquatic larval phase, and metamorphic remodeling adapts the aquatic larva to the terrestrial environment. The aquatic larva almost certainly represents a retained primitive feature; this suggests that the evolution of increased terrestriality in adults was tied to the evolution of a biphasic (metamorphic) life cycle. If this occurred before the divergence of the living amphibian groups from their common ancestor, we should expect to find ancestral metamorphic changes preserved in the ontogeny of recent forms. Here I compare metamorphic changes among the three living amphibian groups using examples from my own work on the skull and the olfactory organ, as well as literature data on other organ systems. The data generally do not support the notion of a retained ancestral metamorphic pattern in the modern groups. They also show that a simple correlation with environmental change cannot fully explain the metamorphic changes we do see. However, the lack of data on an appropriate outgroup makes it unclear whether both larvae and adults of the modern groups have merely diverged since their most recent common ancestor, or whether they have independently pursued the path to a biphasic life history and terrestriality.

Dual Coupled Respiratory Oscillators in Amphibian and Mammals: Are they Homologous?

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Gill or buccal ventilation and lung ventilation in the tadpole and frog are driven by separate buccal and lung neural oscillators which appear to be coupled by postsynaptic inhibition. The respiratory rhythm in rats also derives from two separate but coupled oscillators: the pre-inspiratory (pre-I) and the pre-Botzinger (pre-Bot) rhythm generators. The sequence of activation of the coupled oscillators in both animals suggests possible homology, since in both cases a "preparatory" burst (buccal or pre-I) in oropharyngeal dilators immediately precedes the "power stroke" burst (lung or pre-Bot). The rat oscillators display differential opioid sensitivity (pre-Bot $>$ pre-I), a μ-agonist, causes quantal slowing, i.e., "dropped beats." Here we report similar behavior in the frog. In intact unanesthetized frogs morphine caused a replacement of lung events with buccal events without changing the overall frequency of respiratory events. In the isolated brain stem of tadpoles and frogs, the μ-agonist, DAMGO, preferentially decreased the lung frequency in a dose-dependent fashion. When frequency was increased by hypercapnia in frogs, DAMGO caused a quantal increase lung period reminiscent of that reported for the rat. We suggest that the respiratory CPGs of mammals and amphibia have a common origin in an early air breather using a buccal "force pump."

Sex, Soma, and Evolution: Insights From the Developing Marsupial

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Marsupials are distinguished from eutherian mammals in their mode of reproduction and their greater dependence on the teat and mammary gland than on the placenta for development. They give birth to a highly altricial young that completes its development while firmly attached to a teat, usually within the confines of a pouch. They have many characteristic features that make them ideal models to study the control of sexual differentiation and development. At birth, the marsupial neonate has a well-developed digestive, respiratory, and circulatory system but retains its fetal excretory system with a fully functional mesonephric kidney and undifferentiated gonads and genitalia. Almost all of their sexual differentiation takes place after birth. Although the role of genes in the differentiation of the testis and ovary has been extensively studied in the human and the mouse, the precise roles of genes and their interactions in the pathway of sex determination is still not fully understood. The genes and hormones involved in gonadal differentiation are highly conserved between eutherians and marsupials, but the timing of the developmental events differ. By taking a comparative look at sex determination and differentiation we have gained some surprising insights into the evolution and conserved functions of the developing mammalian urogenital system and the genes and hormones that control this process.

Comparative Analysis of Ossification in the Presence/Absence of a Defined Growth Plate

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Evolutionary diversity of skeletal form is partially achieved through modifying physeal growth. While the molecular mechanisms regulating chondrocyte proliferation and maturation are being clarified, little is known regarding how the location and growth rates of physes are specified. Because metatarsals develop only a single growth plate, proximal and distal ossification patterns differ substantially. We compared protein signals in these two areas of ossification in order to identify factors responsible for the formation and establishment of growth plates, as well as to potentially uncover targets by which natural selection can specify longitudinal growth. Thin-sliced, paraffin-embedded metatarsals from neonatal to 14-day-old mice were stained with safranin-O or monitored for protein expression via immunohistochemistry. While initially similar, the histomorphologies of the two ends diverge with respect to the organization and size of their proliferative and hypertrophic zones. However, PTHrP, Ihh, and Bcl-2 protein can still be detected in the chondrocyte populations of both ends. This suggests that the PTHrP/Ihh feedback loop may not be the specific signal that initiates growth plate formation. Other signals may modulate Ihh and PTHrP expression levels or may specify growth plate formation independently.

Organization of Discrete Fibers in Dinosaur Bones

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The directional organization of the fibers in bone is important because it influences both the Young's modulus and the resistance of the tissue to fracture. Measurements of the birefringence in thin sections of bone under polarizing microscopy have recently shown an association between fiber direction and tensile stress direction. The degree of birefringent brightness correlates with the degree of divergence of fibers from the plane of the section, but does not resolve the directions of the fibers within that plane. We have found bone tissue of several late Cretaceous dinosaurs in which directions of discrete fibers are visible in thin sections with plane light microscopy. Secondary osteons in these specimens typically have an outer zone in which the direction of fibers is circumferential but may deviate from the horizontal plane. Between the zone of circumferential fibers and the central canal is a thicker zone in which the average fiber direction is longitudinal. Near the junction of those zones, fibers are occasionally seen that progressively change direction to assume that in the adjacent zone. A narrower zone of circumferential fibers may also occur adjacent to the central canal. In secondary osteons of a fibula, zones of circumferential fibers are more extensive than those in ribs of several specimens, consistent with a relatively greater proportion of longitudinal compressive stresses predicted for the fibula.

Beyond Imaging: Using 3D-Datasets in Comparative Morphology

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Imaging modalities such as computer tomography and magnetic resonance have long provided the opportunity to noninvasively peer inside organisms. However, recent technological developments have permitted morphologists to move beyond a series of 2D slices to a 3D digital representation of vertebrate anatomy that may be queried for different kinds of analyses. First, for example, specific tissue elements (e.g., neural structures, inner ear canals, pneumatic sinuses, neurovascular canals, vessels, muscles) can be extracted, or "segmented," from the 3D dataset, rendered in 3D in isolation or with other elements, and manipulated in real time, facilitating the morphological visualization of each element, as well as their interrelationships. Moreover, a wealth of metric data (e.g., volumes, areas, distances, angles) can be calculated for each segmented tissue or cavity with unparalleled precision. Second, datasets from different modalities, such as CT and MR, can be registered and integrated into composite 3D models combining the best attributes of each modality. Third, for fossils, enclosing rock can be digitally removed from the 3D dataset, but, more significantly, the 3D dataset can be modified, allowing "virtual restoration" of not only missing or damaged bony structures but also addition of hypothesized soft-tissue elements. Finally, these 3D datasets can be exported to finite element analysis software for engineering studies, and physical models can be produced through stereolithography for presentations or education.

Breaking Organisms Into Parts: Similarity, Stereotype, and Homology

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There is a well-known tension between morphologists and systematists about the nature of morphological characters used in phylogeny reconstruction. Typically, morphologists find systematists to lack respect for the relevant theoretical context when breaking up organisms into character states that are deployed in phylogenetic analysis. Indeed, contemporary systematic theory accommodates anything arbitrarily chosen as a potentially informative character just as long as the character statements that predicate those properties on organisms or their parts cohere to some degree with one another. The justification for the use of coherence of logically independent character statements in support of hypotheses of phylogenetic relationships is based on an empirical presupposition that is also known as Hennig's auxiliary principle: assume homology in the absence of contrary evidence. Functional morphologists worry that such a method will leave undiscovered coherent sets of interdependent characters that are co-instantiated because of functional correlation, and developmental biologists worry that character statements remain hanging in the air, unless there is one or several ropes that descend to root them in the causal mechanisms of generative entrenchment of the property to which the character statement corresponds. I propose to use Putnam's meaning vector for natural kind terms as a way to approach the issue of morphological characters relevant to the theory of phylogeny reconstruction, building on the idea that the hierarchy of groups within groups is a stereotypical (descriptive) representation of a hierarchy of properties that itself is rendered epistemologically accessible through investigation of its causal roots in functional and developmental morphology.

Kinematics of the Righting Response in Inverted Turtles

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The ability of animals to right themselves from an upside-down position is critical to survival, particularly during predator encounters. In most vertebrates, righting is achieved through vigorous movements of the axial and appendicular skeleton. However, turtles have limited axial mobility because their vertebrae are fused to a bony shell; in turtles, only the head, neck, tail, and limbs are free to transmit forces used to right. How do inverted turtles turn themselves over? We used high-speed video (500 Hz) to compare the righting kinematics of several turtle species (including trionychids, emydids, chelydrids, and kinosternids). All species examined use the neck as a lever to accelerate the body during flipping, and tend to pull the limbs from the substrate and project them in the direction of rotation, possibly adding momentum to the flip. However, other aspects of righting behavior vary substantially among species that differ in neck and tail length and shell height and width. For example, unlike other turtles, chelydrids can use their unusually long tail to initiate righting. In addition, although most species appear to elevate the shell off of the substrate after the midpoint of the flip, sliders lift the shell from the substrate before it is perpendicular to the ground. Morphological comparisons indicate that turtles with high neck-length to carapace-height ratios are able to right most rapidly.

Turning Performance of Freshwater Turtles During Swimming

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Rigid bodies are a stable design for life in aquatic habitats, but a rigid body can limit the ability of animals to maneuver and perform turns while swimming. Rigid-bodied fishes (e.g., boxfish) perform maneuvers using multiple fins supported by flexible bony rays. However, rigid-bodied freshwater turtles possess jointed limbs, rather than flexible fins. How does the use of jointed propulsors, rather than flexible ones, affect the turning performance of swimming vertebrates? To examine this question, we used high-speed video (100 Hz) to record routine aquatic turns in multiple species of freshwater turtles. Agility (i.e., angular velocity of turning) is typically lower in turtles than in other rigid-bodied animals of similar size. However, differences in turning behavior and performance are evident among turtle lineages with different body shapes. For example, softshells, with flat shells and extensive webbing between forefoot digits, tend to make smaller turns during routine swimming (45–90°) than sliders (100–150°), in which the shell has a higher dome and the forefeet are less webbed. Sliders also turn with less translation of the center of rotation and at a higher turning rate ($>200°s^{-1}$) than softshells ($<100°s^{-1}$). These trends appear to correlate with the preferred habitats in which these species live: whereas softshells often live in open water, sliders tend to live in highly vegetated water that may require frequent maneuvering.

Morphological Features in Anuran Development Reflecting the Fish-to-Amphib Transition

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Remarkable anatomical details were preserved in the earliest tetrapods (especially in Ichthyostega and Acanthostega from the Late Devonian); however, they are confined to ossified parts of their skeleton. Consequently, 1) only the situation in adults is recorded, and 2) those skeletal parts which were arrested at the level of cartilage or even membrane were not preserved, although they were still well ossified in piscine ancestors of tetrapods (represented, e.g., by *Eusthenopteron* and *Panderichthys*). Developmental morphology of recent amphibians may provide a useful tool for reconstruction of both cartilaginous skeletal structures (mostly the endochondral part of the skull) as well as developmental processes of early tetrapods and their evolutionary transition from piscine ancestors. Here I present data gained from our research on the endochondral parts of the skull (e.g., structure and development of the ethmoidal region, intracranial joint apparatus), on viscerocranial parts (composite origin of the anuran ear ossicle in the context of new discoveries of the columella in *Ichthyostega,* development of the palatoquadrate and associated structures), of the dermal cranium (e.g., development of skull roof bones), as well as on the pectoral and pelvic girdles. Although adult anurans and their larvae are considerably deviated from the original developmental scheme, I believe that ancestral features in their development may contribute to our understanding of anatomical structure of early land-dwellers that were not preserved in fossils.

Ontogeny in Tertiary Frogs

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A detailed account of the development of skeletal and soft-tissue structures is based on 150 fossil tadpoles and metamorphosing froglets of *Palaeobatrachus* from the Late Oligocene of the Czech Republic. The fossil developmental series was compared with normal development of *Xenopus laevis* (Pipidae) represented by cleared and stained (alizarin/toluidine-blue) whole-mount specimens. The comparison revealed that in spite of differences in the sequence of ossification and its timing (e.g., ossification of the otic capsules and ribs was retarded in *Xenopus*, whereas dermal ossification was retarded in *Palaeobatrachus*), in the number of free ribs, and in composition of the sacral region (the synsacrum in *Palaeobatrachus* involves two posterior presacrals, whereas there is a single sacral in *Xenopus*), both genera were similar in a great number of anatomical features that appear during development. The most important difference is the shape of the vertebral centrum, which is formed in comparatively early developmental stages. A view that could result from anatomical comparisons is that *Palaeobatrachus* could be derived from the Pipidae, but this is doubtful due to biostratigraphic and paleogeographic discrepancies. The earliest palaeobatrachids were recorded from the Late Cretaceous of Europe, but pipids could not invade northern continents after the early Cretaceous, when the Tethys Sea prevented interchanges of anuran faunas. Also, palaeobatrachids retain primitive anatomical features that were more derived even in the earliest pipids.

Development of the Pelvic Girdle in Anurans: Contribution to Understanding the Origin of the Pelvis in Early Tetrapods

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Development of the pelvic girdle and adjacent parts of the vertebral column was studied by means of cleared-and-stained mounts of larval and metamorphic individuals of various anuran genera (*Discoglossus, Bombina, Pelobates, Xenopus, Bufo, Rana, Palaeobatrachus*). These genera should represent taxonomically the most important groups of anurans, as well as principal functional morphology types (swimming, crawling, and saltatory locomotion, burrowing). The common developmental scheme for all these types is: The earliest parts of the pelvic girdle to develop are the puboischiadic plate and ilium, both taking their origin as independent centers of chondrification located ventral and dorsal to the proximal head of the femur. The posterior extremity is already nearly complete at that stage, except for the distal phalanges. The pelvic girdle is located underneath the vertebral column and well separated from it. Only later does the ilium begin to expand dorsally towards the developing sacral vertebra. This elongation continues still later, when the ilia begin to rotate posteriorly into an ultimate horizontal position parallel to fused caudal vertebrae (i.e., urostyle). Except for the rotation, this development supposedly recapitulates evolution from the piscine puboischiadic plate to the tripartite pelvis in tetrapods which is not evidenced in fossils. The development of the anuran pelvis (disregarding heterochrony) and its adult structure seem not to be influenced by the type of locomotion.

Heads or Tails? Anterior Thrust Generation in Numerically Simulated Carangiform Fish

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For carangiform fish, research has focused on the tail and its role in transferring momentum from the body to the water. The body is viewed as a housing for the locomotor muscles. However, because of its anatomical position the head acts as a leading edge and thus may act with the body as a lifting surface. We predict that head, body, and tail act together as a hydrofoil oscillating in pitch and heave, generating lift to supplement other thrust sources. To test this, we created an integrated numerical simulation of the morphology of a pumpkinseed sunfish, *Lepomis gibbosus*, and the inviscid flow of the surrounding water using a Lagrangian formulation. The simulation investigates the interaction of fish and fluid, and the fish body includes realistic shape, viscoelasticity, and contracting muscle. With muscle contraction as input, initial changes in body shape and motion influence the fluid forces, which add load to the muscles. Responding, the muscles alter force production, and so forth. The pressure distribution on the body suggests that the head functions in thrust production. Separate models of pitching and heaving disks indicate that crosswise flow generated by lateral heaving directs a component of body lift anteriorly. For the production of lift the tail functions as a control surface, regulating the position and motion of the pressure distribution anteriorly.

Wet Adhesion in the Feathertail Glider *(Acrobates pygmaeus),* a Mouse-Sized Arboreal Marsupial

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The feathertail glider is small (10–15 g), glides with the aid of a patagium and flattened tail, and is an arboreal forager in eastern Australia. *Acrobates* can run on a vertical pane of glass, but if it stops, it slides down slowly. We provide a morphological explanation of its adhesive abilities based on SEM and histology. The manus and pes bear adhesive pads that are seen externally as arrays of parallel ridges. The ridges consist of tall columns of cells; it is remarkable that the stratum corneum does not form a stratified squamous epithelium. The core of the adhesive pad is packed with sweat glands that drain into the epidermal columns. Thus, the adhesive pads are composed of epidermal ridge-sweat gland complexes. Feathertail gliders have developed multiple mechanisms for adhering to substrates. Claws and epidermal ridges interlock with rough surfaces. Adhesive pad-sweat gland complexes are effective on smooth, vertical, impenetrable surfaces, where a capillary adhesive mechanism comes into play. Forward momentum generated by limb muscles and wet adhesion work together and allow the animal to traverse vertical surfaces. When forward momentum decreases to zero, adhesive forces are sufficient to hold an animal's feet against the glass but sweat is not viscous enough to resist shearing forces due to the animal's mass. We initiated investigations of the fluid and tissue components of adhesion.

Lumbar Vertebral Number in Hominids and Hominoids

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The long lumbar column of modern humans likely represents a key adaptation to bipedality. Three hominid specimens, Sts 14, Stw 431, and KNM-WT 15000, may be sufficiently complete to provide data on its length in early human evolution. Each has been described as possessing six lumbars, in distinction to a modal number of five in modern humans and four in other hominoids. Here we review the fossil specimens in order to clarify this pattern. We find little evidence that can elucidate lumbar number in KNM-WT 15000. Given Sts 14f's mosaic nature, Robinson's original attribution as a lumbar is primarily terminological, but does not preclude a key functional role in lordosis. Using a comparative human and hominoid sample, we agree with Stw 431qb's placement as the sixth presacral element. The next most cranial element, Stw 431l, is likely a last thoracic, given that it exhibits an anapophysis, metapophysis, and orthopophysis. We conclude that Sts 14 and Stw 431 had six lumbars, while the number in KNM-WT 15000 remains unknown. Finally, a recent developmental model supports constraints on precaudal vertebral number in hominoids. However, its authors failed to address issues of *Hox cis*-regulation during vertebral morphogenesis and furthermore conflate the processes of segmentation and vertebral specification. We present an alternative developmental model for the evolution of the lumbar spine in the Hominoidea.

Bone Strain in the Cranial and Postcranial Skeletons of Tetrapods

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Models of bone adaptation have emphasized data from the postcranium; bone strain data from the head have been ignored or suggested to be indicative of different optimality criteria. Bone strain data now available from crania and postcrania of several species of tetrapods make it possible to determine whether cranial and postcranial bones are loaded in similar or different ways. These data suggest that cranial and postcranial bones experience a similar range of strain magnitudes, strain rates, and loading frequencies, with strain rate varying as a function of strain magnitude. While in limb bones strain rate and magnitude are correlated with stride frequency, in skull bones strain rate and magnitude are not correlated with chew frequency. This reflects a fundamental difference in the nature of the external forces acting on cranium and postcranium. Forces acting on the limb bones are largely determined by oscillation of the animal's body mass, which varies with locomotor speed, whereas forces acting on the skull originate primarily from the feeding muscles and bite force and do not increase with chew frequency. Similarities between crania and postcrania in strain magnitudes, rates, and frequencies argue for similar mechanisms of bone adaptation at the tissue level; differences in the external forces acting on them predict different scaling relationships of crania and postcrania with body mass.

Modeling Muscle Function in Finite-Element Analysis: What Matters Most?

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The behavior of finite-element models (FEMs) depends on their geometry, material properties, constraining conditions, and external forces. How variation in these parameters affects FEMs impacts our confidence in the behavior of extinct taxa for which these parameters are estimated. We are investigating the sensitivity of our FEM of the *Macaca fascicularis* skull to variation in external forces applied to muscle attachment sites during mastication. External forces are estimated from in vivo EMG data collected during mastication using different EMG-force delay constants and different physiological cross-sectional areas (derived from two different species of *Macaca*). Responses of the model to different loading conditions are evaluated using strain orientation and magnitude data. Using different EMG-force delay constants has little effect on relative force estimates and behavior of the model. These results suggest that the geometry of the skull may have a greater influence on the behavior of the model than subtle differences in muscle activity. It also emphasizes the importance of sensitivity analyses for assessing the importance of variation in other parameters, such as muscle forces and bone material properties.

Consequences of Giantism in *Xenopus laevis* Tadpoles

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Xenopus laevis tadpoles that arrest development and remain as larvae for more than 1 year occasionally occur in laboratory populations. These tadpoles cease development at an early limb-bud stage and continue to grow, developing into grossly deformed giants which average 4 times longer and 35 times more massive than normal tadpoles of corresponding stage. Nontransforming giant *X. laevis* tadpoles lack thyroid glands and differ in gross morphology and behavior from normal *X. laevis* tadpoles. Giants have spinal scoliosis; their axial and tail musculature is disproportionately large relative to the rest of their body. Giants are negatively buoyant, and frequently rest on the tank bottom. In most cases their lungs are small and partially solidified, with numerous septa and abundant collagen. Fat bodies are greatly enlarged. Although gonads are not differentiated in normal tadpoles of the same stage, ovaries in giants are well-developed and full of eggs. Neoteny has never been reported in anurans, but gonadal development brings these giant individuals as close as any anurans to being truly neotenic. When induced to metamorphose by exogenous thyroid hormone (T3) treatment, giant tadpoles develop forelimbs but fail to completely metamorphose; all die at the stage when the tail normally starts resorbing. Complete metamorphosis may not be possible in giant tadpoles due to a disproportionate growth and development of tissues and organs.

Mandibles of Rodents That Have Cheek Pouches Differ Morphometrically From Those of Rodents That Do Not

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The jaws of rodents are anatomically distinctive and functionally important, but the functional implications of jaw shape variation within the Rodentia (which constitute half the living species of mammals) are poorly understood. In different lineages of rodents, cheek pouches have evolved multiple times. We defined morphometric indices based on observations on New World squirrels by Ball and Roth that we hypothesized would correlate with possession of cheek pouches in other rodents. Phylogenetically independent paired contrasts suggest that the presence of cheek pouches, and the behavioral traits that accompany them, can indeed be inferred from quantitative characterizations of the mandible.

Convergent Cranial Evolution and Development in Mammals and Birds

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Living mammals and birds resemble one another in possessing a large brain, a four-chambered heart, and other anatomical and molecular similarities that have been interpreted as evidence of common ancestry. However, phylogenetic analyses that include fossils favor the hypothesis that acquisition of mammalian features is represented by the rich sequence of extinct synapsids whose fossil record extends from the Late Paleozoic through the Cenozoic, and that the history of birds can be traced back through extinct Mesozoic dinosaurs. Phylogenetic analyses offer a method to map sequences of evolutionary change and character correlation, and a rigorous framework for comparison with ontogenetic changes. New evidence from high-resolution X-ray CT on internal morphology of fossils and Recent specimens suggest that both mammalian and avian histories involved reorganization of the skull around a greatly inflated brain and special sense organs, but in different and distinctive ways. In mammals, relative enlargement of the olfactory bulbs, neocortex, and cerebellum dominate the transformations of cranial structure. The ear evolved a unique architecture, elaboration of an olfactory skeleton is even more profound, and the advent of hair may be reflected in cortical expansion. In birds, the cortex and cerebellum also become enlarged in steps traceable through the fossil record, but it is the visual system that is elaborated to the greatest degree.

Morphology and Function of a Hyobranchial Joint in the Ruddy Turnstone, a Scolopacid Shorebird

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Of all vertebrate feeding structures, the tongue may have the greatest diversity of functions. In nonmammalian tetrapods the tongue is supported by the hyobranchial apparatus, a complex arrangement of small bones and cartilages derived from gill arches. Detailed descriptions of the anatomy of the hyobranchium exist for some taxa, but are relatively rare in birds, as are actual demonstrations of the relationship between hyobranchial structure and tongue function. As part of an investigation of feeding system evolution in shorebirds (Scolopacidae; Charadriiformes; Aves) we demonstrate that in the ruddy turnstone (*Arenaria interpres*), a small shorebird, extreme mobility in an anatomically unique joint at the union of the basihyal and paraglossals facilitates both food transport along the beak by the tongue, and in use of the tongue to ram food into the pharynx. This discovery is particularly surprising, given that tongue-based food transport has never previously been described in the Scolopacidae at all. The use of joint in the tongue skeleton of a bird thought to use the tongue little, if at all, is likely an indication that the structure and function of tongues in birds in particular, and vertebrates in general, warrant much closer attention.

Segmental and Regional Growth in the Rat Vertebral Column

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The vertebral column is a derivative of segmental structures (somites) and the growth of its constituent vertebrae can be examined segment by segment, and also by anatomical region. For mammals, cervical, thoracic, lumbar, sacral, and caudal series are ubiquitous and can vary markedly among taxa in dimensional proportions as well as in number of included vertebrae. We examine growth patterns of the Norway rat (Sprague-Dawley strain) from birth to adulthood via reduced major axis regression and principal component analysis. Rates of growth of individual vertebrae vary within and between regions. The atlas grows very slowly; the remaining cervicals have a higher growth rate than the anterior thoracics, but the posterior thoracics exhibit faster growth, which continues to increase into the anterior lumbars. The posterior lumbars and anteriormost sacral show a diminished growth rate, whereas the posterior sacrals grow increasingly more rapidly. The anterior caudals exhibit depressed growth rates, but the intermediate and posterior caudals have the fastest growth rates of the entire series. Patterns of vertebral growth are correlated with regional functionality, the establishment of curvatures along the series, prenatal retardation of tail growth, and possibly with homeobox gene expression.

Wood-Cutting Functional Morphology and Behavior in an Extant and a Fossil Beaver

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I investigated the functional morphology of wood-cutting in beavers using a combination of morphological, behavioral, and experimental data. The study compared the only known wood-cutting beavers: the extant *Castor* and the fossil *Dipoides*. Compared to *Castor*, the skull of *Dipoides* is smaller by roughly one-third, and the gross morphology of its jaw musculature appears less specialized for gnawing. Moreover, these two beavers differ in the morphology of their cutting incisors: In anterior view, the tip of *Castor*'s lower incisors appears straight-edged, whereas those of *Dipoides* are rounded. To investigate the effect of incisor shape on wood-cutting performance, I modeled the shape of the lower incisors in steel and assessed wood-cutting performance quantitatively by measuring cutting forces qualitatively. The experimental set-up (ex. angle of the stick sample relative to the incisor model) was based on observations of cutting behavior by *Castor* and behavioral artifacts from both *Castor* and *Dipoides*. I found that, compared to the *Castor* incisor-model, similar-width cuts made using the *Dipoides* incisor-model required, on average, less force, although the maximum cut-width produced by the *Dipoides* model was usually less than that of the *Castor* model. That *Dipoides* may have tended to take relatively smaller bites during wood-cutting than *Castor* is supported by fossil behavioral artifacts.

Tooth Cusp Patterning: From Genes to Evolution

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In this article we investigate the interrelationship between development and evolution. In previous work we produced a mathematical model that incorporated basic interactions between signaling molecules and cells. The model was able to predict the morphology and gene expression patterns of developing mouse and vole teeth. In the present work, we tested whether the model is able to predict the diversity of tooth shapes among fossil and extant mammals. Using the model, we first explored how variation at the molecular level maps to variation at the level of tooth morphology. We then estimated the relative importance of ecological and developmental factors in evolutionary transitions of tooth morphology. We compared the morphological variation produced by the model with the Cenozoic fossil record. The model helps to elucidate the frequent parallel evolution of basic tooth types, and the relative time of appearance of certain morphologies. Additionally, the model predicts that developmental factors may contribute to stasis in morphology. These predictions about the roles of development in evolutionary transitions may apply to other morphological structures that use morphodynamic developmental mechanisms.

Ecomorphology of the Hindlimb Skeleton in Afro-Malagasy Tenrecoidea

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Tenrecidae represent an exemplary mammalian ecological radiation and therefore provide an excellent opportunity for exploring adaptive differences in postcranial skeletal morphology. Most of the family's 26± species are endemic to Madagascar and exhibit a range of microhabitat-specific locomotor behaviors, including swimming, climbing, and burrowing. This project is the first analysis of the tenrecid postcranial skeleton, focusing on knee, hip, and foot joint morphology. The pelvic girdle, femur, tibia/fibula, and the tarsus from 10 tenrecid species, as well as one species each from the families Solenodontidae and Macroscelididae, were studied and digitally photographed for acquisition of 2D landmark data. Sections 100 μm thick from the femoral diaphyses of seven tenrecid species were also prepared and analyzed for cross-sectional geometric properties. Results from descriptive, univariate, and multivariate analyses demonstrate significant differences in several aspects of knee and hip joint skeletal form that are supportive of function-based hypotheses. The data are consistent with other studies of eutherian functional postcranial morphology. Analysis of cross-sectional geometry parameters shows correlation between external skeletal morphology and diaphyseal structure. These data support identification of a suite of postcranial characteristics that are widespread among eutherians with variously modified locomotor behaviors. In addition, they contribute to a body of well-tested foundations for functional interpretation of fossil material.

Postcranial Development and the Marsupial-Placental Dichotomy

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Placental mammals show a higher degree of morphological diversity in the postcranial skeleton than do marsupials, as demonstrated by comprehensive character analyses of the major clades of both groups. Are there differences in the relative timing and mode of development of postcranial skeletal structures between the two groups? Two aspects of skeletal development were examined in representatives of most of the major clades: the early development of autopodials, and the sequence in the onset of ossification of postcranial elements. In marsupials, in contrast to placentals, early in perinatal life the number and arrangement of the adult carpals can be identified, even at a mesenchymal stage. Pouch-young marsupials show anlage of most of the processes of the adult carpals and the articular surfaces are also recognizable. Altricial placentals show more a developed skeleton in the forelimbs than does any marsupial examined to date. Many features (several associated with the acceleration of forelimb development) distinguish the sequence of postcranial ossification of marsupials from placentals, some of which are derived within tetrapods.

Dermal Characteristics, Scale Row Organization, and the Origin of Macrostomy in Snakes

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The origin of snakes from varanoid lizards involved changes in the feeding apparatus that eventually led to the evolution of macrostomy. Although the monophyly of the Macrostomata remains controversial, there clearly has been a trend within snakes to evolve attributes facilitating the consumption of relatively large prey. We compared dermal organization in a variety of snakes with that of several lizards and the successive diapsid outgroups Sphenodon and Crocodylia. We also examined the organization of the dorsal scale rows in the major lineages of snakes. The dermis of snakes possesses a relatively thin stratum compactum with parallel orientation of the collagen fibers, rather than the crossed plies of collagen found in other diapsids. Folds of skin between each dorsal scale facilitate stretching in snakes; in macrostomates those folds lie beneath the free edges of scales. The distribution of folded intersquamous skin varies along the length of each scale in such a manner that scales must be staggered in order to achieve substantial stretch. A predicted trend toward greater staggering of scale rows, reflected in lower angles between the rows, is observed among the major clades of snakes. Macrostomates also exhibit greater regionalization of the scale rows along the body axis.

Ontogenetic Development of Locomotion in Small Mammals

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Comparisons of locomotory parameters of eight taxonomically and morphologically different mammals, small to medium-sized, resulted in general principles of therian limb configuration and locomotion (Fischer et al., 2002, J Exp Biol 205:1315–38). The aim of this study was to track the development of locomotion during postnatal ontogeny of mammals. Treeshrews (*Tupaia glis*, Scandentia) and cuis (*Galea musteloides*, Rodentia), animals with altricial and precocial juveniles, respectively, were investigated. Starting with developmental stages performing the first continuous cyclic movements, locomotion was studied daily or at a distance of a few days using cineradiography. Even from the first steps on, juveniles showed the typical limb configuration of adults. Limb positions of fore- and hindlimbs at foot down were nearly constant during development. Remarkable differences were observed in the limb configurations at lift off. Shoulder blade, forearm, and hand, as well as thigh and foot, in younger animals were less rotated in the caudal direction than in adults. The same changes in limb configuration and movement were detected in altricial and precocial young. After the first week of life, kinematic parameters of young cuis were comparable to those of adults. In treeshrews, the adult locomo-

tory pattern was achieved at the time of leaving the nest. Time of development of kinematic parameters was clearly shortened in precocial young relative to altricial juveniles.

Intramuscular Architecture of Paravertebral Muscles in Small Mammals

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Studies of fiber-type distributions in various mammalian limb muscles show differences related to muscle function (e.g., propulsory and antigravity). According to their anatomical position and superficial visible fiber direction, different functional roles were also proposed for paravertebral muscles. Therefore, the question of structural differences between functionally different back muscles arose. Fiber-type distribution in back muscles was mapped in serial sections through complete backs of small mammals. Oxidative regions were found near the vertebral column and adjacent to intramuscular tendons in the quadratus lumborum, multifidus, and erector spinae muscle. The longissimus lumborum muscle possessed the highest proportion of glycolytic fibers. The results suggest that there are clear functional differentiations between various paravertebral muscles and even intramuscular regions. Besides the distribution of extrafusal fibers, number and position of intrafusal fibers are important in order to understand functional roles of paravertebral muscles. According to morphological criteria, intrafusal fibers were assigned to one of the three types: simple, tandem, and compound. In comparison to the semspinalis, the quadratus lumborum muscle contained three times more receptors. Direction and length of fascicles of back muscles were measured and 3D-reconstructed to show intramuscular fiber architecture. Data of intramuscular architecture of the back muscles are a prerequisite to understand their functional role during motion. A synthesis of all data collected with different methods is presented.

Intervertebral Movements During Locomotion in Small Mammals

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Evolution of therian locomotion is characterized by regular use of in-phase gaits (gallop, half-bound, bound) in connection with dorsoventral movements of the body axis, rather than lateromedial, undulatory movements as in reptiles. In therian mammals, sagittal spine movements are used systematically at in-phase gaits, whereas pelvic movements around the longitudinal and dorsoventral axis (tilting, lateral bending) occur during locomotion at symmetrical gaits (walk, trot). Because of the rigid connection of the pelvis to the vertebral column, all pelvic movements are the result of small additive intervertebral movements. The present study is the first cineradiographic analysis that measures sagittal spinal movements in intervertebral joints in mammals. Species with and without tails were examined to test the tail's influence on kinematics. Because of comparable effective angular displacements of the pelvis (30–40°), the contribution of "pelvic movement" to step length is similar in all species at in-phase gaits (40–50%). However, this amplitude is covered in a strikingly different pelvic position in tailed and tailless species. In tailless species, the pelvis is in a nearly vertical position at foot down (100°). At lift off, the cranial angle between pelvis and horizontal line is 130–140°. The pelvic angles for the tailed species are 130–140° and 170–180°, respectively. Independent of the regional classification as "lumbar" or "thoracic" vertebrae, 7 ± 1 intervertebral joints are involved in sagittal spine movements.

Development and Evolution of Placodes From a Common Precursor?

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Placodes are specialized areas of ectoderm in the head of vertebrate embryos that give rise to various nonepidermal cell types. Different types of placodes (olfactory, adenohypophyseal, lens, profundal, trigeminal, otic, lateral line, and epibranchial placodes) differ with respect to their location and the cell types they generate. Nevertheless, the various types of placodes share several properties: They are capable of pronounced cell shape changes and include neurons among their derivative cell types (except lens and adenohypophyseal placodes). Moreover, there is now increasing evidence that all types of placodes originate from a common primordium surrounding the anterior neural plate, which is defined by expression of *Eya1, Six1*, and several other genes. Our recent experiments with *Xenopus* indicate that this panplacodal primordium is induced by neural-plate-derived signals and that *Eya1* and *Six1* play crucial roles in regulating generic aspects of placode development, such as neurogenesis and morphogenetic movements. Based on these insights and recent findings in ascidians and amphioxus, a tentative multistep model for the origin of placodes during the course of chordate evolution is proposed involving 1) acquisition of *Six/Eya*-dependent regulation for the expression of generic placodal properties, 2) recruitment of *Six* and *Eya* genes to the neural plate border, and 3) acquisition of responsiveness to additional inducers for the expression of properties specific to various types of placodes.

Shoulder Mobility of Quadrupedal Primates Related to Fiber Type Distribution of Intrinsic Shoulder Muscles

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Cineradiographic records of shoulder movements during locomotion in arboreal-quadrupedal primates reveal that the well-known shoulder joint mobility of apes and humans is far from typical for primates. Moreover, shoulder joint mobility is acquired stepwise during the evolution of primate locomotion. In most quadrupedal primates, shoulder joint excursions are restricted to flexion and extension, whereas scapula excursions engender forelimb movements in all dimensions. Among quadrupedal primates, mediolateral shoulder joint movements were observed only in the squirrel monkey (Cebidae). According to these findings, questions arise about the functional and morphological conditions and constraints for the evolutionary acquisition of joint mobility. Movements of the shoulder joint are usually not restricted by skeletal arrangements, but by intrinsic shoulder muscles. Enzyme and immunohistochemical studies of primate shoulder muscles show that species that differ in their locomotory shoulder movements differ also in amount and distribution of fatigue resistant, slow twitch oxidative fibers (SO-fibers) in certain shoulder muscles. Except for the teres major muscle, all intrinsic shoulder muscles show distinct regions of SO-fibers, pointing to their role as "antigravity muscles." Compared to nonprimate mammals, the high amount of fatigue-resistant SO-fibers of the infraspinatus muscle indicates that this muscle becomes more important for joint stability in primates. Differences in lateral joint mobility are related to different fiber type distribution in the deltoid muscle.

Is Early Embryonic Development of Zebrafish, *Danio rerio,* Accessible to Selection? A Quantitative Genetic Approach to Study Phenotypic Variation During Early Ontogeny

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Vertebrate embryos pass through a period of remarkable morphological similarity during their early embryonic development (phylotypic stage). Here, we study patterns of embryonic variation to test ideas about modularity, constraints, exhausted additive genetic variance, and directional selection. We assume that each of these processes creates a different pattern of variation and covariation of embryonic traits. Those patterns enable us to find out about the underlying processes. We use the zebrafish in a quantitative genetic breeding design to study development-dependent changes in genetic variability and in environment-induced variability. In particular, we look at the embryonic development from 12–27 h postfertilization. During this time, the development of individual embryos was documented in hourly intervals. We measured eye length, size of somites, shape of somites, body length, and the size of yolk sac and calculated the coefficient of variation as a measure of variability that is independent of organ size. During the observation period the coefficient of variation was always above 4%, indicating a considerable degree of (genetic) variability and accessibility of embryonic characters to selection. Results from a correlation analysis suggest that internal constraints determine patterns of variability during early embryonic development of zebrafish and limit the accessibility towards selection.

Limb Kinematics of Quadrupedal Primates and Their Consequences for Functional Interpretations of Limb Proportions

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For more than 100 years limb proportions of primates have been investigated using traditional anthropological methods, which are defined with reference to the functional anatomy of the human locomotor apparatus, and which consider only two limb segments: upper arm and forearm, thigh and lower leg. Cineradiographic locomotor studies reveal that fore- and hindlimbs of quadrupedal mammals are functionally three-segmented. Therefore, functional interpretations of limb proportions should be based on actual limb kinematics and include the scapula and tarsometatarsus. Compared to the basic mammalian condition of nearly equally sized limb segments, intralimb proportions are altered in primates. Among quadrupedal primates, the percentage of scapula length on forelimb length is highly invariable, and seems to be independent of body size or phylogenetic position. Lengthening of the forelimb involves the middle and the distal segment, whereas hindlimb length increases due to lengthening of the proximal and the middle segment. These proportional changes in primates may conceal the functional equivalence of shoulder blade and thigh, upper arm and lower leg, and forearm and foot. Nevertheless, this equivalence becomes obvious when the kinematics of whole limbs is considered. Despite their different lengths, the touch down and lift off position of the functionally equivalent limb segments are nearly identical. Even the typical extent of humeral protraction in primates matches a stronger protraction of the lower leg.

Using Quail–Duck Chimeras to Elucidate Mechanisms of Craniofacial Morphogenesis

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An essential tool for studying craniofacial development has been the generation of quail–chick chimeras. Quails and chicks are closely related birds that differ only slightly in their gross morphology and rates of early growth. In ovo transplants between them have been advantageous in experimental contexts that require donor and host cells to behave in a nearly equivalent manner, such as lineage analyses (quail cells can be distinguished by a nuclear marker not present in other avian species). In contrast, a novel chimeric system that utilizes quails and ducks exploits the substantial differences that exist between these birds in morphology and maturation rates, and provides a potent method for elucidating cellular and molecular mechanisms underlying craniofacial morphogenesis. For example, transplanting neural crest cells between quail and duck embryos results in chimeric ducks with quail-like beaks and chimeric quails with duck-like bills. These transformations arise because donor neural crest cells 1) execute autonomous molecular programs and regulate gene expression in adjacent host tissues; 2) control the size, shape, and location of anatomical structures originating from both the donor and host; and 3) establish when their own derivatives, such as cartilage and bone, and host tissues, such as adjacent epithelia, undergo differentiation. Thus, the quail–duck chimeric system demonstrates that neural crest cells are a key source of spatiotemporal patterning information during craniofacial morphogenesis.

Waterfall Climbing by Hawaiian Gobies: Factors Affecting Climbing Performance

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Juveniles of three species of Hawaiian gobies (fishes under 3 cm) must climb waterfalls to reach adult habitats. For two of these species (*Lentipes concolor* and *Sicyopterus stimpsoni*), the total height climbed can exceed 10,000 times body length. High-speed video analyses of short-distance locomotion (<5 body lengths) revealed that these species use two different climbing styles. *Lentipes* uses bursts of axial undulation initiated by a single adduction of the pectoral fins, and rests between bursts by attaching a ventral sucker to the substrate. In contrast, *Sicyopterus* inches up surfaces by alternately attaching the ventral sucker and a second, oral sucker. To evaluate differences in climbing performance related to differences in climbing style, we used standard video to record climbing bouts over long distances (nearly 100 body lengths) and a variety of surfaces (smooth, fine-grained, medium-grained). Variations in climbing surface affect these species differently. In *Sicyopterus*, higher surface roughness does not affect climbing velocity, but does increase the ratio of time in motion to time resting. In contrast, *Lentipes* shows no change in motion-to-rest ratio on different surfaces, but its climbing velocity increases on textured surfaces. Nonetheless, on all surfaces *Sicyopterus* shows a much higher ratio of motion to rest than *Lentipes*. These distinct effects emphasize that considerable locomotor diversity can evolve even in the context of extreme environmental demands.

Bracing of the Trunk and Locomotion in Dyrosaurid Crocodilians

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In contrast to recent crocodilians, the axial skeleton of dyrosaurs possess higher neural spines throughout the entire vertebral column, and the dorsal osteodermal shield is unique in lacking an external dermosteal keel. The height of the neural spines in the trunk results in dyrosaurs in steeper insertion angles of the epaxial muscles at the osteoderms than in recent crocodilians. The segments in the bracing system of the trunk of dyrosaurs can be described in technical terms as inverse T-beams. Because that type of bracing together with the dorsal osteodermal shield did not stabilize the vertebral column effectively against transverse shear-loads, high-walk was probably impossible for dyrosaurs exceeding 2 m in length and gallop was restricted to individuals smaller than 75 cm in length. A high mobility of the lumbar region of dyrosaurs, the extremely high neural spines and large muscles of the tail, as well as the extremely large and well-muscularized scapula and forelimbs are indicative of improved axial and paraxial swimming capacities and further aquatic locomotor options.

Soft-Part Reconstructions and Biomechanics of the Axial Trunk Skeleton of Sauropods

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The pneumatization of the sauropod axial skeleton has been known for quite a while, but investigations were focused mainly on the neck of sauropods. For reconstructions of the degree of pneumatization throughout the presacral vertebral column of sauropods, calculations of air volumina were made with high-resolution 3D-images with neutron radiography. The reconstruction of the soft-part anatomy around the trunk vertebrae of different sauropod genera forms the basis for a biomechanical analysis to discuss a model of the bracing of the trunk of sauropods as well as different roles for the extensive pneumatization in the sauropod axial skeleton.

Anatomy of the Circadian Clock in Avesuchian Archosaurs

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The Harderian-pineal-retinal-hypothalamic axis (HaH) and its relation to circadian rhythms (cyclical behavioral patterns regulated by indoles) is a critical component of amniote biology. Little is known of this system in Crocodylia, a clade that purportedly lacks a pineal gland but demonstrates a rhythmic melatonin cycle. Crocodilians and birds (Avesuchia) are further derived in the absence of the vomeronasal organ, a structure functionally linked to the Harderian gland in many tetrapod groups. To further elucidate the evolutionary history of the HaH in amniotes, we embarked on a descriptive and experimental comparative study of this system in various amniote clades, with special attention given to avesuchian archosaurs. Although there are some structural similarities of the Harderian gland between crocodilians and lepidosaurs that are not shared with birds, there are more, far-reaching similarities within the avesuchians. This includes the high level of vascularity in the three components (retina, Harderian, and "pineal" glands), the secretory and immunological nature of the Harderian gland, and the presence of a follicular "pineal" gland. The follicular nature of the crocodilian "pineal" does bear some resemblance to that of basal birds. Additionally, there are distinct neural and vascular paths that avesuchians share. This implies a role for the Harderian gland as a component of the circadian endocrinological network.

Marsupial Cleavage and Blastocyst Formation: Insights Into Evolution of the Mammalian Embryo

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Early development in mammals, as in other amniotes, involves a cell lineage allocation into pluripotent future embryonic cells (pluriblast or

ICM) and extraembryonic nutritive cells (trophoblast). Later, the pluriblast separates into epiblast (embryo and extraembryonic membranes) and hypoblast (nutritive lineage). Associated with early lineage allocation are establishment of the body axes (dorso-ventral and anterior-posterior) and changes in cell potency, processes fundamental to formation of the amniote body. Despite differences in yolk content, the common theme in mammals is retention of pluripotency in pluriblast and epiblast lineages, as evidenced by marsupial OCT expression in the epiblast and downregulation in other lineages. In eutherian mammals, a critical step in the first lineage allocation is formation of the morula. No morula forms in metatherian mammals because cell–zona adhesion precedes cell–cell adhesion. It is relatively simple to convert a marsupial conceptus during cleavage into a morula-like form, suggesting that the morula could have evolved from this stage. Despite structural differences, all mammals probably use similar mechanisms to pattern the embryo. Possible mechanisms are 1) polarization of the oocyte and conceptus, leading to uneven distribution of determinants that influence cell fate or positional value; 2) positional signaling between cells and their environment; 3) mitotic asynchrony; 4) sperm entry point; and 5) gravity.

Variation in Mammalian Proximal Femoral Ossification Patterns

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The developmental anatomy of the proximal femur is highly complex. In some mammals, including humans, the femoral head and greater trochanter emerge as separate ossification centers within a common chondroepiphysis, and remain separate throughout ontogeny. In many other mammals the secondary centers merge to form a single epiphysis, as in the proximal humerus. A preliminary analysis using juvenile specimens revealed clear differences in femoral anatomy between these two classes of epiphyseal ossification. However, it was not possible to resolve the effects of age and size with this sample. We therefore examined adult femora in order to better quantify these two morphological patterns. Here we present a comprehensive analysis of the morphometric variation associated with proximal femoral ossification patterns. Our data suggest that geometric form, rather than physical size, is the primary determinant of ossification type. We found that species with "separate" ossification have longer femoral necks and deeper trochanteric notches than do those with "coalesced" ossification. Additionally, "separate" species have more constricted and well-defined femoral necks. These developmental differences are critical to an understanding of femoral architecture across a wide range of mammals.

Sperm Aggregations in the Spermathecae of Torrent Salamanders

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Female salamanders in the suborder Salamandroidea store sperm in cloacal glands called spermathecae. Scanning electron microscopy was used to study these glands in females of the torrent salamander, *Rhyacotriton variegatus* (Rhyacotritonidae), from northern California. Sperm initially enter the cloaca in a tangled mass from the spermatophore cap, but within the spermathecal tubules, small groups of sperm are aligned along their long axes. Sperm nuceli typically are embedded in apical microvilli of the secretory cells forming the distal acini of the spermathecae. Junctional complexes between apices of adjacent epithelial cells are occasionally broached or otherwise absent, and sperm can be found in the intercellular canaliculi between such cells. Sperm associations are most similar to those reported for the Plethodontidae.

Antler Stiffness in Reindeer: Testing Variation in Bone Material Properties Between Males and Females

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The mechanical properties of bone material from different body locations can vary substantially, especially among bones with major differences in function (e.g., skull vs. limbs). However, less is known about the interspecific and intraspecific correlates of material property variation of specific types of bone. For example, deer antler has long been known to exhibit distinctive mechanical properties relative to other types of bone, but little is known about variation in antler mechanical properties among and within deer species that might correlate with behavioral, ecological, or evolutionary patterns. To evaluate a potential source of such variation, we compared the stiffness (Young's modulus) of antler from male and female reindeer (*Rangifer tarandus*), the only deer species in which both sexes grow antlers. We used a screw-driven materials testing machine to measure the stiffness of machined bone specimens in three-point bending. Stiffness values for reindeer specimens were similar to those for most other odocoileine deer, with a mean stiffness near 5 GPa. However, specimens from males, whether from bulls or steer, did not differ significantly in stiffness compared to specimens from females. Thus, although previous comparisons across deer species have shown differences in antler material properties that appear to correlate with differences in patterns of antler use, such differences are not apparent within a single species.

Genetic Architecture of the Human Craniofacial Complex With Paleontological Implications

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Basicranial traits are often used in phylogenetic analyses and are commonly discussed as comprising an anatomical complex. These traits, however, are frequently treated as individual, independent characters of equal phyletic value. Implicit in such considerations is the assumption that the genetic contribution to morphological variation is high and equivalent across traits, and that underlying genetic correlations between traits introduce a negligible confounding effect in phylogenetic reconstruction. We discuss here the phyletic value of craniofacial traits in the context of recent work we conducted elucidating the genetic architecture of human craniofacial variation. Thirteen craniofacial measures were taken from lateral cephalograms of 508 participants in the Fels Longitudinal Study. These individuals are from 90 kindreds and ranged in age from 13 to 72 years at the time of examination. Heritability (h^2) of each trait, and additive genetic and random environmental correlations between traits, were estimated using a maximum likelihood method for pedigree data. The results demonstrate that basicranial traits have significant heritabilities ranging in magnitude from moderate to high ($\sim$0.35–0.80). Various degrees of pleiotropic and shared environmental effects among basicranial traits were also observed. The most pertinent implication of these findings for paleoanthropology is that the genetic architecture of basicranial morphology is characterized by discernable patterns of genetically and environmentally mediated covariation between traits that should be considered in phylogenetic analyses.

Molecular Bases for Evolutionary Novelty: Vertebrate Jaw and Turtle Shell

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Evolutionary novelty can be gained by overcoming ancestral developmental constraints, whereby morphological homology is often lost. As vertebrate examples of such cases, developmental patterning of the jaw and turtle carapace was examined. In gnathostomes, upper and lower jaws are both derived from the mandibular arch, specified from neural crest-derived ectomesenchyme through epithelial–mesenchymal interactions involving FGF8 and BMP4 signaling cascades. Mandibular- or oral-ectomesenchyme is specified as a domain of the early mesenchyme that expresses downstream genes of these cascades. Although the homologous set of genes is functioning in lamprey oral patterning, they act not only on the mandibular ectomesenchyme but also the premandibular domain to pattern the upper and lower lips. Thus, heterotopic shift of gene regulation is implied in the agnathan-to-gnathostome transition. Likewise, patterning of the turtle shell is characterized by unique topographical displacement of the rib primordia during development. In association with rib growth, an embryonic structure called the carapacial ridge (CR) appears on the lateral aspect of the embryonic thorax. By systematically searching for CR-specific genes and analyzing their expression, de novo expression of old regulatory genes shared by other amniotes was revealed in the acquisition of the carapace, not simply a shifting of the gene expression domains.

Development of Putative Placode Homologs in *Ciona intestinalis*

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Vertebrate cranial placodes contribute to the specialized sense organs and associated ganglia of the vertebrate head, and as such are a key component of what makes a vertebrate different from its closest surviving relatives, amphioxus and tunicates. Two structures of the tunicate *Ciona intestinalis* tadpole larva have been suggested to be homologous to vertebrate cranial placodes. These are the buccal cavity, which is situated just anterior to the brain and is hypothesized to be homologous to adenohypophyseal and/or olfactory placodes, and the paired atrial openings, which are hypothesized to be homologous to the otic placode. A prediction of these hypotheses is that the development of these structures will be regulated by a developmental pathway conserved with that regulating vertebrate placode development. Correspondingly, we have identified a panel of molecular markers involved in the regulation of vertebrate placode development, and assayed them during *Ciona* development by in situ hybridization. Our results support both of the above hypotheses. In further experiments we are testing the interactions between these genes to identify how regulatory mechanisms confine gene expression to specific areas of ectoderm fated to form the buccal cavity and atria, with the aim of identifying how primitive mechanisms have been modified and coopted in the evolution of the complex assemblage of vertebrate placodes.

Evolution of Urodele Metamorphosis as a Guide to Early Tetrapod Metamorphosis

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A life cycle with metamorphosis was characteristic of early tetrapods. Among recent amphibians, salamanders display a life history that most closely resembles that in early tetrapods. Consequently, salamanders are a model system for studying the origin and evolution of metamorphosis in tetrapods. Urodele evolution is accompanied by the progressive divergence between larval and adult morphology via the progressive accumulation of larval and adult specializations. Also, many adult structures which in primitive salamanders start to develop at a larval stage postpone their development until metamorphosis in advanced urodeles. As a result, metamorphosis becomes more complicated at the transition from primitive to advanced salamanders. In parallel, urodele evolution is accompanied by an increasing significance of thyroid hormones as metamorphosis-regulating factors. The role of TH is minimal in the ontogeny of primitive salamanders and maximal in advanced ones. Developmental events which in primitive salamanders are under nonhormonal control become shifted under endocrine control in advanced ones. Such a transition from inductive interactions to hormonal factors as regulatory mechanisms of development allows elimination of some intermediate larval structures and the shortening of both the whole developmental process and metamorphic transition. Moreover, it allows decoupling of the larval and adult developmental programs in some metamorphic systems.

Toe Pad Morphology and Adhesion in Tree Frogs

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Toe pad morphology is very similar in climbing frogs from several different families, suggesting that the structure of the pad has evolved for a specific adaptive function. Considerations of the ability seen in many tree frogs to adhere to smooth and vertical surfaces concur that it is these specialized disc-like digital pads that facilitate it. Pads adhere through a wet adhesive mechanism, dominated by surface tension-dependent capillary forces that scale directly with contact area. Adhesive forces recorded in adult hylids scale directly with the toe pad area in contact with the surface. In addition, force per unit area correlates with the linear dimension, i.e., pads of larger species adhere more efficiently than those of smaller species. In spite of the wide recognition of the link between the presence of toe pad discs and climbing ability in frogs, few studies have actually considered the direct influence of the morphology of the toe pad in relation to adhesion. SEM studies were made of the toes of frogs whose sticking abilities on smooth substrates were determined prior to sampling. Many aspects of toe pad morphology differ between species, particularly cell size, groove development, and mucosal pore size and structure. Crucially, although differences in pad morphology appear small, they have demonstrable effects on the adhesive efficiency of the pads.

Striking Out

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The strike of the rattlesnake is an extremely fast event in which venom is injected followed by the release of the prey. The complex strike is usually completed in less than 0.5 sec, and is based on great versatility and variation in recruitment of body segments from many different initial body postures. The vertebrae and epaxial muscle complex of the axial region, together, launch a strike upon which successful capture of prey depends. Therefore, it is the purpose of this study to determine, descriptively and through modeling, if and how this axial region in rattlesnakes functions as an anatomically unique "strike zone." To do so, we: 1) characterized (qualitatively and quantitatively) the axial region of the rattlesnake; 2) conducted a comparison with the constricting, nonvenomous gopher snake; and 3) used a modeling system to construct a simulation of the vertebrae modeled as cylinders and the muscles as modified springs. By modeling the two snakes, using the collected mass distribution and vertebral measurement in constructing our model, mechanical differences exist that suggested that, compared to the gopher snake, rattlesnakes exhibit differences in mass distribution, moments of axial musculature, and a distinctive "pivot" region within the vertebrae. These are correlated with mechanical demands of launching a rapid strike.

Mechanical Implications of Nasal Fusion in Tyrannosaurid Dinosaurs

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Tyrannosaurids have the highest calculated bite forces and thickest teeth among carnivorous dinosaurs, and are characterized by apparent fusion of the nasals throughout their phylogenetic history and across their ontogenetic size range. Computed tomographic (CT) scans of tyrannosauid specimens, of four different sizes, confirm that the fusion extends fully through the nasals rather than being isolated to ornamental fusion of the dorsal suture. Fusion and thickening of the nasals, and a staircase-style nasomaxillary joint in giant individuals, contributed to reinforcement of the snout for feeding activities.

Neuromuscular Organization of the Rat Tongue: Is it Mammal or Reptile?

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The rat tongue is a model system for study of human oromotor disease, yet little is known about its neuromuscular organization. Here we describe rat tongue muscle architecture. Our findings include: 1) Superficial circular fibers form the outermost muscle layer of the anterior tongue. 2) Longitudinal muscle fibers are located both peripherally and centrally in the anterior tongue. 3) A discrete superior longitudinal muscle is only present in the posterior tongue. 4) Hyoglossus and styloglossus muscle systems are each composed of a parallel-fibered component posteriorly and an in-series fiber component anteriorly; the anterior components of these muscles form the bulk of "intrinsic" longitudinal muscle fibers. 5) Ventral fibers of the transverse muscle course bilaterally, with origin and insertion on different sides of the tongue. We suggest that differences in anterior versus posterior tongue morphologies relate to different functions of these regions in food acquisition/transport versus swallowing. Current description of in-series organization in longitudinal muscles provides morphological support for previous physiological demonstration of anteroposterior localization of longitudinal motor units. Interestingly, a peripheral location of circular fibers and central location of longitudinal fibers is typically found in reptiles but not mammals. The functional significance of a combined "reptile–mammal" morphology in the rat, and whether it is present in other mammals, awaits further investigation.

Neuromuscular Compartment: Fact or Fiction?

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Many muscles are composed of discrete subregions that are innervated by a unique population of motor units (MU, a motoneuron and the muscle fibers it innervates). These "neuromuscular compartments" are hypothesized to be functional output elements of the neuromuscular system. Support for this hypothesis derives from the differential electromyographic activity (EMG) of different compartments in many behaviors. For example, EMG from the two compartments of the pigeon pectoralis muscle reveals preferential sternobrachialis (SB) activity during level flight, but combined SB and thoracobrachialis (TB) activity during take-off. Previously, we suggested that SB/TB EMG patterns reflect a compartment-based strategy of activation. We now recognize an alternate, equally plausible explanation: that SB/TB EMG patterns reflect a cross-compartment strategy in which MUs are activated by virtue of biomechanical properties but independent of compartment identity. For example, some MUs from adjacent compartments typically overlap in the direction of torque they exert at a joint, and thus differences in compartment EMG may reflect a differential selection of MUs according to torque direction and not compartment membership. Tests of these strategies require in vivo investigation of individual, characterized MUs and cannot be made with multiunit EMG. These considerations apply equally to muscles, and thus we conclude that it is currently moot under what conditions, or whether, compartments and/or muscles are functional output elements of the neuromuscular system.

Meatal Diverticulum and Conchae of Tapirs

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The nasal cartilages of *Tapirus terrestris* and *T. indicus* are not lost. The proboscis (nasal tubes, surrounding lining, muscles, and skin) develops rostrally to the nasal cartilages up to the external nostrils. Unlike other perissodactyls, the external nares (nostrils) are physically separated (disjointed) from the nasal cartilages. The nasal bones, lateral dorsal nasal cartilage, and nasal cartilages (including alar) probably receded simultaneously. The nasal cartilages merged (blended in) with the dorsal lateral nasal cartilage to form a twisted structure termed the meatal diverticulum. The meatal diverticulum leaves a fossa on the maxilla, lacrimal, and frontal bones. Two specimens of tapirs from the zoo (housed in the SPGM, Munich) show an abnormal development of that region where no bony fossa is discernible. The anterior region of the conchae rotates dorsally from a primitive condition being parallel to the hard palate. The degree of rotation seems to be correlated with the length of the proboscis in *T. terrestris* and *T. indicus*. In addition, the inferior concha has multiplied into four. The posterior collagenous fascia of the straight fold of the nasal cavity pushes onto the anatomically rostral portion of the dorsal concha, leaving a dish-shaped osteological depression that relates to the motion of the proboscis. This disk-shaped osteological marker is of potential significance to reconstructing aspects of the nasal region in extinct tapirs.

Fast Muscle Function in the European Eel (*Anguilla anguilla,* L.) During Aquatic and Terrestrial Locomotion

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Eels are capable of locomotion both in water and on land using undulations of the body axis, powered by the lateral musculature. Differences in kinematics and the underlying patterns of fast muscle activation are apparent between locomotion in these two environments. The change in isometric fast muscle properties with axial location was less marked than in most other species. Time from stimulus to peak force (Ta) did not change significantly with axial position and was 82 $\pm$ 6 ms at 0.45 BL and 93 $\pm$ 3 ms at 0.75 BL, where BL is total body length from the snout. Time from stimulus to 90% relaxation (T90) changed significantly with axial location, increasing from 203 $\pm$ 11 at 0.45 BL to 239 $\pm$ 9 at 0.75 BL. Fast muscle power outputs were measured using the work loop technique, under conditions that simulated their use during aquatic and terrestrial locomotion. Maximum power outputs at $\pm$5% strain using optimal stimulus parameters were 17.3 $\pm$ 1.3 W kg^{-1} in muscle from 0.45 BL and 16.3 $\pm$ 1.5 W kg^{-1} in muscle from 0.75 BL. Power output peaked at a cycle frequency of 2 Hz. The muscle strain and stimulus parameters associated with swimming generated greater force and power than those associated with terrestrial crawling. This decrease in muscle performance may occur because on land the eel is constrained to a particular kinematic pattern in order to produce thrust against an underlying substrate.

Morphine Withdrawal-Induced Abnormalities in the Spine Dendritic in Nucleus Accubens of Rat

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The largest part of studies on neuroadaptament induced by drugs has centered on the effects produced by opiates like morphine or by psychostimulant drugs like amphetamine or cocaine for the ability they have to alter biochemical processes of cells. In this phenomenon the dopaminergic mesolimbic system that begins in the ventral tegmental area (VTA) and projects in several areas of prosencephalon like the accumbens nucleus (ACC) with its divisions seems to play a crucial role. In this work we demonstrate that both natural and induced withdrawal of morphine produces a strong reduction in the number of dendritic spines in medium spiny neurons, above all in the shell of ACC. We suppose that this synaptic remodeling depends on an altered transmission of dopaminergic afferences of VTA and from the direct action of morphine on cytoskeletal remodeling. In fact, other studies have shown that in rats the spontaneous neuronal dopaminergic (DA) activity was strongly reduced by withdrawal of morphine (Diana et al., 1995). This has been confirmed by other studies (Spiga et al., 2003) that document anatomic structural anomalies in DA cells during the withdrawal phase.

Biological Attachment Systems as a Possible Source for Biomimetics: What Can We Learn From Evolution?

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In their evolution, animals have convergently developed hairy attachment pads to attach themselves to a variety of substrates during locomotion. Using various microscopical techniques (Cryo-SEM, TEM, X-ray microscopy) and force measurements on biological systems, we analyzed which structural and mechanical features of convergently developed adhesive structures might be important for biomimetics of artificial adhesive systems. Most recent data on biological systems have demonstrated their excellent adhesion and high reliability of contact. Contacting surfaces in such devices are subdivided into patterns of micro- or nanostructures with a high aspect ratio. The size of single points gets smaller and their density gets higher as body mass increases. The fundamental importance of contact splitting for adhesion on smooth and rough substrata has been previously explained by a very small effective elastic modulus of the fiber array. We provide experimental evidence of adhesion enhancement by division of contact area. A patterned surface made out of polyvinylsiloxane has significantly higher adhesion on a glass surface than a smooth sample made out of the same material. This effect is even more pronounced on curved substrata. An additional advantage of patterned surfaces is the reliability of contact on various surface profiles and the increased tolerance to defects of individual contacts.

Applications of Doppler Ultrasonography in Vertebrates

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Doppler (duplex) ultrasonography uses frequency shifts of ultrasound echos to visualize and quantify direction and speed of moving objects (e.g., erythrocytes) in an acoustic field. Duplex ultrasonography produces color-coded images and renders straightforward, fully noninvasive, and quantitative information about blood flow volume and velocity under different physiological conditions, even in small vertebrates. This technique is frequently used in human and veterinary diagnostics, but has rarely been applied in vertebrate morphology. Spatial resolution depends on the frequency of the probe, while sensitivity to detect blood flow depends on dynamic range and the pulse repetition frequency. Today, most commercial systems allow the detection of blood flow in vessels of a few mm in cross section, and thus have become helpful tools in vertebrate morphology. Besides the broad advantages of noninvasive ultrasound imaging of undisturbed morphology in vertebrates (and invertebrates), Doppler (duplex) ultrasound imaging provides an outstanding opportunity to study the vascular system in functional condition. In this presentation, I present selected examples of studies of the vascular system and patterns of blood flow under different physiological conditions in snakes, crocodiles, and mammals.

Role of Phenotypic Flexibility for Vertebrate Morphology

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Phenotypes are not rigid entities but may respond flexibly to fluctuations in environmental conditions as well as changes in internal demands. Such phenotypic flexibility / phenotypic plasticity includes adjustments of internal and external morphologies to periodically extreme conditions, e.g., adjustments of the gastrointestinal tract in birds to periods of fasting and hyperphagia during long-distance migration. However, flexible phenotypes may evolve under different selective pressure, i.e., predictable seasonal fluctuations versus unpredictable short-term fluctuations of the environment. While seasonal changes of the phenotype may be linked to internal endogenous rhythms, responses to short-term fluctuations require immediate organism–environment interactions. In this presentation we discuss examples of both systems to point out to the importance of including seasonal and environmental information in any study of the vertebrate phenotype. Examples will cover long-distance migration in birds as well as experimentally induced changes of the gastrointestinal tract in domesticated birds. The cellular mechanisms of organ size change strikingly in different organ systems, indicating tremendous evolutionary pressure on the organism to flexibly adjust its organ size to changing environmental conditions. Flexible phenotypes broaden the ecological niche of an organism and allow for survival in environments where stable phenotypes would be eliminated. We position phenotypic flexibility in an explicitly evolutionary framework and discuss its potential role in speciation processes.

Recurring Morphological Patterns in the Evolution of Herbivory in Lizards

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As herbivory has independently evolved at least 15 times within the Lacertilia, this group presents an excellent opportunity for investigating patterns of the origin and elaboration of this dietary strategy. Although patterns of convergence among independently evolved herbivorous lizards have been documented, there has been no work done concerning quantitative patterns of morphological evolution and character acquisition among herbivores. The documentation of such patterns is important, as it allows inferences concerning the process of the evolution of herbivory. I combined a geometric morphometric analysis of lizard skull shape with phylogenies of herbivorous lizards to determine if there are any common patterns of evolution of herbivory. Seventeen functionally relevant landmarks were digitized on 1,105 lizard crania and lower jaws and the data were examined using shape-based analyses. Thin-plate spline visualizations of relative warps were used to construct variables that discriminate herbivores from their carnivorous relatives. Characters were then mapped onto lizard phylogenies using both quantitative and qualitative methods and the order of acquisition of characters was compared. Results show that the order of acquisition of characters is not similar for all clades of lizards. However, herbivorous lizard clades that have evolved on islands show similar patterns of evolution. This suggests that the mechanism driving the evolution of herbivory on islands may differ from that on the mainland.

Phylogenetic Comparative Analysis of Multivariate Data as Exemplified by Comparative Quantitative Genetics and the Evolution of the G-Matrix

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In recent years the development of comparative quantitative genetics and related subjects like phenotypic integration and developmental biology has revealed limitations in several methods of analysis. Most significantly, multivariate data are difficult to analyze in a phylogenetic framework, and there is no standard means of comparing matrices among taxa to examine patterns of variation among traits. I discuss the challenges presented by multivariate data in comparative studies and illustrate some solutions using comparative quantitative genetics. Quantitative genetics provides one of the most promising frameworks to unify the fields of macroevolution and microevolution, and the genetic variance-covariance matrix (G) is crucial to quantitative genetic predictions about macroevolution. I summarize what is known about several key questions in the field and compare the strengths and weaknesses of several statistical and conceptual approaches now being employed, highlighting those approaches using common principle components analysis, ancestral reconstruction, and MANOVA. It is now clear that the key question is no longer if G evolves, but how fast and what evolutionary processes affect the rate and direction of evolution.

Stability, Substrate Characteristics, and Limb Coordination: The Ecological Relevance of Gait

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The coordination of limb movements during mammalian locomotion has been well documented. Most mammals use lateral sequence (LS) gaits, in which a forelimb follows an ipsilateral hindlimb during the stride cycle. Diagonal sequence (DS) gaits, in which a contralateral forelimb follows a given hindlimb during the stride cycle, are utilized by far fewer groups. This study explores potential explanations for the use of DS gaits by considering the mechanical challenges experienced by one of these groups, the primates. A number of scenarios have been offered to explain why primates favor DS gaits, most of them relating to the use of the arboreal habitat and, in particular, the exploitation of a terminal branch niche. This experimental study examines the effects of branch diameter, orientation, and flexibility on gait sequence patterns in six species of quadrupedal primates. Interestingly, there is little evidence to suggest that DS gaits offer advantages for moving on narrow, steeply angled, or moving supports. Some individuals even respond to such balance challenges with a greater proportion of LS gaits. Nonetheless, it would appear that primates possess a higher than previously recognized degree of flexibility in gait sequence patterns, which likely offers some advantage for moving on discontinuous and unstable supports.

Development of the Extraembryonic Membranes of Oviparous and Viviparous *Lacerta (=Zootoca) vivipara* (Squamata: Lacertilia)

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Lacerta vivipara is a reproductively bimodal species. Viviparous populations are widely and contiguously distributed throughout Europe and northeastern Asia. Oviparous populations, which occur in southwestern France and northwestern Spain, northern Italy, Slovenia, and Croatia, are geographically isolated from each other and from viviparous populations. Recent analyses suggest that viviparity evolved from oviparity fairly recently (Pleistocene) in a single event in these lizards. Viviparous species of lizards and snakes differ from oviparous species in the development and structure of the extraembryonic membranes. We used light microscopy to compare ontogeny of the extraembryonic membranes of an oviparous population and a viviparous population of *L. vivipara* to determine if patterns of variation expressed among species of squamates are evident within this species. We found no differences in ontogeny of the allantois or the yolk sac membranes or in the structure of the chorioallantoic membrane and bilaminar omphalopleure. Development of the yolk sac membranes is unusual in this species compared to other squamates, but is similar in both reproductive modes. We confirmed conclusions from previous studies that the tertiary envelope of the egg, the eggshell, is much reduced in the viviparous population. The evolution of viviparity in this species was not accompanied by modification of the gross morphology of the extraembryonic membranes.

Conquest of Land by Temmospondyls

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With more than 160 genera from the Early Carboniferous to the Early Cretaceous, temnospondyls are the most diverse early tetrapods in the fossil record. Most of them were aquatic but some (e.g., eryopoids, dissorophoids) were terrestrial. The first terrestrial tetrapod is considered to be the temnospondyl *Balanerpeton* (Early Carboniferous of Scotland), because of its robust girdles, well-ossified carpal and tarsal elements, possible presence of eyelids, large tympanic ear, and absence of ossified branchial elements. Other terrestrial adaptations in temnospondyls are observed in bone histological structures, such as an expanded medulla, a reduced spongiosa, and a thin cortex in femoral sections of *Onchiodon*. Colonization of terrestrial ecosystems occurs during ontogeny or phylogeny. Concerning ontogeny, temnospondyls are the best-documented fossil tetrapods showing growth sequences from larval to adult individuals. Loss of lateral line sulci and branchial ossicles, development of large septomaxillary and choana, and a voluminous narial passage suggest a transition from water to land during ontogeny. These changes also occur during metamorphosis in lissamphibians, but metamorphosis in temnospondyls (when it occurs) is not necessarily linked with colonization of the land (e.g., *Onchiodon* becomes terrestrial from its juvenile stage, not from its larval stage). Concerning phylogeny, the relationships of temnospondyls within basal tetrapods is still debated, but a consensual phylogeny shows that tetrapods invaded land several times in their evolution.

Did the First Developmental Studies Lead to the Concept of Evolution?

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Comparison between development and evolution is the subject of a proper and tremendous field in natural history called "Evo-Devo." The link between evolution and development is now evident for a majority of naturalists (paleontologists included), but this was not always the case. In 1603 or 1604 (before the term "development" was used by Haeckel), Fabrici Girolamo d'Acquapendente made one of the first developmental observations, an embryological plate describing the transformation of the human embryo (*De formato foetu*). He was one of the first embryologists, but not an evolutionist. In 1800 (before the term "evolution" was used by Darwin), Lamarck presented the first evolutionary theory he called "transformism" (*Le Discours d'ouverture du cours de l'an VIII au Muséum*). He was the first evolutionist, but not an embryologist. According to these two points, one could conclude that the first developmental studies did not lead to the concept of evolution. However, the first embryological observations were often compared with a sequence of adult individuals of other species. Moreover, development and evolution kept the same sense before Haeckel (cf. the German word *Entwicklung*), and development was often used to illustrate evolution (once accepted). It is therefore difficult to answer the title's question: even if developmental and evolutionary studies have apparently different origins, both fields remained imbricate in the history of natural sciences.

Origins and Adaptations of Early Hominids

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Hypotheses explaining the origin and initial radiation of early hominids have focused primarily on diet and locomotion. The evolution of bipedal locomotion is considered the seminal event in the origin of humans, although disagreement persists as to why bipedalism evolved, and what mode of locomotion preceded it. Moreover, it is widely hypothesized that a shift towards a diet of hard, tough food items may also have played a role in hominid origins, and that diet influenced subsequent patterns of hominid diversification. These hypotheses are evaluated using an analysis of character evolution. Cladistic analysis was performed on 110 craniodental characters using an ingroup of five extant hominoid and 13 extinct hominid species. Results indicate that *Homo* and *Paranthropus* are each monophyletic, while the "gracile" australopiths are paraphyletic. By mapping postcranial characters onto the tree, it can be inferred that the last common ancestor of chimpanzees and humans most likely employed both terrestrial knuckle-walking and arboreal vertical-climbing behaviors. This contradicts hypotheses suggesting that hominids evolved from a fully arboreal ancestor. However, the node at which bipedalism first evolved cannot be precisely identified due to a dearth of postcranial fossils. Regarding craniodental characters, most of the apomorphies in basal nodes of the hominid cladogram may be functionally related to mastication. This suggests that dietary factors played a significant role in early hominid diversification.

Primate Masticatory Biomechanics Examined Using Finite Element Analysis

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Primates exhibit considerable diversity in facial morphology, and mastication is thought to be one of the variables influencing craniofacial evolution. However, masticatory and other orofacial hypotheses are difficult to test because the complex geometry of the facial skeleton confounds attempts to investigate the face with simple biomechanical models. Such hypotheses can be evaluated using finite element analysis (FEA), an engineering method that examines how objects of complex design resist loads. A model of a *Macaca fascicularis* skull was constructed using 145,680 elements. Muscle forces were modeled using data on physiological cross-sectional area (Anton, 1993) and simultaneous electromyograms for the anterior temporalis, deep masseter, superficial masseter, and medial pterygoid muscles. Material properties data were obtained using ultrasonic analysis from 25 locations on the skull. The model was constrained at a fixed bite point, and at the temporomandibular joints (where rotational displacements were allowed). These constraints produced reaction forces at those locations. Preliminary results suggest that the model is realistic. At eight facial locations, the magnitude of maximum shear strain generated by FEA falls within the range observed in vivo in chewing experiments. Similarly, at most locations the orientation of maximum principal strain is consistent with experimental data. Validation of a model using experimentally derived data is a critical stage in FEA.

Olfactory Metamorphosis in the Pacific Giant Salamander (*Dicamptodon tenebrosus*)

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The gross morphology and histology of the olfactory organs of larval, neotenic, and terrestrial adult Pacific giant salamanders from Humboldt County, CA, were examined. In all stages, the external naris opens into a nonsensory vestibule; this leads into the main olfactory chamber (MOC), which opens into the buccal cavity through the choana. The vomeronasal organ (VNO) projects forward from the ventrolateral side of the MOC as a blind tube. In larvae and neotenes the MOC is tubular, with at least six paired lateral and medial pouches lined by ciliated sensory epithelium with multicellular glands, and separated by angled internal ridges or constrictions composed of ciliated respiratory epithelium. By contrast, in terrestrial adults the MOC has lost the ridges; instead, the MOC is a dorsoventrally flattened sac, smooth interiorly, although still having regions of sensory epithelium separated by respiratory epithelium. In small larvae the VNO is lined with ciliated respiratory and ciliated sensory epithelium; it is wedge-shaped, with a lumen about 1/9 the length of the MOC. The VNO of larger larvae and mature animals is predominantly lined with ciliated sensory epithelium; it is more cylindrical in shape and is longer in proportion to the MOC. The VNO shows no evidence of glands or secretory cells at any stage.

Sexual Dimorphism in Normal Craniofacial Growth

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Since the development of standardized cephalometric techniques, facial growth has been the subject of extensive investigation. The purpose of this investigation was to reevaluate an existing sample of North Indian people, who have been characterized as having excellent occlusions and balanced facial relationships. The focus is the emergence of sexual dimorphism in the skeleton and dental relationships (age range, 16–25 years). Cephalometric evaluation indicated that the length of the anterior cranial base was larger in males but the cranial base angle was similar for both sexes at all age intervals studied. The effective lengths of maxilla and mandible were similar in both sexes up to 16 years; thereafter, in females this length remained relatively constant while in males it increased. The direction of facial growth was similar for both sexes, with a tendency towards a more horizontal growth pattern in females.

Morphological Variation in Eurasian Perch (*Perca fluviatilis*): Linking Performance and Ecology

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Most fish species increase several orders of magnitude in size during their ontogeny, and along with that they change their foraging abilities and diet. Recently, it has been found in several fish species that individuals, independent of size, occupy either the littoral or the pelagic zone of a lake. These differences in habitat choice have been connected to differences in morphology between the habitats. In Eurasian perch (*Perca fluviatilis*), we found that individuals in the littoral zone are deeper-bodied than individuals from the pelagic zone. Littoral perch are more efficient at foraging in the vegetated littoral zone compared to the pelagic perch, which have a higher foraging efficiency in the unstructured pelagic zone. The morphological growth trajectories over ontogeny in both habitats are different, and this can be due to either genetic differences or a plastic response to habitat/diet choice in perch. Our experimental work demonstrates that, even though there are small genetic differences between littoral and pelagic perch, most of the morphological variation between the two habitat types is due to phenotypic plasticity. Studies of perch and other fish species show that there are strong links between performance and ecology through morphological variation over ontogeny.

Gene Duplication and Evolutionary Novelties: Studies On Plants and Vertebrates

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Although Lewis' classical hypothesis of homeobox gene duplication in dipteran evolution was wrong in its details, the idea that the establishment of new paralogs of developmental genes might underlie morphological change is still interesting. In plants, the MADS-box gene family of transcription factors, encoding, for example, floral homeotic genes, can be compared with the homeobox genes of animals. This presentation will discuss that, unlike the rather conserved animal homeobox genes, the MADS-box gene family has undergone tremendous change in land plant evolution, involving both gene loss and extensive duplication. In animals, gene duplication apparently has been more important in vertebrate evolution than among protostomes. Whereas tunicates have around 16,000 genes, comparable to *Caenorhabditis elegans* and *Drosophila,* vertebrates have 30–40,000 genes. Developmental biologists sometimes ignore gene duplication and assume all vertebrates to have the "same genes." This has, for example, been the case concerning the EPH-receptor family and their ligands, the ephrins. These genes, as well as bagpipe-like homeobox genes, might have been important in the evolution of neural crest-derived structures in the vertebrate head. A hypothesis of the potential role of the bagpipe genes in the evolution of the anuran tadpole mouth apparatus is presented. The relation between homology at the morphological level, and gene expression patterns, important for all hypotheses of this type, are discussed.

Maintenance of Morphological Diversity in a Polymorphic Cichlid Fish

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Polymorphisms in animals are an important source of diversity and may shed light on the evolution and maintenance of species differences. This study uses a polymorphic Mexican cichlid (*Herichthys minckleyi*) as a model to study the maintenance of morphological diversity. This species has pharyngeal jaw morphotypes specialized for generalist feeding and durophagy. Here, we examine the feeding behavior, ecology, and morphology of this species in a broad attempt to elucidate the mechanisms underlying the polymorphism. We found that morphotypes use kinematically distinct feeding behaviors and tend to feed in different habitats. These differences in feeding behavior appear to allow niche partitioning. However, these differences seem to be driven by individual variation in behavioral preference. Caged competition experiments indicate that morphotypes do partition resources under high-density conditions. This suggests that the observed morphological variation is most important in times of resource limitation. Finally, a common garden experiment with different food types is being used to determine the amount of morphological variation that can be attributed to plasticity. The observed behavioral and ecological differences between the morphotypes appear to be mechanisms that can maintain morphological diversity in this species. It is our hope that these findings will provide a model of how morphological diversity is maintained in other fish communities.

Kinematic Correlates of Lift Production in Flying Bats

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To understand the mechanistic basis of animal flight it is crucial to document the dynamic changes in the 3D conformation of the wings. Two parameters of likely aerodynamic importance are wing camber and angle of attack, but assessing their relative importance, or even measuring them accurately, in small, nocturnal animals is technically challenging. We employed a two-camera IR-based video system for kinematic analysis of nine species of Australian mega- and microchiropteran bats flying under controlled conditions in wind tunnels. At each increment of the wingbeat cycle, we computed vertical acceleration of the animals' center of mass; for positive values, lift is greater than body weight. We compared the timing of peak wing camber and angle of attack to timing of lift. We find that both camber and angle of attack vary substantially throughout the wingbeat cycle, and with large peaks during the lift-generating portion of wingbeat. However, high lift values persist longer than the peaks in either camber or angle of attack. Instead, camber and angle of attack peak sequentially. We tentatively conclude that bats employ both means of increasing lift, and extend the lift-generating portion of the locomotor cycle by this dual mechanism not seen in birds or insects.

Pineal Gland and the Regulation of Cell Proliferation

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In the daily dynamics of the mitotic index (MI) epithelium crypt of the intact animals' jejunal, the circadian as well as the ultradian (8–9-h period) rhythms of cell proliferation were observed. Pinealectomy caused the absence of the circadian MI rhythm, but had no influence on the manifestation of the ultradian rhythm. This result shows that the pineal gland is an essential factor in the circadian rhythm proliferation. The pineal gland produces the hormone melatonin and the complex of neuropeptides (epithalamin), whose functional role is yet to be investigated. In our experiments, epithalamin was injected once a day starting on the 26th day and ending on the 40th day after pinealectomy, and this circumstance caused the restoration of MI circadian rhythm in the pinealectomized animals. The character of the ultradian rhythm stayed unchanged. The data show that epithalamin contains neuropeptides that participate in the regulation of the circadian rhythm of cell proliferation. These data also indicate the need for study of the interaction between melanin and pineal gland neuropeptides in the formation of this rhythm. It can be concluded that the regulation of the circadian rhythm of proliferation occurs with the participation of the pineal gland neuropeptides. The regulation of the ultradian rhythm of proliferation seems to occur at the tissue level.

***Hox* Genes Expression Patterns in Japanese Lamprey (*Lethenteron japonicum*) During Development and Evolution of the Gnathostome Jaw**

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The *Hox* gene family has important roles in the patterning of the anterior–posterior axis of various metazoans. In the craniofacial region of a mouse, *Hox* genes show nested expression patterns, whereby every two rhombomeres are specified by the number and types of *Hox* genes as segmental units. Each unit is related to each pharyngeal arch (PA) by means of cephalic crest cell populations. Thus, the cephalic *Hox* code of vertebrates is established. To elucidate the evolution of the *Hox* code as known in gnathostomes, we analyzed *Hox* gene expression patterns in the lamprey, the sister group of gnathostomes. We isolated *Hox* cDNA fragments (*LjHox*). By in situ hybridization, *LjHox2* was expressed in the ectomesenchyme caudal to pharyngeal arch 2 (PA2). Both *LjHox3d* and *-4g* were expressed in the ectomesenchyme caudal to PA3. Notably, *LjHox4h, -5i, -6k*, and *-8q* were expressed in the same caudalmost pharyngeal pouch endoderm. No *Hox* genes were expressed in the mandibular arch. These results indicate that the default state of the mandibular arch and specification of the second arch, as opposed to the more caudal arches, were established in the common ancestor of gnathostomes and lampreys. We assume that the mandibular arch derivatives, such as lamprey-specific velum and lower lip, and gnathostome jaw, evolved independently in each lineage based on the *Hox*-default ectomesenchyme after the split of agnathans and gnathostomes.

Diversity of Position and Morphology of Vertebrate Limbs

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Studies on limbs or fins, locomotor organs that are unique to vertebrates, are often done in paleontology and phylogeny because the structures are clearly visible and their bony patterns are well preserved in fossils. The sizes of limbs or fins and their positions along the primary body axis are considerably diverged in vertebrates; they are mainly determined during development and often characterize the external morphology of each species. We sought to obtain insights into the developmental mechanisms responsible for the diversity of positions of limbs by comparing the process of limb or fin development in several species, including mouse, chick, frog, and several kinds of teleost and cartilaginous fishes. We found that the AER, which is an essential structure for outgrowth of the limb bud, can be induced on the dorsal midline in mouse and chick embryos. Our findings, together with results of studies showing that the dorsoventral boundary in the flank also has the ability for AER induction, suggest that limb-growing ability in all vertebrates is latently provided in both the flank and dorsal region, and each species may use particular parts of the limb-growing ability as windows to make limbs in appropriate positions.

Possible Neuroanatomical Basis for Central Control of Cardiorespiratory Interactions in Vertebrates

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Vagal preganglionic neurons (VPN) are typically found ipsilaterally in two major nuclei, the dorsal vagal nucleus (DVN) and the nucleus ambiguus (nA) in vertebrates. This dual location may contribute to the central control of cardiorespiratory interactions. In mammals about 30% of VPN are located in the nA. However, 70–80% of those innervating the heart and lungs are located in the nA and it is here that the central interactions generating respiratory sinus arrhythmia are thought to occur. In the elasmobranch fish *Scyliorhinus caniculata,* 92% of VPN are found in the DVN, but VPN with a scattered ventrolateral distribution outside the DVN contribute axons solely to the heart. Cardiac VPN in the DVN show respiration-related activity that may generate cardiorespiratory synchrony. In the African clawed toad, *Xenopus laevis*, 32% of VPN are in the nA. Each target organ, including the heart and lungs, is innervated by VPN in both the DVN and the nA. In the axolotl, *Ambystoma mexicanum*, the number of VPN increases at metamorphosis, with 15% relocated in a lateral nA. This may in part relate to the switch from gill to lung-breathing. The extent of the nA is highly variable in reptiles. In the tufted duck, *Aythya fuligula*, only 3% of VPN are located in the nA, but about 30% of these innervate the heart.

Periosteal Vasculature and Bone Organization

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The caudal border of the mandible is an active site of bone apposition during growth of mammals. We examined the association between vascular pattern and the architectural organization of newly formed trabecular bone. It was expected that the orientation of nascent bone should correlate with the vessels in the periosteum. Four juvenile pigs (*Sus scrofa*) were injected with Microfil and calcein so that both the vasculature and newly formed bone could be visualized. The regions of interest were sectioned parasagittally and horizontally; images of the sections were then captured. In selected images bone and vessels were separated digitally, converted into black and white, and subsequently analyzed using a stereological analysis program. The vessels and nascent trabeculae showed a general horizontal orientation within the osseous layer. Two highly vascular zones were evident: the fibrous periosteal zone and the subperiosteal zone. Stereological analyses indicated that the spatial orientation of the vessels in the fibrous layer varied markedly from those in the osseous tissue. Surprisingly, the cambial periosteal layer was relatively devoid of vessels. The vascular subperiosteal zone was dense and mat-like—while difficult to quantify, it was clearly different from the other zones. The images suggest that apposition is directed from the bone itself rather than the periosteum.

Biometric Analysis of Populations of *Lebias fasciata* (Valenciennes, 1821) From Sicilian, Sardinian, and Adriatic Coasts (Teleostei, Cyprinodontidae)

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Osteological characters play an important role in the phylogenetic relationships of teleosts. Multivariate character analysis is regarded as an appropriate method for determining morphological relationships among populations of a species and it can be influenced by both current ecology and phylogenesis. In this study the amount of osteological variation between 11 Italian populations of *Lebias fasciata* was examined using multivariate analysis of 40 morphometric and meristic variables of the skull and vertebral column. A total of 268 specimens from three groups of Italian populations (Sardinian, Adriatic, Sicilian) were counterstained with Alcian blue and alizarin red. The discriminant analysis revealed the greatest discriminating power of the morphometric variables compared to the meristic ones and the importance of the bony elements of the pharyngeal jaws, of the supraoccipital and of the parasphenoid in discriminating populations. The dendrogram based on the UPGMA cluster analysis showed the separation of the Sardinian and Sicilian–Adriatic populations and isolation of the Sardinian populations of Pauli Figu (PF) and Pilo pond (S) from the remaining populations. The morphological variation is supported by allozymic, molecular, and cytogenetic researches in this species and could be explained as the result of a combination of restricted gene flow (due to the limited dispersal potential of the species and its naturally fragmented distribution) with morphological differences due to local adaptations.

Functional Morphology of the Pes of Tardigrada

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The skeletal architecture of the pes of Tardigrada is unique among mammals, especially those of large body size, and reflects locomotor behaviors that have no analogs in other mammals. A conspicuous feature is the tendency for medial rotation or torsion of the pes, a condition commonly termed "pedolateral" in the literature. Other characters common to all fossil and living tardigrades are the presence of very large and elongated unguals, and the fact that unguals are not present on all digits, especially those involved in bearing weight. The result is a complex structure that, although seemingly fragile, is efficient and robust, particularly in very large forms, such as Megatheriinae, having a capacity for bipedal progression. Although torsion of the pes is apparently an ancient feature of Tardigrada and is recognized in taxa at least since the Miocene (e.g., *Hapalops*), the degree and type of torsion nonetheless differ among the various tardigrade lineages and seem to correlate with body size and locomotory tendencies. Number of digits and weight-bearing surfaces apparently correlate strongly with type of torsion, but not degree of torsion. For example, *Hapalops* and *Megalocnus* both possess five complete and functional digits, but torsion is much more marked in the former.

Neural Crest Cells: Development and Patterning of a Stem Cell Population in Craniofacial Development

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Cranial neural crest cells are a pluripotent migratory population that gives rise to the majority of nervous, skeletal, and connective tissue in the vertebrate head. Combined with their capacity for self-renewal, neural crest cells are often considered to be stem cells. Classic models for craniofacial development argued that neural crest cells are autonomous, in that their identity and fate is established in the neural tube prior to migration. Through a combination of interembryo cell transplantation and transgenic analyses in mice, we demonstrated at the genetic and cellular level that neural crest cells are plastic in mammals. This has important evolutionary implications, as neural crest cells are synonymous with the evolution of the vertebrate head. Given that many congenital craniofacial abnormalities arise through defects in neural crest cell development, we began transplanting stem cells into the neural plate and observed that they can regenerate migrating neural crest cells which follow appropriate pathways and express typical neural crest cell markers. Sox2 appears to be an integral signal for maintaining neurospheres in a proliferative and undifferentiated fate and Sox2 is downregulated in stem cell-generated migrating neural crest cells. Currently, we are screening for genes that pattern the identity and/or migration pathways of cranial neural crest cells, which should enhance our understanding of the genetic basis underlying congenital craniofacial abnormalities.

Bone Surface Textures as Ontogenetic Indicators in Archosauria

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General ontogenetic decrease in bone surface porosity has long been recognized in many tetrapod groups. Applying surface textures as ontogenetic indicators for fossils is tempting, as the method is theoretically broadly applicable across taxa. Prior understanding of textural change in extant taxa is critical, however, to determine whether universal patterns exist, identify biological causes of textural types, and evaluate effects of growth regime on textural change. Such testing was recently begun with a study of three archosaur species, the Canada goose *Branta canadensis*, American alligator *Alligator mississippiensis*, and the horned dinosaur *Centrosaurus apertus*. A regular pattern of decreasing surface porosity occurs in *Branta*, with juveniles, subadults, and adults distinguishable by long bone textures. No consistent pattern of textural change is apparent in long bones of *Alligator*. Adult *Centrosaurus* are distinguished from juveniles and subadults by both postcranial and cranial textures; cranial textures may further distinguish juveniles from subadults. Results suggest textural aging may be applied with varying success to taxa with determinate growth (*Branta, Centrosaurus*), but is not useful for taxa with indeterminate and/or interrupted growth (*Alligator*). Application to fossil taxa without knowledge of growth regime is therefore risky at best. Surface texture types were not directly comparable across taxa, and varied between cranial and postcranial bones in *Centrosaurus*. Development of universal textural aging criteria may thus not be possible.

Plasticity and Conservation of Functional Design in the Teleost Fish, *Archosargus probatocephalus*

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Postrecruitment populations of the ubiquitous fish, *Archosargus probatocepalus,* inhabit estuaries with variable prey-resource bases. Field studies revealed a strong correlation between the type of prey consumed and the functional design of the feeding mechanism in populations that inhabit two sections of an estuary in east-central Florida. A laboratory common garden experiment was conducted to investigate the effects of rearing fish on a diet that is characteristic of each of the two field populations on the development of the feeding mechanism and the subsequent effects of rearing fish on variable prey on the kinematics of prey-capture. Young individuals of fish in one population were reared on either hard or soft prey in the laboratory. Postrearing analyses revealed that the overall body size of fish was similar in both diet treatments; however, the oral-jaw bones and muscles as well as the teeth of fish fed a hard-prey diet were more massive than in conspecifics fed a soft-prey diet. Interestingly, rearing fish on two extremely different prey types had no significant effects on the kinematics of prey-capture (e.g., the feeding kinematics of fish reared on a hard-prey diet when capturing soft prey was similar to fish reared on a soft-prey diet). Results of these studies indicate diet-induced changes in the key morphological and biomechanical properties of the feeding mechanism. However, these changes were not reflected by the kinematics of prey-capture. It is apparent that selection pressure acts on different levels of design in an organism.

Myotomal Anatomy in Zebrafish: Mapping Three-Dimensional White Muscle Fiber Angles Using Cross-Correlation Image Analysis

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Cross-correlation based image analysis techniques, such as particle image velocimetry (PIV), have been used successfully to track particles moving in fluids. While these techniques are normally applied to a series of particle images over time, they can in principle track any texture through a series of images taken over time or space. This study applied a modified PIV algorithm to serial sections of white muscle in zebrafish, *Brachydanio rerio*, to determine the 3D fiber angles. Thick sections of whole adult zebrafish were taken in the transverse and horizontal planes and optically sectioned using confocal microscopy. 3D vector fields showing the fiber orientations were then produced at each plane throughout the body. The surfaces of the myosepta in 3D were also reconstructed by manual digitization from the serial sections. Previous studies have constructed "muscle fiber trajectories" by following a muscle fiber through many myomeres, assuming that separate muscle fibers follow an overall trajectory through the myomeres. This assumption will be evaluated by comparing the orientation of muscle fibers inserting on a myoseptum to the angle of those originating from the same myoseptum. Finally, muscle fiber trajectories from many points in the body are calculated and compared to the previous results.

Development of the Pituitary Gland in the Lamprey: Evolution of Epigenetic Patterning Programs in Organogenesis

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The pituitary gland, consisting of the adenohypophysis and the neurohypophysis, is found in all vertebrates. In gnathostomes, the adenohypophysis is considered to develop through hierarchically organized epigenetic interactions based primarily on the topographical relationships between tissues. FGF- and BMP-signaling molecules derived from hypothalamic and adenohypophysial anlage are cooperatively involved in pituitary organogenesis. From a comparison of developmental processes and expression patterns of pituitary-related genes between lampreys and gnathostomes, we speculate on the evolutionary pathway of the vertebrate adenohypophysis. In the lamprey, the adenohypophysis was derived from the nasohypophysial placode (NHP) that developed anterior to the oral ectoderm. The NHP was identified by the expression of *LjPitxA*, before actual histogenesis, but it was initially distant from the future hypothalamic region. Subsequently, the NHP expressed both *LjFgf8/17* and *LjBmp2/4a* gene transcripts, whereas no signaling molecules could be identified in the hypothalamic anlage. The NHP grew caudally to establish a de novo contact with the hypothalamic region by the mid-pharyngula stage, and gave rise to both the adenohypophysis and an unpaired nasal organ. Thus, the topographical relationship between the NHP and the hypothalamic region is established secondarily in the lamprey, unlike gnathostomes. We hypothesize that a modification of the regulation of the growth factor-encoding gene may have been involved above heterochrony and heterotopy.

Innovations in the Locomotory Abilities of Pterosaurs and Their Evolutionary Implications

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Several complementary lines of evidence, including anatomical and arthrological studies, computer-based modeling, and a rapidly growing ichnological record show conclusively that grounded pterosaurs employed a quadrupedal, plantigrade stance and gait. In basal forms ("rhamphorhynchoids") the body must have remained almost horizontal during terrestrial locomotion because the shoulder-hand distance is similar to that for the hip-foot. Computer modeling indicates that "rhamphorhynchoids" moved with an ungainly waddle. A cruropatagium, stretched between the hind limbs as far as the ankles and attached to the fifth toes, is inferred to have been present in all "rhamphorhynchoids" and further restricted their terrestrial mobility. In all probability, basal pterosaurs were predominantly (or entirely) arboreal/scansorial when grounded, which is consistent with the almost complete absence of "rhamphorhynchoid" tracks. Pterodactyloids, by contrast, had a shoulder-hand distance that was considerably greater than the hip-foot distance, enabling a subvertical orientation of the body that, as computer models show, permitted a relatively effective gait. Separation of the cruropatagium into narrow crescents attached to the inner margin of each leg severed the mechanical and functional linkage between the hindlimbs, relaxing constraints on terrestrial locomotion. These innovations enabled pterodactyloids to radiate into a range of "terrestrial" niches that were not exploited by "rhamphorhynchoids" (e.g., filter feeding), resulting in the generation of an extensive ichnological record.

Mechanics and Orientation of Transverse Processes of Lumbar Vertebrate in Simians

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Thirty specimens from 26 species of simians (8 specimens of platyrrhines and 22 specimens of catarrhines, including *Australopithecus africanus, Homo erectus,* and *H. sapiens*) were studied. The lumbar vertebrae from each specimen were projected cranially and dorsally. On these projections, the orientation angle of the transverse processes in a horizontal plane (TPAH) and the orientation angle of the transverse processes in a transverse plane (TPAT) were measured. The individual angles obtained in this way were analyzed by means of the circular statistical package ORIANA in order to calculate the mean angle, the circular standard deviation, and the confidence intervals. Similarly, the angles measured, reported to radians, were regressed to the corresponding body masses. Finally, an estimation of the volume of the main back muscles inserting on the lumbar region, that is, the m. psoas and the m. longissimus and m. iliocostalis, by means of the orientation angles of L3 was carried out. The TPAH of any vertebra in catarrhines scaled faster than in platyrrhines, while statistical differences for TPAT between both groups were only found for L3 and L5. In relationship to muscle, the absolute volume calculated for the m. psoas was higher in *A. africanus* than in *H. sapiens*, while inversely the m. longissimus and m. iliocostalis absolute volume was more important in *H. sapiens*.

Modeling the Soft-Body Mechanics of Snake Tongues, Larval Fish, and Primitive Chordates

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We developed a simulation model for soft tissues that undergo large deformations. The mass distribution of the tissue is represented by a series of point masses that are interconnected by tensile elements. The tensile elements not only can be given nonlinear properties, but also muscular characteristics such as active force production, and length- and velocity-dependence of force. In addition, fluid-pressure gradients are taken into account as driving forces on the point masses. From the initial geometry, internal fiber arrangement and time-dependent activation of various muscle groups, the model computes the deformation of the soft body in a forward-dynamics manner. The model was used for the study of the design and control of soft bodies and movement reconstructions of extinct soft-bodied animals. Predicted protrusion and flicking motions of the tongue in snakes resembled actual movements that were recorded with 3D high-speed video. The model also predicted the cambering of the finfold of larval fish observed in high-speed movies. Finally, the model was also used to reconstruct the body mechanics of the fossil, Cambrian chordate, *Haikouella*. Given *Haikouella*'s reconstructed muscle architecture and the large ventrally positioned notochord, and making several assumptions about the material properties of the various tissues, the model predicts that *Haikouella* could effectively bend its body. *Haikouella* most likely used traveling body waves to propel itself through the water.

Somatic Growth and Growth of the Erupted Dentition in a Marsupial

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Studies of nonmammalian vertebrates have found that the erupted dentition grows as the body grows. Mammals differ from most other vertebrates in that they have both reduced tooth replacement and a limited period of growth, characteristics thought to be functionally related and which figure in interpretations of the biology of early mammals. This study examines the relationship of overall growth and the eruption of the dentition in a mammal. I determined the trajectories of growth of the occlusal area of the dentition and of overall body size (mass) in 10 individuals of the opossum *Monodelphis domestica* (Marsupialia: Didelphidae) from the second to the sixth month. There is rapid growth in the occlusal area from 30 days after birth until the end of the weaning period (45–60 days). This is accompanied by an extremely rapid increase in mass (4–8% per day) during the weaning period. The area of erupted dentition per unit mass reaches a sharp peak at the beginning of the weaning period and declines fairly rapidly. Growth of the body and dentition in *Monodelphis* is characterized by rapid rates and dramatic changes in rate around the time the dentition becomes functional. The sequence and timing of these events shows little variation between individuals, but I could discern no simple relationship between size of the dentition and mass.

Feeding Morphologies and Strategies in Carnivorous Synapsids

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Synapsids include modern mammals and their fossil ancestors, the nonmammalian synapsids ("mammal-like reptiles"). Extant synapsid predators are extremely diverse, ranging in size from less than 5 g (shrews) to over 500 kg (polar bears, dinocephalians). Nevertheless, they all capture, kill, and consume prey, and killing large prey loads jaws and teeth heavily. Consequently, similar adaptations for craniodental strength have evolved repeatedly in the course of synapsid evolution, allowing for fascinating comparisons between species as well as among assemblages of coexisting species. Living carnivorans display a variety of predatory techniques and diets and provide the models for reconstructing extinct predators. There are those that kill with single, crushing bites (e.g., felids, mustelids), and those that kill with multiple, more shallow bites (e.g., canids, hyaenids). There are those that are capable of consuming entire carcasses (hyaenids), and those that specialize on softer tissues (felids). These different behaviors can be read from skulls and teeth using quantitative estimates of muscle leverage, mandibular rigidity, tooth shape and size, enamel microstructure, and even tooth fracture frequency. These same measures can then be used to infer the behavior of fossil species, including those without modern analogs, such as sabertooth cats and therapsids. Such studies reveal that large body size and hypercarnivory has evolved repeatedly within predator clades, probably due to interspecific competition and energetic constraints.

Scaling of Prey Capture Kinematics in the African Catfish *Clarias gariepinus*

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Changes in body size can have important consequences on the feeding mechanics of animals. Previous studies dealing with size effects on prey capture movements in vertebrates have found conflicting results, indicating that the scaling strongly differs among taxa. Consequently, such inconsistent scaling effects may affect feeding behavior and ecology differently during growth. In this study, the effects of body size on prey capture kinematics were examined in the African catfish, *Clarias gariepinus*, a generalist predator that uses suction feeding to draw the prey towards the mouth followed by rapid closure of the mouth. High-speed videos were recorded of 16 individuals of which total length ranged from 11.0–92.3 cm during feeding on a standardized attached prey. While all previous studies on scaling of feeding in aquatic vertebrates tend to support the scaling model of Richard and Wainwright, the present study supports the alternative model of Hill: maximal angular velocities of mouth opening and closing, neurocranial elevation, and lateral hyoid dilatation decreased in proportion with skull length. Moreover, maximal linear velocities of gape size, hyoid depression, and movements of the branchiostegal membrane remained approximately constant despite the increases in absolute size of the musculoskeletal elements involved. The significance of the relatively slower kinematic velocities in prey captures of larger catfish on feeding performance is discussed.

Phylogenetic Analyses of Adaptation and Constraint in Lacertid Lizards

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Whereas "traditional" evolutionary biologists believed in the omnipotent power of evolution by natural selection, emphasis in recent years has been on processes that slow down or constrain adaptation (e.g., genetic constraints, developmental constraints, phylogenetic inertia, trade-offs). To gain insight into the evolution of locomotor performance in lizards, we tested both constraint and adaptive hypotheses. In doing so, we compared locomotor performance (i.e., sprint speed, endurance, climbing speed), limb morphology (i.e., lengths of different limb segments), and ecology (i.e., microhabitat use, antipredator behavior) across lacertid lizard species. Since species share (parts of) their evolutionary history and cannot be regarded as independent data points in statistical analyses, we used the comparative method to analyze our data. When testing whether species occurring in various microhabitats differ morphologically, the importance of taking the phylogenetic relationships between species into account becomes obvious. While results from traditional statistical analyses suggest that lacertid lizards are adapted to their respective lifestyles, phylogenetic analyses (Monte Carlo simulations) do not support this view. Moreover, simulations show that the statistical power of our test is greatly influenced by the fact that microhabitat use is clustered along the branches of the phylogenetic tree. On the contrary, when testing for the existence of evolutionary trade-offs in locomotor performance among different species, similar results were obtained for both "traditional" and phylogenetic analyses (independent contrasts).

Development of the Skeleton in the Alpine Newt, *Triturus alpestris,* and Its Bearing to Reconstruction of Larval Development in Early Tetrapods

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Caudata are the most primitive contemporary tetrapods, which suggests that their anatomical structure is comparatively close to that of early tetrapods. We investigated development of *Triturus alpestris* from late embryonic stages until the end of metamorphosis. In the earliest stage investigated (TL 4.9 mm), the rudimentary skull consists of viscerocranial elements and of independent otic and optic capsules, and only scapulocoracoid and humerus are present but neither vertebrae nor posterior limbs. The braincase walls begin to develop by means of dorsal expansions from the trabeculae. The posterior margin of the palatoquadrate is attached to the otic capsule (still free from the parachordals) by means of the processus oticus. The neural arches of the anterior two vertebrae (occipital and the first trunk vertebra) are developed, as well as complete anterior extremities; hindlimbs are still little buds and their skeleton develops much later (TL 20 mm). The scapulocoracoid is a single, undivided element. Dermal ossification begins with the tooth-bearing bones (intermaxillary, dentary, coronoid, vomer, and palatines). The first endochondral ossification of the skull is the lateral occipital, which only follows ossification of vertebrae. The ossification sequence is approximately the same in larval *Triturus* and larval temnospondyls: in both, the skeleton is ossified (except for the hyobranchial skeleton and epiphyses of the long bones) as early as at the beginning of metamorphosis.

Functional Morphology of the Hominoid Foot–Ankle Complex

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Structure and function of the foot–ankle complex of gibbons, bonobos, and humans were investigated and correlated with their specific locomotor repertoire. Ape species were selected for: 1) their different degree of arboreal specialization; 2) their bipedal behavior; and 3) their close relationship to humans. Detailed dissections of the lower limb were carried out on two bonobos and two gibbons and combined with CT-scanning and 3D visualization. Muscle function and mobility of the joints were investigated through manipulation and digitalization. These data were compared with the extensive literature on human foot function. The joint surfaces and relative development of the muscles point at a mobile foot with a primarily prehensile function in the arboreal gibbon, along with a propulsive function in the more terrestrial bonobo. Gibbons also have lower relative leg muscle masses compared to the more robust bonobo. However, the differences between both nonhuman ape feet are subtle in comparison with the diverging locomotor repertoire. In both cases, the emphasis is clearly on a flexible foot, capable of adapting to many different locomotor modes. This contrasts with the rigid human foot, which is highly specialized for bipedal walking. The comparative study of primate locomotor anatomy provides an insight in form–function relationships and may be used in the interpretation of primate and prehominid fossils.

Comparative Study of Osteoderm Development in *Alligator mississippiensis* and *Dasypus novemcinctus*

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Although representative members of various amniote lineages demonstrate osteoderms, their development is poorly known. This study offers preliminary data on the ontogeny of osteoderms in alligators and armadillos. Skeletally mature alligator osteoderms are coin-shaped, with a small keel or point. Mature armadillo osteoderms dorsal to the head and across the pectoral and pelvic regions form mosaics of interlocking polygonal-shaped elements without keels. Between the pectoral and pelvic regions, armadillo osteoderms are rectangular and imbricated. Presumptive osteoderms of both taxa do not demonstrate any signs of cartilage, but do show strong positive reactions for various connective tissue stains. In alligators, presumptive osteoderms begin as domes of loose mesenchyme that are eventually replaced by thick bundles of highly organized collagen. Mineralization occurs well after hatching, with incipient centers of ossification developing within the keels of the cranialmost elements, dorsal to the thick collagen network. Armadillo osteoderms begin to develop prior to parturition and are first noted in the pectoral and imbricated regions. Presumptive armadillo osteoderms also develop networks of collagen, although the bundles are thinner and less organized than those of alligators. Furthermore, mineralization begins within the middle of the element. Details of comparative histology and development are discussed.

Relationship Between Head Morphology and Feeding Performance During Ontogeny in Two Snake Species *(Nerodia fasciata* and *Agistrodon piscivorous)*

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The scaling of form and function has long been of interest to biologists. However, relatively few studies have examined the ontogenetic relationships between an animal's trophic morphology and feeding performance. To address this issue, I examined how the scaling of head morphology and feeding performance (number of pterygoid walks per item and swallowing time) are related in a semiaquatic pitviper (*Agkistrodon piscivorus*) and a similarly sized water snake (*Nerodia fasciata*). For feeding performance trials, I fed each species a "bulky" prey item (i.e., a mouse for the pitviper and a frog for the water snake) as well as a "slender" prey item (i.e., fish for both species). Both prey types were scaled to the snake's head width so that feeding performance would be comparable across size classes. In both species, head dimensions scaled with negative allometry relative to snout–vent length, but isometrically to head length. However, the scaling patterns of head elements did not accurately predict feeding performance for bulky prey items (i.e., swallowing time did not decrease with increasing head length for bulky prey items in either species). For slender prey, however, swallowing time dramatically decreased with increasing head length throughout ontogeny in both species. These results thus provide unique insights into functional relationships likely important during prey selection by snakes.

Mechanisms of Development of the Neural Crest-Derived Skeleton in *Hymenochirus boettgeri*

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A wealth of information has been collected regarding the mapping and development of the larval cartilaginous skeleton of anurans (frogs and toads). However, little is known about the mapping of the adult bony skeleton, or the mechanisms mediating replacement of the cartilaginous skeleton by the bony skeleton during metamorphosis. Of particular interest is the development of the skull, which is largely derived from neural crest, a secondary germ layer arising from neural ectoderm during neurulation. The current study utilized organ culture of presumptive mandibular mesenchyme, from variously aged tadpoles, to determine the major control mechanisms of larval (cartilaginous) and adult (bony) mandibular development in the Dwarf African Clawed Frog, *Hymenochirus boettgeri.* Some cultures were supplemented with either exogenous thyroxine or thiourea (a thyroxine inhibitor). These cultures were used to assess 1) whether an epithelial–mesenchymal interaction is involved in initiating skeletogenesis; 2) whether thyroxine, a hormone essential to amphibian metamorphosis, plays a role in skeletogenesis, specifically by mediating development of the adult bony mandibular skeleton; 3) whether skeletogenesis involves a combination of 1 and 2. Preliminary results address stage specificity, survival, growth, differentiation, and the role of thyroxine in the organ cultures. This approach should provide important information regarding the mechanisms by which both the larval cartilaginous and the adult bony skeletons develop in anurans.

Maximum Bite Forces Among Three Sympatric *Hapalemur* Species at Ranomafana National Park, Madagascar

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Hapalemur griseus, H. aureus, and *H. simus* coexist at Ranomafana. Each species specializes in eating different parts of bamboo—an unusual food for primates (Tan, 1999). These circumstances have created a natural experiment for investigating the relationship between masticatory performance and the external environment, in this case, food resources. We recorded maximum bite forces at the P3 while stimulating the jaw muscles to tetanus in anesthetized animals. Our sample included four *H. griseus*, five *H. aureus,* and six *H. simus*. We controlled for the influence of jaw-muscle stretching on bite force by recording maximum bite forces at one-half and one-third maximum gape for each animal. Maximum bite forces at one-third gape averaged 100.8 Newtons in *H. griseus*, 216.2 N. in *H. aureus,* and 317.1 N. in *H. simus*. Bite forces increased with strong positive allometry relative to jaw length (RMA slope $\approx$ 4.0) across individuals from these three species. Thus, individuals from the larger *H. simus* can generate absolutely and relatively greater bite forces than members of *H. griseus*, the smallest species. There is, however, overlap in maximum bite forces between individuals of *H. simus* and the intermediate-sized *H. aureus*. This overlap indicates that biting performance by itself cannot explain differences in bamboo feeding behavior among these bamboo lemurs.

Evolution of Labroid Fishes: New Hope for a Key Innovation Poster Child

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The Labroidei (labrids, cichlids, damselfishes, and surfperches) were hypothesized to be monophyletic based primarily on a shared derived condition of the pharyngeal jaw apparatus (PJA). The labroid PJA includes a single fused lower jaw bone and a muscular sling that suspends the jaw from the neurocranium and permits a mechanically direct bite. This innovation became famous as a putative key innovation that may have been involved in the radical success and diversity of labroid fishes. However, the PJA key innovation hypothesis has been criticized because of the apparent uniqueness of its origin and resulting difficulty in linking success of the group to the innovation. We tested the monophyly of the Labroidei using DNA sequence from the cyt b locus of representatives of 75 groups of teleost fishes, primarily perciforms. The resulting tree indicates that the Labroidei are not monophyletic because the Labridae falls well away from the other groups. Our studies of the PJA in these groups indicate functional differences between labrids and the other labroids. The implications of this study are that the labroid PJA has evolved at least twice, once in association with the evolutionary success of cichlids and damselfishes, and once in association with the evolutionary success of labrids. This result reignites the candidacy of the labroid PJA as a key innovation in fish evolution.

Development of the Pectoral Fin Musculature in Zebrafish

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The pectoral fin musculoskeletal system in fishes is relatively simple. Teleost fishes typically have six or seven muscles that control the movements of the fin. Despite recent work on the migration of muscle precursors into the fin bud, no work has sought to describe the embryology of the pectoral fin musculature following the migration of the muscle cell precursors into the fin bud. The goal of this study is to describe the development of the pectoral fin musculature in *Danio rerio*. This study approaches muscle embryology using fluorescent antibody staining of muscles and endochondral bony elements to distinguish the origination and insertion of the pectoral fin musculature across ontogeny. Preliminary evidence indicates that the fin musculature begins as two single-fiber thick muscles: an adductor on the medial side of the scapulocoracoid and an abductor on the lateral surface of the scapulocoracoid. Later in ontogeny these muscles increase in the number of fibers and differentiate into the more specialized abductors and adductors. This study provides the embryological basis for ongoing studies on a comparative analysis of pectoral fin muscular development in fishes. By comparing musculature development in groups of fishes with different levels of muscle differentiation, we hope to develop hypotheses concerning the molecular control and evolutionary basis of increased muscle differentiation.

Comparative Primate Bone Microstructure: Records of Life History and Mechanical Adaptation

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Bone tissue can both respond to and record the processes and behaviors that characterize individual life histories. It therefore offers a unique opportunity for expanding insights derived from macromorphological studies of the skeleton. This project examines the significance of bone microstructural features with respect to life history and mechanical adaptation. The comparative sample includes both strepsirhine and haplorhine primates and a selection of phylogenetically relevant nonprimates. These taxa were chosen to provide a range of body sizes, growth and metabolic patterns, positional behaviors, and evolutionary relationships. Ground sections 100 μm thick from the midshafts of major long bones were imaged in transmitted and circularly polarized light. Images were then processed to provide qualitative and quantitative information regarding: 1) the proportion of primary bone tissue types, examined relative to life history features; 2) the degree of secondary remodeling, considered with respect to both life history and locomotion; and 3) patterns of preferred collagen fiber orientation, as they relate to mechanical adaptation, element-specific growth patterns, and tissue types. These points are considered in light of the phylogenetic relationships among taxa. Results indicate that, despite the near-restriction to a single mammalian order, bone microstructure is highly variable yet distinctly nonrandom in its variation. Data from this project have significant implications for the interpretation of primate paleobiology and evolution.

Adaptations for Fossoriality in Tadpoles

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Many anuran species have adults that actively burrow, yet burrowing tadpoles are rare. The majority of fossorial tadpoles are extremely elongated, with reduced tail fins; this morphology allows them to sequester themselves into small spaces. These attenuate tadpoles are found in wet leaf litter along streams and in leaf axials of bromeliads and other phytotelms. An alternative morphology for burrowing tadpoles is seen in the microhylid genus *Otophryne.* These larvae have broad, shovel-like snouts and extra cranial chondrifications. They actively burrow into wet sand by rapid oscillations of the snout. Why aren't there more burrowing tadpoles? Several features that favor rapid growth and then metamorphosis in most tadpoles may account for the relative rarity of fossorial tadpoles. Active burrowing requires a certain amount of strength and mass. Most tadpoles, however, have relatively little mass in the musculoskeletal system. Growth (and metamorphosis) can consequently be quick, but at the expense of the tissue firmness necessary to pierce resistant substrates. To grow quickly, tadpoles also need microhabitats rich in food resources. The dark places where fossorial animals usually reside are not high in primary productivity. Little is known about developmental rates for *Otophryne.* One prediction, though, from this ecomorphological perspective on what makes tadpoles well designed (or not) for burrowing, is that *Otophryne* larvae may take months to years to metamorphose.

Tooth Shape in Eretmodini (Teleostei, Cichlidae): An Ontogenetic and Multivariate Morphometric Analysis

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The Eretmodini are cichlids endemic to Lake Tanganyika. Although the tribe currently comprises four nominal species mainly defined by distinctive tooth shapes (*Eretmodus cyanostictus, Spathodus erythrodon, S. marlieri*, and *Tanganicodus irsacae*), six genetic lineages (A–F) have been identified. As part of a study to elucidate how similar tooth shapes could have evolved repeatedly and independently, we performed extensive analyses of tooth shape in these taxa. Here, we report results of a multivariate morphometric analysis of tooth shape and size in a considerable size range of subadult and adult specimens in four lineages (*Eretmodus cyanostictus* lineages A and C, *Tanganicodus irsacae* lineages D and E). Our results show that, in general, a large portion of the observed variation in tooth linear measurements can be explained by a linear regression on SL, and thus by growth. Regressions on SL were not significant for most tooth angular measurements. In a few cases, the regression was nevertheless significant but the amount of variation explained by the regression was low. From these results, and from the observation of a dramatically different tooth shape in larvae and early juveniles, we conclude that the adult, taxon-specific, eretmodine tooth shape is established early in adult life, and remains relatively unaltered afterwards, whereas tooth size further changes with increasing fish size.

Facial Bone Modeling and Muscle Attachment in the Juvenile Pig (*Sus scrofa*)

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Facial bones develop their characteristic shapes by modeling (apposition or resorption) of the periosteal surface and by growth at sutures, and an important factor in bone modeling is muscular attachment and loading. This study tested the hypothesis that a single muscle, the levator labii superioris (LLS), is associated with a single modeling pattern in the three bones to which this muscle attaches. In the pig, the maxilla, lacrimal, and zygomatic bones contribute to a distinct fossa which is the attachment site for the LLS muscle. Modeling of the fossa was examined in juvenile pigs using scanning electron microscopy ($n = 12$) and histology ($n = 5$). Large areas of bone resorption were found on the maxillary part of the fossa, while resorption was less frequent on the zygomatic part and uncommon on the lacrimal part. Similarly, osteoclasts were common in the maxillary part of the fossa and rare in the lacrimal part. The bone microstructure, sutural morphology, and osteoblast morphology also indicated that the three bones have different modes of growth to achieve the same (concave) shape. Thus, the attachment of the LLS muscle was not associated with a single modeling pattern in the three bones. However, it is still possible that the LLS muscle loads the three bones in different ways, and this might account for the observed variation in modeling.

Ear and Swim Bladder Morphology in Chaetodontid Fishes: Adaptations for Enhancement of Hearing?

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The recent finding that one *Chaetodon* species produces sound in the noisy environment of a coral reef supports the notion that sound reception is important in the natural behavior of *Chaetodon*. The laterophysic connection (LC), a specialization found only in *Chaetodon*, is defined by bilaterally paired, swim bladder extensions ("horns") that approach or come in contact with a medial opening in the supracleithral lateral line canal. Like the otophysic connection in other taxa, the LC is thought to enhance sound reception by the ear and by the lateral line system, which is not sensitive to sound. If the LC enhances auditory capabilities, then we expect the ear morphology of species with (*Chaetodon*) an LC to reflect those features reported for "hearing specialists." Since the swim bladder likely transmits and transduces sound pressure stimuli, we expected similar trends in its morphology. We used CT to reveal the 3D structure of the otoliths, the dimensions of the swim bladder and swim bladder horns, and their relative positions in live, anesthetized butterflyfishes. Histological and SEM analyses determined the size and shape of the sensory epithelia in the inner ear and the structure of the wall of the swim bladder. The evolution of the laterophysic connection and the significance of sound reception to *Chaetodon* behavior are discussed.

Shock Absorbers and More: Design Principles of the Lower Hindlimb in African Elephants *(Loxodonta africana)*

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African elephants can reach a weight of up to 6 tons and a speed of 40 km/h, but their preferred type of locomotion is a meandering walk. Although the larger forelimbs support more than half of the body mass, the hindlimbs are also well adapted to weight bearing. The toes are enclosed within a flexible skin-shoe and the tarsals and metatarsals are arranged similar to the human foot, forming both a transverse as well as a paramedian arch, although the *Tuber calcanei* does not reach the ground in the elephant. None of the phalanges touch the ground directly. The toes are supported by toe cushions and a well-structured sole cushion lies between the tarsals and metatarsals and the sole skin. In the African elephant a strong toe-flexing Musculus (M.) flexor digitorum superficialis is absent, as it is in humans. Small flexor muscles also supporting the metatarsophalangeal joints as well as adductors and abductors of the toes are present. The long extensors of the toes do not insert only on the dorsal surface of the distal phalanx, but also attach to the medio- and lateroplantar edges of the phalanges. The tendons of the Mm. fibulares brevis, longus, and tibialis caudalis pass dorsodistally over the ankle joint, thus providing a strong support for this joint.

Ontogeny of Cranial Sexual Dimorphism in Hominoids: Implications for Hypotheses of Sexual Selection

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A comparative ontogenetic approach was utilized to examine sex differences in hominoid facial morphology. Scaling relationships that occur during the postnatal development of different skull components within each sex were estimated for *Pan troglodytes* and *Gorilla gorilla*. We show that chimpanzees exhibit clear sexual dimorphism in face width, over and above that expected on the basis of sex differences in body size. This type of facial dimorphism manifests itself relatively late in postnatal ontogeny, indicative of secondary sexual development. In contrast, the facial skeleton of the male and female gorilla is ontogenetically scaled. Furthermore, through the analysis of cranial data from published sources it is shown that such facial dimorphism is negatively correlated with canine dimorphism among anthropoid primates. Our findings thus suggest that the lack of canine dimorphism in anthropoid primates is not due to weak sexual selection, but rather is associated with strong sexual selection for broader face width. Enlarged cheekbones have been linked with attractiveness in humans, but it is unclear whether such morphological variation is purely allometric in nature. Sexual variation of face breadth in *Homo sapiens* was reevaluated in light of this study's findings. We propose that the evolution of a broad face in male anthropoid primates results from intersexual selection (mate choice), as opposed to intrasexual competition.

Behavioral and Morphological Specializations for Aerial Prey Capture in the Silver Arowana, *Osteoglossum bicirrhosum*

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Silver arowana *Osteoglossum bicirrhosum* capture prey at or just below the water's surface and leap out of the water to capture prey. Prey capture events of *O. bicirrhosum* (n = 4) feeding both above and below the water's surface were recorded at 500 fields per second by two synchronized video cameras. Timing and displacement variables of the feeding apparatus, pectoral girdle, and entire body were quantified to compare aquatic and aerial strikes. Results indicate that aerial bites generally involve shorter durations and larger excursions than aquatic bites, although strike durations were not different (~65 ms for both). Thrust generation during aerial capture is characterized by more extensive pectoral fin depression and caudal fin motion. We hypothesize that at least four behavioral and morphological attributes contribute to the ability of *O. bicirrhosum* to obtain prey in an otherwise unattainable environment: 1) delay of mouth opening until the fish leaves the water during aerial capture; 2) an elongate, flexible, laterally compressed body capable adopting an "S" posture; 3) large anal and second dorsal fins that contribute to body-caudal fin propulsion; and (4) a fused pectoral basal plate with an associated twisted j-shaped abductor profundus muscle that is able to rapidly pull the pectoral fins posteroventrally.

Mandibular Form and Masticatory Bone Strain in Alpacas

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Alpacas (*Lama pacos*) are South American selenodont artiodactyls belonging to the family Camelidae. In addition to having a solidly fused mandibular symphysis, compared to other selenodont artiodactyls, camelids also have relatively longer symphyses anteroposteriorly and relatively wider mandibular corpora. Because these patterns indicate increased resistance to lateral transverse bending of the symphysis and corpora, respectively, it suggests that this loading regime is an important determinant of mandibular form. Here, we present the first in vivo mandibular strain data in a camelid to better understand the nature of mandibular loading during mastication. Rosette strain gauges were attached to the mandibular corpora and symphyses of four female alpacas. Both the magnitude and direction of principal strains were calculated for the power stroke of mastication of alfalfa hay. Results indicate that the working-side corpus is twisted about its long axis and/or sheared perpendicular to its long axis during the power stroke. On the balancing-side, the corpus undergoes a combination of parasagittal and, as predicted by the morphological data, lateral transverse bending. The symphysis strain data suggest that the symphysis is sheared dorsoventrally and/or twisted due to twisting of the mandibular corpora about their long axes. Consistent with the morphological data, the symphysis is also bent due to lateral transverse bending late in the power stroke of mastication.

Comparison of the Ontogeny of Prey Capture Kinematics and Feeding Morphology in Wild and Hatchery Florida Largemouth Bass *Micropterus salmoides floridanus*

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Historically, stocking programs for the largemouth bass have poor success of fingerling survival. This study investigates this problem in light of functional morphology. Fifteen wild and hatchery bass from four size classes (20–99 mm TL) were filmed feeding on prey appropriate for their lifestyles, with hatchery bass consuming pelleted food and wild bass feeding on evasive mosquitofish. Kinematic analysis revealed that wild bass used a ram-based strategy, while hatchery bass utilized more suction. Wild individuals reached a larger maximum gape earlier, had greater and longer hyoid excursions, had a shorter duration of maximum gape, and closed their mouths more quickly than their hatchery counterparts. Analyses across size classes show that the degree of ram feeding, the distances of maximum jaw and hyoid excursions, and the lengths of timing variables typically increased as the size of wild fish increased. Similarly, as hatchery fish grew larger, they employed more suction during feeding. Trends in other kinematic variables for hatchery fish, however, were masked by atypical feeding patterns of individuals in size class 3 (60–79 mm TL). These findings are examined with regard to whether such alternate methods of prey capture translate to variations in the osteology of the feeding apparatus, as well as if behavioral plasticity can allow hatchery bass to overcome any such physical limitations postrelease.

Fleshing Out Fossils: The Present as the Key to a Very Different Past

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Fossils tend to preserve only bones and teeth, and so morphologists are challenged to reconstruct those aspects of biology that have been lost. Soft tissues are particularly important, because they not only animate the skeleton, but form the basis for broader biological inferences. Information on any unpreserved feature must come from modern taxa, most relevant being the two extant outgroups of the fossil, which form the extant phylogenetic bracket (EPB). Central to EPB studies is the specification of the causally associated osteological correlates of the inferred attributes, because these bony signatures link the past and present. Based on the phylogenetic support for inferred attributes of extinct taxa, different levels of inference can be identified, with strong level I inferences drawing the most support and weak level III inferences drawing least. Remarkably, level III inferences are common and among the most interesting, because they represent the evolution of anatomical novelties. Inferring novelty in fossils is tractable when grounded in the extant realm. Consideration of unpreserved features (soft tissues, physiology, behavior) of extinct taxa is often necessary for extant studies because modern species have an evolutionary history and the current time plane does not sample the full range of organismal form and function. Ironically, rather than "modernizing" fossils, using the present to reconstruct the past often reveals the uniqueness of extant taxa.

What Happens to the Kype of Male Atlantic Salmon (*Salmo salar*) That Survive Spawning?

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The return of Atlantic salmon (*Salmo salar*) to their home river for spawning involves drastic skeletal alterations in both sexes. The development of a kype (hook) at the tip of the lower jaw in males is the most prominent feature. Unlike Pacific salmon that die after spawning, male Atlantic salmon that survive would have to cope with the kype throughout their life, unless the structure disappeared after spawning. To understand the fate of the kype skeleton, we compared morphological and histological features of kypes from prespawned anadromous males (obtained in the fall) with postspawned surviving males (obtained in the following spring). In the fall, the kype is supported by fast-growing needle-like skeletal structures that contain chondroid bone and thus differ substantially from regular dentary bone. In the following spring, growth of the kype skeleton has stopped and skeletal needles are resorbed distally by osteoclasts. Simultaneously, and despite the animals' severe starvation, bone formation continues. Proximal parts of the kype skeleton are remodeled and converted into regular dentary bone. Distal resorption of the skeleton explains reports of a decrease of the kype in kelts. The conversion of basal kype skeleton into regular dentary bone contributes to the elongation of the dentary and likely provides the basis for the development of a larger kype in repetitive spawning males.

Breeding Teeth in Atlantic Salmon: Fact or Fake?

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The diadromous life cycle of Atlantic salmon (*Salmo salar*) involves drastic skeletal alterations. Connected to the animals' spawning migration, a toothless stage followed by the appearance of breeding teeth has been suggested. We elucidated the pattern of tooth initiation and replacement in different life stages of wild Atlantic salmon using serially sectioned and X-rayed jaws. The first teeth develop directly from the buccal epithelium. In all subsequent stages, a replacement tooth is connected to the lingual and caudal side of the enamel organ of its predecessor. In juveniles, every position in the tooth row holds a functional tooth and a replacement tooth. Odontogenic waves link teeth in similar developmental stages every three positions; replacement waves link teeth in alternate positions and slope down cephalad. This pattern is maintained in prespawning animals, but every position now holds either a functional or a replacement tooth (through wider spacing of odontogenic waves). In postspawning animals the pattern is obscured. However, the abundance of functional teeth indicates that teeth are not lost and that replacement teeth become attached over winter. Our studies provide no indication for a complete change of the dentition prior to spawning. At no time in the life cycle have we found edentulous stages and the pattern of tooth replacement observed in juveniles is continued in prespawning animals.

Finite Element Model Construction for the Virtual Synthesis of the Skulls in Primates

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The analysis of strains in real skulls is an inductive method that yields information about the stresses occurring in the a priori existing shape. We prefer on the basis of Wolff's law the deductive technique of structure synthesis. We start from an unspecific homogenous body that offers the stresses ample volume for spreading between force application and bearing. We used ANSYS 7.0 forming 10-node-tetrahedral finite elements (maximum of 130,000 nodes). Only functional spaces for the sensory organs, the nasal channel, and the brain are taken as preconditions, as well as muscle forces and the placement of the dental arcade. Equilibrium of forces must be considered. The primary 3D stress flows found for each load case are summarized by a "load case technique." If the stress-free parts are eliminated and the summarized stress flows are maintained, a "reduced" model appears that is very similar to the real skull. This "reduction" of shape can be repeated iteratively and leads to a more exact form. Changes in the form of dental arcade, its position relative to the braincase, or the origins of muscles, or the height of the face, lead to models that clearly resemble morphological differences between genera.

Abdominal Gut Appendage of Mesopelagic Fish Larvae

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The abdominal gut appendage (AGA) or "trailing gut" is an unusual feature of some mesopelagic fish larvae (Stomiatoidea). It is a long, thin, cylindrical extension of the ventral body wall, coelom, blood vascular system, and hindgut. The AGA, which arises via differential growth, can attain 5× the body length. In *Heterophotus*, the tubular foregut within the body has a ridge-shaped invagination of the gut wall like a typhlosole. In contrast, the hindgut intestinal epithelium of the AGA has developed into longitudinally oriented, scroll-like sheets that extend from the gut wall into the lumen, similar to a spiral valve. Thus, absorptive surface area is greatly increased. Longitudinally oriented smooth muscle is associated with the exterior surface of the hindgut. A large blood vessel is in contact with the gut wall and runs the length of the AGA. A series of bands, 5 μm wide, comprising cells with pleated apical surfaces, extends along the exterior of the AGA. TEM shows fine filaments filling their cytoplasm. At its distal tip, intestinal tissue that protrudes from the terminal gut orifice forms prototypic trophotaeniae. SEM and TEM of the AGA hindgut in museum specimens reveal tall columnar cells with basal nuclei, relatively few apical microvilli, limited endocytosis, a very well-developed endoplasmic reticulum, and an extensive vacuolar system. These cells may function in absorption.

Hindlimb Use During Bipedalism in Primates: A Comparative Study

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Bipedalism is rare among mammals, yet has evolved in two distant primate groups, hominoids and indrids. We examined foot use and hindlimb kinematics during bipedalism in one hominoid, *Pan troglodytes*, and one indrid, *Propithecus verreauxi*, in order to assess the extent to which adaptation to a particular mode of arboreal locomotion constrains terrestrial bipedal locomotion and the extent to which the fundamental mechanical demands of terrestrial bipedalism constrain movement patterns. We collected plantar pressure distribution and video data on five *Propithecus* and two *Pan. Propithecus* uses a sideways bipedal galloping gait characterized by high hip excursions and preparatory countermovements. Lead and trail limbs exhibit different kinematics, footfall patterns, and propulsive forces but similar peak vertical forces. Peak forefoot pressures are on the first and fourth digits. *Pan* exhibits a compliant walking bipedal gait in which the hindlimb joints are flexed, load is highest on the heel and medial midfoot, and limbs move symmetrically. Peak forefoot pressures are on the first and third metatarsals and are low on the toes. Peak vertical forces in bipedalism are relatively lower than in the habitual forms of locomotion for both species (quadrupedalism, *Pan*; vertical clinging and leaping, *Propithecus*). Primates moving bipedally do so in a way that reduces joint load and takes advantage of morphological and functional adaptations to their habitual form of locomotion.

From Molecular Sequences to Functional Morphology: What Can Phylogenetic Analysis of Snake Toxin Families Tell Us About the Origin of the Venom Apparatus?

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The origin and evolution of the ophidian venom apparatus has had a long history of controversy. Present opinion, based on morphology combined with organismal phylogenetic hypotheses, favors a single early origin of venom at the base of the Caenophidian radiation, followed by extensive "evolutionary tinkering." However, the venoms themselves have, until now, contributed little to the debate. Here, we analyzed the origin and evolution of eight snake venom toxin families represented in both viperid and elapid snakes by means of phylogenetic analysis of the amino acid sequences of the toxins and related nonvenom proteins. Out of eight toxin families analyzed, four provided clear evidence of recruitment into the snake venom proteome prior to the diversification of the advanced snakes, and two were equivocal. In two others (phospholipase A2 and natriuretic toxins), the nonmonophyly of venom toxins demonstrates that the presence of these proteins in elapids and viperids results from independent recruitment events. These results provide strong additional evidence that venom evolved once, at the base of the advanced snake radiation, rather than evolving multiple times in different lineages. Moreover, they provide a first insight into the composition of the earliest ophidian venoms, and point the way towards a research program that could elucidate the functional context of the evolution of the snake venom proteome.

Comparative Anatomy of the Pulmonary Artery Sphincter in Marine Turtles: Gross and Microscopic Structural Adaptations

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Sea turtles are secondarily aquatic, migratory specialists that possess suites of adaptations for prolonged swimming and diving. We describe the gross and microscopic structure of the pulmonary artery sphincter, an unusual adaptation found in marine turtles. We examined great vessels in hatchling and adult leatherback (*Dermochelys coriacea*) and green turtles (*Chelonia mydas*). In leatherbacks, the pulmonary sphincters are located closer to the lung than in green turtles. The smooth muscle layers are thick in both species and the muscle fibers are helically wound, a characteristic of blood vessels under high pressure. The sphincter appears to regulate pulmonary artery resistance, so flow is selectively shunted from the pulmonary to the systemic circuit, and is more robustly developed in deep-diving leatherbacks than in shallower-diving green turtles. We hypothesize that blood flows freely through the pulmonary sphincter into the lungs during breathing and when lung oxygen levels are high, but during prolonged apnea (diving), pulmonary artery sphincters constrict and either reduce flow or shunt blood away from the pulmonary circuit into the systemic circuit. This pulmonary artery sphincter is unlike other flow controlling structures found in other vertebrates.

Frog (*Rana pipiens*) Amelogenin Sequence and Enamel Biomineralization

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Vertebrate enamel formation is a highly coordinated process that involves the formation of long and parallel hydroxyapatite crystals coordinated by the macromolecular control of enamel extracellular matrix molecules, mostly amelogenins. Advances in mouse genetics and amelogenin biochemistry have provided significant information toward the process of mammalian enamel formation, leaving nonmammalian enamel formation as a fascinating area to reveal the origins and evolution of enamel as a tissue. In the present study, we focused on frog enamel formation as a model to further understand the process of enamel evolution. Leopard frog (*Rana pipiens*) tissues were fixed and processed for electron microscopy, immunohistochemistry, and in situ hybridization. RNA was extracted from frog teeth and processed for sequence analysis using polymerase chain reaction (PCR) methodology. Electron microscopy revealed frog enamel to contain long and parallel crystals similar to mammalian enamel. Immunoreactions and in situ hybridization studies confirmed the site-specific localization of amelogenin in frog enamel. Sequencing of amelogenin PCR products revealed a 782 bp cDNA with a 546-nucleotide coding sequence encoding 181 amino acids. The homology of the newly discovered frog amelogenin sequence with the published mouse amelogenin was 38.6%. Our findings indicate a close homology between mammalian enamel formation and enamel biomineralization as described in *Rana pipiens.*

Comparative and Functional Morphology of Venom Ducts in Snakes

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The phylogeny of Serpentes remains unresolved; nevertheless, there is a general consensus that a venom delivery system has evolved independently in multiple snake taxa. Venom injection is a characteristic feature of the Viperidae, Atractaspidae, Elapidae, and Hydrophiidae, and is present to varying degrees in several groups within the Colubridae. Some aspects of these venom delivery systems, particularly the related musculature and dentition, have been well studied. This contribution will center on one of the most poorly known aspects of the venom delivery system, the venom duct. There is considerable variation in the morphology of the venom duct among different taxa, including the number of ducts, the orientation of the duct (vertical or horizontal), and the spatial relationship between the duct and the venom delivery tooth or fang. The different suites of morphological features suggest a range of functional roles in venom delivery. While some venom ducts may be simple conduits, others appear capable of influencing or regulating the flow of venom. Experimental evidence suggests that the venom ducts of different taxa may be exposed to significantly different internal pressures. Understanding the possible transitions between the different types of venom ducts may provide some insight into the phylogeny of venom delivery in snakes.

Canalization, Developmental Stability and Integration of Rodent Skulls

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Canalization and resistance to developmental noise indicate that development is stabilized against genetic and environmental perturbations. How these components of developmental stability are causally related, and how each is related to morphological integration, have long been subjects of theoretical interest. We examined these relationships in the skulls of two rodents, cotton rats (*Sigmodon fulviventer*) and house mice *(Mus musculus domesticus)*, over ontogeny. In both, variance of skull shape decreases markedly early in postnatal development and thereafter stabilizes. Fluctuating asymmetry shows a similar temporal pattern but a different spatial distribution; matrix correlations between symmetric and asymmetric spatial patterns never exceed 0.12. At all ages, the patterns of variation appear to be nearly random except that some landmarks vary more than others. However, those highly localized patterns of variation change from age to age. Fluctuating asymmetry also seems to be nearly random in its spatial distribution, indicating that the processes that act differently on both sides are also localized. Despite the differences in spatial patterning, variance and fluctuating asymmetry may have a common explanation: the poor organization of musculoskeletal and neuromuscular interactions early in postnatal ontogeny. As these become organized, variance and fluctuating asymmetry decrease, and the remainder of ontogeny is characterized by a dynamic equilibrium between processes generating and regulating deviations from both the mean and symmetry.

Stem Species Patterns of Mammalian Reproduction

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Monotremes, marsupials, and eutherians differ remarkably in their reproductive patterns. Monotremes are oviparous and cleavage is meroblastic. However, the monotreme egg is small, contains little yolk, and absorbs nutrients from uterine gland secretions. The hatchlings are very immature and are nourished with milk. In contrast, marsupials and eutherians are viviparous, but their reproductive strategies differ. The marsupial neonate is extremely altricial, climbing to and remaining fixed to the nipple for several weeks. The eutherian neonate is relatively precocial, never fixed to the nipple, and can be left in a nest. Marsupials with yolk sac placentation have short gestation lengths, whereas, in eutherians with allantoic placentation, long gestation lengths are possible. In contrast to eutherians, the oocyte of marsupials contains "yolk," and the conceptus is surrounded by a shell coat. Lactation is always longer than gestation in marsupials but can be shorter than gestation in eutherians. We conclude that the total energy cost is higher in marsupials than eutherians. The advanced lung development of eutherian neonates allows a high metabolism and thermoregulation, which might be of advantage in a changing environment. We suggest that these differences in reproductive strategies influenced differences in extinction rates, radiation, and migration between both groups at and after the K/T event. Besides these differences, the mammalian stem species had a short gestation, lactation, and altricial offspring.

Studies on Myofibrillogenesis in Developing Hearts of Cardiac Mutant Axolotls

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Mexican axolotls provide an excellent model system for studying embryonic heart development. Cardiac mutant axolotls form hearts that are deficient in tropomyosin, lack myofibrils, and fail to beat. The defect can be corrected by culturing the hearts with normal anterior endoderm, in media conditioned by normal endoderm, or in RNA isolated from endoderm or conditioned media. We have identified a single novel gene that directs the synthesis of the bioactive myofibril inducing RNA (MIR) capable of promoting tropomyosin synthesis and myofibrillogenesis in the mutant hearts. These results suggest that the bioactive RNA plays an essential role in normal embryonic cardiac myofibrillogenesis in axolotls. Using Fluro-4, a calcium indicator in both normal and mutant embryonic hearts, we demonstrated a normal pattern of calcium spikes in the mutant embryonic hearts, which ruled out lack of normal pacemaker or electrical activities in mutants or a cause of the defect. The unique and novel RNA appears to induce the synthesis of tropomyosin and allows myofibrils to form, via gene regulation, most likely at the transcription level.